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The California Spotted Owl:

A Technical Assessment of Its Current Status

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This report is based on the Final Report submitted on May 8, 1992 by the Technical Assessment Team to the Interagency Steering Committee for the California Spotted Owl Assessment. The 13 chapters cover the assessment of the current status of the California spotted owl, its biology and habitat use, and forests where the subspecies occurs in the Sierra Nevada and southern California. The report suggests the direction of future inventories and research, identifies projected trends in habitat, and offers guidelines and recommendations for management of the California spotted owl.

Retrieval Terms: Strix occidentalis occidentalis, habitat attributes, old-growth, resource management, Sierra Nevada, southern California

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The Forest Service, U.S. Department of Agriculture, is responsible for Federal leadership in forestry. It carries out this role through four main activities:

- Protection and management of resources on 191 million acres of National Forest System lands
- Cooperation with State and local governments, forest industries, and private landowners to help protect and manage non-Federal forest and associated range and watershed lands
- Participation with other agencies in human resource and community assistance programs to improve living conditions in rural areas
- Research on all aspects of forestry, rangeland management, and forest resources utilization.

The Pacific Southwest Research Station

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Forest Service

Pacific Southwest Research Station

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Acronyms

AK--------- Adaptive Kernel estimates of home-range size
BLM------- Bureau of Land Management (USDI)
CDF-------- California Department of Forestry and Fire Protection
CDFG------ California Department of Fish and Game
CVs-------- Coefficients of Variation
d.b.h.------- Diameter at breast height
EIS -------- Environmental Impact Statement
ESA ------- Endangered Species Act
FS---------- Forest Service (USDA)
FWS ------ Fish and Wildlife Service (USDI)
GIS ------- Geographic Information System
HCAs ----- Habitat Conservation Areas
IPs --------- Industrial Private (Timber Companies)
ISC -------- Interagency Scientific Committee
LMPs------ Land Management Plans
LTBMU -- Lake Tahoe Basin Management Unit
MBF------- Thousand Board Feet
MCP------- Minimum Convex Polygon estimates of home-range size
MIS ------- Management Indicator Species
MMBF ---- Million Board Feet
MPs ------- Miscellaneous Private Parties
NFs ------- National Forests
NFMA ---- National Forest Management Act
NPs ------- National Parks
NPS ------- National Park Service (USDI)
PNW ------ Pacific Northwest Research Station (FS)
PSW ---------Pacific Southwest Research Station (FS)
RD&A ------ Research, Development, and Application Program
R5 ---------- Region 5, Pacific Southwest Region (FS)
R6 ---------- Region 6, Pacific Northwest Region (FS)
RSAs -------- Random Sample Areas
SEIS ---------Supplemental Environmental Impact Statement
SFs ---------- State Forests
SHPs -------- State Historical Parks
SOHAs------ Spotted Owl Habitat Areas
SPs ---------- State Parks
UC---------- University of California
USDA------- United States Department of Agriculture
USDI --------United States Department of Interior
USGS ------- United States Geologic Survey (USDI)

Metric Equivalents:

1 inch = ---------- 2.54 centimeters
1 foot = ---------- 0.305 meters
1 square foot = ----- 0.09 square meters
1 acre = ----------0.405 hectares
1 mile = ----------1.609 kilometers
1 square mile = ----- 2.59 square kilometers
1 ounce = ----------28.35 grams
1 pound =---------- 454 grams

Preface

Maintaining viability of northern spotted owl populations in Washington, Oregon, and California, in the face of the many activities that take place in their habitats, especially logging, has challenged public land managers for nearly two decades. Policies and guidelines established by the USDA Forest Service during the late 1970s and early 1980s were challenged repeatedly, and from opposing camps. The timber industry is concerned that management of the owl's preferred habitat unnecessarily restricts commodity production, while environmental interests contend that Forest Service plans for the owl fall short of assuring long-term viability of the bird. Although the controversy has been more hotly debated over the northern spotted owl, the California spotted owl has recently taken part of the spotlight.

The Report and Its Origin

During most of the 1980s, the Forest Service implemented a conservation strategy based on retention of Spotted Owl Habitat Areas (SOHAs) capable of supporting one to three pairs of owls, separated from each other by distances ranging from 6 to 12 miles, edge-to-edge. A recent, comprehensive assessment of management for the northern spotted owl identified serious weaknesses in the SOHA strategy, however, and gave rise to a markedly different approach for conserving the owl.[1] Because the SOHA strategy is currently used to manage for the California subspecies, in June 1991 the Forest Service and various agencies of the State of California initiated a technical assessment of the current status of the California spotted owl, under auspices of an Interagency Steering Committee for the California Spotted Owl Assessment (the "Steering Committee").

The Steering Committee formed two investigative, advisory teams-the Technical Assessment Team and the Policy-Implementation Team. This report contains findings of the Technical Assessment Team, as transmitted to the Steering Committee on 8 May 1992. The Team's findings will be further evaluated by the Policy-Implementation Team, which will suggest policies and guidelines for implementing recommendations of the Technical Assessment Team. Final recommendations will then be made by the Steering Committee.

In developing this technical assessment, we have drawn information from many sources-the owl's biology, including its geographic distribution, habitat associations, life history, demography, and ecological relations; historical aspects of land management and disturbance in the Sierra Nevada and southern California; fuels management; principles of conservation biology; and risk analysis. This was consistent with our assignment, as set forth in the charter that established the Technical Assessment Team. The charter also directed the Team to "follow accepted scientific standards and practices." Accordingly, to the extent possible, we have used the hypothetico-deductive process to guide our assessment of available information. We sought to falsify specific null hypotheses by using empirical data, computer models, widely accepted concepts and theories, and professional judgment (common sense!), rejecting hypotheses that failed these tests. This does not mean that surviving hypotheses are necessarily correct, only that they were not falsified by present information. This is the way of science. It inevitably leaves us with areas of uncertainty. How we deal with that uncertainty in the end depends, of course, on society's objectives.

The next step in following accepted scientific standards and practices was to submit a nearly final draft of our report for peer review by five other scientists not selected by the Team. This was accomplished by requesting that the Presidents of five learned societies-The American Ornithologists' Union, The Ecological Society of America, The Society of American Foresters, The Society for Conservation Biology, and The Wildlife Society-personally select one reviewer each, at their discretion. We then sent the draft document to each of these reviewers, whose critical comments and suggestions were taken into account in the revisions leading to this final report.

Although the report focuses on the California spotted owl, much more is at issue here. The owl is designated as an "indicator species" for old-growth ecosystems even though, as detailed in some of the chapters beyond, it is not restricted to just those habitats. But owl pairs use inordinately large areas in the course of their daily, seasonal, and annual activities, making the species an effective "umbrella" for a host of other species that satisfy their life requisites in the same habitats. Certainly commodity production must figure prominently when we weigh the pros and cons of maintaining viable populations of spotted owls. But prudence demands that the assessment be exhaustive and extend beyond the bottom line for the next year, or even the next decade. For the forest ecosystems we consider, our appraisal must look many decades, even centuries, into the future to be certain that decisions we make today are sustainable into the future-that they do not compromise future benefits from these ecosystems. A truly balanced assessment, therefore, "...must consider water quality, fisheries, recreation, soils, stream flows, scenic values, biological diversity, and other species of wildlife. All aspects of such a decision should be weighed in the balance. The issues are not limited to questions of owls and timber supply, as important as those are. The matter is not that simple--it never has been."'

[1]Thomas, Jack Ward; Forsman, Eric E.; Lint, Joseph B.; Meslow, E. Charles; Noon, Barry R.; Verner, Jared. 1990. **A conservation strategy for the northern spotted owl.** Washington, DC: U.S. Government Printing Office; 427 p.

Some Guidelines for Using the Report

The report consists of 13 chapters covering various aspects of the information needed for the assessment. Chapter 1 is an extended summary of Chapters 3-13, providing the bare essentials about key findings to establish the basis for our final conclusions, and presenting our recommendations. It is the essence of our assessment. Chapter 2 presents the consensus of the Technical Assessment Team's recommendations about what we think future efforts on the California spotted owl should be, and why. Readers can explore any or all of the remaining chapters, as needed or desired, for details on statements and conclusions summarized in Chapter 1. Chapter 3 presents the general background leading up to the present issue and summarizes what we know of the owl's distribution throughout California, and how the subspecies is being managed. The next seven chapters describe the owl's general biology and ecological relations, results of studies on its habitat associations, its demography and projections of population stability, and its major prey species. Finally, Chapters 11-13 consider how conifer forests in the owl's range came to be what they are today, review the fire history and current fuels problems in owl habitat, and identify projected trends in the forested habitats used by the owl. Four appendices conclude the report: Appendix A identifies the Technical Assessment Team and provides a brief chronology of Team activities leading to the report; Appendix B is a glossary of terms used in the text; Appendix C lists the common and scientific names of plant and animal species mentioned in the text; and Appendix D identifies authors of the various parts of the document.

We adopted some policies in the preparation of this report that we believe will ease the reader's task. Figures and tables are labeled by number for the chapter in which they appear, and by letter for their order in that chapter (for example, figure 4C is the third figure in Chapter 4). This procedure allows us to cross reference figures and tables from one chapter to another without confusion. In addition, a set of color photos of owl habitat taken during the Team's field trips are aggregated at the end of Chapter 5; these are identified as "colored photo 5-1," colored photo 5-2," and so on. We have substituted acronyms for several entities that are mentioned frequently in the text. Some are already familiar to most readers (for example, USDA = the United States Department of Agriculture), but in each chapter we define anew each acronym when it is first used. A list of many of the common acronyms appears after the Contents pages in this volume, for quick reference in case readers momentarily forget what one represents. All measurements are expressed in English units (for example, feet, acres, ounces) instead of metric units (meters, hectares, grams). This decision was made because English units are still used by Federal land-management agencies and by the forest industry, and because most of the general public still thinks in terms of English units, not metric units.

Acknowledgments

To complete this assessment, we have relied upon assistance, input, information, and general cooperation from literally hundreds of persons. To acknowledge each one is clearly not possible. We could not even rank them in order of the importance of their contributions. Certainly our biggest debt is to the many biologists from all the State and Federal agencies and private entities-both in management and research-who have spent countless hundreds of hours in the field, mostly at night, hooting for owls, searching for their nests, measuring nest trees and stands, locating owlets, recording data, and generally accumulating the wealth of information now available about the owl and its habitats. In particular, we thank the Forest and District Biologists from the National Forests within the range of the California spotted owl who have responded, again and again, to specific requests for information that we needed. They have met all of our requests unfailingly, pleasantly, and quickly.

Another major group of folks that worked largely behind the scenes, and essentially anonymously as far as we on the Team were concerned, were persons on the National Forests who compiled and mapped habitat information for us in electronic form. We have all learned much from this exercise, which should result in significant improvements in the way habitat information is collected, classified, and stored in the future.

Many others operated behind the scenes to implement data summaries, analyses, and syntheses, particularly at the Pacific Southwest Research Station's Redwood Sciences Laboratory in Arcata and Forestry Sciences Laboratory in Fresno. And a special thanks to folks in the California Department of Forestry's Forest and Range Resources Assessment Program, whose willing applications of their geographic information system made possible the mapping of all known California spotted owl sites and an assessment of high, medium, and low likelihoods of owls in riparian/hardwood forests in the Sierran foothills and Coast Ranges.

The administrative side of the Team's operation was made possible largely through the Regional Office of the Forest Service in San Francisco, which covered nearly all of the costs, and the Pacific Southwest Research Station in Albany, California. We were blessed by the wisdom of a couple folks in the Regional Office who saw and met a need to provide us with "scissors" to cut through the red tape that occasionally threatened to bring our progress to a temporary halt.

Technical Coordinators:

Jared Verner, Kevin S. McKelvey, Barry R. Noon,
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Chapter 1

Assessment of the Current Status of the California Spotted Owl, with Recommendations for Management

Jared Verner, Kevin S. McKelvey, Barry R. Noon, R. J. Gutierrez, Gordon I. Gould, Jr., and Thomas W. Beck

Release of a proposed conservation strategy for the northern spotted owl in April of 1990 (Thomas et al. 1990) raised concern in Region 5 (R5) of the U.S. Department of Agriculture, Forest Service (FS) about the adequacy of their regional guides for managing the California spotted owl (Barker and Jay pers. comm.). This concern was amplified by a decision formally announced on 26 June 1990 by the U. S. Department of Interior, Fish and Wildlife Service (1990) to confer "threatened" status on the northern spotted owl throughout its range. Negotiations began shortly thereafter to undertake an assessment of the current status of the California subspecies. This process led to the formation of the California Spotted Owl Assessment Team Steering Committee, with members representing several State of California (Resources Agency, Board of Forestry, Department of Fish and Game, and Department of Forestry and Fire Protection) and Federal entities (U.S. Department of Agriculture, Forest Service; and U.S. Department of Interior-Bureau of Land Management, Fish and Wildlife Service, and National Park Service). Observers represented the California Farm Bureau, California State Association of Counties, California Forestry Association, National Audubon Society, Nature Conservancy, private timber companies, Sacramento Chamber of Commerce, and the Wilderness Society. The Steering Committee held its first meeting on 11 May 1991, in Sacramento, CA, and established two teams to implement the assessment--a Technical Assessment Team to be designated by the FS and a Policy-Implementation Team to be designated by State entities. The charter for the Technical Assessment Team specified submission to the Steering Committee of a report on the current status of the California spotted owl (the "CASPO Report"), following "accepted scientific standards and practices." The report would:

1. Present, analyze, and interpret relevant information currently available on the biology of the owl-its distribution, abundance, density, movements, breeding biology, diet, demography, habitat associations, and so on.
2. To the extent possible, characterize the attributes of various habitats used for foraging, roosting, and nesting by the owl throughout its range in California.
3. Evaluate current land-management practices throughout the range of the owl, recognizing that more detailed informa tion may be available for some ownerships than for others.
4. Evaluate a range of options to achieve an amount and configuration of suitable habitat to provide for the long-term maintenance of the owl throughout its range.
5. Identify research, monitoring, and inventory programs needed to answer existing critical questions and to provide for adaptive management of the owl in the future.

The Technical Assessment Team consisted of a Core Group of six members (see Appendix A), consultants from the State and Federal entities represented on the Steering Committee, observers from the timber industry and the environmental community, and staff. This volume is the CASPO Report to the Steering Committee; this chapter synthesizes the Team's findings and presents its recommendations.

Producing the Technical Assessment

We established an agenda, schedule, objectives, and operating procedures (see chronology of Team activities in Appendix A). We spent 19 days on field trips throughout the range of the owl in the Sierra Nevada and southern California, including 5 days on private industrial timberlands. Arrangements were made for a professional photographer to accompany the Team on all field trips and to search archives for historical photos of locations that might be rephotographed now. Workshops were held to exchange information and explore concepts with agency biologists from throughout the State of California, with leading authorities in silviculture, and with some of the Nation's leading conservation biologists. Numerous other informational meetings were held with smaller groups and with more focused objectives. An extensive reference library, including most published literature and unpublished reports (from many very recent field studies of California spotted owls), was assembled and made available to the Team in its offices in Sacramento. We acquired all other relevant information currently available on the owl, its habitats, and its biology; reviewed the current-management situation; and identified the major factors leading to concern for the well-being of the California spotted owl throughout its range. The Team and staff analyzed and synthesized all information obtained from the variety of sources mentioned above. Various Team members and other specialists prepared the supporting chapters contained in this report.

Background and the Current Management Situation

As done for the northern spotted owl (Thomas et al. 1990, p. 12), we have subdivided the range of the California spotted owl into two major physiographic provinces, based on a variety of factors. These are the Sierra Nevada Province and the Southern California Province, with Tehachapi Pass as the dividing line between provinces. These regions are clearly distinct geographically; owl populations in the two provinces probably seldom exchange individuals; most owls in the Sierra Nevada Province prey mainly on northern flying squirrels, but all owls in the Southern California Province prey almost exclusively on dusky-footed woodrats (table 4A); the predominant threats to owl populations differ markedly between provinces; and feasible options for dealing with those threats also differ markedly between provinces.

The administrative history of the California spotted owl is closely tied to that of the northern spotted owl. Detailed research began in 1969, with studies on the northern subspecies, and early surveys for both subspecies of spotted owls in California were done in 1973 and 1974. Those surveys located owls at 159 sites (Chapter 3), primarily by visiting selected late-successional forests and areas with known historical sightings. Region 5 (R5) of the FS designated the spotted owl as a "Sensitive Species" on National Forests (NFs) throughout California in the late 1970s. In spite of this and increasing concern over the status of the northern spotted owl, FS surveys in the range of the California spotted owl did not begin in earnest until 1981.

Sierra Nevada Province

Primary concern for the status of the California spotted owl has been in regard to timber management on the seven westside Sierran NFs and on private industrial timberlands. The Sierra Nevada owl population is contiguous and fairly evenly distributed throughout its 400-mile length (figs. 4A and 4B) but is probably poorly linked to the southern California population. Connectivity may exist through the Tehachapi Mountains and the Liebre/Sawmill area east of Interstate Highway 5 (fig. 9A). The California spotted owl connects to the northern spotted owl in Shasta County (fig. 4A).

Standard survey and monitoring protocols have been established by the FS to locate owl sites; these protocols have been used by most other entities involved in owl inventories. An owl site is an area of unspecified dimensions where a single owl or a pair of owls has been located, usually repeatedly. In demographic and radio-tracking study areas, where efforts to locate all owls are more intense than elsewhere, most owl sites with single owls have eventually been found to have a pair. All owl sites have been mapped and given unique spatial references, so they can be tallied. Designation of an owl site makes no assumption about home-range or territory boundaries of the owls, although usually a center of activity can be identified by the location of a nest or a primary roosting area. The terms "owl site" and "site" are general and often used generically to refer to home ranges, territories, or to sites designated by agencies for special owl management (see glossary in Appendix B).

Surveys, inventories, and other field efforts produced an estimated 1,250 spotted owl sites in the Sierra Nevada during the period 1987-1991, 92 percent on public lands (table 1A). Pairs were confirmed at 697 of those sites (table 3B). Only 162 of the sites were in reserved lands [National Parks (NPs) and Wilderness Areas in NFs]. Biologists have estimated an additional 305

Table 1A-*Known California spotted owl sites (1987-1991 surveys) and estimated acreages of suitable habitat, by ownership and physiographic province (see tables 3B and 3J).*

	California spotted owl sites						Estimated acres of potential suitable habitat[1]	
	Sierra Nevada Province		Southern California Province		Statewide			
Ownership	Known	Additional estimated	Known	Additional estimated	Known	Additional estimated	Sierra Nevada	Southern California
Federal ownerships								
Forest Service	1,028	250	294	190	1,322	440	3,500,000	540,000
National Park Service	120	55	0	0	120	55	461,000	0
Bureau of Land Management	1	?	1	?	2	?	68,500	7,600
Subtotal of Federal	1,149	305+	295	190+	1,444	495+	4,029,500	547,600
State of California	3	?	7[2]	14[2]	10	14+	26,000	25,000[2]
Private ownerships	98	?	37	?	135	?	2,408,000[3]	?[4]
Native American Nations	0	?	4	?	4	?	?[4]	?[4]
Grand total	1,250	305+	343	204+	1,593	509+	6,463,500	572,600

[1] Acreages are based on forested land currently known to be suitable habitat (dominant tree size ≥12-14 inches in diameter at breast height, with ≥40 percent canopy cover) or land that is currently not suitable but has high timber-producing capability, providing for a relatively rapid return to suitable habitat.
[2] Includes some local governmental ownerships.
[3] Figure is only for known forested lands in private ownership in the Sierra Nevada; an unknown amount of that is unsuitable.
[4] The quantity of suitable habitat on private ownerships in southern California and on Native American Nations' lands has not been determined.

sites, based on unsurveyed areas in habitats considered to be suitable (tables 1A and 3B). We have assigned owl sites in the Sierra Nevada Province to one of five general habitat types, based primarily on tree-species composition:

1. *Foothill riparian/hardwood forest*-This type generally occurs at low elevations in the Sierran foothills. It includes denser stands of hardwoods immediately adjacent to streams, as well as denser stands of hardwood forests on the adjoin ing slopes. Tree species along streams include cottonwood, California sycamore, interior live oak, California buckeye, Oregon ash, and occasionally white alder. Tree species on the adjoining slopes include blue oak, interior live oak, and digger pine.
2. *Ponderosa pine/hardwood forest* (montane hardwood)--This habitat blends with the upper elevations of riparian/ hardwood forests. In the southern Sierra Nevada, ponderosa pine at its lowest elevation generally occurs with interior live oak, canyon live oak, and black oak, with incense-cedar and white fir coming into stands at slightly higher elevations. In the northern Sierra Nevada, tanoak and Pacific madrone commonly contribute to the hardwood component of this type.
3. *Mixed-conifer forest*-This type is the predominant timber-producing forest of the Sierra Nevada, consisting of various mixtures of white fir, ponderosa pine (at lower elevations), incense-cedar, sugar pine, black oak, and red fir (at higher elevations). Douglas-fir is an important component from Yosemite NP northward, and giant sequoia occurs in widely scattered localities.
4. *Red fir forest*-This type blends with the higher zones of mixed-conifer forest. It is dominated by red fir, with increasing amounts of white fir at lower elevations until it becomes mixed-conifer forest. At upper elevations it often includes some lodgepole pine and occasionally quaking aspen.
5. *Eastside pine forest*-This type occurs generally east of the Sierran crest and is dominated by ponderosa and/or Jeffrey pine.

Most known spotted owl sites (82 percent) on Federal lands in the Sierra Nevada are in mixed-conifer forests. Indeed, about 62 percent of all California spotted owl sites on Federal lands are in Sierran mixed-conifer forests, making this by far the most significant habitat for the subspecies (table 1B).

Approximately 8.6 million acres of forested or potentially forested lands occur in the Sierra Nevada; 71 percent are on public lands. Of these lands, 6.5 million acres are either suitable or potentially suitable owl habitat, and about 4 million acres are owned by the public. Because we lack a full understanding of all attributes that comprise suitable owl habitat, however, we cannot determine the exact amount of suitable habitat for the owls on any ownership.

Forest Service

NFs of the western Sierra Nevada with major owl populations have a total land base of 6,978,900 acres; about 5,260,611 acres are forested and about half of that is current or potential habitat for spotted owls (Chapter 3). An estimated 1,028 spotted owl sites, probably most capable of supporting a pair of owls. have been located on NFs in the Sierra Nevada (table 1A). About 80 percent of those are in the zone of mixed-conifer forests. about 10 percent in red fir forests, and about 7 percent in ponderosa pine/hardwood habitats. The remaining 3 percent are in eastside pine forests and foothill riparian/hardwood habitats in the western Sierran foothills (table 1B).

In July 1981, the Regional Office of R5 notified Forests with the California spotted owl to provide in their Land Management Plans (LMPs) a strategy for maintaining viability of the owls. This led to the designation of Spotted Owl Habitat Areas (SOHAs) in a "network" on each of the westside Sierra Nevada NFs with owl populations and major timber-management programs. The network concept was patterned after a similar approach adopted by the FS in Washington and Oregon to manage for northern spotted owls. SOHAs are designated stands of habitat to be managed to maintain suitable owl habitat. They may occur singly, in pairs, or in triplets. If single, they may be no more than 6 miles from at least two other SOHAs, edge-to-edge; if pairs or triplets, they may be up to 12 miles from other SOHAs. Management direction for SOHAs is to maintain at least 1,000 acres of suitable owl habitat within a 1.5-mile radius of the known or potential nest site. Suitable habitat is described as mature timber stands having (1) multi-storied canopies with 70 percent or greater total cover, (2) 40 percent or more of the total canopy in trees at least 21 inches in diameter at breast height (d.b.h.), and (3) extensive decadence-cavities, broken tops, snags, and so on (Chapter 3).

Directions for Sierran Forests resulted in the designation of 264 SOHAs in approved or draft Forest LMPs (Lassen 40; Plumas 54, Tahoe 33, Eldorado 32, Stanislaus 36, Sierra 29, and Sequoia 40). Of this number, 249 are on lands suitable and

Table 1B- *Distribution by major habitat types of known California spotted owl sites, based on 1987-1991 surveys in National Forests and National Parks (see tables 3A and 3I)*[1]

Forest type	Known sites	Percent of province	Percent of total
Sierra Nevada Province			
Mixed-conifer	959	81.5	62.4
Red fir	114	9.7	7.4
Ponderosa pine/hardwood	79	6.7	5.1
Foothill riparian/hardwood	19	1.6	1.2
Eastside pine	6	0.5	0.4
Subtotal	1,177	100.0	76.6
Southern California Province			
Live oak/bigcone Douglas-fir	147	40.8	9.6
Riparian/hardwood	116	32.2	7.6
Mixed-conifer	95	26.4	6.2
Redwood/California-laurel	2	0.6	0.1
Subtotal	360	100.0	23.4
Grand total	**1,537**		**100.0**

[1] Subtotals and totals do not match those in table IA because values given here were based only on numbers supplied by National Forests and National Parks. The figures occasionally include habitat descriptions from sites on private lands within NF boundaries and from single owl locations. We believe the percentages shown here correctly display the relative proportions of owl sites in these habitat types.

otherwise available for timber management. The total allocation for the 264 SOHAs is about 454,000 acres, of which about 110,000 acres would be managed under low-yield, even- or uneven-aged management (Chapter 3).

Other Public Ownerships

Lassen, Yosemite, Kings Canyon, and Sequoia NPs occur within the range of the California spotted owl in the Sierra Nevada. These have a total land base of 1,719,039 acres, but only about 28 percent of that is judged to be suitable owl habitat, and only 120 owl sites are known to occur in the four NPs combined (table 1A). Even though the NPs experience high recreation impacts in local areas, NP management has not been an issue, because the emphasis in the Parks generally is believed to be compatible with habitat needs of the owls.

The Bureau of Land Management (BLM) administers scattered public lands along the foothills and lower slopes of the Sierra Nevada and southern Cascades, some with forests, woodlands, and riparian habitats that are potentially suitable for California spotted owls. About 68,500 acres of BLM lands are potential for spotted owls (table 1A). Although owls have been observed at a few sites on BLM lands, a general lack of inventory precludes an estimate of the total number.

Seven State Parks (SPs) total an estimated 16,580 acres in the Sierra Nevada, with perhaps as many as six sites suitable for owls. Because all wildlife and plants are protected in SPs, habitat for any owls there is probably secure. Two State Forests (SFs) in the Sierra Nevada, totaling 13,830 acres, are managed for demonstration of forestry practices and to support cooperative research with other agencies. Uneven-aged silviculture is featured on these lands, which may have three or four pairs of owls. In addition, the University of California administers the 3,000-acre Blodgett Forest in El Dorado County and the 320-acre Whittaker Forest in Tulare County. About 2,000 acres at Blodgett are suitable owl habitat and typically one or two pairs nest in the area (Chapter 3).

Private Lands

Industrial timberlands total 1,451,000 acres and miscellaneous private timberlands total 957,000 acres in the Sierra Nevada (table 3D). The latter group includes both large landowners, such as utilities and water districts, and small landowners. About 58 percent of the combined total of these private lands are surrounded by NF lands, much in the form of alternating sections of private and public lands in "checkerboard" pattern, especially in the Tahoe and Eldorado NFs. Significant additional parcels of private timberlands, not in checkerboard arrangement, are included within boundaries of the Lassen, Plumas, and Stanislaus NFs. Most of the best forest-growing lands in the Sierra Nevada are owned by commercial timber companies in the mixed-conifer zone. The majority of the private land has not been inventoried for owls yet, but it is apparent that some industry lands with a long history of logging have spotted owls comparable in density to adjacent NF lands. Other private lands lack nesting owls, however, even though nest sites occur in adjoining NF lands (Chapter 5). Decisions are still pending on possible enactment of forestry reform legislation to provide new rules for logging on private lands in California. Although we cannot now assess the effects of any new forestry regulations on the capability of private lands to support spotted owls, we believe that any new regulations would be more beneficial for owls than past policies.

At the north end of the Sierra Nevada, private timberlands along the east side of Shasta County provide an essential habitat linkage for movement back and forth by both northern and California spotted owls, between the Lassen and Shasta-Trinity NFs. Maintenance of this connection is believed to be essential to the long-term conservation of both subspecies of spotted owls (Dawson et al. 1987, Thomas et al. 1990).

Spotted owls breed in dense stands of hardwoods along stream channels at low elevations on the western edge of the Sierra and Sequoia NFs. These habitats, generally not classified as commercial timberlands, are similar in most respects to habitats commonly used by spotted owls in southern California. Similar habitats occur along riparian zones west of the boundaries of all NFs in the Sierra Nevada. Livestock grazing, type conversions, firewood cutting, and logging in and adjacent to riparian zones have affected these habitats. Many are now being affected by an increasing trend of residential developments in the foothills. These potential habitats have not been adequately surveyed for spotted owls, although they may support many pairs (see fig. 4D).

Areas of Concern

Our over-riding concerns for spotted owls in the Sierra Nevada conifer zone involve potential impacts of logging practices on their habitat (details in Chapter 13) and the extent to which selective logging and aggressive fire suppression in this century have created incendiary conditions in a majority of the low- to mid-elevation conifer forests (details in Chapters 11 and 12). In addition, we have identified several conditions that will bear further study and evaluation (table 3G, fig. 3A). These involve bottlenecks in the distribution of habitat or owl populations, gaps in the known distribution of owls, locally isolated populations, fragmented habitats, and areas with low densities of owls.

Concerns for spotted owls in foothill riparian/hardwood forests in the western Sierra Nevada primarily involve increasing development of residential properties. This is the case for dispersed, rural homesites and growth of existing communities in the foothills. Both potentially impact spotted owls directly by reducing the amount of owl habitat and by bringing dogs and cats into potential contact with fledgling owls that may spend some period of time on the ground before they are capable fliers. These developments would also affect the owls indirectly by reducing the area suitable for woodrats. Grazing in the foothills may also impact owls by influencing shrub cover needed by woodrats. We cannot evaluate possible effects on owls that may result from the increasing need for surface and ground water to provide for residential developments in the foothills. None of these potential impacts has been studied.

Southern California Province

Spotted owls occur in all major mountainous areas of southern California, but they are not continuously distributed like those in the Sierra Nevada. Instead, we believe that each major mountain range has a relatively isolated subpopulation of birds that is separated from its nearest neighboring subpopulation by distances ranging from 6 to 45 miles (fig. 9A, table 9A). Inventories in these mountains since 1987 have produced a total count of 343 known owl sites; 295 of these are on Federal lands (table 1A). Estimates by biologists of additional sites in southern California range from 155 to 254 (table 3J); taking the midpoint of these gives an estimate of 204 additional sites or an estimated total of 547 spotted owl sites in southern California. This is not out of line with an independent estimate of 578 (known + potential) owl sites in southern California by Stephenson (1991). We have assigned owl sites in southern California to one of four general habitat types, based primarily on tree-species composition:

1. *Riparian/hardwood forest*-This type varies considerably in different parts of southern California. In deep canyons in the Los Padres NF, for example, it occurs in narrow strips adjacent to permanent or near-permanent streams. Common tree species include coast live oak (near coast), canyon live oak (interior locations), California sycamore, white alder, California-laurel, and cottonwood. In shallower canyons in the Cleveland NF, these forests may consist almost exclusively of coast live oak.
2. *Live oak/bigcone Douglas-fir forest*-This habitat occurs in a narrow band mostly at mid-elevations in mountains of all four NFs in southern California. Dominant tree species are canyon live oak, coast live oak, and bigcone Douglas-fir.
3. *Mixed-conifer forest*-This type is best developed at relatively high elevations in the San Gabriel and San Bernardino Mountains, and on Mount San Jacinto. Species composition is similar to that of Sierran mixed-conifer, although Coulter pine occurs and bigcone Douglas-fir occasionally occurs at lower elevations. Red fir, Douglas-fir, and giant sequoia are missing.
4. *Redwood/California-laurel forest*-These forests are restricted to the coast range, where coast redwood, California-laurel, tanoak, Pacific madrone, red and white alder, coast live oak, Santa Lucia fir, and bigleaf maple form various mixtures.

About 41 percent of the owl sites in southern California are in live oak/bigcone Douglas-fir forests, 32 percent are in riparian/hardwood forests, and 26 percent are in mixed-conifer forests, mainly in the San Bernardino Mountains (table 1B). Southern California has an estimated potential of about 573,000 acres of suitable owl habitat (table 1A), but we still cannot characterize the full range of conditions that comprise suitable habitats there.

Federal and State Lands

Regional direction for the four NFs in southern California is to protect all known spotted owl sites and to manage the habitat based on local information about suitability and availability. One owl site is known on BLM lands, where only about 7,600 acres of potential owl habitat occur; habitats are managed for wildlife, riparian habitat quality, water quality, and dispersed recreation. Camp Pendleton probably had spotted owls in the past, but long-term effects of military training activities have degraded habitat to an extent that little exists today. State Parks have several thousand acres of potential owl habitat, perhaps enough for 13-15 pairs.

Other Lands

Over the past 5 years, 41 owl sites have been found on private and Native American Nation lands in southern California (table 1A). Most private lands are at lower elevations than "traditional" spotted owl habitat.

Areas of Concern

Several significant factors threaten the long-term maintenance of spotted owl populations in these relatively isolated mountain ranges in southern California. Probably of most concern is the likelihood of a decline in the capability of landscapes between the mountains to support owls that would otherwise disperse from one subpopulation to another. Only in this way can the decline in one subpopulation be offset naturally by immigration from other subpopulations (so-called demographic "rescue effects"). As urban and residential areas expand in the valleys between mountains, the suitability of dispersal habitat may decline to the point that successful dispersal is too restricted for demographic rescue. Subpopulations must then survive demographically on their own or decline to extinction (Chapters 8 and 9). We are similarly concerned about what appears to be a tenuous linkage between owls in the southern Sierra Nevada and owls in the Transverse Ranges (see fig. 9A).

In addition to maintaining connectivity, the integrity of each habitat "island" must be maintained. An additional concern, therefore, is a decline in the amount, or an increase in fragmentation, of currently suitable habitat within any of the many isolated mountain ranges.

Direct surface-water diversions and "mining" of ground water for human needs deplete water in permanent or near-permanent streams, threatening the associated riparian woodlands. Loss of the woodlands would mean the loss of spotted owls and numerous other riparian species found in these habitats. Stand-destroying fires, and increasing concentration of recreational activities in prime owl habitat are additional threats to spotted owls in southern California. Maintenance of a viable population of spotted owls in southern California may be impossible without changes in land-use policies on private lands, especially those that adjoin public lands.

Assessing the Owl's Status: The Sierra Nevada

Determining the owl's status depends on answers to three fundamental questions: (1) Is the California spotted owl's population declining in all or part of its range? (2) Is the California spotted owl a habitat specialist? (3) If the answer to question 2 is yes, then is the habitat upon which the California spotted owl specializes declining? We have endeavored to answer these questions by attempting to falsify the implied null hypotheses:

H_o: California spotted owl populations in demographic study areas are not declining.

H_o: California spotted owls use all habitats in proportion to their availability.

H_o: Habitats used in excess of availability by California spotted owls are not declining in abundance.

All sources of information available to us have been important in this effort, including common sense, professional judgment, empirical data, widely accepted concepts and theories, and mathematical modeling.

Failure to falsify a null hypothesis does not necessarily mean that it is true. When data are insufficient to provide a powerful test of the hypothesis, we are likely not to falsify the hypothesis even when it is false. This is known to statisticians as a type-II error. In all cases where it was possible, we have estimated the power of tests that failed to reject a null hypothesis. This information is critical to the conclusions and recommendations we have made in this report.

Is the Owl's Population Declining in All or Part of Its Range?

Demographic studies of California spotted owls are currently underway in five locations-Lassen NF (2 years), Eldorado NF (6 years), Sierra NF (2 years), Sequoia/Kings Canyon NPs (4 years), and San Bernardino NF (5 years). Owls are captured and color-banded with unique band combinations that can be identified in the field without recapturing the birds. In this way, a history of each color-banded bird can be accumulated for as long as it remains in the study area. Sex is determined by voice, and age (up to 2 years) can be determined by plumage characteristics. Critical parameters needed to determine whether a population is stable, increasing, or decreasing are stage-specific birth rates and death rates. The parameter we need to estimate is lambda (λ), the finite rate of population growth ($\lambda = 1.0$ indicates a stable population; $\lambda > 1.0$ indicates an increasing population; and $\lambda < 1.0$ indicates a declining population). Lambda is computed from estimates of three classes of parameters: age at first reproduction, age-specific survival rates, and age-specific fecundity (for simplicity in modeling population trends, we use a females-only model, so fecundity is defined here as the expected number of female fledglings produced per female of age *x* per year). In the Lefkovitch stage-projection matrix model (Lefkovitch 1965) used for this assessment, the value of lambda indicates the annual rate of change in the size of a population.

Results

Owl banding has been underway long enough to compute estimates of lambda for only three study areas-Eldorado NF, Sequoia/Kings Canyon NPs, and San Bernardino NF. We could estimate juvenile survival rate only for the San Bernardino study area, because data were insufficient for the Eldorado and Sequoia areas. Consequently, the San Bernardino value was used as a reasonable approximation for the other two locations. It was in line with estimates of juvenile survival rates from studies of northern spotted owls (Chapter 8), and lambda was not especially sensitive to variations in juvenile survival rate (figs. 8C and 8D). Results from the Eldorado and Sequoia/Kings Canyon studies follow; results from the San Bernardino are deferred to the section dealing with southern California.

Eldorado Study Area-The estimate of lambda for the Eldorado population was 0.947, suggesting about a 5 percent annual rate of population decline during the period of study (1986-91). This value was not significantly <1.0 (a = 0.05, *P* = 0.1271), however, so we cannot reject the null hypothesis that the population is not declining. The test, however, had a power of only 0.30. Even if the population were truly declining at 5 percent per year, we would fail to detect that decline 70 times in every 100 studies of equivalent size. The low power resulted from a relatively small number of marked birds, and the large standard errors of parameter estimates (table 8E). The correct inference to draw from this result is that we are uncertain about the true trend of this population. The power of the test is much too low to infer that the population is stable.

Sequoia/Kings Canyon Study Area-The estimate of lambda for this population was 0.969 (table 8F), suggesting about a 3 percent annual rate of population decline during the period of the study (1988-91). As in the Eldorado study, the statistical test (a = 0.05, *P* = 0.2709) failed to reject the null hypothesis of no decline in the populaton. The power of this test-0.30-was identical to that for the Eldorado study, so we must infer again that we are uncertain about the trend of this population.

Is the California Spotted Owl a Habitat Specialist?

Results from Landscape Studies

This question was explored in several ways and at three scales, with details given in Chapters 5 and 6. We know, for example, that California spotted owls use forested habitats almost exclusively, although they occur and breed in a greater variety of habitats than does the northern spotted owl. Within forested landscapes, we found that 45 percent of all nests of California spotted owls in the conifer zone of the Sierra Nevada were in M4N and M4G stands, significantly more than expected based on availability (table 5A) [table 1C explains codes designating timber strata, or see "timber strata" in the glossary (Ap-

pendix B)]. All other habitat types that we evaluated were used less than or equal to their availability (table 5A). These results indicated that, for nesting, the owls selected stands with relatively large trees and closed canopies.

Densities of owl sites in 1:24,000 U.S. Geological Survey quadrangles were significantly related to the percentage of forests having medium-sized and larger trees and high canopy closure. These results generally corroborated those of the previous analysis.

Results from Home-Range Studies

At a home-range scale, attributes in nest stands were compared with those in randomly selected stands in the general forest matrix. Significant differences were found for several attributes, most or all of which were consistent with the previous conclusion that the owls tended to select stands of large, old trees with closed canopies for nesting. Results of identical analyses in roost stands produced parallel results. Nest and roost stands showed consistent, often significant differences from random locations in the forest in having higher canopy cover, greater snag basal area, greater total basal area of live trees, and greater softwood basal area (tables 5B and 5D). Mean values for canopy cover ranged from about 75 to 96 percent in the different studies; similarly these studies suggested a range for total basal area of live trees from 185 to 350 square feet per acre, and basal area of large snags (>15 inches in d.b.h. and >20 feet tall) from 19 to 31 square feet per acre in nest and roost stands ("Recommendations" in Chapter 5). Many of these parameters varied considerably, and not all measures of habitat used by spotted owls and at random locations differed significantly within a given study. The data were, however, consistent and mutually supportive among all studies. California spotted owls in these various studies chose to nest and roost in stands that were denser than average and that contained a large-tree component. Most nest sites were selected in dense mixed-conifer stands with average quadratic mean diameters of canopy trees >24 inches in d.b.h. We know of no studies that consistently contradicted these findings.

Table 1C-- *Explanation of codes used to designate timber strata in the Sierra Nevada.*

Attribute	Code used	Identification	
Timber type	M	Mixed-conifer	
	P	Ponderosa pine	
	R	Red fir	
Tree size-class[1]	2	<12 inches	
	3	12-23.9 inches	
	4	>24 inches[2]	
Canopy closure	P	Poor	0-39 percent
	N	Normal	40-69 percent
	G	Good	>70 percent

[1] Mean diameter at breast height of dominant trees.

[2] Code 5 has been used to designate larger size-classes, and code 6 has been used to designate multi-layered stands; most National Forests in the Sierra Nevada no longer make these distinctions in their timber inventories.

Results of similar analyses at foraging locations indicated that the owls foraged in stands characteristic of nest and roost sites, as well as in a wide variety of other habitats having lower canopy cover and a greater range of tree sizes and ages. Nonetheless, in comparison with random locations within the forest, owls tended to forage in sites with higher canopy closure; greater basal areas of live trees combined and of softwoods; greater basal areas of snags; and more dead-and-downed wood (tables 5G and 5H). In general, they foraged in forests of intermediate to old age, typically with >40 percent canopy closure.

Results from Studies at Nest Locations

Data from 276 nests located throughout the range of the California spotted owl provided the most conclusive evidence of selection by the owls of very large, old trees. In Sierran conifer forests, for example, nest trees averaged about 96 feet in height and 45 inches in d.b.h., with a surrounding canopy cover of about 75 percent (table 5K). A prevalence in these forests of cavity nests (66 percent) and nests on broken-topped trees (10 percent) showed that most nest trees were not only large but also old and decadent. For example, many of the natural cavities used for nests were created when decay invaded a wound on the side of the tree where a branch tore out of the trunk. These cavities must have room to accommodate an owl's nest, the female, and her (usually) two nestlings, so only very large trees have branches and trunks of sufficient size to produce such cavities. Not only were the diameters of nest trees significantly larger than the average tree in today's conifer forest (fig. 5K), but also they exceeded the mean diameter of trees in plots sampled in the Sierra Nevada at the turn of this century. The owls are apparently nesting today in a legacy of very large, old trees that were present in 1900 and before.

Results from Radio-Tracking Studies

Radio-tracking studies of California spotted owls in the Lassen NF and the Sierra NF provide some insights into habitat selection in conifer forests of the Sierra Nevada. Studies of this nature have shortcomings that can lower our ability to draw inferences from them, however. First is the need for a large number of owl locations during a brief period of the year (for example, the breeding period or the winter period). But to meet assumptions of independence in the locations, required by statistical tests, locations should be recorded only about every 2-3 days. In the 6-month period that approximates the breeding cycle of the spotted owl, only about 72 locations could be obtained without violating assumptions of independence. Second is the fact that a small sample size results in low power of the tests to detect habitat selection. A mean of 57 locations was available for the radio-tagged spotted owls reported in the home-range studies (Chapter 6) upon which the following summary is based. The power of statistical tests ranged from about 15 to 80 percent, so failure to detect significant overuse or underuse of habitats, based on availability, probably resulted from low power in many cases. This means that any consistent pattern in habitat selection among birds with samples large enough for tests with ample power should be given additional

weight when evaluating the suitability of habitats for spotted owls from studies of radio-tagged birds.

Habitat selection was more consistent and more pronounced for canopy closure than for tree size-class among radio-tagged California spotted owls in the Sierra Nevada. Chi-square values were consistently higher for canopy closure, and more owls had significant tests of habitat use for canopy closure than for tree size-class in 18 site-by-season comparisons. Differences between total and dominant canopy closure were minor (Chapter 6). Because more owls showed selection for cover of the dominant trees in a stand, however, it appears to be a better measure of habitat quality for California spotted owls than total canopy cover.

The amount of medium and large sawtimber in individual home ranges did not appear to be a good indicator of the amount of habitat needed to sustain the owls, unlike the case for the northern spotted owl (Chapter 6). Most owls did not have significant tests of habitat use for tree size-class. Nearly all owls in the Sierra NF used size-classes in proportion to their availability; patterns were stronger in the Lassen NF during the breeding season, where about half of the birds used medium and large sawtimber greater than expected.

Based on overall use by radio-tagged owls of habitats with $\geq$40 percent canopy cover and those with $\leq$39 percent canopy cover, stands with $\geq$40 percent canopy cover should generally be considered suitable owl habitat. Stands with $\leq$39 percent canopy cover should generally be considered unsuitable (Chapter 6). The data show that owls exhibited lower selectivity for habitats when foraging than they did when roosting (Chapters 5 and 6).

Results from Studies in Foothill Riparian/Hardwood Forest

Results of habitat studies and home-range use by owls in lower-elevation, riparian/hardwood forests and adjacent stands of oak-pine woodlands in foothills of the Sierra Nevada generally agree with those in conifer forests. The birds nest and roost in stands with mean canopy cover of about 89 percent and in trees generally large for those habitats (mean d.b.h. = 29.5 inches, table 5K).

Is the Habitat Used Selectively by the California Spotted Owl Declining?

Having concluded that California spotted owls are not habitat generalists, particularly for nest stands, we next must determine whether any evidence indicates a decline in the amount of habitat used more than expected by the owl. Forests of the Sierra Nevada have been markedly impacted in a variety of ways by human intervention, especially during the past 150 years (Chapter 11). The first major perturbation was grazing by millions of sheep from about 1860 to the first decade or so of this century; peak numbers occurred in the early 1870s. Coincident with sheep grazing was extensive early logging, mainly at low elevations near towns, mines, and along transportation routes. Timber production-in billions of board feet-reached a peak about 1950, dropping some from that level but remaining relatively high in most years since. Fire suppression began in the early part of this century and has become increasingly effective and aggressive since.

With removal of sheep and some measure of fire control in place, forest stands became subject to ingrowth of shade-tolerant conifers such as white fir and incense-cedar (Chapter 11). A combination of logging and natural attrition of the old forest led to a decline in the number of large, old trees. Past logging activities that concentrated on removal of the largest, most valuable trees broke up the patchy mosaic of the natural forest, further encouraging the development of dense conifer regeneration. These developments, especially in the ponderosa pine and mixed-conifer forests of the Sierra Nevada, reduced large-diameter trees in many areas to small remnant populations. Concurrently, surface fuels have been accumulating in forest stands and the extensive ingrowth of shade tolerant trees has resulted in vertical fuel ladders that essentially connect the surface fuels to the dominant tree crowns over much of the Sierra Nevada. These changes have not occurred to the same degree in the red fir type, where fires were less frequent historically, and logging was generally uncommon until recent decades.

Because of current stand structures and excessive fuel loadings in much of the Sierran mixed-conifer type, fires that escape initial suppression efforts-usually those occurring during extreme weather conditions-tend to become large and severe. Fire trends in the Sierra Nevada can be expected to continue along their current trajectories. As the human population increases in Sierran forests and woodlands, the presence of so many houses within the forest will shift further the emphasis of suppression from one of saving forests to one of saving property. The fuels will also continue to accumulate, with the recent drought-induced bark beetle infestations contributing a major pulse of new fuels over the next few decades. We expect the net result to be a much higher incidence of stand-destroying fires in the future than was characteristic of the Sierran fire regime prior to this century. And with those fires we will continue to lose remnant, individual old trees, stands of old trees, and other old-growth attributes.

Timber cutting trends also point to a continuing decline in the number of old trees and remnant old-growth stands. Sixty-five percent of the forested acres on all Sierran NFs are classified as suitable for timber production (Chapter 13). If we discount forested acres that cannot produce timber commercially because they are too poor in quality, they cannot be successfully regenerated, or they have unstable soils, 74 percent of the lands that can potentially produce timber will be harvested in some manner (table 13A). Seventy-two percent of the timber volume removed from these lands will be taken through even-aged systems--mostly clearcuts. Of the 528,474 acres of suitable timberlands on the Tahoe NF, for example, 68 percent will be managed for even-aged silviculture (24 percent long rotation, 44 percent short rotation) (Chapter 13). On the Plumas NF, 52,000 acres are scheduled for even-aged cutting per decade, with 8,000 acres in selection cutting methods.

Clearcut, seed-tree, and shelterwood cutting techniques all have the same goal: produce even-aged stands. In this regard,

seed-tree and shelterwood systems can generally be thought of as two-stage (sometimes three-stage) clearcuts. In all of these cutting systems, the original stand will be totally removed before the new stand is scheduled to be cut. In terms of owl biology, the primary impact of traditional, even-aged harvesting practices lies in the creation of simple stand structures and, probably more importantly, the removal of all large trees from vast areas of the forest. Even if prescriptions are modified so that snags and live culls are left at the first cutting, no provision is made for a predictable recruitment of replacement trees for these relics when they fall. This, in turn, will lead to a loss of large-diameter downed woody material important for production of the fungi that are a primary food source for flying squirrels-the main prey of spotted owls in the Sierra Nevada (Chapter 4). Log slash can create much small-diameter woody debris, but it cannot replace the large logs. In an even-aged system, these old-growth features can be created only by an extreme extension of the rotation interval. Even if the rotation is extended to 150 years, for instance, no trees will match the average age of the forest at the beginning of this century (Chapter 11). Decadent features in stands are functions of age, not just d.b.h. (fig. 13G); and any animals that depend on decadent features (cavities, broken-tops, snags), or the large woody debris that they create, will simply drop out of these forests (see Chapters 4, 5, and 10 for examples specific to the spotted owl and its prey species). The rate of conversion to even-aged systems in the western Sierra Nevada is estimated by the LMPs to be 229,000 acres per decade.

Even on lands planned for selection harvest (about 80,000 acres/decade), we have no guarantee that harvest prescriptions will leave any of the large, old trees. Ideally, stands managed for individual selection are harvested in a manner that brings the diameter distribution in the stand into conformity with an idealized distribution, which is characterized by a declining exponential function (in forestry referred to as an inverse "J"). The number of large trees in the stand is dictated by the slope of this curve and the designated diameter of the largest tree. In selection-logging systems, timber is removed from all diameter classes as required to maintain this diameter distribution. Little evidence exists, however, that historical patterns of partial cutting have followed the classic single-tree theory. "Selective" harvest in the Sierra Nevada has, in the past, primarily targeted the large trees. This system, sometimes called "pick and pluck," will not produce the simple, even-aged structures that characterize clearcutting techniques, but its effect on the presence of large, old trees is similar. If the large trees are removed and no stocking control is done on the smaller stems, replacement trees in these diameter classes will be produced very slowly, if at all, and they will consist primarily of the more shade-tolerant species. Even with classical single-tree selection, a gradual loss of shade-intolerant species would be likely.

The future forest of the Sierra Nevada, as projected by the LMPs, will very likely be split between areas of even-aged plantations and areas of dense and increasingly small-diameter stands. Given these projections, it seems most likely that the forest to be generated by adherence to current LMPs will be susceptible to fire disturbance, nearly devoid of large, old trees, and depauperate in terms both of plant and animal species that depend on attributes of the older forests that were common last century. We conclude that the key elements of spotted owl nest and roost stands, under current LMPs, will decline sharply over most of the Sierra Nevada in the next few decades. If they disappear, a hiatus of well over 100 years will pass before more can be grown to take their place. In the process, the spotted owl would probably be markedly reduced in numbers over most of the Sierra Nevada, but probably with viable subpopulations surviving in Yosemite and Sequoia/Kings Canyon NPs.

Conclusions

Is the Sierran population declining? We cannot be certain. Failure to detect significant declines in the two Sierran study areas must be interpreted cautiously, because the power of both tests was very low. We know nothing about the normal, long-term fluctuations of spotted owl populations in the Sierra Nevada. If the California spotted owl has experienced gradual declines in habitat quality in these mountains, the effects may be subtle and difficult to detect. Because we lack adequate, historical inventories of spotted owls in the Sierra Nevada, we have no basis for comparison with our current knowledge. Their current distribution and abundance, however, do not suggest that they have declined either in their overall distribution in the Sierra Nevada or that they have declined markedly in abundance within any forest type.

Selective logging of the largest trees from the most productive sites in the Sierra Nevada has resulted in significant changes in diameter distributions of trees, leaving relatively few very old, large trees that are clearly selected by the owls for nesting (Chapter 5). Consequently, we are far from comforted by results from the demographic studies. Before reaching a final conclusion on this matter, we need to continue these studies until the power of their tests on lambda is greatly increased.

Do Sierran owls exhibit selective use of habitats? Yes. The overwhelming weight of evidence is that California spotted owls in the Sierra Nevada select habitats differentially from among all habitats available to them. Selectivity is strongest for nesting and roosting habitats, weaker for foraging habitats. Even for foraging, however, we conclude that a target for suitable owl habitat should include at least 40 percent canopy cover in stands with trees averaging at least 11 inches in d.b.h. Data from direct measures of foraging stands further suggest that suitable foraging stands have snags, dead-and-downed woody debris, and some large trees (Chapter 5).

Are key habitat elements declining in the Sierra Nevada? Yes. Of greatest concern to us at this time is the rapid disappearance of the large, old, and generally decadent trees that are the focus of nesting by spotted owls. Given projections from approved and draft LMPs for NFs in the western Sierra Nevada, where the vast majority of Sierran owls occur, these important stand components will disappear at a rapid rate over the next few decades. They cannot be replaced quickly.

Considering the present state of our knowledge about spotted owls in the Sierra Nevada, we can identify eight major factors of concern about owl habitats there (table 1D). These have resulted from a combination of selective logging removing

Table 1D-*Summary of major factors of concern in habitats of California spotted owls in the Sierra Nevada, reasons for those factors, and their impacts on the owls.*

Factor	Reason(s) for the factor	Impact on spotted owls
Decline in abundance of very large, old trees	Selective logging of the largest trees from stands	Loss of the owl's preferred nest sites
Long recovery period for spotted owl habitat after logging	Selective logging of the largest trees from stands	Less of total landscape in suitable owl habitat at any given time
Ingrowth of shade-tolerant tree species, creating unnaturally dense stands with ground-to-crown fuel ladders	Selection harvest; aggressive fire suppression; sheep grazing, which created ideal seedbeds for conifer germination late last century	Increased threat of stand-destroying fires
Excessive build-up of surface fuels	Aggressive fire suppression over the last 90 years, leading to higher densities of trees, more competition for space and water, so a higher death rate of trees	Increased threat of stand-destroying fires
Loss of large-diameter logs from the decaying wood source on the ground	Intentional fires by sheepherders; selective logging of largest trees; piling and burning logs after logging; domestic fuel-wood removal	Potential decline in flying squirrel densities via loss of fungi that are a dietary staple for the squirrels
Decline in snag density	Selective logging of the largest trees from stands; salvage logging; fuel-wood removal	Loss of potential nest sites for owls; loss of den sites for flying squirrels; loss of a source of large logs for decay needs on the ground
Disturbance and/or removal of duff and topsoil layers	Sheep grazing; mechanical disturbance from logging equipment, skid trails, and so on; increased surface fuels that burn hot enough to destroy duff layer	Potential decline in flying squirrel densities via loss of fungi that are a dietary staple for the squirrels
Change in composition of tree species (fewer pines and black oaks, more firs and incense-cedar)	Selective logging of the largest trees, particularly pine species, from stands; aggressive fire suppression	Some loss of nest sites; other effects unknown

mainly the largest trees from stands, aggressive fire suppression beginning shortly after the turn of this century, and the combination of human-ignited fires and extensive sheep grazing in the Sierra Nevada during most of the last half of last century.

Assessing the Owl's Status: Southern California

Here we summarize available evidence for the spotted owl in southern California as it relates to the three fundamental questions, and null hypotheses, posited for Sierran owls. Less is known about the habitat relations of spotted owls in southern California, but we can say much about the likely stability of the owl population there in relation to its pattern of distribution-in relatively isolated blocks with potentially hostile habitat between them, through which the owls must disperse.

Does Evidence Indicate a Decline in the Southern California Population?

Yes. The estimate of lambda for the San Bernardino demographic study area was 0.827 (table 8G), suggesting about a 17 percent annual rate of decline in the resident, territorial population during the study period (1987-91). The statistical test (alpha = 0.05, $P < 0.0001$) strongly rejected the null hypothesis of a nondeclining population. The correct inference for this population is that it has been in a steep decline for at least the past 5 years.

We do not know the reason(s) for this decline. Much logging occurred there in the 1960s, but we doubt whether that disturbance can explain the current decline. Chronic air pollution in southern California may be directly or indirectly linked to the declining population of owls, for example by way of the plant foods important to woodrats. A more plausible hypothesis involves either direct or indirect effects of the drought in southern California, where precipitation from 1984 through 1990 averaged about 60 percent of normal at one weather station and about 67 percent of normal at another near Big Bear Lake, near the center of this demographic study area. Precipitation was below normal in all 7 years at one station and above normal in only 1 of the 7 years at the other (figs. 8A and 8B). In 1991,

when precipitation was above normal, it exceeded the long-term average by about 10 percent. Most of this came in a series of strong storms that coincided with the laying period for most owl pairs that attempted to breed that year.

One working hypothesis is that numbers of dusky-footed woodrats, the primary prey of the owls in the San Bernardino Mountains (Chapter 4), have declined as a result of the drought. If the decline in owl numbers is related in some way to the drought, it suggests that the owl population there is subject to high levels of environmentally induced variation in its demographic parameters. As the population declines, individuals may be lost from marginal habitats, where survival and reproduction are possible only during "good" times (Chapter 8). Individuals that survive, and even reproduce, during the decline may be those occupying better, more stable, habitats, as where more mesic conditions prevail (for example, riparian areas). Such refuges would be critically important to the species' long-term persistence, and any destabilization of them-by logging, water diversion, depression in ground-water levels, excessive development of recreational activities, or further development of communities and dispersed housing-could pose a significant threat to the owl's survival.

Do Spotted Owls in Southern California Exhibit Selective Use of Habitats?

Yes. The same basic patterns found at the home-range scale for Sierran owls have been observed in studies of habitat use by spotted owls in southern California. The most detailed study was done in the San Bernardino Mountains (table 5C). Compared to randomly located sites, nesting and roosting stands had significantly higher canopy cover, total live basal area, hardwood basal area, softwood basal area, and snag basal area. Nest trees were very large for the area, averaging 37 inches in d.b.h. and 88 feet in height. The mean age of nest trees in the San Bernardino Mountains was 230 years based just on the core length that could be extracted from the trees (table 5M).

Are Key Habitat Elements Declining in Southern California?

We do not know. We were not able to bring quantitative information to bear on this question. Little commercial logging occurs in southern California, but "timber-sale improvements" and firewood cutting have negative impacts on owl habitat there. In addition, wildfires occasionally burn through suitable owl habitat, rendering it less suitable, or even useless. The extent to which these events result in a net loss of suitable owl habitat is unknown, however. We also know that urban and dispersed residential expansion is occurring in suitable owl habitat in southern California, especially at lower elevations between relatively isolated subpopulations of the owl. Those are the places where dispersing owls must move from one subpopulation to another, and such dispersal is the only method whereby a decline in one subpopulation can be compensated by "rescue" via immigrants from another. We also know that many owl pairs in southern California, especially in the southern portion of the Los Padres NF, occupy narrow strips of riparian/hardwood forest. These forests will survive there only as long as the stream system from which they get their water survives. In some of these areas, water mining in the forms both of diverting surface water and drilling into underground aquifers threatens to dry up streams to the point that they will lose their riparian forests.

Stability Properties of the Spotted Owl Metapopulation in Southern California

Spotted owls in the Southern California Province have an insular population structure, ranging in size from about 1-4 pair sites to about 125 pair sites, distributed among discrete mountain ranges (fig. 9A, table 9A). This distribution of habitat islands is discontinuous across the landscape, reflecting natural discontinuities in vegetation structure and composition, in topographic conditions, and in the effects of extensive human-induced habitat disturbance and fragmentation. The largest population is in the San Bernardino Mountains, with considerably lower population sizes in the other areas. This "archipelago" is estimated to have 376 pair sites (table 9A), with an approximate population of 300-350 pairs at any point in time. Based on theory and limited empirical data, we believe the ultimate stability of this metapopulation will depend on several factors, including the persistence of one or more populations of sufficient size to avoid negative effects of demographic stochasticity, and with demographic characteristics that result in production of excess individuals to serve as potential colonists for other local populations (Chapter 9).

The sensitivity of the southern California metapopulation to a variety of perturbations was tested by performing multiple simulations, using a spatially explicit model developed to examine effects of spatial aspects of the distribution of the northern spotted owl (Chapter 9). Interpreting model results in a visual and spatially explicit way allows insights into areas of the landscape that are especially vulnerable to local extinction events, as well as those areas that represent sources for immigrants to other local populations. We did not, however, project extinction likelyhoods from the model runs.

The arrangement of owls and owl habitat across the landscape shows that most of the population is concentrated in the San Gabriel/San Bernardino Mountain complex. Smaller populations in the archipelago will continue to function as a part of the larger metapopulation only if they remain connected through dispersal. If these smaller populations become increasingly isolated, via reduction in size of their habitat islands or creation of barriers to dispersal, the likelihood of their extinction increases. Although these small, isolated populations will be the first to go, even the largest, most continuous ones will experience increased risks as smaller populations drop out of the metapopulation.

The many factors discussed earlier-for example, wildfires, urban and dispersed residential expansion, water mining, and increased recreational use of riparian areas that are prime owl habitat-can all add their seemingly insignificant, individual bits

of erosion into the existing population of spotted owls in southern California. To the extent that this leads eventually to fewer pairs overall, fewer pairs in individual "islands," greater distances between pairs, and reduction in the rate of successful dispersal between populations (to maintain smaller ones), the spotted owl population in southern California appears to be fragile.

On the other hand, we know that inventories of spotted owls in southern California have not been completed. If more pairs were known to occur in some of the habitat islands, it could markedly increase estimates of the stability properties of those subpopulations. Particularly important in this regard are the possibilities of more pairs in and near the Cleveland NF and in and near the San Rafael Wilderness in the Los Padres NF. Increasing cluster size (number of pairs with essentially shared home-range boundaries) to 45 or 50 pairs in each of these areas would have a strong stabilizing effect on the metapopulation in southern California.

Conclusions

Several uncertainties are associated with the status of spotted owls in southern California. The only population studied demographically has been declining at a high rate for at least 5 years, but this has all taken place during the recent drought. We cannot separate the possible effects of the drought from other possibilities. Indeed, no other explanations are immediately evident. It is possible that some subtle, even unsuspected phenomenon is the real cause of the decline. Although the owls in southern California use only a subset of all available habitats, we do not know if those selected types are undergoing a net decline. Our modeling suggests that the metapopulation structure of the owls, there is especially sensitive to diminishing sizes of smaller, local populations. And it is also especially sensitive to any reduction in the effectiveness of dispersal by owls among the various "island" populations. We have identified several factors that could be, and probably are, affecting the sizes of the "island" populations and the effectiveness of dispersal among them. For this reason, we believe that more inventories and research are needed on the spotted owl metapopulation in southern California.

Considering the present state of our knowledge about spotted owls in southern California, we have identified seven major areas of concern about owl habitats there (table 1E). These have resulted from a combination of two major factors: (1) The overall population is naturally fragmented into small, relatively isolated subpopulations by the topography, precipitation patterns, and fire regime. (2) Extensive growth in the human population in the Los Angeles basin, and in other valley and foothill areas within commuting distance of Los Angeles, is encroaching on owl habitat.

Table 1E--*Summary of major factors of concern in habitats of California spotted owls in southern California, reasons for those factors, and their impacts on the owls.*

Factor	Reason(s) for the factor	Impact on spotted owls
Fragmented distribution of suitable owl habitat into small, relatively isolated "islands"	Mainly a natural result of topography, precipitation patterns, and fire regime in southern California	Creation of a metapopulation structure overall population is fragmented into numerous relatively small populations
Small population units are relatively unstable	Demographic stochasticity (random events in breeding, such as most or all young in a given year being males)	Increased likelihood of local extinction of small population units
Extent of demographic rescue of small populations by immigration of owls from other populations is relatively impeded	Distances between isolated populations, and the nature of the habitat between them, directly affect the likelihood of successful dispersal among populations by owls	Increased likelihood of local extinction of small population units
Wildfires	Natural fire regimes in southern California; additional human-caused fires; difficulty of fire suppression in rugged, remote terrain	Loss of suitable habitat will exacerbate problems of small owl populations and restricted dispersal among populations
Expansion of communities and dispersed housing developments in suitable owl habitat, especially in dispersal areas between isolated owl populations	Human population growth in southern California	Further decline in effective dispersal among isolated owl populations; possible loss of suitable breeding habitat
Increasing recreational impacts in owl habitats	Human population growth in southern California	Possible loss of additional owl habitat; possible disturbance effects inducing owls to leave otherwise suitable habitat
Surface and subterranean mining of riparian water sources	Human population growth in southern California	Loss of suitable owl habitats in riparian/hard wood forests

An Assessment of Current Management

Forest Service Lands

Regional Policy-The SOHA Network

Based on available information, we estimate that 83 percent of all California spotted owls occur on NFs, overall; 65 percent of the total are on NFs in the Sierra Nevada (table 1A), and only 4 percent of those are on reserved lands. All known spotted owl sites on NFs in southern California are to be protected. We were not able to assess the extent to which the implementation of this policy is adequate for those owls, because we have incomplete knowledge of the range of habitats in which the birds can maintain self-sustaining populations. In general, we agree with the policy. We are concerned, however, about the current level of information on owl sites in southern California, as well as with the ability of the FS to manage habitat to provide adequate protection from fire and other factors. We recommend that current policy be reviewed periodically to determine (1) that it is being implemented adequately, and (2) that measures taken to implement it reflect the latest information available on the owls in each locality.

The FS's Regional policy for maintaining a viable population of California spotted owls in the Sierra Nevada is the network of SOHAs described in a previous section of this chapter. Because SOHAs provide habitat for only one to three owl pairs in a unit, separated by 6-12 miles from other units, the Interagency Spotted Owl Scientific Committee (ISC) that proposed an alternate strategy for the northern spotted owl (Thomas et al. 1990) concluded that the SOHA strategy had an unacceptably low likelihood of maintaining the owl population over the next 50 to 100 years. We agree that a SOHA strategy, culminating in a network of small, relatively isolated "islands" of older forest suitable for breeding by spotted owls and separated by a "sea" of younger, less suitable or unsuitable habitat, is not a workable strategy to assure long-term maintenance of spotted owls. The underlying principles are the same whether for the northern or the California spotted owl:

1. Every empirical study available on the persistence of bird populations in relation to the number of pairs in the population shows that the likelihood of extinction increases dramatically with decreasing numbers of pairs in a block of habitat. Isolated pairs exhibit excessively high extinction rates. Modeling studies show the same thing. Consequently, we expect that owl pairs in SOHAs would disappear at a relatively high rate, leaving the SOHAs unoccupied and at least temporarily nonfunctional. This loss would considerably exacerbate dispersal problems. Replacement of members lost from pairs would occur very slowly because recruits would have to search extensive areas of unsuitable landscape before locating a vacancy in an isolated SOHA.
2. Social interactions among pairs of owls almost certainly increase calling frequency where several pairs of birds arc clustered. If this were not true, observers should not be able to elicit calling from silent owls by imitating their calls. The increased calling rate in clusters of several pairs should provide a sort of "vocal guidance" that would help dispersing birds locate other owls of the opposite sex in good, occupied habitat. This effect would be minimal at SOHAs because calling neighbors could be too far away to hear, and thus to stimulate counter-calling (see Thomas et al. 1990. appendix O).
3. Although SOHAs must provide at least 1,000 acres of suitable owl habitat, and some specified amount of replacement habitat, this can be (and usually is) accumulated by summing acreages of several smaller patches. A result is that SOHAs have a high ratio of edge to area. Some studies indicate that fundamental changes occur in the microclimate of a forest interior, at about 525 feet from an edge (Harris 1984, Franklin and Forman 1987). A 20-acre circular patch, therefore, is essentially all "edge." A 100-acre circular patch has a core of only 32 acres that would be sheltered from edge effects. In addition, allowing a SOHA to consist of several small patches of habitat, instead of a single large one, results in each patch being more susceptible to blowdown of trees around its edges.
4. Being relatively small, SOHAs are vulnerable to small-scale catastrophes. Destruction of a SOHA removes it from the network for perhaps 80 to 150 years and increases the mean dispersal distance between remaining SOHAs, further reducing the chance of nonterritorial owls finding unoccupied but suitable sites.
5. Floaters (nonterritorial birds) behave toward populations of breeding birds in ways that seem unlikely toward isolated pairs of breeders. We believe SOHAs would fail to provide sufficient conditions for recruitment of floaters into a breeding population, because the extent of suitable habitat in a SOHA is too limited to accommodate much more than a nesting pair.

All of the above problems are markedly reduced if owl populations are maintained in relatively large clusters in extensive landscapes where most or all owl pairs have one or more adjoining neighbors (Thomas et al. 1990).

Cumulative Effects Analysis

In 1991, the FS implemented a cumulative effects analysis (CEA) to evaluate green timber sales and other projects within the range of the California spotted owl in the Sierra Nevada. Its objective is to maintain a full range of options for managing spotted owls in the future, while still allowing logging. First, all known and probable spotted owl sites for pairs or resident singles are identified that could be directly or indirectly affected by a project that might remove or affect owl habitat. Directly affected sites are those in which project activities will occur; indirectly affected sites are those in which owl use areas during the breeding period adjoin directly affected sites. The analysis area generally corresponds to the combined use areas of the known and probable owls that are determined to be directly and

indirectly affected by a given project. The outer boundary of this combined area may be constrained on one or more sides by topographic barriers or unsuitable vegetation types.

The process next calls for mapping all nesting and foraging habitat available within the analysis area before the project is done, using the most current information. This can include recent aerial photography, Landsat imagery, LMP database, timber stand inventory, and especially ground verification. All components of suitable habitat-total canopy closure, dominant overstory trees, multi-storied canopy structure, decadence, dead-and-downed wood, and hardwoods are considered. The amounts of suitable nesting and foraging habitat that will remain in each owl use area after completion of the proposed project are then mapped. Effects of other actions that are reasonably forseeable are also considered (for example, other sales under contract, other projects with signed decision notices, timber harvest plans, or predictable actions on private lands that will remove suitable habitat). The amounts of suitable foraging and nesting habitat that will remain after project completion are next evaluated against that determined to be needed by the owls in that locality, using the best available information from research and other sources. If the proposed action would reduce the total suitable owl habitat blow levels needed to support the current estimated number of owls in the analysis area, adjustments are made in the project. These may include deleting portions of the sale, modifying prescriptions so that suitable habitat remains after logging entry, or moving sale units into unsuitable habitat. If the project would leave the needed amount of suitable foraging and nesting habitat per owl use area, it may proceed subject to any other Forest standards and guidelines that apply.

We have reviewed this process and believe that it will accomplish its objectives in many cases. We are concerned, however, that it lacks specific guidance for retaining the very large trees that are selected for nesting by the owls. Although the procedure calls for at least half of the canopy cover retained in the project area to be in the dominant overstory, which would undoubtedly spare many larger trees in a project area, it would not necessarily spare the largest or the oldest trees. The process also lacks specific guidance for retaining snags and maintaining some quantity of dead-and-downed woody material in specific size-classes. Finally, the CEA process has no provision to retain important habitat attributes in areas not now classified as suitable nesting or foraging habitat, even though these may have the potential to become suitable at varying times in the future--some sooner and some later. Results presented in Chapter 5 of this report could be used to craft specific recommendations for these attributes.

Other Public Ownerships

Only 130 owl sites located from 1987 to 1991 were on SPs and NPs, where management appears to be consistent with maintaining their habitat. The single known owl site on BLM lands certainly underestimates the true number of owl pairs, present, although the final count is not likely to be large. Logging occurs on much of the forested land managed by the BLM. Even though BLM's stated management emphasis will shift toward managing for old-growth, wood products, stand maintenance, and to meet wildlife and vegetation objectives, we cannot be certain that this will suffice to maintain the number of owl pairs that probably occur now on BLM lands. The matter needs to be addressed in detail along lines recommended in later sections of this chapter. A similar approach should be taken for State-owned forests where logging occurs.

Private Timberlands

Timberlands in the Sierra Nevada that are owned by commercial timber companies and miscellaneous private parties exceed 2 million acres. Presumably much of this acreage has habitat suitable for spotted owls. Inventories have not been completed on most of these lands, and we have not been provided with full information about results of some inventories that have been done. It is clear, however, that much commercial timberland still supports breeding pairs of spotted owls, even though that has not been an objective. Breeding pairs are missing from other private timberlands, however (Chapter 3). Management across all private timberlands is consistent to the extent that policies and practices mandated by the State Forest Practices Act are followed on all private lands. Even with these constraints, however, we cannot easily characterize timber management on private ownerships because practices differ markedly among them. The fact that some private timberlands have breeding pairs of owls, while others do not, suggests to us that existing State regulations do not assure maintenance of owl sites on private lands. The difference lies in the different policies and practices of individual land owners. Whether or not new forest management practices will be enacted by the State of California remains to be seen, as does their contribution to the maintenance of breeding pairs of spotted owls on private lands.

Management Recommendations for Southern California

We regard the status of the spotted owl in southern California as serious and meriting annual attention into the foreseeable future. We are deeply concerned that the largest subpopulation in southern California, in the San Bernardino Mountains, has been declining at an average annual rate of about 17 percent, at least since 1987. Of equal concern is the fact that the overall population is fragmented into many smaller populations. This metapopulation structure is mainly a natural result of vegetation patterns created by topography, precipitation, and fire regimes. Consequently, we are unaware of significant management opportunities to create additional, large areas of suitable dispersal habitat between the isolated populations, or to add markedly to the amount of suitable breeding habitat within those population areas. Our modeling studies strongly suggest that the stability of

the entire southern California metapopulation depends on the populations in the San Bernardino and San Gabriel Mountains (Chapter 9). If they collapse, the entire metapopulation will collapse with them. Although the observed steep decline in the San Bernardino population may be related to current drought conditions, and so be transitory, this is not a certainty (Chapter 8). The large number of factors leading to concern for the owls in southern California (table lE) only add to our concern for what appears to be a very fragile balance for the spotted owl metapopulation. Accordingly, we recommend the following:

1. Immediately implement a program to complete inventories of spotted owls in the remainder of their range in southern California (Chapter 2). If inventories and assessments of total populations, based on our understanding of habitat, have led us to markedly underestimate the number of owls occurring in various parts of their range, it could significantly change conclusions from our modeling.
2. Continue to monitor the demographics of the San Bernardino population annually, and implement at least two additional demographic studies-one centered on Palomar Mountain and the other in an area with reasonable road access in the Los Padres NF. These additional demographic studies would help (1) to determine whether our conclusion from modeling is correct that owl subpopulations in these locations depend for their maintenance on immigrants from the San Bernardino and San Gabriel subpopulations, and (2) if so, to establish the rate of immigration from other subpopulations needed to maintain them.
3. Continue existing management direction on FS lands, and extend that policy to other Federal lands and to State lands, to maintain all known pairs of spotted owls in southern California. To the extent possible, implement the same policy on private lands.
4. Finally, we recommend that a team of specialists be assembled immediately to formulate guidelines that they believe would best assure maintenance of owl pairs in various parts of their distribution in southern California. This team should include biologists with the most knowledge of spotted owl biology and habitats in southern California, silviculturists, specialists in fuels management and wildfire suppression, county planners, and probably others.

Management Recommendations for Private Timberlands in the Sierra Nevada

Management of private timberlands in California are regulated by the State, which appears to be in the process of promulgating new policies in this arena. We hope that some of the information provided in this full report may influence the final form of those new policies.

Recently, some of the larger private timber companies have begun to develop guidelines for their lands that they contend will maintain populations of breeding spotted owls. We laud those efforts and believe they should be encouraged, but under the provision that results are carefully studied and documented using standard, scientific methods, including scientific peer review, and that they are shared openly with the public at least annually. Specifically, for private timberlands, we recommend the following:

1. Private timber companies that have developed management practices that they contend will maintain nesting or foraging habitat, or both, for spotted owls, should be permitted to test those practices, contingent upon submission of detailed plans to, and subsequent approval from, the State Board of Forestry. It would be the Board's responsibility to determine whether a particular plan has reasonable merit, vis-á-vis spotted owl biology.
   A. These plans should clearly identify how resulting forest structures and configurations are likely to provide owl habitat, as it is presently understood, or additional information presently known only to a given timber company should be made public, in detail, for evaluation.
   B. Approval of a plan by the State Board of Forestry would be contingent upon the concurrent implementation by the timber company of a long-term demographic study (see Chapter 8) over a large enough sample of its ownership to determine whether or not its management leads to predicted results. Such a demographic study would follow the same standards and protocols already established for spotted owls, and results would be open for scrutiny, at any time, by the public.
2. Operations on other private timberlands should continue to be regulated by existing State policies.
   A. All information about spotted owls on these lands should be shared openly with all adjoining ownerships. Indeed, this needs to be a two-way street so that all parties can maximize the efficiency of their planning and the evaluation of their land managagement, vis-á-vis the owls.
   B. Further, overall plans for management of spotted owls need to result from coordinated efforts with adjoining landowners, including all public ownerships. This recommendation is not leveled as a criticism of private landowners. On the contrary, we believe that all parties-public and private-share equally in the general failure to work cooperatively to develop solutions to common problems.

Management Recommendations for Public Timberlands in the Sierra Nevada

A successful strategy for the California spotted owl in the Sierra Nevada must be designed to ameliorate the negative effects on owls of several important trends that have been underway for at least the past 100 years (table 1D). Furthermore, if the FS moves ahead with its current generation of LMPs, the dramatic shift toward clearcutting would add considerably to the fragmentation of Sierran forests. This would lessen the ability of spotted owls to find mates and increase the distances that the birds would need to fly to find sufficient food. In addition to ameliorating the several negative trends itemized in table 1D, a successful long-term strategy for spotted owls in the Sierra Nevada must result in the clustering of pairs such that many occur as neighbors with overlapping home ranges in the same general area.-This is the same reasoning advanced by the ISC in the case of the northern spotted owl (Thomas et al. 1990), which recommended multiple Habitat Conservation Areas (HCAs) large enough to provide habitat for at least 20 pairs of owls.

Evaluation of an HCA Strategy for the California Spotted Owl

Both the northern and California spotted owls select forest conditions commonly associated with very old forests. Consequently, logging is responsible for much of the concern about long-term maintenance of the populations of both subspecies. As two of our five peer reviewers pointed out, the ISC strategy proposed for the northern spotted owl (Thomas et al. 1990) set new precedents in conservation biology, so it should not be lightly dismissed as an option for the California spotted owl. We agree. In five important ways, however, the current situation for the California subspecies differs from that of the northern subspecies.

First, by some estimates the numbers and distribution of the northern spotted owl have been reduced by about 60 percent as a direct result of logging, land clearing for agriculture, urbanization, and other human developments (Thomas et al. 1990, p. 20). We have no evidence of similar declines in the number or distribution of California spotted owls, however, either in the Sierra Nevada or in southern California. In spite of the fact that logging has occurred over nearly all of the conifer forests of the Sierra Nevada in the past 100 years, and especially in the past 50 years, spotted owls continue to be widely distributed throughout most of the conifer zone. Indeed, spotted owls may be more abundant in some areas of the Sierra Nevada today than they were 100 years ago. Late last century, sheep and sheepherders so depleted the understory vegetation and the supply of dead-and-downed wood at some locations in the Sierra Nevada that flying squirrel populations may have been depressed. We would expect owl numbers to decline proportional to the decline in numbers of flying squirrels (see table 4A), unless the owls preyed mainly on other species in the latter part of last century. With the burst of regeneration that followed removal of the sheep and introduction of reasonably effective fire suppression (fig; 11I), stand densities increased markedly and this led to an increase in the amount of decaying wood on the ground. The absence of periodic fires also permitted greater accumulations of duff and decaying wood.

Second, clearcutting is still held by many foresters and silviculturists to be the prescription of choice for most of western Washington and Oregon, west of the Cascade crest. Partial cutting there leads to extensive blowdown of remaining trees, and regeneration of preferred timber species is poor after partial cutting compared with clearcutting. The result is a scant record of experience with partial cutting in most of the Pacific Northwest, and certainly no experience with how to maintain spotted owls in logged forests by applying a variety of partial-cutting prescriptions. As a result, the ISC opted for a strategy that separated HCAs from areas where logging could occur, and they prudently held that experience with silvicultural procedures that could both generate timber volume and maintain owls should be acquired outside of HCAs. On the other hand, partial cutting has been the predominant method over most of the Sierra Nevada for decades. We know that stands there do not "fall apart" when partially cut. We also know that most of what has been done there has not yet excluded spotted owls from Sierran forests.

Third, because clearcutting practices have dominated silviculture in the Pacific Northwest, most forests there today are either relatively undisturbed or they are in various stages of regeneration from clearcuts done mostly within the past 50 years. Consequently, distinguishing between suitable and unsuitable owl habitat in the Pacific Northwest was relatively easy, compared with the same task in most of the range of the California spotted owl. Tallying total acres of suitable owl habitat, although not easy, was nonetheless feasible over most of the range of the northern spotted owl. This has not been the case throughout the range of the California spotted owl for three primary reasons: (1) Logging practices in the Sierra Nevada and southern California have not typically involved the creation of nonforests where once forests stood. Instead, logging's impacts have been incremental. (2) We have no studies to show what sorts of forest stands can support *self-sustaining* populations of California spotted owls. (3) Nearly all of the quantitative research done on the California spotted owl began in 1987 or later-the same time the present drought began (fig. 4H). Therefore, all results must be interpreted against that background.

Fourth, fire is not a major threat to most existing stands west of the Cascade crest in Oregon and Washington (Agee and Edmonds 1992). Setting aside large blocks of forested land to be left nearly intact, with little or no logging or other stand-altering activities, does not entail a big risk that fires will destroy major portions of. those blocks at an unacceptable rate. We have little confidence that the same is true in the Sierra Nevada. Sierran mixed-conifer forests, where most California spotted owls oc-

cur, are drier and, given the effects of fire exclusion, much more prone to stand-destroying fires than are most forests in western Washington and Oregon. This creates a challenge when trying to establish procedures for maintaining spotted owls in Sierran conifer forests. An HCA strategy there could deal with the uncertainties associated with logging, but HCAs would sometimes be reduced in extent by stand-destroying fires. Prescribed fires and other methods of fuel treatment can be used to reduce the excessive fuel loads that are now so common in Sierran forests (Chapter 12). These procedures are costly, however, and we believe it is folly to imagine that sufficient funds would be forthcoming to implement an effective fuels management program in HCAs excluded from logging. Furthermore, regulations on air quality standards are making it increasingly difficult for agencies to obtain the burning permits needed to implement effective prescribed burning programs.

Fifth, the northern spotted owl is considerably more numerous than the California spotted owl. This contrast is even greater, of course, for the Sierra Nevada-the only area where an HCA strategy might be considered for the California spotted owl (see prior discussion of the southern California case). Thomas et al. (1990, p. 20) stated that "...results indicate about 2000 pairs located during the last 5 years, representing some unknown fraction of the true number of pairs. Because a census of the total population is not available, we have no statistically reliable population estimate. Recent claims of actual counts of some 6000 birds in 1989 are not out of line with other information from monitoring and inventory efforts." The HCAs recommended by the ISC were estimated to set aside habitat for 1,743 pairs of northern spotted owls (Thomas et al. 1990, p. 33). "In a worst-case scenario, we estimate that the strategy could result in a 50 to 60% reduction in current owl numbers," stated Thomas et al. (1990, p. 34). Given the relatively large number of northern spotted owls, and the extensive distribution of HCAs throughout the range of the subspecies, the ISC believed that such a reduction in total population would not preclude attaining a stable, equilibrium population within 100 years.

We expect that an HCA strategy in the Sierra Nevada could be implemented only on Federal lands, where we have estimated 1,454 known and possible owl sites (table 1A). If 75 percent of the owl sites have pairs at any given time, and assuming that an HCA strategy in the Sierra Nevada might result in only a 40 percent decline in the number of owl pairs, we would expect only about 650 pairs of owls to be protected by HCAs (which would be structured to include reserved lands-NPs and Wilderness Areas). This number may be sufficient to maintain a viable population of owls over the short- to mid-term in the Sierra Nevada, depending on the sizes and positioning of the HCAs. But the number is small enough to introduce additional risks associated with catastrophic events, such as stand-destroying fires in HCAs. Because fire events and subsequent impacts on owl numbers are inevitable, we must maintain a balance between the rate of habitat loss to fires and the rate of habitat recovery from fires.

From the above considerations, we believe an HCA strategy for the Sierra Nevada has as many faults as it has benefits. It should not be undertaken lightly, and evidence of the need for such a strategy must be compelling. Here we briefly summarize that evidence.

Although both study populations suggest the possibility of population declines, evidence of declining owl populations in the Sierra Nevada was inconclusive. Because the power of the test of the null hypothesis of no decline was very low in both cases, the correct inference to draw from results is that we are uncertain about the status of these populations. Condition this inference, however, with the additional facts that (1) one of the two demographic studies was done in Sequoia/Kings Canyon NPs, where logging and other habitat disturbances have not occurred, and (2) the second demographic study was done in an area of checkerboard ownership where owl density was considerably less than in areas of continuous public ownership in the Sierra Nevada, and where no nests and few roosts of owls were found on the private timberlands that were part of the checkerboard. Even if this population actually declined during the period of study, it may not have been representative of owl populations occupying areas of more contiguous, suitable habitat in Sierran conifer forests.

As for northern spotted owls, strong evidence from several sources indicates that California spotted owls select nest and roost sites in stands with very large, old trees, high canopy closure, and snags. Clear evidence from past logging practices and from the LMPs for Sierran NFs indicates that most of these stands will soon be gone if the direction of forest management in Sierran conifer forests is not changed. At the present time, however, the owls are widely and evenly distributed throughout nearly all of the westside conifer forests on NF lands. We know less about their occurrence on private lands, but we do know that owls occur on many of them. Apparently, even though the total amount of old-growth forest has been markedly reduced in the Sierra Nevada during the past century, enough very old trees remain today, widely distributed, that the owls do not exhibit major gaps in their distribution that can be clearly attributed to logging.

Given these circumstances, we do not find a case sufficiently compelling at this time to recommend setting aside large blocks of Sierran forests as HCAs for the California spotted owl. Instead, we believe the situation calls for several steps needed during an interim period to preserve for the future significant management options for owls in the Sierra Nevada. These are aimed primarily at saving the older forest elements that the owls appear to need for nesting and roosting, and at reducing the excessive build-up of surface and ladder fuels.

A Recommended Interim Approach

We believe the current status of the California spotted owl in the Sierra Nevada is more amenable to improved management practices throughout public lands (Federal and State) than it is to any of the variety of reserved block designs we have examined. Because spotted owls are still widely and fairly evenly distributed throughout the conifer forests of the western Sierra Nevada, we favor an alternative strategy that maintains that number and distribution at least for an interim period. Management of the

forests during this interim should not foreclose options for whatever long-term management scenario may be adopted for the owl at the end of the interim period. The desired objective, of course, would be to determine how to maintain spotted owls throughout Sierran conifer forests in a manner compatible with some sustainable level of timber production. The advantages of such a strategy are many. No decisions must be made about the number of owl pairs needed in blocks of habitat or how far apart to space blocks, because most of the Sierran conifer forest would be suitable for foraging by owls, and nesting and roosting habitat would be widely available. Commodity production associated with maintenance of suitable owl habitat would result in funds for fuels management. And much of the fuels management problem could be approached physically as part of the strategy to maintain suitable owl habitat by removing the dense surface and ladder fuels that now facilitate stand-destroying fires. Finally, we contend that such a strategy is more likely to sustain viable populations of most or all other plant and animal species in the Sierra Nevada than is any block strategy.

Whatever interim strategy may be adopted, it should accomplish three primary objectives: (1) protect known owl nest stands (or main roost stands if nest stands are not known) from any significant degradation; (2) protect very large, old trees throughout Sierran conifer forests; and (3) begin to cope with the excessive fuels problem. The duration of the interim period will depend on how quickly we can determine, with certainty, the status of the owl population in the Sierra Nevada and attain a relatively full understanding of the range of habitats in which the owls can maintain self-sustaining populations. We recommend an initial period of 5 years, although whatever period is chosen must extend well past the present drought into the next "normal" or "wet" climatic period.

General Recommendations

1. Maintain all existing SOHAs, as presently specified in LMPs, until a long-term strategy is implemented. Although the SOHAs do not, by themselves, constitute a viable strategy for the owls, we cannot anticipate what role they may play, if any, in a long-term strategy.
2. Continue to monitor the demographies of spotted owls in the Lassen NF, Eldorado NF, Sierra NF, and Sequoia/ Kings Canyon NPs. Enlarge these studies enough that the power of their tests of lambda can provide a reasonable likelihood of detecting real population declines when they occur (Chapter 8).
3. Implement ecological studies of the primary prey species of spotted owls in the Sierra Nevada Province, especially the northern flying squirrel in the conifer zone and the dusky-.footed woodrat at lower elevations (Chapter 2). The objective should be to develop a full understanding of the key ecological linkages among trees, soil, water, prey, and owls (Chapter 4).
4. Undertake an extensive inventory of potential spotted owl habitat in riparian/hardwood forests and adjoining woodlands in the foothills of the western Sierra Nevada and in the inner coast ranges to estimate the number of nesting pairs there (Chapter 2).
5. Through coordination between managers and researchers, initiate a program of experimental forestry in Sierran NFs within the interim period, as recommended in Chapter 2 and elucidated in Chapter 13, so that we may observe these modified forest systems and determine their effects on spotted owls.
6. Develop a time schedule that identifies specific, annual accomplishments that can be monitored to assure satisfactory progress toward attaining information needed to craft a longer-term strategy for the California spotted owl.

Specific Recommendations

The following guidelines (table 1F) should not preclude options for the future. The protections afforded to owl sites and preferred nesting habitat are intended to stabilize owl habitat acreage in the short-term. Taking a longer look, the basal area retention in larger tree size-classes will ensure that old-growth elements will not be lost from these systems. Existing Experimental Forests and Demonstration Forests are expressly exempted from all of the following recommendations.

Spotted Owl Sites on Public Lands

1. Establish a *Protected Activity Center* at all known California spotted owl sites in the Sierra Nevada. Locate owl sites using the California Department of Fish and Game's database, and identify the activity center in each, defined either by a known nest site or by what is judged by a Forest Biologist knowledgeable about owl biology to be the best roost location in the site. Delineate an area of 300 acres around this activity center (see "Size of Activity Centers" in Chapter 5) following boundaries of known habitat polygons and topographic features such as ridgelines, as appropriate. The *intent* here is to include in the 300 acres the best possible owl habitat available, blocked up into as compact a unit as possible. Ideally, each unit would consist of 300 acres of P4G, M4G, or better stands (M5G, M5N, M6) (see table 1C for code definitions), but this will likely not be possible in all instances. To assure that the unit includes the best owl habitat available, augment the acreage of P4G, M4G, or better with the following timber strata, arranged here in descending order of priority: M3G, P3G, M4N, M3N, P3N, R4G, R4N, P4P, and M2G (see table 5A and fig. 5B, and the discussion of ponderosa pine strata under the heading "Selective Use of Forest Types" in Chapter 5).
2. Undertake no stand-altering activities within *Protected Activity Centers*, other than light underburning.
3. Light underburning in these stands would be permissible, given careful review by biologists and fuels management specialists, on a case-by-case basis. Any underburning should be done in a manner that minimizes removal of duff and large woody debris.
4. Remove no snags or large culls from *Protected Activity Centers*.

Table 1F-*Summary of primary recommendations for stand retention and special stand treatments to maintain options for spotted owls on public timberlands in the Sierra Nevada during an interim period.*

Attributes	Protected[1] Activity Centers	Selected[2] Timber Strata	Other[3] Timber Strata
Large, old trees			
Basal area	No logging	Retain 40 percent basal area from the largest healthy trees and culls	Retain 30 percent basal area from the largest healthy trees and culls Retain at least 50 square feet basal area per acre
D.b.h.[4]	No logging	Retain all live trees ≥30 inches in d.b.h.	Retain all live trees ≥30 inches in d.b.h
Percent canopy cover	No reduction	≥40 percent	No restriction
Snags	No reduction	Save the largest snags ≥30 inches in d.b.h., to a maximum of eight snags per acre; if this is < 20 square feet basal area per acre, save snags < 30 inches in d.b.h., from the largest down, to a total of eight snags per acre or 20 square feet basal area per acre, whichever comes first; need not retain snags <15 inches in d.b.h. or < 20 feet tall	
Downed woody material	Reduction only in relation to light underburning	Beginning with the largest downed logs (by volume), sequentially retain pieces of downed wood until an average of *at least* 10-15 tons/acre are retained over a cut unit. Do not include pieces <11 inches in diameter to meet the tonnage limit. The intent here is to retain as many as possible of the existing large pieces of decaying wood present on a site before any treatment (for example, a timber sale or prescribed burn). Cull logs created by a sale should be left at or near where they fall and be included when totalling the downed wood to be retained	
Fire threats	Light underburning	Positive fuels management	Positive fuels management

[1] Block of 300 acres of suitable nesting/roosting habitat delineated around nest site or primary roost site in all known spotted owl sites in the Sierra Nevada, as identified in the California Department of Fish and Game database.

[2] Timber strata selected for nesting by spotted owls in the Sierra Nevada (P4G, M4N, M4G, and better-strata codes explained in table 1C).

[3] Other timber strata used for nesting by spotted owls in the Sierra Nevada (MG, P3N, P4P, M2G, M3P, M3G, M3N, M4P, R3P, R3G, R4G, R4N-strata codes explained in table 1C).

[4] Diameter at breast height, in inches.

Other Forested Public Lands

1. *Selected Timber Strata:* Stands shown to be selected for nesting by the owls (P4G, M4G, M4N, M5G, M5N, M6--see table 5A and section on "Selective Use of Forest Types" in Chapter 5) may be entered only once for commercial logging prior to implementing a long-term strategy for managing the California spotted owl on public lands. Remove no live tree ≥30 inches in d.b.h. Retain 40 percent of the basal area, consisting of the largest of the healthy trees and culls in each cut unit, using the following steps:
   A. Do not rely on current timber inventories to determine stand strata. Base this determination on field verification of each cut unit during stand inventories in preparation for sales. When a cut unit is borderline between two timber strata (for example, between M4N and M3N, between M4G and M3G, or between M4N and M4P), assign it to the stratum with higher canopy cover and/or larger stem diameter. Develop diameter distributions of live trees (including culls) from the inventory data for each cut unit separately, by 2- to 4-inch d.b.h. groupings.

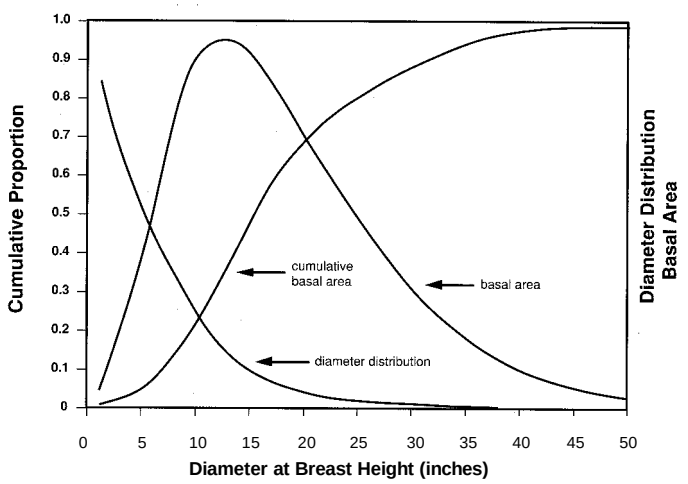

Figure 1A-Diameter distribution (stems per acre), basal area distribution (square feet per acre), and cumulative basal area distribution of a hypothetical, uneven-aged stand of trees.

B. For each cut unit separately, construct basal-area distributions for live trees.

C. Next form *cumulative* basal-area distributions for live trees in each cut unit (see fig. lA), and draw a horizontal line from the 0.6 proportion on the *y* axis to the cumulative basal-area distribution curve. From that point, draw a vertical line down to the *x* axis (see fig. 1B).

D. Cut no live trees with diameters equal to or larger than the diameter intersected by the line perpendicular to the *x* axis.

Maintain an average crown closure ≥40 percent in the remaining overstory. If the largest live trees retained in the cut unit do not yield a canopy closure ≥40 percent, make up the difference with stems 12-24 inches in d.b.h. Treat surface and ladder fuels as necessary to create a mosaic of fuel profiles that will minimize the probability of extensive, stand-destroying wildfires. Fuel profiles should consider other objectives of land management, including the needs for site productivity and for habitat of species other than spotted owls.

2. *Other Timber Strata:* Stand types used for nesting by the owls, but not significantly selected based on availability (P3G, P3N, P4P, M2G, M3P, M3G, M3N, M4P, R3P, R3G, R3N, R4G, R4N-table 5A), may be entered only once for commercial logging prior to implementing a long-term strategy on public lands. Remove no live tree ≥30 inches in d.b.h. Retain 30 percent of the basal area, consisting of the largest of the healthy trees and culls in each cut unit, following the same steps described for *Selected Timber Strata.* In this case, begin the horizontal line to the cumulative basal area distribution curve from 0.7 on they axis (fig. 1B). Live trees remaining in these stands must have a cumulative basal area of at least 50 square feet per acre. Remove surface and ladder fuels that would threaten to carry fire into the crowns of remaining trees, and undertake on the sale unit other fuels treatments that are considered necessary.

3. *Snag Retention:* Retain all snags in Protected Activity Centers. In all other habitat that is currently or potentially suitable for foraging, roosting, and/or nesting by spotted owls, including salvage sales and instances of catastrophic stand loss, use the following guidelines: Save the largest snags ≥30 inches in d.b.h. (starting with the largest snag and working down) to a maximum of eight snags per acre, averaged over the cut unit. If this guideline does not result in at least 20 square feet basal area of snags per acre, continue adding snags, from the largest ones remaining, down to a total of eight snags per acre or 20 square feet basal area, whichever comes first. Snags <15 inches in d.b.h. or <20 feet tall need not be retained.

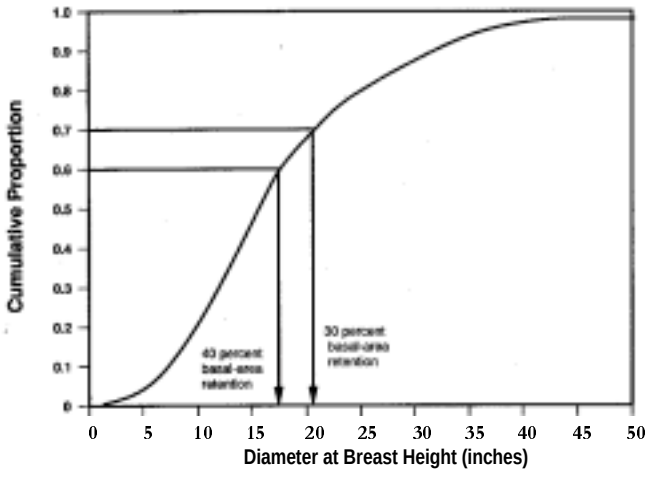

Figure 1 B-A cumulative basal-area function from a hypothetical stand, showing how to relate the proportion of the total basal area subject to logging to the diameter limit of the trees to be retained.

4. *Downed Wood Retention:* In all habitat that is currently or potentially suitable for foraging, roosting, and/or nesting by spotted owls, use the following guidelines: Beginning with the largest downed logs (by volume), sequentially retain pieces of downed wood until an average of *at least* 10-15 tons/acre are retained over a cut unit. Do not include pieces smaller than 11 inches in diameter to meet the tonnage limit. The intent here is to retain as many as possible of the existing large pieces of decaying wood present on a site before any treatment (for example, a timber sale or pre-=scribed burn). Cull logs created by a sale should be left at or near where they fall and included when totalling the downed wood to be retained. For the mass calculation, assume a specific gravity of 0.4.

5. *Exceptions to Guidelines 1 and 2:* Guidelines 1 and 2, above, require that large, live trees be left where they are found. In certain cases, based on concurrence between wildlife biologists and silviculturists, compelling reasons may exist to reduce the areas of tree crowns and roots in portions of a cut unit. These include the need to break up a uniform distribution of leave trees to allow regeneration of shade intolerant species, to reduce the spread of dwarf mistletoe from the overstory to regenerating conifers in the understory, or to protect dense leave patches from bark beetle attack by killing high-risk trees. In such cases, we recommend the following guidelines:

If the total basal area of snags ≥30 inches in d.b.h. is less than 20 square feet per acre, live trees greater than the diameter limit for *Selected Timber Strata* or *Other Timber Strata,* as appropriate, may be girdled to create snags. Add the basal area of the girdled trees to the snag basal area, but leave an equivalent live basal area in the dominant and codominant tree classes to compensate for the loss in basal area of large live trees that were girdled. A maximum of 10 square feet basal area per acre, or one stem per acre if that stem contains ≥10 square feet basal area, may be girdled. As with all other retention figures, the evaluation is averaged over the cut unit, which means that a minimum of 40 trees may be treated in this manner on a 40-acre cut unit. The following steps would serve to implement this strategy:

A. Develop a diameter distribution and mark leave trees in a given cut unit.

B. Determine whether the stand is deficient in large snags.

C. If more large snags are desirable, mark desired snags as "wildlife" trees and measure their diameters at breast height.

D. After all "wildlife" trees have been selected, mark to leave enough additional live trees from the dominant

Table 1G-*Estimates of the effects of leaving the largest trees in stands, accumulating to various percentages of total stand basal area, for four timber strata, using actual mean stand-diameter distributions from the Tahoe NF. When the value in column seven ("Percent of basal area retained by 30-inch limit") exceeds the corresponding value in column one ("Percent basal-area retention"), the 30-inch limit is more constraining. Similarly, when the value in column five ("D.b.h. of smallest tree left") is larger than 30, the 30-inch limit is more constraining than "Percent basal-area retention."*

Percent basal-area retention	Strata[1]	Initial basal area	Basal area left after, logging	D.b.h. of smallest tree left[2]	Mean d.b.h. of trees remaining	Percent of basal area retained by 30-inch limit	Number of trees left per acre with basal-area rule
Stands affected by the 40-percent retention rule							
20	M4G[3]	254.61	50.92	34	37	27	6
25	M4G[3]	254.61	63.65	31	37	27	7
30	M4G	254.61	76.38	29	36	27	10
35	M4G	254.61	89.11	27	34	27	14
40	M4G	254.61	101.84	25	32	27	18
45	M4G	254.61	114.57	23	30	27	23
50	M4G	254.61	127.30	22	30	27	26
Stands affected by the 30-percent retention rule							
20	M4P[3,4]	126.45	25.29	32	38	24	5
	M3G[3,4]	213.43	42.69	34	38	26	4
	M3P[4]	138.06	27.62	30	38	19	3
25	M4P[4]	126.45	31.61	30	38	24	4
	M3G[3]	213.43	53.36	31	38	26	6
	M3P[4]	138.06	34.52	28	35	19	5
30	M4P[4]	126.45	37.94	26	35	24	6
	M3G	213.43	64.03	29	37	26	8
	M3P[4]	138.06	41.39	26	33	19	7
35	M4P[4]	126.45	44.26	24	33	24	7
	M3G	213.43	74.70	27	35	26	11
	M3P[4]	138.06	48.32	25	32	19	9
40	M4P	126.45	50.58	22	30	24	10
	M3G	213.43	85.37	25	32	26	15
	M3P	138.06	55.33	24	31	19	10
45	M4P	126.45	56.90	21	28 .	24	13
	M3G	213.43	96.04	24	31	26	17
	M3P	138.06	62.13	22	29	19	13
50	M4P	126.45	63.23	20	27	24	14
	M3G	213.43	106.72	22	30	26	21
	M3P	138.06	69.03	20	28	19	16

[1] Strata codes defined in table 1C.
[2] Diameter at breast height, in inches.
[3] Does not satisfy the 30-inch d.b.h. rule, which then takes effect.
[4] Does not satisfy the rule of retaining a basal area of at least 50 square feet.

and codominant classes to equal the basal area of trees to be girdled.

E. Girdle the marked "wildlife" trees after the sale. If trees marked to leave were inadvertently removed during harvest, make up for the lost basal area by NOT girdling some of the "wildlife" trees.

A Rationale for the Recommendations

Having decided that a major part of an interim strategy for spotted owls in the Sierra Nevada needed to save the largest, oldest trees, we then had to determine what level of retention would be sufficient. For this, we obtained plot-level data from timber-strata inventories in the Tahoe NF. From these data we defined diameter-distribution and basal-area functions for each stratum in the mixed-conifer group. We then generated cumulative distributions for each stratum, determined the diameter limits, and computed the number of trees per acre that would remain for basal-area retentions between 20 and 50 percent (table 1G). Evaluation criteria were based on the need to leave both the large, old trees and to leave sufficient "dominants" as replacement trees so that these structures would be retained into the future. Because we wished to establish a limit, not a target, we aimed to set minimum retention values.

An additional objective for *Selected Timber Strata* was to leave such stands in or near a structural condition corresponding to suitable foraging habitat for spotted owls. For these stands, it is clear from study of values for M4G strata in table 1G that basal-area retentions of <30 percent would not accomplish our main objective of retaining large, old trees AND providing a succession of replacement trees for them. The smallest of the large trees under 20-percent retention would be 34 inches in d.b.h.-too large to be considered candidates for replacement of the large, old trees when they die and fall. Only six large trees per acre would remain with 20-percent retention, but the 30-inch

d.b.h. rule takes over in this case and leads to retention of 10 trees per acre. A 40-percent retention nearly doubles the number of trees retained per acre, and the smallest of the large trees would be 25 inches in d.b.h. Trees of this size can easily be produced in less than 100 years on most commercial timberlands in the Sierran mixed-conifer zone, providing ample replacements for the large, old trees that range upward in age from 200 years.

A challenge arises with stands having a very high proportion of very large trees. Even with a 40-percent retention rule, the smallest of the large trees retained could be too large to qualify as a replacement tree. For this reason, we added a recommendation to retain all trees ≥30 inches in d.b.h. When the basal-area retention rule fails to include such trees, the 30-inch rule is more constraining and determines the smallest stem diameter to be retained.

The criteria outlined above for retaining large trees will result in unique residual stand structures. In contrast to the uniform spacing of trees common to seed-tree and shelterwood methods, we expect large trees to be irregularly distributed in a stand and to exhibit varying degrees of clumping. This pattern of distribution would result in some large openings in the canopies of units logged following the retention guidelines, and thus promote the regeneration of shade-intolerant species like ponderosa pine and black oak. Our next concern was with the final canopy closure in these stands, which should be ≥40 percent to be within the range of suitable owl foraging habitat. Given 18 trees per acre with a 40-percent retention, and assuming an average crown diameter of 30 feet, final canopy closure would be <30 percent. This led to our final recommendation of retaining sufficient trees 12-24 inches in d.b.h. to bring total canopy closure up to ≥40 percent. Not only would this provide adequate canopy closure, but also it would provide an intermediate range of tree sizes as later candidates for replacement of large, old trees.

The thought process was similar for *Other Timber Strata,* represented by M4P, M3G, and M3P stands (table 1G), although it was not our intention that these should qualify structurally as suitable foraging habitat for owls after logging. Retaining 30 percent of the total basal area in the largest tree sizes would maintain some trees <30 inches in d.b.h., which would provide replacements for the largest trees. As added protection for very sparse stands, we have recommended a minimum basal area of 50 square feet per acre, accumulated from the largest trees in the stand. For the M3P and M4P stands (table 1G), approximately 40 percent of the basal area must be retained to leave 50 square feet per acre, and 10 of the largest trees per acre would remain.

As described in Chapter 5, under the section entitled "Selective Use of Forest Types," we lacked data to analyze whether or not spotted owls select nest sites in various ponderosa pine strata in excess of expectation. Because we have strong reason to believe that at least P4G strata would be selected, however, we recommend a cautious approach in treating ponderosa pine types during the proposed interim period, especially because NFs are likely to classify them as unsuitable owl habitat for lack of sufficient crown closure, even though they may have plenty of hardwood cover in the understory. Accordingly, we recommend that P4G stands, so classified *after* hardwood and understory conifer components have been included in an assessment of stem diameter and canopy closure, should be treated as *"Selected Timber Strata"* during the proposed interim period. P3N, MG, and P4P, again as classified after inclusion of their hardwood components, should be treated as *"Other Timber Strata."*

Table 1H *Summary of major factors of concern in habitats of California spotted owls in the Sierra Nevada, and which of the recommended actions are intended to ameliorate effects of those factors.*

Factor	Recommended actions
Decline in abundance of very large, old trees	Saving live trees ≥30 inches in diameter at breast height; saving the largest trees in stands, by percentage of basal area
Long recovery period for spotted owl habitat after logging	Emphasizing retention of largest, trees shortens the recovery period after logging
Ingrowth of shade-tolerant tree species, creating unnaturally dense stands with ground-to-crown fuel ladders	Thinning; emphasizing removal of small-diameter trees; clearing fuel ladders from around largest trees
Excessive build-up of surface fuels	Implementing aggressive fuels management program, especially to reduce amount of downed wood <10 inches in diameter
Loss of large-diameter logs from the decaying wood source on the ground	Retaining the largest trees and snags in stands, which will eventually be recruited as logs; meeting guidelines for large-diameter logs on the ground
Decline in snag density	Retaining at least 20 square feet basal area per acre of the largest snags in stands; in addition, sparing the largest trees will assure a continuing source of large snags and downed logs
Disturbance and/or removal of duff and topsoil layers	Reducing surface fuels so ground fires burn cooler; reducing mechanical impact of logging and other projects on top soil and duff layers
Change in composition of tree species-fewer pines and black oaks, more firs and incense-cedar	Leaving largest trees and removing smaller trees should result in many openings large enough for germination by shade-intolerant species

Evaluation of the Recommendations in Relation to the Problem

Our recommendations address all factors in Sierran conifer forests that we believe have negative effects on California spotted owls (table 1H). Of the eight factors identified, six would be alleviated by a strategy that saves the largest trees in stands and removes some significant proportion of the smaller trees. In effect, the approach recommended here tends to invert silvicultural practices of the last 100 years. What has been characterized as "top down" logging (concentrating on the largest trees) would become primarily a "bottom up" approach (leaving the largest trees and concentrating on the smaller trees). Although not

excluding certain kinds of silvicultural prescriptions that are sometimes associated with clearcut logging, the steps recommended here preclude "clearcutting" in the sense that much of the public perceives it-as creating unsightly patches of land from which all trees have been removed. It also prevents the high-grading of scattered remnant trees.

We do not contend that the approach recommended is without risks. No approach is risk-free. The guidelines suggested for *Other Timber Strata* are not so restrictive that they would guarantee stand conditions suitable for owls immediately after logging. We have focused on setting strong rules to retain stand components that are most at risk and hardest to replace. For instance, to replace large logs in late decay-classes after clearcutting, we first must grow large-diameter trees, allow them to become snags, fall over, and subsequently rot. This is a process measured in centuries. On the other hand, a clearcut site can return to a dense stand of small to medium sawlogs in a few decades (see figs. 11P-11S). We are therefore more concerned about the former than the latter. The spotted owl population in the Sierra Nevada persists despite 100 years of logging injurious to its habitat, and it is still widely and relatively evenly distributed. We thus believe the recommended changes in traditional silvicultural practices in Sierran forests are unlikely to significantly degrade spotted owl habitat over the short-term, and they may even improve habitat over the long-term.

In contrast to the case for *Other Timber Strata*, recommendations for *Protected Activity Centers* should maintain existing nest/roost habitats in a condition suitable for continued use by the owls for those purposes. And guidelines for *Selected Timber Strata* should at least maintain suitable foraging habitat, as recommendations would retain all structural attributes associated with foraging owls (Chapters 5 and 6). We know, for example, that spotted owls regularly used some stands, but not others, that had been recently logged in the Lassen NF (Chapter 7). We would not be surprised to find that a brief period (probably less than 5 years) elapses after logging operations before the owls resume foraging in *Selected Timber Strata*. This is a primary question to be studied through radio-tagged owls (see recommendation in Chapter 2). If the approaches recommended here can be implemented faithfully and studied carefully, we are hopeful that they might lead us to a feasible, long-term solution to the owl problem and to many other problems that follow from the loss of attributes associated primarily with forests in late seral stages.

The recommendations DO NOT REPRESENT TARGETS. Instead, they should be viewed as limits that allow a wide range of silvicultural options. Their main purposes are to arrest the decline of very large, old trees; to save younger, "dominant" trees as replacements for older trees as they die and fall; to reduce risks of catastrophic fire; to promote recruitment of shade-intolerant tree species; and to retain large-diameter dead-and-downed woody materials. These goals can be achieved, in most cases, by leaving *more* trees than the guidelines suggest. For instance, guidelines proposed for *Selected Timber Strata* would be perfectly acceptable for *Other Timber Strata*. Examples of some silvicultural options compatible with the recommendations are described in Chapter 13.

Most or all biomass sales (see glossary) are probably also consistent with the guidelines. In particular, these sales can deal effectively with the serious problem of accumulating surface and ladder fuels. This situation strikes us as being akin to the general deterioration in the nation's infrastructure-bridges, highways, railroads, and so on. We have enjoyed relative luxury while postponing the inevitable costs of maintaining these structures. Someday, someone must pay for this negligence, and it will certainly cost more in the long run than it would if we simply dealt with maintenance needs as they arise. In the case of the current, serious fire threats to conifer forests of the Sierra Nevada, the money spent to suppress just one very large, stand-destroying fire would go a long way toward lessening the threat of such fires if it were spent in an aggressive fuels management program. Instead, we continue to behave like a person who fails to see the wisdom of owning fire insurance on an expensive home.

Conclusions

We suspect that some of the interim guidelines proposed here-those intended to retain various stand attributes found most often in older forests-would also be a necessary part of any strategy to maintain California spotted owls over the long-term. The best long-term solution for the owl in the Sierra Nevada would be to maintain the population in its current, relatively even distribution throughout the forests of the western slopes. If that distribution can be maintained, no need may arise to block up numerous areas large enough to contain many pairs of owls that can share home-range boundaries, as proposed for the northern spotted owl (Thomas et al. 1990). Such a policy in the Sierra Nevada would bring with it a high risk of stand-destroying fires (Chapter 12) that was not a major concern over most of the range of the northern spotted owl. Further, if an acceptable way can be found to maintain attributes of older forests generally throughout the Sierra Nevada, such a plan might go a long way toward meeting the needs of most or all other plant and animal species that thrive in older forests. The spotted owl issue is only the first in a potentially long list of such species awaiting our attention.

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Chapter 2

Future Directions for the California Spotted Owl Effort

Jared Verner and Robert J. Taylor

The chapters that follow summarize most of what we presently know about California spotted owls-their biology and general ecology, their habitat requirements, their demography, and so on. Most chapters contain references to information still needed and suggest further studies and inventories of California spotted owls-their habitat associations, their prey, and their demography. Here we offer tentative directions for proceeding with these tasks, which we believe will speed our progress compared with the past. This chapter is intended to satisfy item #5 in the Charter that established the Technical Assessment Team for the California Spotted Owl: "Identify research, monitoring, and inventory programs needed to answer existing critical questions and to provide for adaptive management of the owl in the future." The need to continue any phase of the effort to fully understand the current status of the owl must be conditioned on the extent to which remaining areas of uncertainty will lead to incorrect decisions. The objectives of this chapter are to identify remaining areas of uncertainty that can be reduced by further inventory, monitoring, and research work, and to recommend at least a broad approach for moving forward with these efforts in a more systematic and coordinated way than has been the case in the past.

Major Uncertainties About California Spotted Owls

Inventory

Significant areas of uncertainty still preclude conclusive recommendations about how best to manage for California spotted owls. For example, inventories have not yet been completed over much of the range of the owl in southern California. Our present information indicates that the largest area of fairly clustered owl sites in the Cleveland National Forest (NF) and adjacent areas has only 37 sites. Similarly, the largest group anywhere west of the San Gabriel Mountains in southern California contains only 25-30 sites. Sites in both localities are not tightly clustered, so they would not function efficiently to foster internal recruitment of dispersing juveniles. The numbers of sites in both are also near the lower limit of stability for isolated populations (see fig. 9G). Consequently even small increases in numbers of pairs there can be expected to have large, positive effects on estimates of stability properties of the populations in those two areas and of the entire metapopulation in southern California.

Further, we know little about the full extent of winter use or the presence of breeding owls in riparian/hardwood habitats in foothill woodlands of the western Sierra Nevada or other parts of the owl's distribution in the Coast Ranges (Chapter 4). This information is critical for two reasons. First, significant numbers of breeding pairs in these habitats, combined with owls in the adjacent conifer forests, would markedly increase the overall size, and thus the stability, of these owl populations. Second, their presence and importance there would merit serious consideration in planning for residential expansion into those localities. We know little about the possible impacts of current land uses in relevant hardwood habitats on spotted owls or their prey species. These are major uncertainties that need resolution. Inventories in these hardwood types could be planned in a way that tests, on a sample basis, habitat suitability models developed by Steger and Greenwood (pens.' comm.) to estimate the possible distribution and abundance of spotted owls in foothill woodlands (fig. 4D).

Finally, the presence of California spotted owls along the central coast of California is well-established as far north as Monterey County, where they occur in mixed conifer-hardwood habitats and coast redwood/Douglas-fir forests. Similar habitats occur to the north, especially in the coastal mountains from the Santa Cruz area northward at least into San Mateo County. Inventories are needed there to determine whether the coastal arm of the California spotted owl's distribution extends northward beyond Monterey County.

Monitoring

A detailed monitoring procedure was designed to detect declining trends in the occupancy and breeding status of territorial spotted owls in the SOHA network (see Chapter 1) on Forest Service lands in California. In the range of the California subspecies, this procedure was implemented in 1987, 1988, and 1989. Analyses done in the course of developing a proposed conservation strategy for the northern spotted owl, however, showed that this monitoring procedure was relatively insensitive to declines in the overall population (Thomas et al. 1990, appendix M). This was the case because of two significant lag effects that accompany habitat-induced declines in the number of territorial owls.

The first lag effect arises from the fact that spotted owls can live for 10-20 years. Even in a SOHA that has declined in suitability to the point that a pair of owls can no longer breed successfully there, the pair may survive for a long time, still be counted as a viable pair, but never replace themselves. Spotted owls often do not breed annually; they may even fail to do so for several successive years. For this reason, little concern is raised when a pair does not nest in a given year. Furthermore, the monitoring protocol does not always detect nesting when it does occur. Consequently, a gradual decline in habitat quality could be overlooked and, over the short term, the overall population would be judged to be stable.

The second lag effect results from the fact that only the resident territorial population is monitored. Floaters (nonterritorial birds) are an integral part of the total owl population (Chapter 4), but they are seldom or never detected by any standard sampling protocols. When territorial adults die in the vicinity of floaters, their places are quickly filled, leaving no indication that the total population has actually declined. This continued occupancy of pair sites would last as long as required to exhaust the floater population. Only then would we expect to see a decline in the territorial component of the total population. This may be the reason why 1991 was the first year in the several years of studying the declining population of spotted owls in the San Bernardino Mountains that the number of occupied territories showed a marked drop (LaHaye pers. comm.).

Modeling work done for the northern spotted owl (Thomas et al. 1990, appendix M) indicated that the combination of these lag effects might delay by as much as 15-20 years the period before a significant decline could be detected in the territorial component of a population of spotted owls. By that time, conditions might already have worsened to a point that some critical threshold in the amount or quality of suitable habitat could have been crossed, resulting in a precipitous decline in the owl population with little chance of recovery. For these reasons, Thomas et al. (1990, appendix R) recommended that the emphasis of the monitoring program be shifted from tracking trends in the occupancy rate and breeding status of owls in SOHAs to detailed monitoring of birth and death rates, turnover rates (replacements of territorial birds lost from the population), and finite rates of population change (lambda-see Chapter 8) of spotted owls in several demographic study areas. Only in this way could we know whether a population is reproducing with sufficient success to maintain itself.

We are still uncertain about whether the Sierran population has been declining during the years since demographic studies began (Chapter 8). Lambda was <1.0 in two populations in which it could be estimated (Eldorado NF and Sequoia/Kings Canyon National Parks), but not significantly less. The power of the tests on lambda, however, were so low that we were not likely to detect a significant decline even had it been occurring. Furthermore, even if the test results had suggested that a significant decline had taken place, it would be impossible to infer whether the population decline resulted from changes in the amount or quality of available habitat or because of ecological relations mediated by the present drought (fig. 4H).

Research

Habitat Capability for Spotted Owls

Explicit characterizations of superior, suitable, marginal, or unsuitable habitats for California. spotted owls still elude us. This contrasts sharply with the case for the northern spotted owl, for which most land capable of growing forests in the Pacific Northwest could easily be identified as either suitable or unsuitable for the owls-most was either regenerating from clearcuts less than 50 years old, or it had been altered little or not at all from its pristine condition. Either it was or it was not suitable habitat.

The past 150 years or so of forest management in the Sierra Nevada, where most California spotted owls occur, have involved relatively little clearcutting, especially on lands presently within NF boundaries (Chapter 11). The present character of these forests resulted from combined effects of (1) the natural fire regime before European settlement (Chapter 12), (2) massive overgrazing by sheep over a 50-year period beginning in the early 1860s, (3) increasingly effective fire suppression since about 1900, and (4) extensive selection logging in the past 5-6 decades. Currently, most of these forests are unnaturally dense, have large components of young and intermediate-aged trees but few surviving older trees, have extensive vertical fuel ladders linking ground fuels with crowns, and are highly susceptible to stand-destroying fires (Chapters 11, 12, and 13). But these same forests have a relatively uniform density of spotted owls, dispersed in a mostly even pattern over the forested landscape. At the landscape scale, we see little in the overall distribution pattern of California spotted owls to suggest how we might distinguish between suitable and unsuitable habitat (but see Chapter 5).

We have learned much about particular stand attributes that are used selectively by California spotted owls (Chapters 5 and 6), but we have been unable to connect them with studies of the owl's reproductive success-or failure. We still are uncertain about what levels of canopy cover, tree densities and sizes, snag densities and sizes, quantities and sizes of downed woody debris, and so on, are found where owls reproduce consistently and well. Only by linking demographic rates with habitat attributes can we eventually distinguish among superior, suitable, marginal, and unsuitable habitats.

Owl/Prey Relations

Studies of many owl species from around the world suggest that variations in available prey affect their breeding behavior in many ways (table 4B). We contend that the spotted owl is typical in this regard and that an essential component of suitable owl habitat is a consistent abundance of available prey. We know much about the diets of California spotted owls, but no studies have been done on relations between the availability of prey species and the presence, density, or reproductive success of California spotted owls. Only one definitive study of this sort has been completed on northern spotted owls (Carey et al. 1992). Carey et al. found evidence that the area used for foraging by northern spotted owls increased as the densities of their primary prey species declined. Our ultimate understanding of why some

habitats tend to be superior for the owls, while others are only marginal, may depend on knowledge of this sort. It remains as a major uncertainty.

In addition, we know little about the ecologies of the prey species that dominate the owl's diet in different parts of its range. For example, it is generally unknown if the primary prey species show cyclic variation in response to either endogenous or exogenous factors, or to what extent their populations track environmental variation. Furthermore, understanding how prey availability differs with changes in habitat structure is essential if we are to indirectly manage spotted owl populations by increasing suitable habitat for their prey.

Addressing Uncertainties

Additional Inventories

Deficiencies in our knowledge about the presence and reproductive status of California spotted owls in localities like the hardwood zone of the Sierran foothills, or in large parts of southern California, can be met with relative ease and speed, and at a modest cost compared with other major uncertainties. The needed inventory work can follow established protocols and draw upon a wealth of prior experience in such endeavors. Planning for it should begin immediately to assure that field work is completed no later than September 1993. If inventories show that a substantial number of owl pairs breed in these hardwood habitats, studies will be needed to investigate the range and scale of the impacts on owls and their prey that result from the variety of current uses of these lands by humans. Such studies are almost certainly needed in relation to where migrant owls from the conifer zone spend their winters.

Results of complete inventories in potential habitats throughout the range of the spotted owl in southern California will probably require additional modeling efforts to ascertain the stability properties of that metapopulation.

Monitoring

Population Trends

We recommend that the direction of the monitoring program for California spotted owls be shifted to demographic studies. Using this approach, uncertainties about population trends can be resolved more quickly and with a better chance to identify cause-and-effect relations than would be the case with simple measures of occurrence or breeding by owls at selected sample points.

Existing demographic studies in the Sierra Nevada must continue and be enlarged (see recommendations in Chapter 1). It is critical that the continuity of these be maintained, because just a single year's interruption in the series of years needed to estimate vital demographic rates means that the study essentially must begin anew. Generally, 5-6 consecutive years of banding all territorial owls in a demographic study area are required to attain a reasonable estimate of the vital rates, assuming that the study area is large enough that a sufficient number of birds is banded and reobserved each year (see Chapter 8). Enlarging the studies to include more owls in each year's sample can shorten the time needed to attain accurate and precise estimates of lambda. For example, if current vital rates remain stable and the study is not enlarged, we would need 9 more years of banding in the Eldorado Study Area to attain a statistically significant estimate of the population's trend. On the other hand, by enlarging the study to double the number of banded owls, we might confidently estimate the population trend in only 4-5 more years. In any case, demographic studies in these populations need to continue well beyond the current drought cycle before we will have a chance to fully understand the significance of observed birth and death rates, turnover rates, and estimates of lambda.

The demographic study in the San Bernardino Mountains must also be continued, especially considering the modeling results indicating that the collapse of this population would probably result in the extinction of the entire population of spotted owls in southern California (Chapter 9). Banding in the San Bernardino study area has been done for 5 years, so the study is just getting to a stage that payoffs from its continuation become especially significant. In addition, we need to enlarge the effort in the San Bernardino to include studies of those owl sites where breeding is most consistent and successful. If the present drought is causing the significant decline in the population there, sites that still allow successful breeding are certainly the ones most in need of protection. They are the "sources" of birds that can maintain this population through the "crunch" of the present drought (Chapter 9).

Additional demographic studies are needed to broaden our monitoring sample in southern California-one centered on Palomar Mountain and one in the southern block of the Los Padres NF (Chapter 9). These would also serve to test our current hypothesis that these subpopulations depend for their maintenance on immigrants from the relatively large population center in the San Gabriel and San Bernardino Mountains. If that proves to be the case, the studies would also provide quantitative measures of the rates of immigration needed to maintain each subpopulation.

Effects of Logging

Monitoring the effects of various logging prescriptions on the foraging, roosting, and nesting activities of spotted owls is an especially high priority. Analyses reported in Chapter 7 provide one model of how such studies can be done. If recommendations proposed in Chapter 1 are implemented to maintain options for spotted owls in the Sierra Nevada during some interim period, we consider it essential to monitor owl activities and movements before and after logging operations that follow those recommendations. This can be done on a sample basis, following a study plan developed jointly by managers and researchers. It will require studies of radio-tagged owls, although some concern

exists about possible effects of radio tags on breeding and survival of the owls. Using the latest tail-mounted radio transmitters, however, should reduce impacts on the owls compared to back-pack models used in earlier studies.

Research

Uncertainties About Habitat Capability

Because an accurate determination of the suitability of owl habitat must be linked to the birds' reproductive success (specifically, demographic rates), we believe that advances in dealing with these uncertainties will be most rapid when habitat studies are coupled with demographic studies. The specific details of what habitat parameters should be measured, how they should be measured, and at what scale, need to be given a thorough review by a team of experienced owl biologists, foresters, silviculturists, and others. Implementing these efforts should be contingent upon developing a fully interactive Geographic Information System (GIS) for each demographic study area, with layers for all relevant attributes (for example, vegetation types, locations of owl nests and roosts, hydrographic features, topography, and so on).

Uncertainties About How Silvicultural Systems Affect Owl Habitat

Current Land Management Plans (LMPs) of the various NFs propose to emphasize silvicultural methods and to attain levels of timber removal that will result in significant changes in forest structure. Conversion of most of the lands suitable for timber production to a regulated state will largely result in even-aged plantations and areas with dense, and increasingly smaller-diameter stands (Chapter 13). The LMPs make no reference to the natural conditions of forest ecosystems when proposing the timber programs leading to regulated forests, but the short- and long-term effects of these changes are unknown. No certainty exists that ecosystem processes, whether the population dynamics of spotted owls or the successional trends of multi-species plant communities, will be maintained in regulated forests. We propose that the FS move away from its goal of regulating forests and develop, instead, the knowledge to manage for more natural stand structures, compositions, and functions. Given incomplete knowledge of natural forest conditions and, once known, the uncertainties of how to produce such stands, this is clearly an area for high-priority research.

To the extent that spotted owls nest in stands that retain remnants of historical structure (Chapter 5), data available from habitat-capability studies can provide a useful starting point. In this regard, extensive studies within NPs of stands occupied by owls may prove particularly valuable. We propose that quantitative characterizations of the structure and composition of stands used by owls be expanded and that these data be made available to research silviculturists.

Uncertainties About the Role of Prey

First in priority, we need to know whether prey availability is a primary causative factor in whether or not the owls breed in a given year. If that proves to be the case, as we believe is likely, we will then need to understand better how we might manage habitats to assure sufficiently dense (and available) prey populations. As with studies of habitat suitability, studies of prey ecology and owl-prey relations would be best done within the boundaries of demographic study areas. For this reason, some decisions about where to initiate additional demographic studies could be determined according to perceived needs to study prey relations.

Several approaches might be suggested to falsify the null hypothesis that the availability of prey is unrelated to the likelihood that a pair of owls will or will not breed in a given year. The hypothesis might be tested by measuring densities of key prey species in many owl home ranges over some period of time (probably a few years) and comparing prey densities available to pairs that did and did not breed. We believe this approach is unfeasible. We know from experience, for example, that it can cost as much as $50,000 to $100,000 per year to obtain reasonably precise estimates of prey densities in just a few owl home ranges. A second option might be to supplement artificially the prey available to various pairs of owls in a set of pair-wise comparisons among owl pairs randomly selected from the population. The latter experiment might be more direct and less costly than the former, but it may also prove to be unfeasible for a variety of reasons. Other alternatives need to be considered before we move forward with research on this question. This example points up the need to establish a coordinated effort and a rigorous process for deciding what the major uncertainties are that we need to study, and what are the most efficient ways to reduce those uncertainties.

Establishing a Process

Coordinating studies of owl demographics, habitat attributes, and prey relations promises to significantly streamline research and to speed answers to critical questions needed for a more definitive assessment of the owl's status. Simultaneously, we should learn more about the spatial scales at which these components of the overall system should be considered and how differences in functional scales can best be dealt with in management plans. For example, frequent disturbance events in pristine forests, resulting from fire, insect outbreaks, and wind storms, probably affected relatively small areas ranging from 0.5-2 acres (Chapters 12 and 13). The result was a relatively fine-grained pattern of variability in the vegetation, modified by topography, at a landscape scale. Logging and fire suppression have changed the scale of frequent disturbance to one of about 5-30 acres. Spotted owls, on the other hand, operate in home ranges of hundreds of acres (hardwood habitats where woodrats dominate the diet) to thousands of acres (conifer habitats where flying squirrels dominate the diet) (Chapters 4 and 6). As a result, their home ranges generally incorporate a mosaic of stand structures,

the distribution of which may determine habitat quality. Finally, owl prey populations probably respond to variation in vegetation at scales more like those of pristine forests.

Research Approaches

The style of research best suited to issues at hand is a fusion of two emerging trends in wildlife science. First is an emphasis on hypothesis testing (Romesburg 1981, 1989, 1991; Bailey 1982; MacNab 1983; Eberhardt 1988; Keppie 1990; Murphy and Noon 1991; Nudds and Morrison 1991; Sinclair 1991). Second is adaptive management (Holling 1978, Walters 1986, Walters and Holling 1990).

Hypothesis Testing

Experimentation is the essence of the hypothetico-deductive method. It may be done in many ways, not all requiring direct manipulation of a system under study (Sinclair 1991). It requires formulation of null hypotheses, based on application of common sense to observed natural phenomena and stated in terms that can be falsified. For example, the null hypothesis that the population of spotted owls in the San Bernardino Mountains did not decline from 1987 to 1991 was falsified by estimates of demographic rates from the area. Problems with routine experiments in wildlife biology are many: the scale of the landscape is often immense; variability in data may be too large to reveal treatment effects; replication may be difficult or impossible. These challenges are not insurmountable, but they require that careful attention be given to experimental design.

No style of experimental research has been more effective than a protocol called "strong inference" (Platt 1964). Strong inference is simple in principle. The phenomenon to be explained is described and defined thoroughly. An exhaustive set of explanations (hypotheses) is then devised, which constitutes the core of the process. All hypotheses must be initially plausible, and they should be as diverse and complete as possible to avoid the common pitfall of premature commitment to a single explanation (Chamberlin 1965). They must lead to precise, falsifiable predictions. This process is facilitated if the hypotheses can be stated as quantitative predicitons. The predictions are examined and compared until natural circumstances are found that can, if studied, discriminate among hypotheses.

These circumstances define the conditions of a traditional "crucial experiment" (Romesburg 1991). The experiment may involve only the taking of a set of measurements in the field without causing disturbance; the important feature of the experiment is not that it is manipulative but that it allows alternative hypotheses to be compared in a definitive way. In principle, only one hypothesis will survive the tests and comparisons. In practice, however, crucial experiments are seldom perfectly unambiguous (Hempel 1965). Their design and conduct come under attack. More often, the "exhaustive" set of alternative hypotheses is found to be missing a reasonable new idea. In spite of its logical flaws, this style of research has proven to be remarkably productive in those sciences, such as chemistry and physics, where it is routinely practiced.

Platt's (1964) paper on strong inference is widely cited and equally widely misunderstood. In particular, strong inference is not equivalent, as Sinclair (1991) claimed, to the hypothetico-deductive method-it is a subset of that method. To illustrate the difference, the rejection of the null hypothesis that California spotted owls use lakes in their home ranges in proportion to their availability is a reasonable application of the hypothetico-deductive method. The fact that it is a trivial null hypothesis, the rejection of which does not really advance our understanding of the owl's habitat needs, renders this research far from strong inference.

A strong-inference approach to habitat selection would consist first of compiling a list of alternative hypotheses that span the range of possible cause-and-effect relations. The only constraint on these hypotheses is that they must be consistent both with what is known of owl biology and with previous research in animal ecology. This list might contain, for example, a physiological hypothesis (owls choose habitats that minimize thermal stress), a foraging hypothesis (owls require a mosaic of habitats that support their preferred prey), and a cover hypothesis (owls choose habitats that minimize risks of attack by great horned owls and goshawks). The hypotheses are not necessarily mutually exclusive, and thus may allow the possibility of multiple causation. Some set of predictions from the hypotheses, however, must differ so that all predictions cannot be jointly true (Romesburg 1991).

Implementing tests of these hypotheses would require some quantitative assessment of specific attributes of both spotted owls and their territories, resulting in sets of measurements collected across a range of occupied sites. Further, each hypothesis would need to be formulated in terms of specific predictions that discriminate among them. Data used to test the truth of these predictions could be collected from either observational (nonmanipulative) or manipulative studies, in which the researcher experimentally alters one or more components of the system. The design of such studies is difficult and requires much creativity, but those sciences in which it is taught and routinely practiced profit enormously from the exercise.

Adaptive Management

This is an emerging style of management planning that provides an intelligent response to uncertainty (Walters and Holling 1990). Its essence is the use of management decisions to gain knowledge, which may then be used to improve subsequent management decisions. In effect, it integrates management with research and uses feedback loops to progress from acquired knowledge to iteratively improve management paradigms. One might respond that this is not new, that the history of environmental management has always been "adaptive." In its precise meaning, however, the point of adaptive management is to progress from mere trial-and-error learning to a systematic and efficient process of acquiring new knowledge.

Adaptive management offers a major additional benefit deriving from the fact that most conflicts over environmental issues result as much from uncertainty as from fundamental differences in the social valuation of resources. If these uncer-

tainties are acknowledged and a systematic effort is begun to reduce them, most management conflicts tend to moderate.

Walters (1986, p. 9) suggested that adaptive management requires attention to four basic issues: "(1) bounding of management problems in terms of explicit and hidden objectives, practical constraints on action, and the breadth of factors considered in policy analysis; (2) representation of existing understanding of managed systems in terms of more explicit models of dynamic behavior, that spell out assumptions and predictions clearly enough so that errors can be detected and used as a basis for further learning; (3) representation of uncertainty and its propagation through time in relation to management actions, using statistical measures and imaginative identification of alternative hypotheses (models) that are consistent with experience but might point toward opportunities for improved productivity; (4) design of balanced policies that provide for continuing resource production while simultaneously probing for better understanding and untested opportunity."

The construction of models is central to the adaptive-management approach. Models are not new to wildlife biology, but Walters intended for them to be used in a novel way. If one can say that a model-building tradition exists in wildlife biology, then it is to build a single model that captures the essence of existing data and leads to the formulation of rational projections of a population, habitat, or whatever the variable of interest. This activity, usually the capstone on a series of empirical studies, is not what Walters intended. He meant for the scientific manager to identify areas of uncertainty and then build a set of models that both incorporate what is known and allow rational evaluation of the consequences of what is not known.

We contend that adaptive management, in its most elegant form, is the application of strong inference to environmental problems, with the additional constraint that experimental treatments are limited to management protocols that are at least minimally acceptable. That is, most treatments should involve some level of logging with positive economic value. In this light, adaptive management can be the best hypothetico-deductive science applied directly to a management problem.

The Next Phase

The question of how to implement an adaptive management approach is open to discussion. Holling (1978) and Walters (1986) advocated a workshop approach, which has both advantages and disadvantages. Its primary advantage is its contribution toward conflict resolution-if the owl is determined to be in trouble, conflicts will probably be intense. When all interested parties participate both in formulating the set of models considered as management alternatives and in identifying hypotheses to be tested, it strips the mystery from those activities and turns resulting products into common property. Most or all participants feel "ownership."

A problem with relying entirely on a workshop approach is that modeling is a difficult process under the best of circumstances, requiring much effort, time, and creativity. A workshop environment is far from the best arena-time is short, tensions may be high, and participants are often tired and irritable. We contend, however, that a relatively structured "workshop" format is appropriate to formulate a program to proceed with management and research on the California spotted owl.

The process requires a team and a leader; the leader should not be affiliated with any of the entities involved. The team should include at least a computer scientist with GIS experience, a population biologist, a community ecologist, a forest ecologist, and a forest products economist. These theoreticians could come from the organizations with a stake in the outcome of the plan, with the stipulation that no single organization can be allowed to dominate the team. In addition, the team should have access to other experts, as needed, to deal with various phases of the planning. A central office/work facility should be provided, with a staff to implement routine duties. We envision seven steps in the overall process:

Step 1: Define Issues and Develop an Agenda

The initial stage of the effort should bring together representatives of all affected parties. Each must attempt to gain a clear understanding of the components of the problem and understand both objectives of and constraints on solutions. Existing datasets should be examined to assess their usefulness, and unavailable but needed datasets should be identified.

Step 2: Develop Alternative Models

This is a brainstorming exercise designed to identify as large a set of component processes, and alternative representations of each, as possible. These should be cast in symbolic form suitable for computer models. The modeling team must include the best available theoreticians in all important aspects of the problem. The resulting models should be compared with available data to see if the models are at least consistent with what is known. The necessary precision of outputs will almost certainly require that alternative models be cast in spatially explicit forms and be based upon GIS-derived, landscape descriptions. Parameters to which the models appear to be sensitive should be identified.

Step 3: Assess Uncertainty

This is an intensive workshop exercise to identify uncertainty, both socio-economic and physical-biological. Again, participants should represent all parties with a stake in the issue, and they need to be at ease with quantitative reasoning. They should be teamed with the model builders from Step 2 to forge a set of alternative models that bracket our range of ignorance.

Step 4: Design Experiments

Models coming from Step 3 should be tightened and analyzed by the model builders until they yield predictions that lead to crucial experiments. To the extent possible, the modeling team should focus on predictions that differ qualitatively and that do not require precise parameter estimates. Assuming that multiple experiments will emerge from this exercise, the participants have an added responsibility to prioritize them in rank order, listing first those likely to remove the most uncertainty from critical aspects of our ignorance about the owls in relation to their environment.

Step 5: Forge a Management Plan

Representatives of all groups involved in Steps 3 and 4 should meet to examine the models and the proposed crucial experiments. If the experiments seem plausible, the group should consider the practical problems of their implementation, determining how they can be done and ensuring that sufficient data are collected to discriminate among alternative models.

Step 6: Conduct Experiments

This task would fall to various scientists and study teams from among the entities cooperating in the effort. Success will depend to a major extent on the degree to which the several participating entities can cooperate: (1) to assure that funds are available on a sustained basis to see each experiment through to a logical conclusion; (2) to plan the total set of studies to assure that sensible priorities are followed; (3) to coordinate all studies to avoid needless duplication; (4) to standardize the data to be collected, the methods for collecting them, the forms used to record them, the computer filing and operating systems for manipulating them, and the methods used to analyze them; (5) to assure that political boundaries become as invisible to researchers and their respective affiliations as they are to the owls; and (6) to assure that all results obtained are freely and openly shared, discussed, and interpreted. The nature of the experiments, and their likely duration and cost, are impossible to predict. Ideally they would involve existing manipulations of habitats, but this must not be assumed *a priori*.

Step 7: Feedback Loops

Knowledge gained from the experiments and tests of hypotheses (models) feeds back to managment, and the process goes through another iteration.

Completing the Tasks

It is no more likely that a single pass through this process will completely reduce uncertainty than it is that a few laboratory experiments will solve a major scientific question. These steps may need to be retraced a second or third time. The likelihood is high, however, that the process will identify a management solution much faster than current process-oriented research. In particular, the likelihood is high that a blend of strong inference and adaptive management will distil] the extent of our uncertainty about the biology of California spotted owls and highlight areas of ignorance that matter the most.

Conclusion

The primary barrier to finishing what is needed to remove the remaining uncertainty about the status of the California spotted owl is administrative, not scientific. Before it can begin, much discussion is needed at the highest levels of the organizations involved to discover whether they are prepared, or even legally able, to accept and implement the changes that will be needed. For example, if a crucial experiment requires designating as "experimental land" a substantial fraction of a forest--public or private, will support be there for retraining local managers and for temporary reorganization of management authority? Will permitting processes be re-examined? Will citizen and environmental groups refrain from pressuring local managers as experiments proceed? If the answers to these questions are "no," then the political will is missing for any sort of systematic hypothesis testing and adaptive management in forest/wildlife issues.

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Chapter 3

Background and the Current Management Situation for the California Spotted Owl

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The administrative history of the California spotted owl is closely tied to that of the northern spotted owl. Detailed research first began in 1969, with studies on the northern subspecies (Forsman 1976). Forest Supervisors in California were first alerted in 1972 by the Pacific Southwest Regional (R5) Office of the U.S. Department of Agriculture, Forest Service (FS) about concern for the owl in Oregon, based on logging-related habitat changes. Wildlife biologists were advised to seek information on the presence of spotted owls in their respective forests.

Administrative Events

1972-1980

Shortly before passage of the Endangered Species Act (ESA) of 1973, the spotted owl was designated by the U.S. Department of Interior, Fish and Wildlife Service (FWS) as a "threatened species," including the California subspecies. This designation was intended to stimulate interest, impart knowledge, and solicit information about wildlife that appeared to be endangered. With passage of the ESA, however, an official list of Threatened and Endangered Wildlife and Plants did not include the spotted owl (USDI, FWS 1973).

In 1973 and 1974, the PSW Region, the California Department of Fish and Game (CDFG), and the U.S. Department of Interior, National Park Service (NPS) jointly financed the first survey for spotted owls in California. Locations of historical observations and selected late-successional forests were chosen for surveys. Spotted owls were located on most National Forests (NFs) and were found to be much more abundant than previously known, with 159 owl locations documented within the range of the California spotted owl (Gould 1974).

The Oregon Endangered Species Task Force was formed in 1973, at a time when spotted owls had been located at only about 100 sites in that state. The Task Force recommended that 300 acres of old-growth be retained around each northern spotted owl location, as interim protection until permanent guidelines could be adopted. FS Region 6, Pacific Northwest Region (R6) and the Oregon State Office of the U.S. Department of Interior, Bureau of Land Management (BLM) rejected the recommendation (Thomas et al. 1990).

Concern over the status of the California spotted owl was slow in developing compared to that for the northern spotted owl in the Pacific Northwest. During the mid-1970s, additional surveys were done on individual Forests and Ranger Districts in the Sierra Nevada but not in response to Regional direction or policy.

Passage of the National Forest Management Act (NFMA) in 1976, and regulations pursuant to that Act, established the basis for maintaining well-distributed, viable populations of all native vertebrate species on NF lands. NFMA also required the use of Management Indicator Species (MIS) to guide management for certain wildlife groups or critical habitats. The spotted owl was designated as an MIS for wildlife requiring large areas of late-seral-stage conifer forests by all NFs in the western Sierra Nevada.

Early in 1977, the Oregon State Director of BLM and the Regional Forester for R6 agreed to protect northern spotted owl habitat in accordance with interim recommendations of the Oregon Endangered Species Task Force. This included protection of habitat where spotted owls and their nest sites had been found. Late in 1977, agency administrators agreed to the Oregon Spotted Owl Management Plan, which recommended clusters of 3-6 pairs, 300-acre core areas for each pair, pairs in a given cluster no more than 1 mile apart, and clusters no more than 8-12 miles apart, edge-to-edge. The plan was to be implemented through the land-management process and individual land-management plans for NFs and BLM Districts (Thomas et al. 1990).

In 1978, the Oregon-Washington Interagency Wildlife Committee replaced the Oregon Endangered Species Task Force with the Spotted Owl Subcommittee, to represent both Oregon and Washington. In 1979, a Washington Spotted Owl Working Group was established, and in 1980 the FS afforded the same protection to spotted owls in Washington that had already been provided in Oregon.

Because of the rapidly growing issue of logging vs. habitat management for the northern spotted owl, surveys to locate owls increased sharply in 1978 on NFs in Oregon, Washington, and northern California, but FS surveys in the range of the California spotted owl did not begin in earnest for another 3 years. The initiation of systematic surveys in the Sierra Nevada responded to the need to verify designated spotted owl territories for land management plans, as well as to provide wildlife input to planned timber sales. Designated spotted owl territories were later called Spotted Owl Habitat Areas, or SOHAs.

The spotted owl was designated a "Sensitive Species" on NFs throughout FS R5 in the late 1970s (Carrier pers. comm.).

CDFG, with jurisdictional boundaries almost identical to R5, classified both subspecies as "Species of Special Concern" in 1978 (Remsen 1978).

1980-1991

Based on study results by Forsman (1980, 1981), the Spotted Owl Subcommittee revised the Oregon Spotted Owl Management Plan in 1981, recommending that 1000 acres of old-growth forest within a 1.5-mile radius of the nest area be maintained for each pair. R6 agreed to the new recommendations only to the extent that they would "maintain the option" to manage for 1000 acres if further research proved it to be necessary. The BLM in Oregon continued to protect only 300 acres for managed pairs (Thomas et al. 1990).

In early 1981, R5 initiated a meeting on spotted owls that brought interested State and Federal agencies together for the first time. This included BLM, NPS, California Department of Forestry and Fire Protection (CDF), CDFG, and both the administrative and research branches of the FS. The purpose of this meeting was both to share information and to discuss development of management policies and research needs.

FS Regional planning direction for both subspecies of spotted owl in California was issued in June 1981 and closely followed the Oregon Spotted Owl Management Plan. The final revised direction issued in 1984 included the concept of replacement habitat, explained below. In July 1981, the Regional Office, R5, notified Forests with the California spotted owl to provide a strategy for maintaining viability in their Land Management Plan (LMP). This led to the development of designated SOHAs in a grid configuration or "network" on each of the seven westside Sierra Nevada NFs, and prompted those NFs to verify occupancy of the designated sites.

The Portland Regional Office of the FWS conducted a status review of the northern spotted owl in 1981 because of concerns about the effects of the decline of old-growth forest (USDI, FWS 1982). Although the species was described as "vulnerable," the FWS review concluded that the species did not meet the listing requirements of the ESA.

In 1982, the Washington Office of the FS analyzed and clarified existing national policy for management of Sensitive Species on NF lands. This policy was seen as a visible, preventive strategy with the following key objectives: (1) identify plant and animal populations that currently or potentially qualify for Federal or State listing as a result of NF management activities, and (2) develop a consistent, systematic, biologically sound strategy to manage these species and their habitats to provide for viable populations so Federal listing as Threatened or Endangered would not be required.

In cooperation with the BLM, R6 initiated the Old-Growth Wildlife Research and Development Program in 1982, which entailed field studies of old-growth wildlife species and their forest habitats in western Washington and Oregon.

In 1982, R5 recognized differences in vegetation patterns between the Sierra Nevada and Pacific Northwest forests. Considering these differences and the observed use of habitats by spotted owls, R5 speculated that home ranges of the California subspecies might be smaller and owls might be using younger and more diverse timber stands than in areas where research had been done to date. Based on this concern, the FS and CDFG planned the first research studies for the California spotted owl. The first of these studies began on the Eldorado NF in 1982.

Throughout 1984, the R5 Regional Office approved the final spotted owl habitat networks for proposed LMPs on most NFs in northern California and the western Sierra Nevada. The policy was to implement Regional standards and guidelines for the networks in advance of LMP approvals to avoid losing management options. No Regional policy was set, however, for management of spotted owls outside of approved networks. Some NFs provided protection for 1000-acre "non-network" SOHAs to maintain options for full spotted owl management, but most provided minimal or no protection.

In 1985, the Deputy Assistant Secretary of Agriculture upheld an appeal against the R6 planning guide. The successful appeal contended that the standards and guidelines for northern spotted owls were inadequate and that an environmental impact statement (EIS) was required. Work on a supplemental EIS (SEIS) began in 1985 and was completed in 1988 (USDA, FS 1988).

The National Audubon Society established a "Blue Ribbon" Advisory Panel in 1985 to review the status of the spotted owl in Washington, Oregon, and northern California. The Panel's report was issued in 1986, with findings and recommendations for the northern spotted owl throughout its range, and for the California spotted owl in the Sierra Nevada portion of its range (Dawson et al. 1987). Recommendations on numbers, home ranges, and distribution relevant to the California spotted owl were: (1) Maintain no fewer than 1,500 pairs in the combined range of the northern subspecies and the Sierra Nevada portion of the California subspecies and discard the earlier view that 500 individuals could represent an effective breeding population; (2) maintain the current distribution with a network system similar to that being used by the agencies, but with maximum emphasis on having networks comprised of SOHAs with verified reproduction; and (3) provide at least 1,400 acres of late-seral forest habitat for each pair home range in the Sierra Nevada. Maintaining the population linkage through Shasta County, where the California and northern subspecies come together, was emphasized to be critically important. The Audubon Panel also recommended a well-designed program of intensive and extensive research on a sample basis to obtain reasonable estimates of the proportion of network home ranges supporting breeding pairs of spotted owls and to document reproductive rates in relation to population maintenance.

In 1987, the Old-growth Wildlife Research and Development Program of 1982 was supplemented by the Spotted Owl Research, Development and Application Program (the RD&A Program) for a period of 5 years. This was a cooperative effort of R6, R5, and the Pacific Northwest (PNW) and Pacific Southwest (PSW) Research Stations. The new spotted owl RD&A program, funded as a line item by Congress, had a mission to develop, apply, and integrate new and improved information into guidelines and procedures needed to manage suitable spotted owl habitat to assure maintenance of viable populations in California, Oregon, and Washington. Under the auspices of this

program, numerous studies of spotted owls, associated habitats, and old-growth wildlife species were done in Oregon, Washington, and California (Thomas et al. 1990), but most research funds went to studies of the northern spotted owl. The monitoring phase of the RD&A Program included the Sierra Nevada portion of the California spotted owl's range.

In early 1987, the FWS received a petition to list the northern spotted owl as an endangered species under the ESA. A new status review was done and the FWS determined that listing was not warranted. That decision was litigated by conservation groups in 1988 in the Seattle Federal Court. The court ruled that the FWS's decision was not biologically based and ordered the FWS to reconsider listing (Thomas et al. 1990).

In December of 1988, the Chief of the FS approved the SETS for spotted owls in R6. The selected alternative maintained the existing concept of network owl reserves but increased the sizes of the SOHAs in Washington and portions of Oregon to range from 1,000 acres in southern Oregon to 3,000 acres on the Olympic Peninsula (USDA, FS 1988).

In 1989 the California State Legislature passed AB 1580 to improve the analysis of the cumulative impacts of logging. The measure directed the CDF to develop a system to better track how harvest planning decisions are made, and to develop a scientific database on timberland habitats and wildlife species (Thomas et al. 1990).

In response to Federal court action, the FWS initiated an other status review of the northern spotted owl in January 1989 to supplement the 1987 review. That review team concluded that the northern spotted owl warranted protection as a Threatened Species under the ESA (USDI, FWS 1989). As required under Section 7 of the Act, FS and BLM immediately began to confer with FWS regarding evaluation of timber sales. A FWS listing team began a review in 1989 of the proposal to list the owl. Its final recommendation, released in June 1990, was to designate the northern spotted owl a Threatened Species throughout its range. The listing became official on 23 July 1990 (Thomas et al. 1990).

An Interagency Agreement among Agency heads of the BLM, FS, FWS, and **NPS** was signed in August 1988; the intent of this agreement was to enable these four Federal Agencies to work together toward a common goal of population viability for the spotted owl throughout its range. Under authority of this agreement, the Agency heads acted upon a 1989 recommendation from the FS to establish an Interagency Scientific Commit tee (ISC) to address the issue of the northern spotted owl. The committee was officially chartered in October 1989 and given 6 months to "develop a scientifically credible conservation strat egy for the northern spotted owl." The ISC's final report was released to Agency heads and Congress on 1 April 1990 (Tho mas et al. 1990). It concluded that existing management for northern spotted owls on NF and BLM lands would lead to increasing loss and fragmentation of suitable owl habitat and imperil the continued existence of the owl. The ISC recom mended an alternative conservation strategy that would desig nate large reserves, called Habitat Conservation Areas (HCAs), to be well-distributed over the range of the owl. Ideally, each HCA should provide sufficient suitable habitat for at least 20 pair-sites, with the lands between managed to facilitate -movement (dispersal) of owls among HCAs.

The implications of the ISC report for management of the California spotted owl became apparent immediately. In May of 1990, the R5 Regional Forester requested assistance from PSW Research Station in additional data collection and analysis for the California subspecies. Emphasis on Sierra Nevada NFs was changed from conducting a third year of RD&A monitoring to inventory of presumed owl habitats not previously surveyed. These habitats were primarily low-elevation oak woodlands, pine-oak forests, and high-elevation red fir forests.

In April of 1991, R5 and PSW Research Station began a cooperative venture with CDF and other State and Federal agencies to assess current information on the California spotted owl. A Steering Committee with representatives from various State and Federal agencies and other interested parties was formed to oversee the entire effort (Chapter 1). The Steering Committee established two teams. A Technical Assessment Team was designated to synthesize and interpret all current information available on the California spotted owl, and to evaluate various management alternatives for the subspecies. A Policy-Implementation Team was designated to evaluate impacts of the Technical Assessment Team's recommendations, to determine whether they fall within existing policies and regulations, and to propose least-cost/low-impact ways to implement them. The Steering Committee will make final recommendations to the responsible agency heads based on reports from the two teams. This report is the product of the Technical Assessment Team.

Current Management

The range of the California spotted owl is considered to include the southern Cascades south of the Pit River in Shasta County, the entire Sierra Nevada province of California, all mountainous regions of the southern California province, and the central Coast Ranges at least as far north as Monterey County (Grinnell and Miller 1944, Gould 1977). Within this range, the owl occurs on 13 NFs, the Lake Tahoe Basin Management Unit (LTBMU) administered by the FS, four National Parks (NPs), several State Parks and Forests, private timber lands, scattered BLM lands, and other minor ownerships (fig. 4A, 4B, and 4C). This includes a portion of the Toiyabe NF, which is administratively a part of the Intermountain Region of the FS.

One of two major subdivisions of the total California spot ted owl population occupies the southern Cascades and the Sierra Nevada, an area roughly 400 miles long by 50 miles wide. The other occupies mountains of southern California, primarily the San Bernardino Mountains and isolated mountains south ward nearly to the Mexican border, the San Gabriel Mountains, the Tehachapi and nearby mountains westward to the coast, and the central coastal mountains (fig. 9A).

Sierra Nevada Province

The Sierra Nevada Province, as used here, includes the conifer forests and foothill riparian/hardwood forests of the Sierra Nevada and the southern end of the Cascade Mountains. Most known California spotted owls and suitable habitat occur on public lands on the west slope of the Sierra Nevada, primarily in seven NFs and in Yosemite and Sequoia/Kings Canyon NPs. Spotted owls also occur on scattered BLM lands along the Sierran foothills, but few surveys have been done on those lands. Large blocks and scattered parcels of private timberland occur within most NFs within the range of the owl in the Sierra Nevada. Recent surveys by timber companies indicate considerable spotted owl use on some of those lands.

Since 1973, agency and public concern for the status of the California spotted owl has been in regard to timber management on the seven westside Sierra NFs and on private industrial timberlands. Even though the NPs experience high recreation impacts in local areas, NP management has not been an issue because the emphasis of the NPS generally is believed to be compatible with maintaining habitats needed by the owls.

The Sierra Nevada owl population is contiguous throughout the mountain range's 400-mile length but is probably poorly linked to the southern California population through the Tehachapi Mountains and the Liebre/Sawmill area east of Interstate Highway 5. The California spotted owl connects to the northern spotted owl in eastern Shasta County.

Forest Service, Pacific Southwest Region (R5)

From north to south, the Lassen, Plumas, Tahoe, Eldorado, Stanislaus, Sierra, and Sequoia NFs in the Sierra Nevada all have major populations of California spotted owls. These NFs have a total land base of 6,978,900 acres, about 73 percent of which (5,093,600 acres) is forested. About 50 percent of this land base, or 3.5 million acres, are forest types considered current or potential spotted owl habitat (USDA, FS 1986b, 1988a,1988c,1988e, 1990, 1991a, 1991b). The major forest types comprising known and potential habitat are Sierran mixed-conifer, red fir, ponderosa pine/hardwood (montane hardwood), eastside pine, and foothill riparian/hardwood (Chapters 5 and 6) (descriptions in Chapter 1). Mixed-conifer is the most abundant type with the most owl sites; the others are less abundant and have far fewer owl occurrences (table 3A).

The LMP directions for Sierran Forests resulted in the designation of 264 SOHAs in approved or draft Forest LMPs (Lassen 40, Plumas 54, Tahoe 33, Eldorado 32, Stanislaus 36, Sierra 29, and Sequoia 40) (table 3B). Of the 264, 249 are on lands suitable and otherwise available for timber production. The other 15 are on lands unavailable for timber production, either because of Congressional classification (Wilderness or Wild Rivers) or because of other Forest LMP allocations. The total land allocation for these 264 SOHAs is about 454,000 acres, of which about 110,000 would be managed under low-yield, even- or uneven-aged management (USDA, FS 1986b, 1988a, 1988c, 1988e, 1990, 1991a, 1991b).

The management direction for SOHAs is to maintain at least 1,000 acres of suitable spotted owl habitat within a 1.5-mile radius of the known or potential spotted owl nest site. Suitable habitat is described as mature timber stands having (1) multi-storied canopies with 70 percent or greater total cover, (2) 40 percent or more of the total canopy in trees 21 inches or more in d.b.h., and (3) well-developed decadence (USDA, FS 1984).

Further, the direction calls for replacement of the suitable habitat over time, based on the certainty that forest stands un-

Table 3A-*Known California spotted owl sites, by habitat type on National Forests and National Parks in the Sierra Nevada, 1987-1991.*

Location	Eastside pine	Red fir	Mixed-conifer	Ponderosa pine/ montane hardwood	Riparian/ hardwood	Number sites sampled[1]	Breeding pairs found[2]
National Forests							
Lassen		8	97			105	36
Plumas	3	9	195	15		222	56
Tahoe		11	135	8		154	38
Eldorado		10	149	1		160	53
Stanislaus		11	97	10		118	26
Sierra		41	86	23	10	160	25
Sequoia	3	9	95	12	9	128	22
Inyo		1				1	1
Lake Tahoe Basin Management Unit		2	1			3	
National Parks							
Yosemite		9	46	1		56	6
Sequoia/Kings Canyon		3	58	9		60	12
Grand total	**6**	**114**	**959**	**79**	**19**	**1,177**	**275**
Percent	**<1**	**10**	**81**	**7**	**2**	**100**	

[1] Data based on NF and NP information for all known owl sites where habitat information was available. (This included some single owl sightings not considered to be "owl sites.") Table 3B should be used for official, total count of spotted owl sites, as it is based on interpretation of NF data along with information from private lands to avoid duplication.

[2] Data on sites where young were produced provided by NFs and NPs.

Table 3B-*Estimated numbers of California spotted owl sites in the Sierra Nevada, by ownership.*

Land	Total known sites (known pairs) 1970-91		Total known sites (known pairs) 1987-91		SOHAs Estimated additional sites	SOHAs Total per National Forest	SOHAs Number with pairs[1]	SOHAs Total number of pairs[2]	Sites in reserved areas 1970-1991	Sites in reserved areas 1987-1991
					Federal Lands					
National Forests										
Lassen	111	(73)	111	(73)	26-31	40	36	42	23	1
Plumas	228	(113)	228	(112)	38-50	54	39	46	5 3	4
Tahoe	150	(83)	118	(75)	46-57	33	28	33	2	2
Eldorado	180	(125)	177	(123)	10-21	32	28	41	0	0
Stanisalus	131	(47)	118	(49)	15-25	36	23	23	3	3
Sierra	175	(86)	157	(81)	50-52	29	16	20	153	12
Sequoia	127	(77)	114	(71)	32-41	40	27	31	22 3	17
Lake Tahoe Basin Management Unit	3	(1)	2	(1)	?	0	0	0	0	0
Toiyabe	2	(0)	0	(0)	?	0	0	0	0	0
Inyo	5	(3)	3	(1)	0	0	0	0	2	1
Subtotal	1112	(608)	1028	(586)	217-277	264	197	236	51	40
National Parks										
Lassen	5	(2)	4	(2)	?				5	4
Yosemite	56	(17)	56	(16)	26-41				56	56
Sequoia/Kings Canyon	60	(42)	60	(41)	20-22				60	60
Subtotal	121	(61)	120	(59)	46-63				121	120
Bureau of Land Management										
All Lands	6	(3)	1	(1)	?				0	0
Total Federal	1239	(672)	1149	(646)	263-340				172	160
					State of California					
State Parks	1	(1)	1	(1)	?				1	1
Other State	2	(1)	2	(0)	?				1	1
					Private Lands					
Industrial forests	58	(32)	49	(29)	?					
Other private	67	(26)	49	(21)	?					
Total Sierra Nevada	**1367**	**(732)**	**1250**	**(697)**					**174**	**162**

[1] Number of SOHAs with at least one pair.
[2] Total number of pairs in all SOHAs (counting all pairs in each SOHA).
[3] Indicates that FS data were augmented by information from CDFG's database.

dergo natural events such as fire, insect and disease attack, and windthrow that may render them unsuitable for spotted owls. The Forests were given a choice of three strategies for replacement: (1) no scheduled harvest, (2) uneven-aged management and (3) even-aged management. An option of no scheduled harvest requires that 650 additional acres of suitable or near-suitable habitat be designated to supplement the 1,000 acres, for a total of 1,650 acres for each SOHA. SOHAs selected for uneven-aged management must have replacement habitat of 1,000 acres and all 2,000 acres can be managed using selection harvests and an implied rotation period of 300 years. SOHAs selected for even-aged management must have 1,650 acres of replacement habitat, and the entire 2,650-acre SOHA is to be managed using clearcut and shelterwood prescriptions and an implied rotation of 240 years (USDA, FS 1984).

Most NFs have already designated management of their SOHAs, but a few will designate the management system as timber sales are planned. Essentially all SOHAs on the Lassen, Eldorado, Stanislaus, Sierra, and Sequoia NFs will be managed as "no scheduled harvest." SOHAs on the other NFs will be a combination of management strategies. The Inyo NF and LTBMU have the same direction as westside NFs, but they were not required to establish SOHA networks because the LTBMU has no regulated timber program and the Inyo timber program is small. Both units have 1-3 spotted owl sites, and essentially all suitable habitat at these sites is protected. The Toiyabe NF, which is adjacent to the Inyo NF and LTBMU on the east slope of the Sierra Nevada is part of Region 4 of the FS. It has only 1-3 spotted owl sites and essentially all suitable habitat is protected (Coburn pers. comm.)

From 1981 to 1987, most spotted owl surveys done on NFs in the Sierra Nevada focused on verification of pairs in network SOHAs. Prior to 1987, this was generally done using a three-visit method without rigid survey requirements. In 1987, however, the Spotted Owl RD&A Program established strict protocols for monitoring SOHAs in R5 and R6. These protocols require up to six visits, methodical coverage of the SOHA and special nest-detection techniques that markedly increased the informa tion acquired. In 1988 and 1989, NFs in the western Sierra Nevada participated in the RD&A Program by monitoring ran-

dourly selected SOHAs and Random Sample Areas (RSAs). Seventy-two SOHAs and 86 RSAs were selected as part of the sample in the Sierra Nevada. Verification of other SOHAs with little or no occupancy history was also made a high priority during this period. Many of those other SOHAs, especially at remote sites, had not been surveyed previously.

In 1988, RD&A monitoring of RSAs began to add information to a meager database of owl locations outside network SOHAs. In 1989, RS direction specified that field surveys be done for the preparation of biological evaluations for spotted owls in proposed timber sales. Surveys in 1989 and 1990 included improved coverage of project areas, similar to the RD&A monitoring method, but they required only three visits. Because of an extended drought affecting the Sierra Nevada, most NFs have had extensive insect mortality among conifers in the last few years, resulting in a much-expanded salvage sale program that involved large portions of the NFs. Spotted owl surveys for proposed green and salvage sales since 1989 have covered much more land outside SOHAs, and to a higher standard, than all previous surveys combined. In 1991 the protocol for project surveys for spotted owls was changed to match that used for the northern spotted owl. This entailed six visits with longer time periods between visits, ensuring a higher likelihood of detecting owls that might be present.

Protecting owl habitat in network SOHAs has been the policy since 1982 except where natural events have impacted the habitat to the extent that management actions to benefit the owl are justified. Direction for management of, spotted owl habitat outside network SOHAs, however, has not been as static. Sites outside network SOHAs received little or no protection before 1989. FS direction in 1989 on field surveys and biological evaluations for owl sites outside network SOHAs created concern and controversy in the NFs. Most Forests were hurrying to complete LMPs based on Regional Guidelines for networks intended to ensure viability. Emerging research on the northern and California subspecies cast doubt on the adequacy of that approach, however, and many biologists preparing biological evaluations concluded that many non-SOHA habitat areas might be needed to maintain viability of the California spotted owl. Release of the ISC report (Thomas et al. 1990) further eroded confidence in the efficiency of the SOHA network.

Protection was given to non-network spotted owls on a case-by-case basis in 1989 and 1990. Generally, more protection was given to pairs and nest sites than to single owls, but policies varied among Forests, Districts, and cases. Where extra measures were afforded, they usually involved habitat protection ranging from 40 to 300 acres and exclusion of sale-related activities between 1 March and 30 August for pairs known to be nesting. For insect salvage sales, protection entailed snag retention in the protected zone comparable to network SOHA standards. Occasionally, similar protection was given to some single birds where pairs were suspected.

In 1991, commensurate with higher standards for field surveys, RS established interim policy for evaluating and mitigating effects of timber sales on spotted owls not otherwise protected in the Sierra Nevada. The direction to NFs was to see that projects did not directly or indirectly affect spotted owls by removing nesting or foraging habitat. This involved the use of home-range study data on the California spotted owl to estimate the territorial needs of known and potential owl pairs. The objective of the policy was to assure a full range of options for managing spotted owls by maintaining the population at current levels until the agencies could consider new directions based on recommendations of the Steering Committee.

Since 1970 biologists have identified California spotted owls at 1,112 sites (an area with either a pair or a single where a pair could be supported-see glossary) in NFs in the Sierra Nevada province. In the last 5 years (1987-1991) 586 pairs have been verified at 1,028 of these sites (table 3B). The NFs estimate a potential for approximately 250 more sites. Of the 264 network SOHAs identified in the LMPs that are managed exclusively for California spotted owls, pairs have been verified at 197 sites, including 107 sites where reproduction has been documented.

National Park System, Western Region

Four NPs are located in the southern Cascades and Sierra Nevada, within the range of the California spotted owl. Sequoia/Kings Canyon NPs, Yosemite NP, and Lassen Volcanic NP have land bases of 863,710 acres, 749,031 acres, and 106,298 acres, respectively, for a total of 1,719,039 acres. Thirty-six percent (315,933 acres) of Sequoia/Kings Canyon NPs is forested and within the elevational range of the owl, and 15 percent (133,561 acres) is considered suitable for foraging or nesting. In Yosemite NP, 75 percent (564,500 acres) is forested, and 35 percent (263,126 acres) is considered suitable for foraging or nesting by owls (Steger pers. comm.). Lassen NP is approximately 94 percent (100,100 acres) forested, but few surveys have been done there; about 60 percent (64,600 acres) of that is in yellow pine and fir forests (Husari 1990), and may be suitable spotted owl habitat.

The NPS manages the Parks to emphasize preservation and maintenance of natural communities and ecological processes. Their policy states that "Natural processes will be managed with a concern for fundamental ecological processes as well as for individual species and features. Managers and resource specialists will not attempt solely to preserve individual species (except threatened or endangered species) or individual natural processes; rather, they will try to maintain all the components and processes of naturally evolving park ecosystems, including the natural abundance, diversity, and ecological integrity of the plants and animals" (USDI, NPS 1988).

In addition, the NPS "will identify all state and locally listed threatened, endangered, rare, declining, sensitive, or candidate species that are native to and present in the parks, and their critical habitats. These species and their habitats are considered in NPS planning and management. Based on an analysis of the status of state and locally listed species throughout their native ranges and throughout the national park system, the National Park Service may choose to control access to critical habitats or to conduct active management programs similar to activities conducted to perpetuate the natural distribution and abundance of federally listed species."

The spotted owl is recognized as a special status species by the NPS, but specific management direction has not been devel-

oped. Resource management plans for the NPs will be revised as each unit determines what special management, if any, is needed (van Wagtendonk pers. comm.).

Known owl sites since 1986 total four in Lassen Volcanic NP, 56 in Yosemite NP (Roberts et al. 1988), and 60 in Sequoia/Kings Canyon NPs (Roberts 1989, Steger pers. comm.) (table 3B). We estimate that the NPs may contain owls at another 55 sites. Most of the information for Yosemite and Sequoia/Kings Canyon NPs was obtained by the CDFG and PSW Research Station in special surveys and studies done since 1988. Yosemite and Sequoia/Kings Canyon NPs are considered critical by the CDFG and FS as reserves for maintaining population viability and for movement by spotted owls between NFs in the Sierra Nevada.

Bureau of Land Management, California Office

The BLM administers scattered public lands along the foothills and lower slopes of the southern Cascades, Sierra Nevada, Transverse Ranges, central Coast Ranges, and southern California mountain ranges. Some of these support forest, woodland, and foothill riparian/hardwood habitats that are potentially suitable for California spotted owls. Commonly, potential owl habitat on BLM land occurs in small tracts (less than a section) and may be located adjacent to NFs or intermingled with private timberlands. Along the Merced, Tuolumne, American, Yuba, Stanislaus, and Mokelumne Rivers, however, their lands are concentrated in blocks of several thousand acres (Saslaw 1991).

In the northern Resource Areas, forest management includes green timber sales, thinning for timber stand improvement, fire and insect salvage, and forest sanitation. Forested lands of the BLM in California are managed primarily under uneven-aged prescriptions that remove 40 to 60 percent of the volume and up to 30 percent of the stems. Between 1981 and 1990, 25,691 acres were logged under a partial-cut prescription, and 238 acres (1 percent) were logged as clearcuts, generally between 2 and 4 acres in size. Many unharvested locations were within riparian buffer areas, usually 100 feet on each side of the stream, and may be within special recreation management areas along major streams. Future management in the Folsom Resource Area is expected to be custodial, with forest management prescriptions designed to meet wildlife and vegetation objectives. Emphasis will be on managing for old-growth, special wood products, and stand maintenance. Logging will be directed to fire and insect salvage and forest sanitation. Forest management on the Redding, Alturas, and Eagle Lake Resource Areas will continue to use uneven-aged methods.

Potential suitable habitat has been mapped based on BLM forest operation inventories, Timber Production Capability Classification maps, CDF oak woodland maps, BLM vegetation surveys, and records of owls from the CDFG and nearby NF lands. About 68,500 acres of BLM land are considered to be potential habitat for the California spotted owl, based on habitats they are known to use elsewhere in the Sierra Nevada (Saslaw 1991) (table 3C).

Inventories for California spotted owls on BLM lands were initiated in 1989 for forest management or land exchange proposals that could potentially affect spotted owl habitat. Because the BLM has only recently begun systematic inventories for spotted owls, information on their distribution and numbers is unavailable. This precludes an estimate of the number of California spotted owls inhabiting BLM lands. They have been observed at six sites on BLM lands in the Sierra Nevada, however, and we believe there is potential for more.

California State Parks

Seven units of the California Department of Parks and Recreation with known or potential spotted owls occur in the Sierra Nevada. Management on State Park (SP) lands is similar to that of the NPs. All wildlife and plants are protected and sensitive species receive special care. Most units are designated as State Parks (SPs) and State Historical Parks (SHPs), with a total area of 16,580 acres. The SPs with the most potential for spotted owl are Plumas-Eureka SP with about 3,000 acres of conifer forest, Malakov Diggins SHP with 1,500 acres of conifer forest, South Yuba River Project with 1,500 acres of conifer and oak habitats, and Calaveras Big Trees SP with 5,750 acres, mostly in old-growth conifer forest (Bakken pers. comm.). Spotted owls have been found on adjacent NFs and Calaveras Big Trees SP (2 pairs), Malakov Diggins SHP (single owl) and Growers Hot Springs SP (single owl). Surveys, none of which are recent, have been conducted only at Calaveras Big Trees and Growers Hot Springs SPs and the potential exists for owls at the other larger units.

California State Forests

Mountain Home State Forest (SF) and Latour SF are State-owned forests managed by the CDF for demonstration of forestry practices and to support cooperative research with other agencies. Uneven-aged silviculture is featured in both SFs, including both single-tree and group-selection methods on a sustained yield basis. Other multiple uses are also emphasized, primarily recreation. Known owl activity centers would be protected from planned projects through review and advice from the CDFG.

Located in Tulare County, Mountain Home SF includes 4,807 acres, with Sierran mixed-conifer and giant sequoia stands that provide potential owl habitat on the entire property. About 960 acres of old-growth forest remain. Surveys have been done only around the edges of this SF by FS biologists, but they provide evidence of use by spotted owls. Probably two or three pairs occur there (Dulitz pers. comm.).

Table 3C--*Potential suitable habitat for California spotted owls on Bureau of Land Management lands.*

BLM District Resource Area	Acres
Susanville	
Alturas	13,337
Eagle Lake	18,936
Ukiah	
Redding	12,250
Bakersfield	
Folsom	24,000
Total	**68,523**

Latour SF is located in Shasta County and encompasses 9,033 acres. It was surveyed for spotted owls in 1990 and 1991, with one pair discovered in 1990 (McNamara pers. comm.). This SF has 7,000 acres of mixed-conifer and fir forest that are potential owl habitat, but only 2,000 acres have significant large-tree components (6+ trees per acre at least 32 inches in d.b.h.).

University of California

Blodgett Forest Research Station, located in Eldorado County within the Eldorado NF, is a 3,000-acre facility owned and operated by the University of California, Berkeley. It provides a setting for research on all aspects of forest management in Sierra Nevada mixed-conifer forests, especially research done as part of the forestry program at the University. Blodgett Forest has approximately 2,000 acres of suitable habitat for California spotted owls and typically one or two pairs nest in the area (Heald pers. comm.).

Whitaker Forest is a 320-acre unit located between the Sequoia NF and the General Grant area of Kings Canyon NP. Most of it is suitable owl habitat including giant sequoia stands. The property is used for research, with emphasis on sequoia natural history (Gasser pers. comm.). This unit has a long history of spotted owl observations and has supported at least a single owl over the last 5 years.

Private Lands

Private lands in the Sierra Nevada that are classified as timberland and have the potential to grow forest habitats used by California spotted owls encompass about 2.4 million acres, much of which is currently in suitable condition. Of this, 1.45 million acres are owned by industrial private timber companies (IPs) and 0.96 million acres are owned by miscellaneous private parties (MPs) not primarily engaged in commercial timber production (Colclasure et al. 1986, Hiserote et al. 1986, Lloyd et al. 1986) (table 3D). The latter group includes both large landowners, such as utilities and water districts, and many small landowners.

Table 3D-*Acres of forest lands owned by commercial timber industries and miscellaneous private parties in the Sierra Nevada, by county, within the range of the California spotted owl.*[1]

County	Forest industry	Miscellaneous private
Shasta	194,000	54,000
Lassen	267,000	42,000
Tehama	120,000	19,000
Plumas	215,000	82,000
Butte	135,000	92,000
Yuba	26,000	23,000
Sierra	49,000	44,000
Nevada	60,000	137,000
Placer	95,000	79,000
El Dorado	121,000	117,000
Amador	25,000	31,000
Calaveras	68,000	71,000
Tuolumne	60,000	50,000
Mariposa	1,000	40,000
Madera	5,000	12,000
Fresno	10,000	22,000
Tulare	Trace	16,000
Kern	0	26,000
Total	**1,451,000**	**957,000**

[1] From Colctasure et a1.1986, Hiserote et al. 1986, and Lloyd et al. 1986.

NFs in the Sierra Nevada include approximately 1.4 million acres of private land within their administrative boundaries (USDA, FS 1986b, 1988a, 1988c, 1988e, 1990, 1991a, 1991b) (table 3E). The other 1 million acres of IP lands are outside of NF boundaries. NF inholdings are much greater in extent in northern NFs (especially the Lassen, Plumas, and Tahoe) than in the southern Sierra Nevada. The Tahoe NF, with about 375,000 acres, includes the most private inholdings, and the Sequoia NF (with about 54,000 acres) has the least.

The spatial arrangement of private lands within NFs varies. Much of the private lands within the boundaries of the Lassen, Plumas and Stanislaus NFs tend to be in contiguous blocks, leaving NF lands also fairly contiguous. Most private lands on the Tahoe NF are in "checkerboard" ownership-alternating sections of private and NF ownership-and the Eldorado NF has a combination of checkerboard and contiguous block patterns. The checkerboard pattern is a vestige of Federal land policies used to stimulate development of the Nation's railroad system prior to establishment of the NFs. The Sierra and Sequoia NFs have relatively little interior private lands, and the four NPs have negligible amounts.

Except for historical railroad holdings, most lands belonging to IP companies were acquired with consideration for growth and yield potential. Therefore, they occupy most of the best tree-growing lands in the Sierra Nevada. Most IP timberlands are at middle elevations, in the mixed-conifer zone, but some are higher and farther east, in red fir and eastside pine zones. Almost all are within the elevation and geographic ranges of the California spotted owl. About 12 major companies have relatively large holdings in timberlands of the Sierra Nevada with eight owning at least 75,000 acres (Swing pers. comm.) Table 3D shows the total amount of IP and MP timberlands by county.

Systematic surveys for owls have not been done on most private lands, although several timber companies conducted surveys, using established FS protocols, starting in 1989, 1990, or 1991. Locations of owls found are not always available from timber companies, but it appears that some IP lands with a long

Table 3E---*Approximate acres of private lands within National Forest boundaries (data from Forest LMPs as listed in references)*

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National Forest	Private land
Lassen	230,000
Plumas	226,000
Tahoe	375,000
Eldorado	190,000
Stanislaus	195,000
Sierra	109,000
Sequoia	54,000
Total	**1,379,000**

history of logging have a substantial number of owls, comparable in density to adjacent NF lands. We also know from one study that some IP lands with a history of intensive logging lack nesting owls, even though nest sites occur in adjoining NF lands (Bias and Gutiérrez 1988).

The public has recently attempted to pass forestry-reform initiatives for California, and the Legislature and Board of Forestry are also moving to provide new rules for logging on private lands. Emergency Regulations were recently in effect for IP timberlands in California, with the expectation they would be replaced with permanent policies. These policies will probably include requirements for sustained yield, less clearcutting, riparian protection, and special requirements for older forest stands. Although we cannot now assess the effects of new forestry regulations on the capability of private lands to support spotted owls, we believe those regulations will be more beneficial than past policies.

At the north end of the Sierra Nevada, a relatively continuous block of private timberlands in eastern Shasta County provides the habitat linkage for movement between populations by both northern and California spotted owls. Maintaining this connection is considered to be critical to the long-term conservation of both subspecies of spotted owls (Dawson et al. 1987, Thomas et al. 1990).

Owls are known to inhabit dense stands of hardwoods along stream channels at low elevations on the western edge of the Sierra and Sequoia NFs. These habitats resemble, in most respects, habitats used by many spotted owls in southern California. Similar habitats, with sparse stands of digger or ponderosa pine over denser stands of mixed hardwoods, occur along riparian zones west of NF boundaries from the Stanislaus NF north. Generally, these areas are not classified as commercial timberland. Livestock grazing has been the primary activity in these low-elevation habitats in the past, and type conversions, firewood cutting, and logging in and adjacent to riparian zones have also occurred. An increase in residential developments in the Sierra Nevada foothills is now impacting many of these potential owl habitats. The combination of residential development and indirectly related increased fire potential represent growing threats to habitat for both year-round and wintering spotted owls (Chapter 13). These areas have not been adequately surveyed for owls, although we suspect that they support many pairs.

Over the last 20 years, spotted owls have been located at 58 sites on IP lands and at 67 sites on MP lands in the Sierra Nevada. Twenty-nine and 21 pairs have been verified on IP and MP lands, respectively, in the last five years (tables 3B and 3F). There is no estimate of the potential number of spotted owl sites on private lands because of the small percent of those lands which have been surveyed and the lack of specific habitat information which could be used to estimate the distribution and numbers of spotted owls in lower elevation habitat types. We expect that these areas contain many owl sites but we estimate, based on the gross mapping of hardwood types, that number to be no more than one-third the total number of sites in conifer types.

Areas of Concern: Sierra Nevada

Spotted owl distribution in the Sierra Nevada Province is characterized by its continuity and relatively uniform density (fig. 4B). The ability of existing habitat to support owls does not appear to be a major problem except at the peripheries of the subspecies' range. This condition is normal for animal populations, however, and is not a concern unless the range begins to shrink. Five conditions give rise to some concern for the integrity of the California spotted owl's range in the Sierra Nevada: (1) bottlenecks in the distribution of habitat or owl populations; (2) gaps in the known distribution of owls; (3) locally isolated populations; (4) highly fragmented habitat; and (5) areas of low crude density of spotted owls. Areas occur throughout the length of the Sierra Nevada where one or more of these conditions currently limit the owl population; it might be of critical concern if conditions were exacerbated, or if they limit our knowledge of the owls there. This might lead to erroneous or more risky management decisions (fig. 3A, table 3G). These conditions may be caused solely or jointly by fire, land-ownership patterns, natural or human-caused fragmentation of suitable habitat, and by natural geographic features that control vegetation patterns. Rather than reflecting current negative effects on spotted owls, areas of concern identified in figure 3A simply indicate potential areas where future problems may be greatest if the owl's status in the Sierra Nevada were to deteriorate.

Areas A and B (fig. 3A) are bottlenecks in distribution where even relatively small losses of habitat could sever the interchange between adjacent populations of owls. In Area A, this would decrease the likelihood of interchange between the California and the northern spotted owl populations. This area of concern was identified for its importance by the Audubon Society's Spotted Owl Advisory Panel (Dawson et al. 1987) and by the Interagency Scientific Committee for the northern spotted owl (Thomas et al. 1990).

Areas A, B, 1, 4, 5, 7, and 8 are characterized by habitat fragmentation that decreases the density of. owl pairs, makes successful dispersal more difficult, and reduces the likelihood of quick replacement of owls in vacated habitat.

Area 2 is a gap in the known distribution of spotted owls from the western to the eastern edge of the owl's range in the northern Sierra Nevada. If few birds and little habitat exist in this area, north-south dispersal could be impeded. This area and others (for example, areas 4 and 5) where few surveys have been done are, however, capable of producing owl habitat and may not be breaks in distribution.

Areas 5 and 6 also have low population densities. As in areas with fragmented habitat, low densities make dispersal more difficult and less likely to result in reoccupation of vacated sites.

Area 8 is characterized, in part, by small isolated populations that are more vulnerable to extinction by local stochastic or catastrophic events.

Table 3F-*Estimated numbers of owl sites (confirmed pairs) on private lands in the Sierra Nevada, by county.*

County	Industrial lands				Other private			
	1970-1991		1987-1991		1970-1991		1987-1991	
Shasta	5	(0)	5	(0)	4	(0)	3	(0)
Lassen	0		0		3	(1)	3	(1)
Tehama	6	(4)	6	(4)	0		0	
Plumas	8	(5)	7	(4)	10	(4)	10	(5)
Butte	9	(0)	5	(0)	7	(4)	5	(4)
Sierra	3	(2)	3	(2)	2	(0)	2	(0)
Yuba	0		0		3	(1)	1	(0)
Nevada	7	(6)	7	(6)	3	(2)	3	(1)
Placer	3	(3)	3	(3)	5	(1)	2	(1)
El Dorado	13	(8)	9	(6)	8	(3)	7	(2)
Amador	0		0		1	(0)	1	(0)
Calaveras	0		0		5	(0)	1	(0)
Tuolumne	4	(4)	4	(4)	7	(3)	3	(0)
Mariposa	0		0		4	(2)	3	(2)
Madera	0		0		0		0	
Fresno	0		0		4	(4)	4	(4)
Tulare	0		0		0		0	
Kern	0		0		1	(1)	1	(1)
Totals	**58**	**(32)**	**49**	**(29)**	**67**	**(26)**	**49**	**(21)**

Southern California Province

Spotted owls in southern California occur in 11 major mountain ranges and mountain complexes, predominantly on NF lands. These ranges and areas are the Santa Ana, San Diego (including the Laguna, Cuyamaca, Pine Hills/Vulcan, and Palomar mountain areas), San Jacinto, San Bernardino, San Gabriel, Liebre/Sawmill, Tehachapi, Tecuya Mountain area, Los Padres, southern Santa Lucia Mountains, and northern Santa Lucia Mountains (fig. 9A). Movement between these major ranges and complexes may be uncommon to nonexistent (Stephenson 1991). Within a given range, however, separate blocks of suitable habitat are relatively close together. For instance, the San Diego ranges include five of the mountain ranges mentioned above with populations 4.5 to 8 miles apart, but distances from the San Diego to the San Jacinto ranges and Santa Ana Mountains are 18 and 33 miles, respectively (Stephenson 1991). Historic records from the turn of the century documented spotted owls in riparian areas on the coastal lowlands, but their occurrence there today is unlikely because of the extensive loss of habitat to urbanization (Bloom pers. comm.).

Besides our concern that successful movement by owls among some of these relatively isolated islands of habitat may be declining or no longer possible, the southern California populations of owls may be isolated from the southern Sierra Nevada because of the nature of available connecting habitat. The Tehachapi Mountains, Liebre/Sawmill and Tecuya Mountain areas are critical for maintaining this linkage, if it still exists, and they are relatively distant from the nearest other known spotted owls in the San Gabriel Mountains and the southern Los Padres ranges.

Estimated owl sites, numbers of pairs, pair status, and distances from nearest neighboring populations of California spotted owls for each of the 11 mountain areas are summarized in table 3H (Stephenson 1991).

Forest Service, Pacific Southwest Region (R5)

Most known spotted owl populations in southern California are on the Angeles, San Bernardino, Cleveland, and Los Padres NFs, with a total land base of 3,643,927 acres. The primary habitat types used are riparian/hardwood, live oak/bigcone Douglas-fir, and mixed-conifer (Chapter 5) (types described in Chapter 1), but in different proportions on the four NFs (table 3I). On the Angeles and San Bernardino, most spotted owls are found in live oak/bigcone Douglas fir at elevations of 2,000 to 5,000 feet and mixed-conifer (mostly Jeffrey pine) at elevations from 5,000 to 8,000 feet. These types cover 137,000 acres on the Angeles NF (20 percent of the landbase) and 308,000 acres on the San Bernardino NF (37 percent of the landbase). On the Cleveland NF most owls are found in similar habitats, including a total of 40,000 acres (9.6 percent of the landbase) but we believe that additional owls will be found in riparian/hardwood habitats when they are surveyed. These habitats make up 1-2 percent of the landbase on all four NFs (USDA, FS 1986a, 1987, 1988b, 1988d).

On coastal portions of the Monterey District of the Los Padres NF, large stands of redwoods on north slopes also provide owl habitat, but population surveys there are incomplete. Most owls on the Los Padres NF, especially in the southern block, are in narrow riparian corridors, where mixed hardwoods are closely flanked by chaparral.

Regional direction for the four NFs in southern California is to protect all known spotted owl sites and to manage the habitat based on local information about suitability and availability (USDA, FS 1984). FS surveys for occupancy and suitable habitat in southern California lags behind the Sierra Nevada Prov-

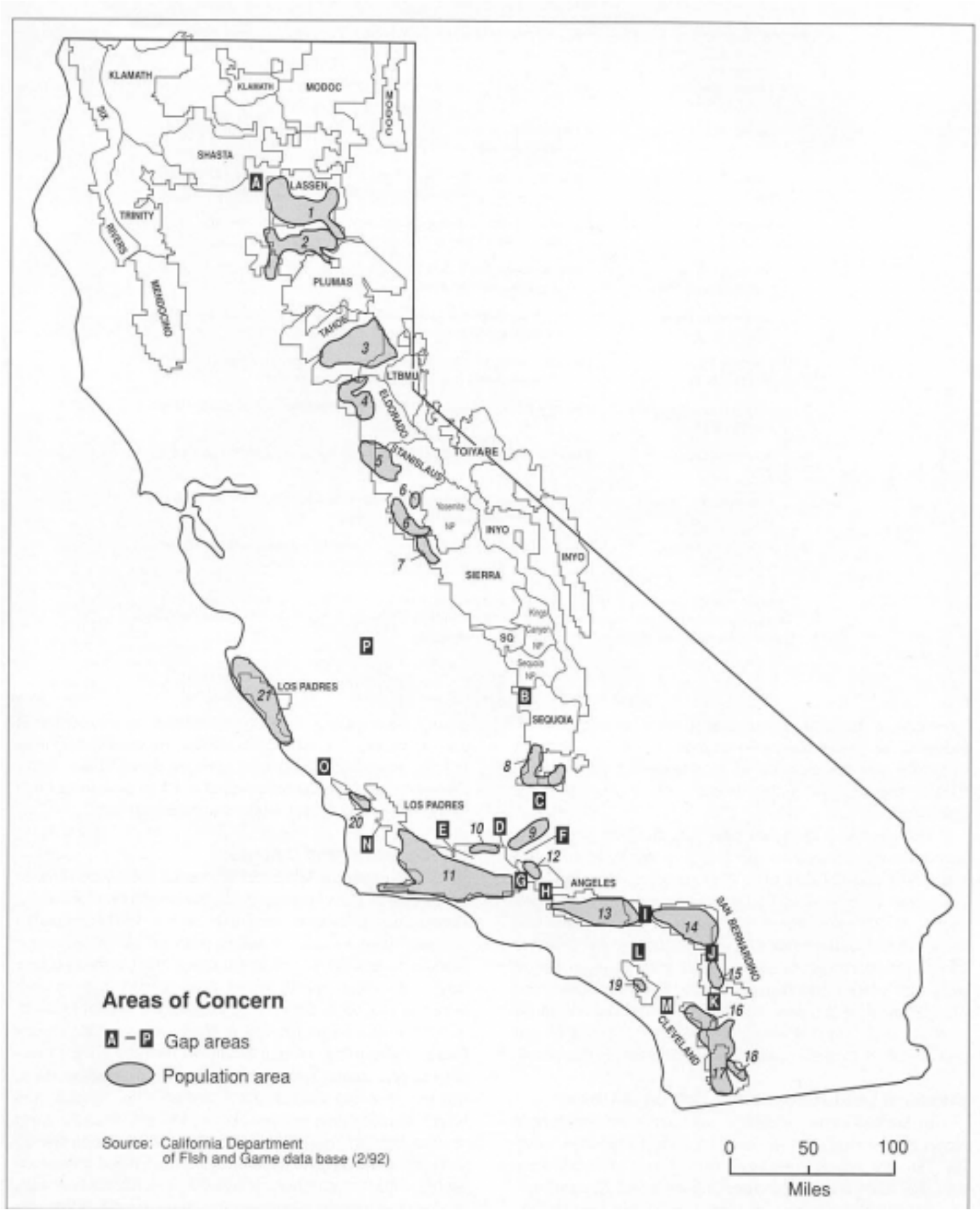

Figure 3A-Areas of current and potential concern for the California spotted owl. Gap areas delineate discontinuities in owl distribution; designated population areas have a variety of real or potential concerns, such as low population density, relatively fragmented habitat, or extensive loss of habitat from recent wildfires. Place names and reasons for concern are identified in tables 3G and 3K.

Table 3G-*Areas of concern for California spotted owls in the Sierra Nevada.*

Area[1]	General location (major ownership)[2]	Reasons for concern
A	Eastern Shasta County (FS, IP)	A natural bottleneck between northern and California spotted owls; habitats are fragmented and owl densities low.
B	Central Tulare County (NPS)	Apparently a natural bottleneck in north-south distribution of owls because steep terrain provides only a narrow band of suitable habitat.
1	Lassen County (FS, NPS, IP)	Habitat in this area is discontinuous, naturally fragmented, and poor in quality due to drier conditions and lava-based soils.
2	Northern Plumas County (FS, IP, Pvt.)	A gap in known distribution, mainly on private lands, extends east-west in a band almost fully across the width of the owl's range.
3	Northeastern Tahoe NF (FS, IP, Pvt.)	An area of checkerboard lands; much dominated by granite outcrops and red fir forests; both features guarantee low owl densities.
4	Northern Eldorado NF (FS, IP, Pvt.)	Checkerboarded lands and large, private inholdings; owl densities unknown on some private lands and very low on others.
5	Northwestern Stanislaus NF (FS, IP, Pvt.)	Has large private inholdings; owl densities unknown on most private lands.
6	Southern Stanislaus NF (FS)	Burned in recent years; the little remaining habitat is highly fragmented.
7	Northwestern Sierra NF (FS)	Habitat naturally fragmented, due partly to low elevations and dry conditions; fragmentation accentuated by logging.
8	Northeastern Kern County (FS)	Only small, semi-isolated groups of owls in the few areas at elevations where habitat persists at the south end of the Sierra Nevada.

[1] Location codes correspond to letters (gaps and bottlenecks) and numbers (population areas) on figure 3A.
[2] Ownership codes: FS = USDA Forest Service; NPS = National Park Service; BLM = Bureau of Land Management; IP = Private industrial lands; Pvt. = multiple, small, private ownerships.

ince because threats to the population from management appeared to be less imminent in southern California. Southern California was not included in the monitoring phase of the RD&A Program, and funding for other survey efforts has been inadequate.

Three hundred seventeen sites with pairs or single owls have been documented on the four southern California NFs since 1970, and 294 sites since 1986 (table 3J). Over the last 5 years, pairs have been verified at 214 of these sites with reproduction at 107 sites. About 42 percent of known sites were located in the San Bernardino Mountains (LaHaye and Gutiérrez 1990). This probably reflects a higher relative abundance of owls over a larger area than elsewhere in southern California. The NFs estimate that approximately 190 additional sites might currently exist. The 294 sites identified since 1986 are 85 percent of all sites located in southern California during that period.

Bureau of Land Management, California Office

BLM lands are relatively few and scattered in the mountain ranges between the coast and inland deserts of southern California. They are located down-slope from, and in more arid areas than, NF lands and they include drainages and riparian/hardwood forests that may provide spotted owl habitat. In the California Desert District and the Caliente Resource Area, potential spotted owl habitats are managed for wildlife, riparian habitat quality, water quality, and dispersed recreation. Total potential owl habitat, based on vegetation, in these two management units is 7,560 acres, but surveys have not been done (Saslaw 1991). One spotted owl site has been located on BLM lands in the last 5 years, the result of survey work on adjacent NF lands.

U.S. Department of Defense

Camp Pendleton Marine Base occupies about 125,000 acres on the coastal plain between the Santa Ana Mountains and the Pacific Coast in northern San Diego County. The higher part of the Base, with a small amount of potential habitat, abuts the Trabuco Ranger District of the Cleveland NF, but no owls have been found there recently (Buck pers. comm.). Spotted owls were observed about the turn of the century at several locations in riparian habitats on the coastal plain, including San Onofre Creek in what today is Camp Pendleton, but none is there today (Bloom pers. comm.). Santa Margarita Creek is another major drainage bisecting the Camp that probably had spotted owls historically, based on remnant bigcone Douglas-fir in the upper reaches, but the habitat has been too degraded by fire to support owls now (Bloom pers. comm.). The Base has a natural resource management program, including wildlife conservation, but long-term effects of training activities have degraded habitat for spotted owls to an extent that very little exists today (Buck pers. comm.).

Table 3H-Owl *sites*[1]*, number of pairs and status* of *pairs at those sites, pair status, and nearest-neighbor distances of California spotted owls in southern California*[2]

Area	Owl sites (all years)	Pairs since 1987	Breeding since 1987	Potential population (no. sites)	Nearest neighbor distances[3]
San Diego Ranges	37	18	6	76	18 -33 miles
Santa Ana Mountains	2	1	-	12	30 -40 miles
San Jacinto Ranges	20	16	9	29	11 -18 miles
San Bernardino Mountains	124	114	66	125	6 -11 miles
San Gabriel Mountains	54	22	5	95	6 -20 miles
Liebre/Sawmill Mountains	14	10	2	20	12 -20 miles
Tehachapi Mountains	4	0	-	12	unknown
Tecuya Mtn area	5	3	-	10	9 -12 miles
Los Padres	65	32	17	100	8 -12 miles
So. Santa Lucia Mountains	12	6	2	19	32 -45 miles
No. Santa Lucia Mountains	39	22	1	80	45 miles
Total	**376**	**244**	**108**	**578**	

[1] See definition of "owl site" in glossary (Appendix B).
[2] Based on Stephenson (1991) and California Department of Fish and Game database.
[3] Where two distance values ate shown (for example, 12-20 miles), they represent the distances to the two closest neighboring populations.

California State Parks

Five units of the SP system, totalling 58,182 acres, are in the vicinity of the Angeles, San Bernardino, and Cleveland NFs. Those with significant owl habitat are San Jacinto SP (about 12,500 acres of conifer and pine-oak forests), Cuyamaca Rancho SP (about 11,000 acres of conifer and hardwood forests), and Palomar Mountain SP (1,000 acres of conifer and hardwood forests) (Bakken pers. comm.). All three of these SPs have been surveyed for spotted owls in recent years. Based on research, existing habitat, and nine known sites, they could support 13 to 15 pairs of spotted owls (Stephenson pers. comm.).

Four additional SP units with a combined total of 300 acres of coastal conifer and hardwood habitats are on the central California coast and have potential for a limited number of spotted owls. These are Julia Pfieffer Burns SP, Pfieffer-Big Sur SP, Andrew Molera SP in Monterey County and and Gaviota SP in Santa Barbara County (Bakken pers. comm.). Nojoqui Falls County Park is a 98-acre park which is part of the Santa Barbara County park system not far from Gaviota SP. It has had records of a spotted owl site since the early 1970s in riparian/hardwood habitat along Nojoqui Creek (Jimenez pers. comm.).

National Audubon Society

Starr Ranch, a 4,000-acre wildlife sanctuary owned and managed by the National Audubon Society, is located on upper Bell Canyon in Orange County, adjacent to the Trabuco Ranger District of the Cleveland NF (DeSimone pers. comm.). This area occasionally has nonbreeding spotted owls that move onto the property from NF lands, but they apparently do not nest there (Bloom pers. comm.).

Native American Tribal Lands

Several Native American Tribal Reservations are located in southern California; these have potential spotted owl habitat and a few documented sightings. The Pala, La Jolla, Santa Ysabel, Mesa Grande, Los Coyotes, and Cuyapaipe Reservations all have potential habitat that has been identified by FS biologists from the Cleveland NF. Sightings indicate a population of at least four pairs, and known potential habitat could support a higher number. Activities and potential threats to spotted owls on these lands are unknown.

Other Private Lands

Major activities that threaten spotted owls on private lands in southern California are recreation, urbanization, fire, and water extraction from stream systems (Chapter 13). Both the San Bernardino and Cleveland NFs include significant areas of private land-about 145,000 and 120,000 acres, respectively (USDA, FS 1986a, 1988d). The San Bernardino NF surrounds the popular and rapidly growing mountain resorts of Big Bear Lake, Lake Arrowhead, Forest Falls, and Idyllwild. This is causing a loss of owl habitat, especially near Lake Arrowhead (Stephenson 1991). The situation on included lands on the Cleveland NF is not so severe, but expanding development and recreation on these lands pose long-term risks for the owl. Direct risks are caused by continual loss of suitable nesting habitat from these activites which fragments the already meager quantity of suitable habitat. An indirect risk is the decreasing ability of the FS to use prescribed burning to reduce fuel accumulations that can lead to stand-destroying fires, because of the potential risk of prescribed fires to residential areas as well as local air pollution regulations.

Urbanization and wildfires also affect owl habitat outside of and surrounding all four NFs. The Angeles and the Los Padres NFs do not have major problems with private inholdings, but they are experiencing residential development around their edges. Loss of habitat in these areas outside the forests reduce the quantity of suitable habitat around the edge of the isolated parcels of NF lands and occasional tracts of habitat on private lands. Additional impacts of urbanization are effects of fire management policies, recreation patterns, and diversions of wa-

Table 3I-*Known California spotted owl sites, by habitat type, on and in the vicinity of National Forest lands in southern California, 1970-1991.*

	National Forests					
	Angeles	San Bernardino	Cleveland	Los Padres	Total sites	Percent
Habitat types						
Riparian/hardwood		2	4	110	116	32
Live oak/bigcone Douglas-fir	48	73	26		147	41
Mixed-conifer	11	72	6	6	95	26
Redwood				2	2	>1
Total Sample[1]	**59**	**147**	**36**	**118**	**360**	**100**
Reproductive sites						
Breeding pairs[2]	10	82	7	8	107	

[1] Data provided by NFs for all sites with available information on habitats. Actual total counts of sites for southern California are given in Table 3J, based on CDFG's database.

[2] Data provided by NFs for sites where young were produced.

Table 3J-*Estimated numbers of California spotted owl sites (pairs) in southern California.*

Location	Total known sites (known pairs)				Sites in reserved areas		Estimated additional sites
	1970-1991		1987-1991		1970-1991	1987-1991	
			Federal Lands				
National Forests							
Los Padres	111	(62)	94	(61)	45[1]	41	58-100
Angeles	59	(31)	56	(28)	9[1]	7	40-80
San Bernardino	126	(114)	126	(114)	8	8	30-45
Cleveland	21	(14)	18	(11)	3	3	14
Bureau of Land Management							
All lands	1	(0)	1	(0)			
Subtotal	**318**	**(221)**	**295**	**(214)**	**65**	**59**	**142-239**
			State and Local Lands				
State Parks	7	(4)	7	(1)			13-15
Other State	1	(0)	0				
Local Parks	1	(1)	0				
Subtotal	**9**	**(5)**	**7**	**(1)**			**13-15**
			Private Lands				
Indian Nations	4	(3)	4	(3)			
Other (by county)							
Monterey	2	(1)	1	(1)			
San Luis Obispo	2	(1)	0				
Santa Barbara	3	(2)	2	(1)			
Ventura	0		0				
Kern	5	(1)	4	(0)			
Los Angeles	3	(2)	3	(1)			
San Bernardino	16	(14)	16	(13)			
Riverside	7	(6)	7	(6)			
Orange	0		0				
San Diego	7	(5)	4	(4)			
Subtotal	**45**	**(32)**	**41**	**(29)**			
Overall total	**376**	**(261)**	**343**	**(244)**			

[1] Data from FS were augmented by information from CDFG's database for historical sightings only.

ter from streams for local residential use. These development; also accentuate the barriers separating owl populations. They also have the effect of reducing dispersal between blocks and the chance for population support from adjacent areas.

Over the last 5 years spotted owls have been found at 37 sites on private lands in all counties along the southern California coast except Ventura, Orange, and San Luis Obispo (table 3J). We expect these numbers to be low because most private lands are at elevations lower than "traditional" spotted owl habitat. Some surveys have been done in the gaps between NF lands and on NF lands with habitats similar to those found on private lands. Spotted owls have been located in local situations and at relatively low densities. We do not expect that further surveys will document additional, extensive populations that would dramatically change our current understanding of the species' distribution and density in southern California.

Areas of Concern: Southern California

Our concern for spotted owl populations in southern California is much greater than is the case for the Sierra Nevada, because processes are at work there that we believe will further isolate populations from one another and reduce the sizes of individual populations. These processes are likely to reduce the interchange of owls between populations (Chapter 9), lowering our estimates of the stability of the metapopulation in southern California. The likelihood of local extinction resulting from stochastic processes will increase if local populations are further isolated and suitable owl habitat declines.

Concern about the stability and persistence of the California spotted owl population in southern California centers on four factors: (1) Every population is separated from neighboring populations by unsuitable habitat; (2) even within mountain ranges, gaps occur in the known distribution of owls; (3) suitable habitat is highly fragmented; and (4) some areas have low crude densities of spotted owls. Whereas the Sierra Nevada contains one relatively contiguous population of spotted owls, southern California contains at least 11 populations separated from their nearest neighbors by at least 6 miles (figs. 3A, 9A; tables 3H and 3K). The gaps, in all but two cases, contain major highways, often urban development, and hotter, drier, lower elevations unsuitable for nesting, foraging, or dispersal.

The owl's habitat in the Sierra Nevada most often consists of relatively large areas with a fairly high proportion of suitable habitat. In southern California, even in areas with owls, the habitat is often restricted to narrow riparian strips separated from adjacent and similar habitat by open expanses of 1/2 mile or more of chaparral (Areas 10,11, 12, 15,17, 19, and 20 in fig. 3A, table 3K). The intervening areas are not amenable to changes that might result in their having suitable owl habitat.

Areas 9, 10, 11, 13, 17, 19, and 20 also have low crude densities, given the potential habitat that might be present. Estimates of low crude densities of owl pairs and individuals in many of these populations may be a result of insufficient survey work.

Conclusions

Diverse in character and geography, habitats of the California spotted owl are managed by several State and Federal agencies and various private landowners, most with different objectives and mandates. The FS has implemented policies to provide for conservation of the California spotted owl, but these policies have been challenged recently as a result of recommendations by the ISC for the northern spotted owl (see Thomas et al. 1990).

The extensive and nearly continuous nature of Federal land ownership in primary habitats of the California spotted owl over the length of the Sierra Nevada makes it feasible to implement a coordinated and effective conservation strategy there. We also believe that lands held by commercial timber companies and other private owners could make a substantive contribution to maintenance of the spotted owl population in the Sierra Nevada. Private timber companies differ in their land-management objectives and policies, however, and it is uncertain the extent to which future management of their lands will maintain suitable spotted owl habitat. The final form of expected new State forestry rules cannot be fully predicted except that, at a minimum, they will change logging practices on some private lands and probably benefit spotted owls as a net effect.

In contrast to the case in the Sierra Nevada, populations of spotted owls in southern California occur in relatively isolated blocks, primarily on mountain tops and in wooded ravines extending down the mountain sides, and most of these populations are small (Chapter 9). This island-like nature of owl distribution in southern California makes it especially challenging to contrive a conservation strategy for the bird, based solely on public lands. For a variety of reasons, southern California is losing spotted owl habitat for breeding, foraging, and dispersal. Among the primary reasons are residential developments in previously remote valleys and mountains, stand-destroying fires, increasing concentration of recreational activities in prime owl habitat, and the "mining" of water from streams within the range of the owl. These impacts will continue, leading to increased insularization of owls in the relatively small mountain ranges where they now occur. These are the primary risks facing continued spotted owl distribution in southern California. It will probably be impossible to maintain a viable population of spotted owls in southern California without stabilizing the amount and distribution of suitable habitat on public lands and without changes in land-use policies on private lands, especially those that adjoin public lands.

Table 3K-*Areas of concern for California spotted owls in southern California.*

Area[1]	General location (major ownership)[2]	Reasons for concern
	Gaps in known owl distribution	
C	East-central Kern County (Pvt., BLM)	A gap of 30 miles in the known owl distribution; believed to contain little or no suitable owl habitat.
D	Tejon Pass (Pvt., FS)	Includes Interstate 5 and has little suitable habitat; most is grasslands and chaparral.
E	Northern Ventura County (FS)	Has little suitable habitat; most is chaparral or pinyon-juniper woodlands.
F	Western Antelope Valley (Pvt.)	High desert with no suitable habitat.
G	Piru Gorge (FS, Pvt.)	Has little suitable habitat and bisected by Interstate 5; most of the area in chaparral.
H	Santa Clara River (FS, Pvt.)	Has little suitable habitat; includes State Highway 14 and associated developed areas; most of the area in chaparral and desert scrub.
I	Cajon Pass (FS, Pvt.)	Consists mainly of chaparral; bisected by Interstate 15.
J	Banning Pass (BLM, FS, Pvt.)	Mostly desert scrub and chaparral at higher elevations; has Interstate 10 and developments.
K	Anza area (BLM, FS, Pvt.)	Mostly chaparral; includes some grasslands, limited riparian woodlands, and semirural housing.
L	Los Angeles Basin (Pvt.)	No owl habitat; fully urban sprawl with some grasslands and residual chaparral areas.
M	Temecula area (BLM, Pvt.)	Mostly chaparral; includes Interstate 5; urbanization is increasing.
N	Cuyama River (FS, Pvt.)	Has little suitable habitat; contains chaparral and some semidesert scrub.
O	Northwestern San Luis Obispo Co. (Pvt.)	May contain some suitable hardwood and riparian habitat, but very poorly surveyed.
P	San Joaquin Valley (Pvt.)	Has little suitable owl habitat; most land in crops, grasslands, or residual desert scrub.
	Population problems	
9	Tehachapi Mountains (Pvt.)	Habitat is fragmented and known owl density is low. This small population is isolated from the population to the south and probably from the population to the west.
10	Tecuya Mountain (FS)	Owl density is low and habitat occurs only in north-slope drainages. This small population is probably isolated from populations to the south and east.
11	Ventura/Santa Barbara (FS)	This is a large area with varying owl densities and distributions of habitat. Except for the San Rafael Wilderness Area, populations are scattered in suitable habitat, mostly in north-slope drainages. The population here is probably isolated from other populations to the northwest, northeast, and east.
12	Liebre/Sawmill (FS)	Area has a limited population in suitable habitat on the north sides of mountains; owls are isolated from the population to the southeast and probably from the ones to the north and west.
13	San Gabriel Mountains (FS)	Large area varying in habitat distribution and owl densities; much habitat is mixed-conifer or bigcone Douglas-fir/oak. This population is isolated from the population to the northwest and probably from the one to the east.
14	San Bernardino Mountains (FS)	Contains the largest population and most extensive owl habitat in southern California; at least partially isolated from the population to the west and maybe totally from the one to the south.
15	Mount San Jacinto (FS)	Most habitat here is bigcone Douglas-fir/oak on south and west sides of the mountain. The limited population is isolated from populations to the north and southwest.
16	Palomar Mountain (FS, IP)	The mountain-top habitat is mixed-conifer and bigcone Douglas-fir/oak. The owl population is isolated from populations to the northwest and northeast but is continuous with the population to the south.
17	Central San Diego County (FS, NATL, Pvt.)	This population is spread sparsely through the canyons at lower elevations south from Palomar almost to the Mexican border. It includes some smaller mountains and links Palomar with Area 18. Habitat is usually oak in canyons. Surveys here have been limited and local.
18	Cuyamaca/LagunaMountains (FS, CA)	Areaconsistsoftwoadjacentmountaintops,bothwithsmall,localpopulations.Habitatismixed-coniferandoak-dominated canyons. This is southern-most population in California and only links to populations further north in San Diego County.
19	Santa Ana Mountains (FS)	This range contains the smallest known population (two sites), both in conifer/oak habitat at heads of canyons on the range's west slope. This population is isolated by the Los Angeles Basin from populations to the southeast and north-northeast.
20	Southern Santa Lucia Mountains (FS, Pvt.)	This limited population exists in canyons dominated mostly by oak habitats. It is probably isolated from populations to the southeast and northwest.
21	Coastal Monterey County (FS, Pvt.)	This is the northern-most population of the California Spotted Owl on the coast. It occurs in a variety of habitats including the southern-most groves of coast redwood. It is isolated from the northern spotted owl by 100 miles of mixed habitat, including the highly developed San Francisco area. It is isolated from California spotted owls in the Sierra Nevada by the San Joaquin Valley.

[1] Location codes correspond to letters (gaps and bottlenecks) and numbers (population areas) on figure 3A.

[2] Ownership codes: FS = USDA Forest Service; BLM = Bureau of Land Management; CA = State of California; NATL = Native American tribal lands; Pvt. = multiple, small, private ownerships.

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Chapter 4

The California Spotted Owl: General Biology and Ecological Relations

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Understanding a species' ecology and life history and its role in ecosystem functions is vital to successful management of that species. The extent to which this understanding is comprehensive and correct is also critical. This chapter emphasizes life history elements and ecological relations of the California spotted owl that bear directly on planning for its management. In that sense, this is not an extensive, detailed treatment of the owl's biology and ecology. Nor does it provide a thorough analysis of some of the primary factors that must be considered, such as habitat relations, home ranges, density, and demography. Instead, because these components are so critical to conservation planning, and each requires extensive analyses, other chapters treat them in considerable detail.

Description and Classification

The spotted owl is generally mottled in appearance, the back is brown with irregular white spots and the underparts distinctly lighter, with white spots and brown barring. The facial disk is pale brown with concentric rings of darker brown and bordered by a ring of dark brown feathers. Pale "eyebrows" and "whiskers" merge into a conspicuous, light-colored "X" between the eyes and above the beak. Unlike most other owl species, which have yellow eyes, the eyes of spotted owls are dark brown. The beak is pale yellowish. Wings and tail are rounded and all flight feathers are dark brown with light-brown crossbars. The legs and toes are fully covered with short, pale-buff feathers, and the claws are dark brown to black. Adult males and females cannot be distinguished by plumage (Forsman 1981), but they are readily identified by voice and size (Forsman et al. 1984, Blakesley et al. 1990). Barrows et al. (1982) indicated that sexes can be distinguished by the number of tail bars, but Blakesley et al. (1990) found this characteristic to be unreliable. Moen et al. (1991) noted that first-year and second-year adults can be distinguished by the shape of the tips of their tail feathers.

Only four of the 19 species of owls occurring in North America are larger than the spotted owl (Johnsgard 1988). Based on live weights from a sample of 46 adult male and 48 adult female California spotted owls captured in the Sierra National Forest (NF) and Sequoia National Park (NP) (Steger pers. comm.), females averaged 22.2 ounces-13.6 percent heavier than the average of males at 19.6 ounces. Weights of individuals captured more than once differed markedly, which is not surprising considering that some common prey items of spotted owls (for example, woodrats) weigh as much as a third of an adult owl's weight. For comparison, live weights of 65 female northern spotted owls captured in northwestern California averaged 23.2 ounces; 68 males averaged 20.3 ounces (Blakesley et al. 1990).

The American Ornithologists' Union (1957) recognized three subspecies of the spotted owl-California spotted owl (*Strix occidentalis occidentalis*) (Xantus 1859), northern spotted owl (*Strix occidentalis caurina*) (Merriam 1898), and Mexican spotted *owl* (*Strix occidentalis lucida*) (Nelson 1903). The Mexican form, found from southern Utah and Colorado southward into Arizona, New Mexico, and Mexico, is geographically isolated from the California and northern subspecies. The California spotted owl is confined to the State of California (figs. 4A, 4B, and 4C), where its distribution in the southern Cascade Mountains adjoins a southeastern extension of the range of the northern spotted owl. This contact zone is along the Pit River, east of Redding.

Barrowclough (pers. comm.) has observed north-south clinal variation (gradual change) in morphology of northern and California spotted owls. Barrowclough and Gutierrez (1990) found no electrophoretic differences between the northern and California subspecies, so their study shed no light on the question of a taxonomic distinction. As in other such studies, however, only a fraction of the total genetic information was compared. The American Ornithologists' Union has consistently recognized two subspecies of spotted owls in California; this position was recently reaffirmed (N. K. Johnson pers. comm.).

Questions about whether the northern and California spotted owls are valid subspecies, however, are essentially irrelevant to concerns about the status of the owls. Spotted owls certainly move back and forth across the Pit River, and interbreeding between northern and California forms undoubtedly occurs in that area. Subspecies, by definition, are not reproductively isolated from each other. The important management questions relate to conditions of populations and habitats in various parts of the spotted owl's overall range, not to details of its subspeciation. The owl may be doing well in some areas but not in others. Where it is not doing well, we need to consider options for improving its status. Generally, this will involve improving habitat conditions and increasing the crude densities of owls to increase the efficiency of dispersal (Chapters 8 and 9). Maintaining the continuity of spotted owl populations from the northern Sierra Nevada into the southern Cascades and northwestern California is an important part of assuring the overall viability of both subspecies (Dawson et al. 1987, Thomas et al. 1990).

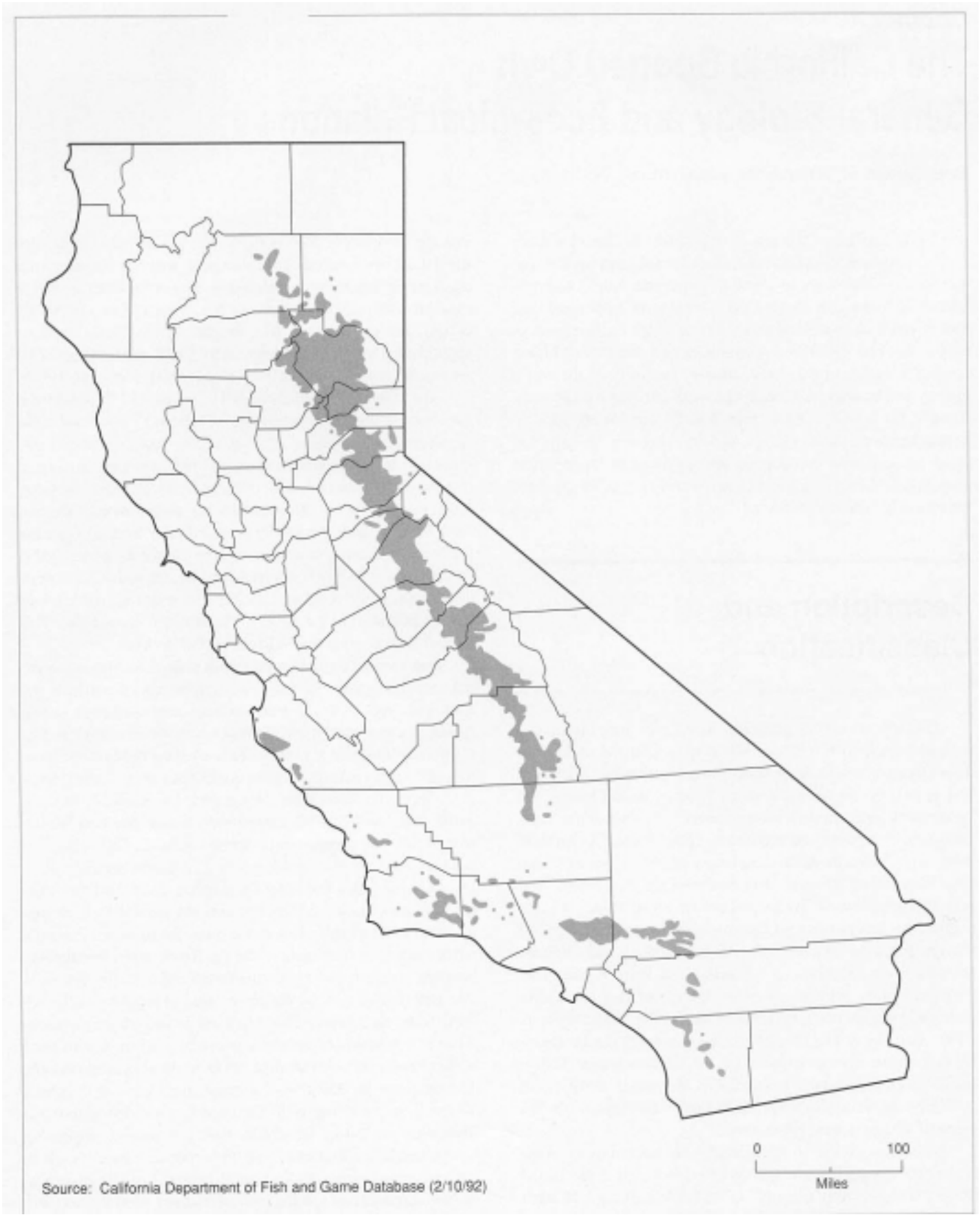

Figure 4A-Distribution of California spotted owls.

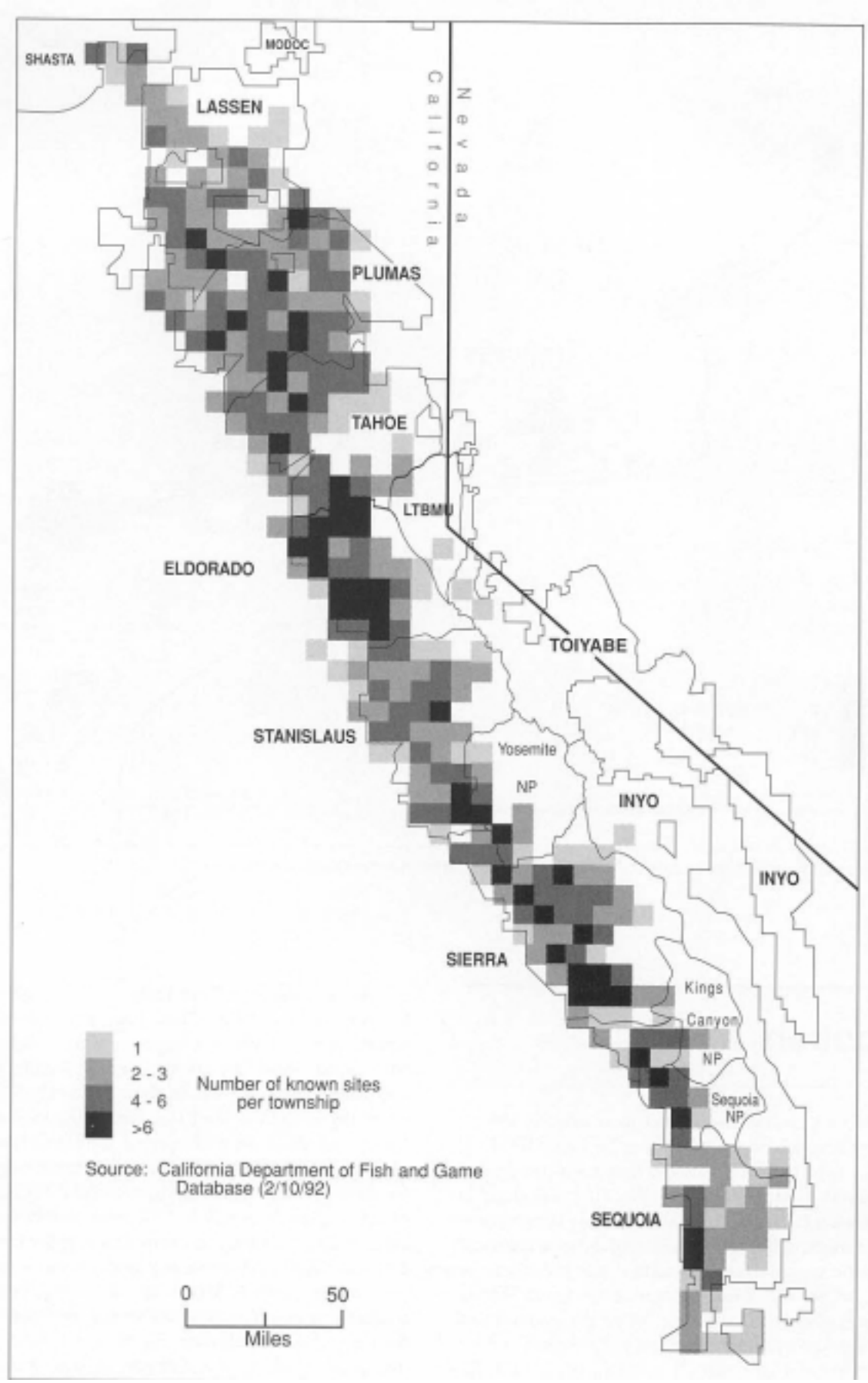

Figure 4B-Detail of the relative abundance of California spotted owls in the Sierra Nevada Province.

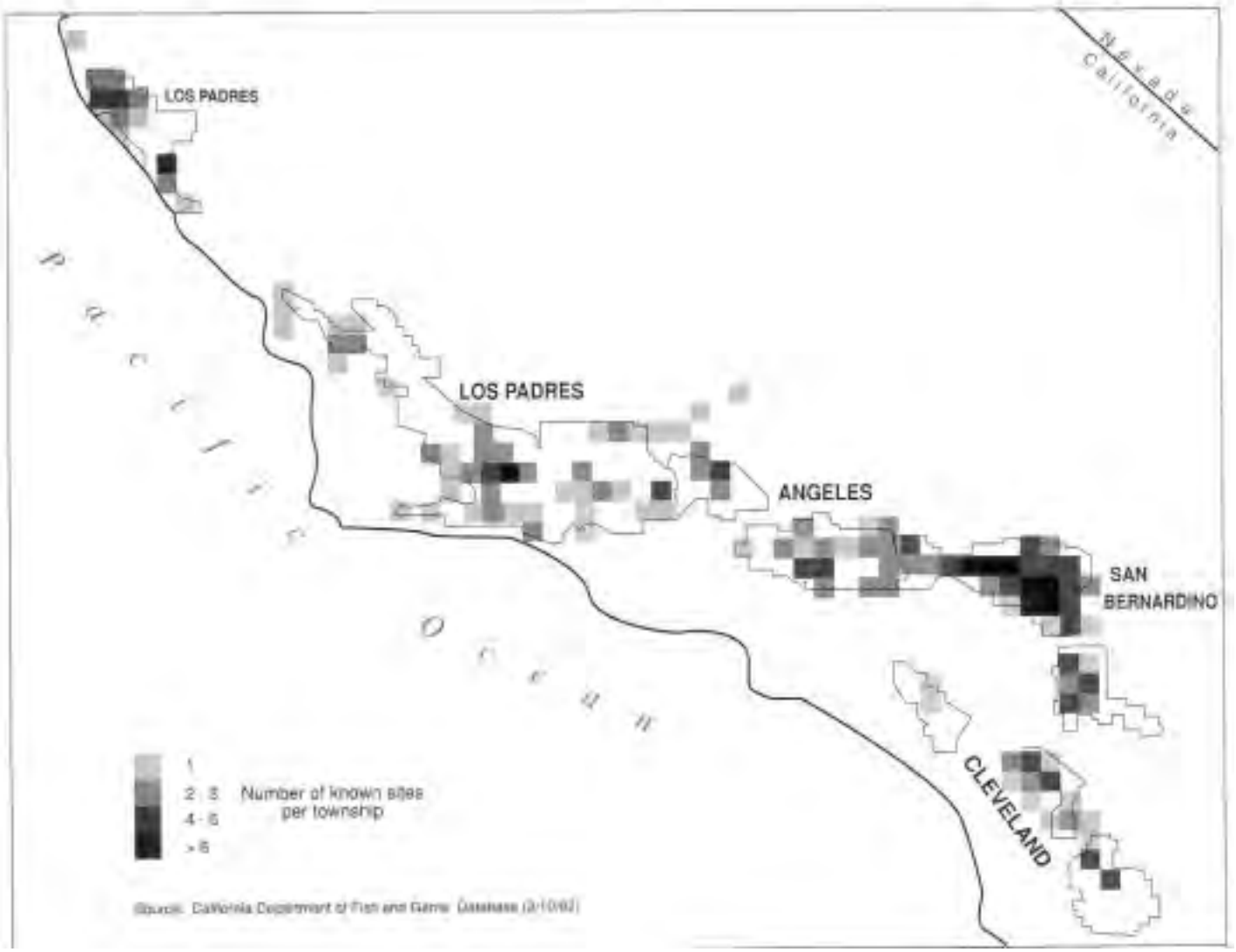

Figure 4C-Detail of the relative abundance of California spotted owls in the Southern California Province.

Distribution

The California spotted owl occurs in coniferous forests, mixtures of conifers and hardwoods, and in hardwood forests in the western Sierra Nevada; few locations have been documented east of the Sierran crest (figs. 4A and 4B). They also occur in conifer, conifer/hardwood, and hardwood stands in mountainous country of southern California, and in coastal mountains and foothills from the Santa Barbara area north at least into Monterey County (figs. 4A and 4C). Most owl pairs in the Sierra Nevada occur in the mixed-conifer forest type, but in the mountains of southern California they are almost equally represented in three major habitat types-mixed-conifer, live oak/bigcone Douglas-fir, and riparian/hardwood (tables 3A and 3I) (habitat types are described in Chapter 1 and Appendix B).

Areas in the coastal mountains north of Santa Cruz appear to have suitable habitats. These have not been inventoried adequately for owls, but they appear similar to others in the State where spotted owls are known to breed. Finally, spotted owls may also occur in denser stands of riparian/hardwood forests, especially in foothills bordering eastern portions of the Central Valley and along the south-central California coast (fig. 4D). The potential spotted owl habitat in lower-elevation hardwood forests depicted in figure 4D includes habitat within the ranges of both the northern and the California spotted owl. It encompasses about 5,000,000 acres, of which about 1,100,000 acres are rated "high" as potential owl habitat (Greenwood and Steger pers. comm.), with 625,000 acres of the high-potential habitat within the range of the California spotted owl. Essentially none of this has yet been surveyed for spotted owls, so we cannot estimate the number of pairs, if any, that may be located there. Obviously surveying these habitats, on a sample basis, is a priority need.

Figure 4D-Statewide distribution of potential California spotted owl habitat in lower-elevation hardwood forests.'

Habitat Associations

Quantitative details about habitat associations of California spotted owls are given in Chapters 5, 6, and 7. Generally, however, the birds occur only in habitats with substantial tree cover and especially with some larger, older trees present (see the set of color photos at the end of Chapter 5).

Nesting Habitat

Habitats used for nesting typically have greater than 70 percent total canopy cover (all canopy above 7 feet), except at very high elevations where canopy cover as low as 30-40 percent may occur (as in some red fir stands of the Sierra Nevada). Nest stands typically exhibit a mixture of tree sizes and usually at least two canopy layers, and some very large, old trees are usually present. Often these have large, natural cavities, broken tops, and/or dwarf mistletoe brooms. Nest stands in conifer forests usually have some large snags and an accumulation of fallen logs and limbs on the ground; downed woody debris is not a major component of nest sites in lower-elevation riparian/ hardwood forests.

Spotted owls do not build their own nests but depend mainly on finding a suitable, naturally occurring site. Nest heights vary regionally-about 38 feet in riparian/hardwood forests at lower elevations; about 65 and 57 feet in conifer forests of the northern and southern Sierra Nevada, respectively; and about 58 feet in conifer forests in the San Bernardino Mountains (table 5K). In Sierran conifer forests, nests are usually in cavities or on broken-topped trees or snags. Less often they are on platforms associated with abandoned raptor nests, squirrel nests, dwarf mistletoe brooms, or debris accumulations in trees (Chapter 5). LaHaye (1988) found an increase from north to south in the proportion of platform nests used by northern spotted owls in a study in northwestern California. Similarly, cavity nests dominate nest types of California spotted owls in the Sierra Nevada, but platform nests predominate in the San Bernardino Mountains (table 5I). These trends probably reflect the distribution of stand ages rather than latitude.

Nest trees (details in Chapter 5) are typically large [mean diameter at breast height (d.b.h.) of about 45 inches for nest trees in Sierran conifer forests and 37 inches in the San Bernardino Mountains] and decadent. Among 124 nests found on NFs in the Sierra Nevada, 34 were in snags and 90 were in live trees. Eighty-two (66.1 percent) were in cavities and 19 (15.3 percent) were on broken tops of living or dead trees, or on dwarf mistletoe brooms. These conditions all tend to develop in older trees. Only 17 (13.7 percent) of the nests were on stick platforms built and used previously by other species (probably including goshawks, sharp-shinned hawks, ravens, and tree squirrels). Some owl pairs use the same nest cavity or platform repeatedly from year to year, some select new sites each year, and yet other alternate nest sites over time (Foreman et al. 1984, p. 31; R. J Gutiérrez pers. observ.; LaHaye pers. comm.).

The species of nest trees used seems to depend on what is available, with 10 species of conifers and 7 species of hardwoods accounting for all nests in our database (table 5J). Locations of nest trees in the Sierran sample ranged in elevation from 1,000 to 7,740 feet, with 86 percent found from 3,000 to 7,000 feet in elevation. The highest elevation of nests increased from the northern to the southern Sierra Nevada (Lassen NF - 6,400, Plumas NF - 6,100, Tahoe NF -7,000, Eldorado NF - 6,340, Stanislaus NF - 7,200, Sierra NF - 7,500, and Sequoia NF - 7,740 feet). The distribution of breeding spotted owls in the Sierra and Sequoia NFs extends down at least to 1,000 feet in elevation (Neal et al. 1989). The lower elevation of the study area with nests at 1,000 feet is bounded by a reservoir, so owls elsewhere may nest at even lower elevations. Few surveys have been done at these lower elevations. In southern California, nests ranged in elevation from 1,000 feet (Los Padres NF) to 8,400 feet (San Bernardino NF). The mean elevation of nest sites in the San Bernardino Mountains was about 6,000 feet.

Roosting Habitat

Stands used for roosting are similar to those used for nesting, with relatively high canopy cover, dominated by older trees with large diameters, and with at least two canopy layers. Studies of roosting northern spotted owls indicate that they respond to variation in temperature and exposure by moving higher or lower within the canopy, or around the roost tree, to access more comfortable microclimates (Barrows and Barrows 1978, Forsman 1980, Barrows 1981, Solis 1983, Forsman et al. 1984). The structure of multistoried stands characteristic of roost sites facilitates this movement. This observed response led Barrows and Barrows (1978) to propose that old-growth forests are necessary for spotted owls to avoid heat stress. Based on the following observations, however, we doubt that avoidance of heat stress is an essential benefit of old-growth forests: (1) California spotted owls are relatively common in riparian/hardwood forests in southern California and the Sierran foothills, where ambient temperatures are high during summer months. (2) A female nested in full sunlight on an abandoned Cooper's hawk nest platform in the Sierran foothills. .While incubating, she was sometimes exposed to ambient temperatures exceeding 100 degrees Fahrenheit, and the developing young experienced like conditions (Steger pers. comm.). (3) Adult California spotted owls often roost in full sunlight or high in the canopy on hot days, which is not typical of northern spotted owls (R. J. Gutiérrez pers. observ.). We agree that the birds probably move about in a forest canopy to find a comfortable microclimate, but they seem to be able to tolerate relatively high ambient temperatures.

Foraging Habitat

Foraging habitats include suitable nesting and roosting sites, as well as more open stands, regularly down to 40-50 percent canopy cover, that are generally similar in structure and composition to nesting and roosting habitat. Typical conditions in conifer forests include:

1. A mixture of tree sizes, usually with some trees exceeding 2 feet in d.b.h., resulting in tree canopies at a wide range of heights in a stand but not necessarily in distinct layers. (Many sites depicted in the color photos at the end of Chapter 5 were taken in areas where spotted owls were known to forage.)
2. Signs, of decadence-snags, overmature trees, downer woody debris (large logs are especially characteristic).
3. The presence of hardwoods probably tends to enhance foraging habitat in conifer forests.
4. Ample open flying space within and beneath the canopy

Conditions in foraging habitat in hardwood stands in southern California, and at lower elevations in the Sierra Nevada, tend to have less downed woody debris than found in conifer forests and stands tend not to be multilayered. Because woodrats dominate the diets of owls in these hardwood habitats, we can infer that they provide good habitat for woodrats as well. Live oaks are common in the canopy and a variety of shrubs provide food (leaves, buds, flowers, and so on) for woodrats (Chapter 10).

Home Range and Territoriality

Spotted owls generally have large home ranges, defined by Thomas et al. (1990, p. 419) as "the area to which the activities of an animal are confined during a defined period of time." By contrast, an animal's "territory" is generally a defended area (Nice 1941) within its home range. Home ranges of radio-tagged, neighboring spotted owls overlap to varying degrees (reviews in Thomas et al. 1990, appendix I; Carey et al. 1992; Chapter 6). Observations by Forsman et al. (1984, p. 52-53) indicate that aggression between neighboring birds is infrequent, apparently confined to interactions between members of the same sex, and generally more pronounced when an intruder is well within the home range of another bird. These observations suggest a form of territoriality in which "...an individual or a pair may be dominant in the core area of its home range but not in the periphery. This tends to produce a regular dispersion by effectively excluding other individuals from breeding in the core without necessarily excluding their presence there as subordinates engaged in other activities" (Brown and Orians 1970, p. 244).

Median, combined home ranges of members of pairs of northern spotted owls, estimated from radio-tagged birds and using minimum convex polygons as the estimator, ranged from 1,411 acres in the South Umpqua River Valley in the Klamath Mountains of southwestern Oregon to 9,930 acres on the Olympic Peninsula in northwestern Washington (Thomas et al. 1990, p. 194). Home ranges were generally larger in Washington than in areas to the south. In Oregon, areas where median pair home ranges exceeded 5,000 acres were usually in heavily logged sites with a low percentage of the landscape covered by older forests (Forsman et al. 1984, Carey 1985, Thrailkill and Meslow 1990). Home ranges of the California spotted owl exhibit similar variation in size, being measured in thousands of acres in higher-elevation conifer forests but only in hundreds of acres in foothill woodlands of the Sierra Nevada (Chapter 6). We strongly suspect that prey availability accounts for a major part of the variation in home-range size of the spotted owl (see discussion below in section entitled "Why Differences in Home-Range Size?").

As in other bird species, some spotted owls do not exhibit fidelity to an area, their movements indicating instead that they do not occupy a specific home range (Chapter 6). Juveniles often wander widely in search of a vacant home range, and similar behavior may occur among adults displaced for some reason from their former home range. They may move within or among the home ranges of other birds, where they await opportunities to join the breeding population when a territorial owl dies or deserts its territory. These birds are referred to as "floaters" by ornithologists (Smith 1978, 1984). Their role in avian population dynamics is believed to be critical (review in Thomas et al. 1990, p. 295; Franklin 1992), but less is known about them than any other subset of bird populations. This is true because floaters are typically quiet and secretive, avoiding contact with territorial birds and being less susceptible to detection by researchers. For these reasons, we have no quantitative information on the ratio of floaters to territorial birds in any population of spotted owls.

Vocalizations

Spotted owls communicate with a variety of hoots, "barks," and whistles (Forsman 1976, Forsman et al. 1984). The context of some of these calls is unknown, but researchers generally agree on the function of some of the more common calls. For example, the most common call is the four-note hoot, phonetically described as "hooo---hoo-hoo---hooooo." It advertizes the fact that an owl is on its territory and probably functions both to repel intruders and to attract potential mates. Given at a lower pitch and intensity, this same call is also used by the male to announce prey delivery to his mate, and in other sexual interactions. Owl biologists most often imitate this call when attempting to locate or attract spotted owls in the field.

Another common call is the multiple-note "series," which is a highly variable rendition of the basic four-note hoot (Fitton 1991). It is used by birds in an excited state. Spotted owls also produce whistles that usually serve to maintain contact between members of a pair (Forsman et al. 1984). The calls of females are higher-pitched than those of males, facilitating identification of sexes in the field. Calls of spotted owls also vary spatially and temporally (Ganey 1990, Fitton 1991).

Pair Bond

All available evidence indicates that spotted owls are monogamous. Forsman et al. (1984, p. 53) concluded that pair bonds are usually maintained from year to year primarily because (1) individuals of both sexes tend to remain within their home ranges, and (2) they tend to exclude other individuals of the same sex from their home ranges. Owls that remain throughout the year in the same home range generally maintain a solitary existence during the nonbreeding period, seldom even roosting near their mates. Mate constancy, therefore, may be "more a function of the attachment to a traditional home range than attachment to a particular mate." Observations of migrant spotted owls support this conclusion. Mates do not migrate or spend the winter months together. Survivors return to their former summer home ranges, where former pair bonds are renewed if both members of the pair survive (Verner et al. 1991).

Not all pair bonds last for as long as both members of the pair survive, however. "Divorces" have been observed in several demographic studies of spotted owls, but they are rare and reasons for them are unknown (R. J. Gutiérrez pers. observ., LaHaye pers. comm., Steger pers. comm.). When an owl of either sex loses its mate, it may desert its old home range and orm a new pair bond elsewhere; it may remain on the old home range and acquire a new mate there; it may remain unmated for an extended period of time; or it may become a floater. Too few instances have been observed to identify a pattern, although LaHaye suspects that females that lost mates left their old home range more often than was the case for males in his study in the San Bernardino Mountains.

The Annual Cycle

Knowledge of the owl's annual cycle is essential for delineating any restrictions on projects and activities that might be planned within owl territories. The following account of the spotted owl's breeding chronology is drawn mainly from Forsman et al. (1984), who have provided the best quantitative information. Although it is based primarily on observations of pairs, nests, and broods of the northern subspecies in Oregon, we believe it is the same or similar for the California spotted owl. Estimated periods for the different stages of the cycle were based on unpublished information and summaries provided by National Forest biologists; by Blakesley (pers. comm.) and Steger (pers. comm.) for the Sierra Nevada; by LaHaye (pers. comm.) for the San Bernardino Mountains; and by Stephenson (pers. comm.) for owls at lower elevations in southern California.

The Breeding Cycle

Available evidence indicates that spotted owls are physiologically capable of first breeding at the age of 2 years (Barrows 1985, Miller et al. 1985), although rare cases of nesting by yearlings are known (LaHaye pers. comm., Steger pers. comm.). Determining the "usual" age at first breeding is complicated by the fact that nesting by the owls does not occur annually, even among older birds. As a result, a bird that has attained reproductive maturity may not nest for one or more years beyond that age, probably for ecological reasons.

Here and elsewhere in this assessment we recognize five stages of the breeding cycle-prelaying, laying, incubation, nestling, and fledgling. The timing of these stages (fig. 4E) is especially important information for management purposes. Because not all birds begin nesting at the same time, the duration of each stage for all owls in a region, such as the conifer forests of the Sierra Nevada, is considerably longer than it is for a single pair.

The breeding cycle of California spotted owls extends from about mid-February to mid- or late September or early October, when young are no longer cared for regularly by their parents (fig. 4E). The cycle apparently begins earlier in some places than in others in a given year. For example, Steger (pers. comm.) believes that spotted owls in the foothills of the Sierra Nevada initiate breeding about 2 weeks earlier than birds in the higher conifer forests at the same latitude. The various stages tend to begin about 4 days earlier in the San Bernardino Mountains than in the conifer zone of the Sierra Nevada (fig. 4E). As in the Sierra Nevada, timing at lower elevations in southern California apparently precedes that in the San Bernardino Mountains by about 2 weeks (Stephenson pers. comm.). Reasons for these differences may be related to local differences in peak periods of prey abundance for the owls. Before this can be determined, however, much more information is needed to refine details of the owl's breeding cyles and periods of prey abundance in all localities.

Prelaying Stage (duration variable) (see Forsman et al. 1984, p. 34)

Members of nonmigrating pairs generally do not roost together during the winter. By late winter, however, they increasingly roost together, engage in mutual preening, and occasionally copulate in the evening. For 2 weeks or so before the date of first laying, paired birds typically roost together every night and copulate once or twice each evening. Beginning about a week before laying, the female spends most of her time near the nest, receiving an increasing share of her food from the male. These activities probably do not last as long for birds that migrate, because members of migrant pairs spend the winter in different locations and do not return to their breeding territories until shortly before laying begins. Because the prelaying stage has no clearly definable beginning, we have arbitrarily designated the 3 weeks prior to laying of the first egg as the prelaying stage.

Laying Stage (1-6 days)

Data suggest that the peak laying period probably occurs from about 7 to 21 April in the San Bernardino Mountains and from about 11 to 25 April in conifer forests of the Sierra Nevada. When egg laying begins, a female spotted owl spends almost all

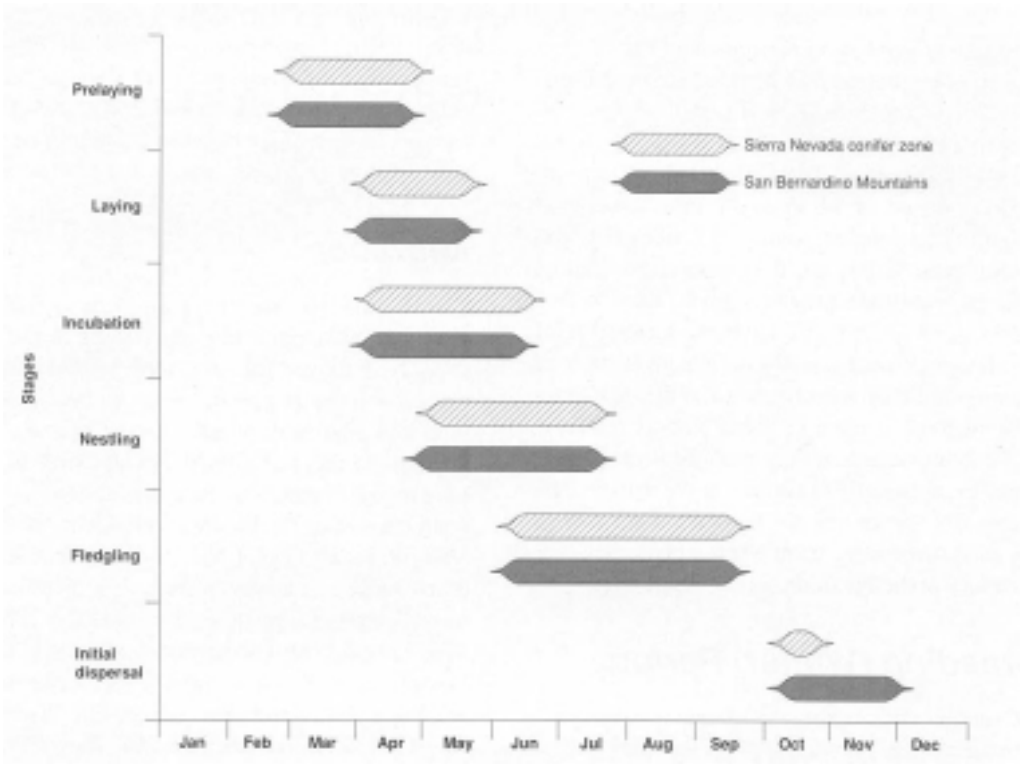

Figure 4E-Chronology of the breeding seasons of California spotted owls in conifer forests of the Sierra Nevada and the San Bernardino Mountains.

of her time in the nest, and her mate provides nearly all of her food. Copulation continues on a daily basis throughout the egg-laying stage and for up to about 4 days after incubation begins.

The clutch size of the spotted owl is one of the smallest among North American owls (Johnsgard 1988). Most clutches contain two eggs; three-egg clutches are infrequent and four-egg clutches are rare (only two records-Bendire 1892, Dunn 1901). The interval between laying of successive eggs is 72 ± 6 hours (Forsman et al. 1984, p. 33), so the laying period would be 1 day for a clutch of one egg, 3 days for a clutch of two, and 6 days for a clutch of three. (A rare clutch of four eggs would presumably stretch the laying period to 9 days.)

Incubation Stage (30 ± 2 days) (Forsman et al. 1984, p. 33)

Incubation begins shortly after laying of the first egg and is done solely by the female, who may leave the nest at night for periods up to 2 hours during the first 2 days of incubation. Thereafter, she only occasionally leaves the nest for periods of 10 to 20 minutes at night to regurgitate pellets, defecate, preen, or accept food from her mate. The female does not forage during the incubation period, receiving all her food from her mate. The male typically roosts within 650 feet of the nest during the daytime and begins to forage shortly after sunset (Forsman et al. 1984, p. 35).

Coincident with the laying of eggs, the female develops a brood patch-"a feather-free area with thickened skin and a rich supply of blood vessels to facilitate the transfer of heat from the body of the incubating bird to the eggs" (Pettingill 1970, p. 355). The presence of a well-developed brood patch is clear evidence that a female has been incubating,

Nestling Stage (normally 34-36 days) (Forsman et al. 1984, p. 37)

The peak hatching period probably occurs from about 3 to 17 May in the San Bernardino Mountains and from about 7 to 21 May in the conifer zone of the Sierra Nevada. The female broods the new hatchlings almost continuously for 8-10 days, still depending on her mate to provide food for herself, and now for the young. By the time her young are 2-3 weeks old, the female begins to forage for increasingly longer periods at night-typically 1-4 hours. The male continues to bring food to the nest, but the female then passes the food to the young. Apparently the male seldom, if ever, passes food directly to nestlings. Forsman et al. (1984, p. 35) reported that they never observed males feeding nestlings. If the male brings food to the nest while the female is away, he simply leaves it in the nest. The female continues to roost in the nest until 3-6 days before the young leave it.

Most young observed by Forsman et al. (1984) fledged (left the nest) when 34-36 days old, occasionally moving off the nest to perch on nearby limbs for a few days before leaving the nest permanently. Occasionally young leave their nest earlier than normal. Because such young are less developed physically, they may spend more time on the ground than young that remain in the nest for the full nestling period. This may increase their mortality rate compared to that of later-fledging young (Forsman et al. 1984, p. 36).

Fledgling Stage (80-120 days) (Forsman pers. comm.)

The fledgling stage covers the period after the young leave the nest until they become independent of their parents. The

peak period of fledging probably occurs from about 8 to 22 June in the San Bernardino Mountains and from about 12 to 26 June in conifer forests of the Sierra Nevada. New fledglings are weak fliers, often falling to the ground, where they may spend several hours to several days. Within about 3 days after fledging (assuming a normal nestling period of 34-36 days), most young can flutter or climb to elevated perches; usually in a week they can fly clumsily between trees. Within about 3 weeks after fledging, they can hold and tear meat from prey brought by their parents (Forsman et al. 1984, p. 37). Although adult males bring food for the fledglings at all ages, they generally do not give the food directly to the young until they have been out of the nest for at least 2 weeks (Forsman pers. comm.). Both parents regularly bring food to the fledglings and generally continue to do so until mid- to late September, apparently regardless of the age or capabilities of the young. Because of this, the fledgling stage may be relatively long or short, depending upon when a given nest was begun and on variations in the age of the young at fledging.

The Nonbreeding (Winter) Period

Activities of spotted owls during this period are primarily related to basic maintenance-capturing prey, securing protection from the elements, avoiding predators, preening; and so on.

The beginning of the nonbreeding period is technically the date when adults quit feeding their young, although this may not be well-defined because feeding may continue sporadically even well after the young can capture and kill prey for themselves. Three changes in owl status indicate that 1 October is a reasonable beginning of the nonbreeding period in the Sierra Nevada, at least for most birds: Young are generally independent of their parents by late September; juveniles begin dispersal as early as 1 October (Laymon 1988); and some adults begin fall migration early in October (Laymon 1988, Neal et al. 1989). The end of the winter period coincides with the beginning of activities characteristic of the prelaying stage. This is also a poorly defined date, partly because the initiation of prelaying behavior is not abrupt and partly because timing differs among pairs. Many pairs, however, have initiated prelaying activities at least by the end of February, and egg laying and incubation begin at some nests by the end of March. For planning purposes, therefore, we can reasonably set the end of the winter period at the end of February, at least for most birds.

Movements

Regular, long-distance movements of birds beyond home-range boundaries are of two types-migration and dispersal. Migration is an annual movement between breeding and nonbreeding home ranges. Natal dispersal is the movement of young birds from their natal territory to a site where they breed or at least establish a territory where breeding could occur (Greenwood 1980). Sometimes adult birds are displaced from established territories by loss of habitat through fire, logging, or other major disturbances. Adults displaced by loss of habitat, or separating from a mate, may begin searching for new territories. Their movement to a new territory is referred to as breeding dispersal.

Migration

Migration is rare among northern spotted owls (Forsman et al. 1984), although a few individuals in the Washington Cascades have moved back and forth several miles between breeding and nonbreeding home ranges without an appreciable change in altitude, latitude, or habitat type (Brewer and Allen 1985). Some radio-tagged California spotted owls in the Sierra Nevada have migrated altitudinally, however, moving downslope for the winter period on the Eldorado NF (Laymon 1988) and the Sierra NF (Neal et al. 1988, 1989, 1990; Verner et al. 1991). At least 8 of 10 birds in Laymon's study left breeding home ranges in mixed-conifer forests (elevations 4,000-5,200 feet) to spend the winter in oak/pine woodlands (elevations 1,000-3,500 feet). The mean elevational displacement between breeding and nonbreeding areas was 2,450 feet; the straight-line distance between areas was 10 to 36 miles (mean = 20). The earliest migrant left its summer home range on 18 October, the latest on 18 November. Dates of return to breeding areas were not determined, because batteries in the radio transmitters failed during the winter. The owls were, however, back in their breeding territories by mid-April.

Six of 18 radio-tagged owls on the Sierra NF migrated from summer home ranges in mixed-conifer forest at 5,700-6,700 feet in elevation to winter home ranges in oak/pine woodlands at 1,100-2,050 feet in elevation. Departure dates ranged from 8 October to 17 December; one female departed her summer home range on 8 October 1987, 8 November 1988, and 20 November 1989. Vertical displacement ranged from 3,680 to 5,541 feet (mean = 4,628) and straight-line distances between areas were 9.6 to 15.3 miles (mean 12.3). Spring return dates ranged from 27 February to 28 March.

None of four owls radio-tagged by Call (1990) migrated during his study on the Tahoe NF (elevations from 2,200 to 5,200 feet), where he tracked from summer through early December in both 1986 and 1987. Call's tracking period in both years lasted well beyond the fall migration dates observed by Laymon, and >2 feet of snow had accumulated in his study area by December of 1986.

No members of any pair in either the Eldorado NF or the Sierra NF study migrated together or established winter home ranges in the same area. In both studies, at least one migrant moved back and forth between winter and summer home ranges once or twice during the winter. Six of the 18 owls in the Sierra NF study whose movements were well-documented were year-round residents, remaining within essentially the same home-range boundaries during summer and winter periods. Two simply enlarged their summer home ranges for the winter period, and five shifted their home range for the winter period but their summer and winter home ranges overlapped. Nine of the 18 were tracked through at least two annual cycles; none of these birds changed behavioral patterns from one year to the next (that

is, once a migrant always a migrant, and so on). The Sierra NF study included another 11 owls that remained as permanent residents in foothill riparian/hardwood forests, at elevations ranging from 1,000 to 4,000 feet. Home ranges of these birds were often shared in winter with migrants from higher elevations.

Data available from these studies thus show individual variation in migratory behavior of the California spotted owl. Collectively, the three studies tracked 32 birds with summer home ranges in the higher-elevation conifer forests long enough to determine whether they did or did not migrate; at least 14 (44 percent) were altitudinal migrants. Because the sample is small, however, we cannot sort out the reasons why some individuals migrated and others did not. Nor can we determine why all 10 owls in the Eldorado NF study migrated, none of the four in the Tahoe NF study migrated, and only about a fourth of the 18 birds in the Sierra NF study migrated. It does not appear to be the case that habitat quality was best in the Tahoe and poorest in the Eldorado study area. Only 35 percent of the Tahoe study area was in stands of large sawtimber (≥21 inches in d.b.h.). Because Call (1990) did not report the proportion of the large sawtimber that also had ≥40 percent total canopy cover, we assume that something less than 35 percent had both large sawtimber and suitable canopy cover. The Sierra study area was only about 14 percent large sawtimber (table 6C). On the other hand, the Eldorado study area, with the highest proportion of migrants, was 39 percent in large sawtimber that also had ≥40 percent canopy cover (Bias 1989). Finally, in the Sierra study area, some owls left areas for the winter that were subsequently used during the winter by other owls (Steger pers. comm.), suggesting that the birds that left them did so for reasons other than food shortage.

Altitudinal migration may expose owls to added sources of mortality, some related to various human activities. They may cross roadways and be hit by a vehicle. In many lower sites, in foothills of the western Sierra Nevada, traditional wintering areas for the owls are being developed for home sites, even communities. And the development of residential properties, with resulting homes, lawns, driveways, and so on, will eliminate otherwise suitable habitat for woodrats-the staple winter diet of spotted owls in these oak/pine woodlands (table 4A). Finally, foothill woodlands are used extensively to graze cattle and to harvest firewood from oaks. Both of these activities can have negative impacts on woodrat populations and on the cover value of the habitat for owls.

Table 4A -*A summary of California spotted owl diets, expressed as estimated percent biomass from different studies.*

	Sierra Nevada								Southern California	
	Sierran mixed-conifer forest						Riparian/hardwood woodland		Mixed-evergreen forest	Riparian/mixed hardwood
	Lassen National Forest	Eldorado National Forest		Sequoia/Kings Cyn. Nat. Prk.	Sierra National Forest				Riverside, San Diego, Orange cos.	Los Padres National Forest
Diet	Spring/summer	Summer	Summer	Spring/summer	Spring/summer	Fall/winter	Spring/summer	Fall/winter	All seasons	Spring/summer
Woodrats[1]	10.1	35.0	37.5	4.0	8.3	0	73.8	88.0	79.3	93.9
Northern flying squirrel	61.1	24.5	31.3	60.0	50.1	76.6	9.6	0	0	0
Mice[2]	1.1	3.0	1.2	1.8	1.5	1.5	1.4	2.6	6.0	1.2
Pocket gophers[3]	6.2	1.3	8.1	26.9	20.4	14.7	11.6	5.6	6.0	2.5
Moles[4]	1.6	4.2	2.0	3.4	3.0	2.1	0.6	0.2	0.2	0
Diurnal squirrels[5]	4.4	16.5	6.8	4.0	1.9	0	0	0	0.2	0
Lagomorphs[6]	6.1	0	0	0	0.8	0	0	0	1.0	0
Shrews and voles	2.1	2.4	0.7	0.2	1.2	0.5	1.1	0.6	0.2	0
Bats	<0.1	0.3	0	0.1	0.1	0	Trace	0	0	0.5
Birds	6.7	12.7	12.4	2.7	12.3	4.3	1.9	3.0	7.1	1.5
Insects	0.6	0.1	0.3	0.3	0.5	0.3	0.1	0.1	0.3	0.3
Number of prey items	1,008	1,232	139	162	531	71	234	556	296	30
Elevation (feet)	4,700-6,800	3,500-5,000	3,000-5,500	5,300-6,900	4,500-7,000	4,500-7,000	1,000-4,500	1,000-4,500	3,000-5,500	1,000 3,600
Source	Blakesley (pers. comm.)	Thrailkill Laymon (1988)	Roberts and Bias (1989)	(pers. comm.)	Steger and Eberlein (pers. comm.)				Barrows (1980)	Smith (pers. comm.)

[1] The Lassen sample included both bushy-tailed and dusky-footed woodrats; only dusky-footed woodrats occurred elsewhere.
[2] Most were white-footed mice (*Peromyscus* spp.), but some samples included minor percentage of pocket mice, jumping mice, or house mice.
[3] As many as three species in some samples.
[4] As many as two species in some samples.
[5] Included ground squirrels, tree squirrels, and chipmunks.
[6] The Lassen sample included one pika; all other lagomorphs identified at all sites were rabbits (*Sylvilagus* spp.)

Dispersal

Successful dispersal is essential for population viability. Without it, a population will slowly decline to extinction, because deceased individuals in the breeding population will not be replaced by recruits from dispersing juveniles or adults that have been displaced or have not yet secured a territory. As Miller (1989, p. 1-2) stated, "The distance between adjacent pairs or groups of breeding owls should be such that dispersal of juveniles can replace losses (deaths or emigrations) among existing pairs and provide for colonization of suitable, unoccupied habitats. An understanding of dispersal in juvenile spotted owls is thus basic to formulation of criteria for appropriate spacing of habitat to accommodate pairs of owls." We especially need data on the variability of dispersal distances, dispersal directions, and habitats used by dispersing birds. We also need quantitative information on the extent to which fragmentation of forest habitats impedes successful dispersal (Chapter 9).

Dispersal Among California Spotted Owls

Unfortunately, information on dispersing California spotted owls is nearly nonexistent. Four radio-tagged juveniles on the Eldorado NF (Laymon 1988) initiated dispersal from 1 to 24 October. One was never relocated, another moved 1 mile before it was found dead on 1 December; the others moved straight-line distances of 8.8 and 11.5 miles from their natal sites. This last bird crossed two major rivers and a major highway before settling in oak/pine woodlands near the town of Columbia, at an elevation of 1,300 feet. Two radio-tagged juveniles on the Sierra NF (Steger and Eberlein pers. comm.) moved straight-line distances of 6.1 miles (radio signal lost) and 12.7 miles from their natal areas. The latter bird moved from mixed-conifer forest into oak/pine woodlands. Three color-banded juveniles in the Sierra study dispersed 3.4, 3.5, and 4.1 miles from natal areas to their first territories; four adults banded as members of pairs later shifted territories, moving 2.1, 2.2, 2.4, and 4.4 miles. All of these banded birds were relocated because they stayed within the Sierra NF demographic study area (Steger and Eberlein pers. comm.).

A male color-banded as a fledgling, probably on the Eldorado NF, was found on the Stanislaus NF on 5 September 1990. It was paired and had raised at least one young. This bird was reared in mixed-conifer forest and later paired with a bird in the same forest type. The straight-line distance from its natal home range to its breeding territory was at least 68 miles.

Observations of Dispersing Juvenile Northern Spotted Owls

Because information on dispersal of California spotted owls is so meager, we rely here on studies of dispersal by northern spotted owls to establish quantitative information needed for this assessment. We believe this is a reasonable course of action, because the two subspecies are so closely related that we have no reason to expect dispersal behavior or capability to differ markedly between them.

Over a 4-year period in western Oregon, Miller (1989) fitted 48 juveniles with radio transmitters and monitored their movements regularly. Thirty-two survived to disperse from natal areas (mean = 104 days after fledging). Twenty-seven (84 percent) initiated dispersal between mid-September and mid-October. Their initial movement was usually rapid, and "...most juveniles settled into well-defined areas for their first winter after the initial dispersal movements. Those...surviving their first winter often began moving again in late winter or early spring." From a subset of birds positively identified to sex, males dispersed an average of 16.2 miles (SD = 14.6; n = 7) and females an average of 20.4 miles (not significantly different--SD = 6.6; n = 6). Initial directions taken by dispersing juveniles did not differ from a random distribution, although six of nine juveniles in 1983 dispersed down the McKenzie River drainage from the H. J. Andrews Experimental Forest. Miller found no significant relation between forest fragmentation and either the final distance moved or the number of days survived by birds in his study. Dispersing juveniles used a wide variety of habitats, but 12 of 18 birds exhibited significant selection for old-growth and mature forests.

In a study of 23 dispersing juveniles in northwestern California (11 in 1983 and 12 in 1984), the birds departed from their natal areas from 22 September to 5 October (Gutiérrez et al. 1985). Dispersing juveniles in 1983 moved a mean of 5 miles per day (range 1 to 11), compared to 1.3 miles per day in 1984 (range 0.8 to 6.4). The difference was statistically significant. Directions taken by dispersing birds varied. They left their natal areas in random directions, with no relation between dispersal direction and the geographic orientation of drainages or ridges. During the first 80 days of dispersal, individuals moved total distances of 15.3 to 92.9 miles (n = 11) in 1983 and 0.7 to 62.8 miles (n = 7) in 1984. Total distance was the sum of all segments between successive locations as birds were followed during dispersal. Total distance is greater than the straight-line distance between beginning and ending points.

In addition to these more extensive radio-tracking studies of dispersing juveniles, we compiled results from all sources to estimate dispersal distances of radio-tagged juveniles after they left their natal areas (fig. 4F). Only one of the 54 juveniles whose dispersal distances are known was later found as a member of a mated pair, but apparently it never nested (R. J. Gutiérrez pers. observ.). All other birds either died (68 percent), their transmitters failed (27 percent), or they disappeared (5 percent). This raises a question about whether estimates of dispersal distance from radio-tagged birds were biased because the birds were wearing radios. Although radios may have affected their survivorship or their ability to form a pair bond, we found no evidence that distances moved by radio-tagged juveniles were affected by radio transmitters.

If juvenile spotted owls carrying transmitters tended to die sooner than normal, that is, before they dispersed as far as they would without a radio, their dispersal distances might be underestimated. Miller (1989) observed that dispersing juvenile northern spotted owls tended to move quickly from their natal area to a point where they settled for their first winter. Our data set on 54 dispersing juveniles includes a subset of 31 with data on the number of days they dispersed and the number of days they survived thereafter. The dispersal period was highly variable ($\bar{x}$ = 128.3 days; SD = 168.5; range = 0-657 days; n = 31). The

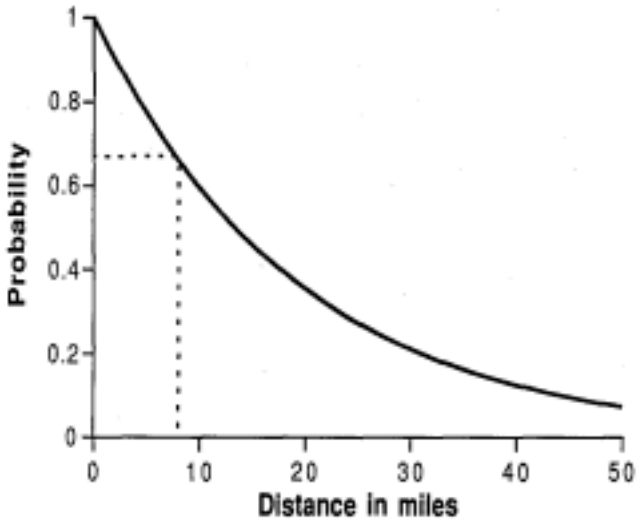

Figure 4F-Probability of dispersing juvenile spotted owls traveling various distances, based on observed dispersal distances of 56 radio-tagged northern spotted owls (Thomas et al. 1990, appendix P). For example, two-thirds of the juveniles would be expected to disperse at least 8 miles (Murphy and Noon 1992).

survival period following dispersal, however, was more consistent ($\bar{x}$ = 119.2 days; SD = 37.4; range = 88-156 days, with one outlier each at 45 days and 284 days). In this subset of 31 dispersers, 13 quit dispersing within 46 days after leaving their natal territory and 11 quit dispersing after at least 83 days (maximum of 657 days). The mean dispersal distances of these two groups were 22.4 miles (SD = 15.7) and 22.0 miles (SD = 8.1), respectively. The correlation coefficient (rho) between maximum dispersal distance and the number of days dispersed was not significant (r = -0.03; P = 0.88; 95 percent confidence intervals were -0.38 and +0.33; n = 31). The power of the test was 0.37 for rho = 0.30, 0.61 for rho = 0.40, and 0.83 for rho = 0.50. The power for any value of rho $\geq$0.70 was 1.0. Consequently, the likelihood of failing to detect a statistically significant correlation that might have had biological significance was slight, and the likelihood of failing to detect a significant rho of at least 0.70, if one truly existed, was essentially nil.

These results suggest that dispersing juveniles quickly attained their maximum dispersal distance from their natal territory. If they continued to disperse thereafter, their movements tended to keep them within that earlier-attained, maximum dispersal distance.

We also computed the correlation coefficient between maximum dispersal distance and the number of days that juveniles carried radio tags (r = 0.02; 95 percent confidence intervals for the true correlation coefficient were -0.25 and +0.30). Rho was not statistically significant (P = 0.87). The power of the test was 0.60 for rho = 0.30, 0.86 for rho = 0.40, and 0.98 for rho = 0.50. The power for any value of rho $\geq$0.60 was 1.0. Examination of scatterplots suggested no patterns that might be missed by just using a correlation coefficient. Additional analyses reported in Thomas et al. (1990, p. 306) corroborate the conclusion from the above results that radio transmitters did not bias estimates of dispersal distance. Lacking critical data from dispersing juvenile California spotted owls, we have therefore used the full data set on northern spotted owls to estimate dispersal distances of radio-tagged, juvenile spotted owls. The function derived from these data (fig. 4F) was used to parameterize one model for assessing the sensitivity of the southern California metapopulation of spotted owls to various changes in its numbers and distribution (Chapter 9).

Mortality

Birds of most species die of undetermined causes, because they simply are not found in the inconspicuous places where they die. In addition, their bodies are often quickly consumed by other animals in the environment. Spotted owls are no exception. We have little information on their sources of mortality, certainly not enough to establish proportions or even to rank the causes of death. Many dead spotted owls have been examined carefully by veterinarians in an effort to determine the cause of death, but even those examinations are generally unable to pinpoint the exact cause. Instead, a variety of contributing factors is typically suggested. We do know, however, that spotted owls die from the usual variety of causes that befall most wild birds (D. H. Johnson pers. comm.).

Predation

Although spotted owls appear to have few predators, we know that great horned owls and goshawks occasionally capture and eat them: Forsman et al. (1984, p. 38) reported seeing a Cooper's hawk attempt to capture a recently fledged owlet and Forsman and Meslow (pers. comm.) reported one incident of predation by a red-tailed hawk. The great horned owl and the goshawk are both larger than the spotted owl, and all three species often occupy the same forested areas. Great horned owls tend to be more common in areas with lower tree densities than is the case for spotted owls, and the smaller size of spotted owls probably enables them to outmaneuver great horned owls in dense forest. Forsman (pers. comm.) suspects that great horned owls only opportunistically prey on spotted owls.

Goshawks kill both adult and juvenile owls (Gutiérrez et al. 1985, Miller 1989, D. H. Johnson pers. comm.), but spotted owls sometimes nest within goshawk territories and defend their young against attacks by goshawks (R. J. Gutiérrez, pers. observ.). We agree with Forsman et al. (1984, p. 38) that goshawks probably are not serious threats to spotted owls.

Accidents and Starvation

A few deaths from accidents (flying into obstacles, automobiles, and drowning) and starvation have been recorded among spotted owls (for example, Gutiérrez et al. 1985, Laymon 1988, Neal et al. 1988, 1989; R. J. Gutiérrez pers. obser., Forsman and

Meslow pers. comm.). Starvation may result from low abundance or availability of prey, or from lack of hunting experience. Death by starvation is more common among juveniles than adults (Gutiérrez et al. 1985, Miller 1989, Sisco 1990, D. H. Johnson pers. comm.).

Shooting

Shooting deaths have also been documented for spotted owls. For example, both members of a pair of birds that occupied riparian/hardwood habitat in the Switzer Picnic Area in the Angeles NF were shot and killed with "BB" guns by two young boys (Stephenson pers. comm.). This was apparently just a thoughtless act, not a malicious effort to destroy spotted owls, but it does raise a question about the safety of owls in heavily used recreation areas.

Diseases and Parasites

Little is known about diseases and parasites of spotted owls, and nothing is known about the extent to which they contribute to mortality, although Forsman and Meslow (pers. comm.) observed several instances of mortality that they attributed to diseases or parasites. Gutiérrez (1989) surveyed blood parasites in all three subspecies, finding an infection rate of 100 percent, exceeding that recorded in nearly all other bird species (Greiner et al. 1975). Spotted owls must be adapted to these high parasite loads, however, because their survival rates are high even where infection rates are high (Franklin et al. 1990). Hoberg et al. (1989) examined 20 northern spotted owls for helminth parasites and found eight species, representing round worms, flat worms, and spiny-headed worms. More than 80 percent of the birds were infected with at least one species, and multiple infections were common.

Young et al. (1992) reported two species of hippoboscid flies from northern spotted owls in northwestern California. One species was found only once among the 382 owls examined, but about 17 percent of the owls they examined had hippoboscid infestations of the other species. Fly densities on owls were higher in years with higher summer and fall temperatures and lower winter precipitation. Young et al. (1992) speculated that low temperatures may have depressed survival of fly pupae. In demographic studies in the Sierra NF and Sequoia/Kings Canyon NPs, hippobiscid flies were detected on 15 of 45 birds (33 percent), but searching for the flies was not an objective of field crews, and limited evidence indicated that the flies were more likely to crawl to the outer surface of an owl when it was handled longer (Steger pers. comm.).

Competition

The barred owl, probably the closest relative of the spotted owl, was historically restricted to eastern North America. Gradually it has extended its range westward through Canada, and finally southward from British Columbia into Washington, Oregon, and more recently into northern California, as far south as the Tahoe NF in the Sierra Nevada (G. 1. Gould, Jr., pers. observ.; R. J. Gutiérrez pers. observ.). Barred owls are larger and more aggressive than spotted owls in interspecific territorial interactions, and they are more generalized in their selection of prey, the habitat types they use, and their nest site requirements (Hamer et al. 1989). Their recent invasion into the range of the spotted owl (Taylor and Forsman 1976) is a possible source of competition between these closely related species. Evidence available already indicates that barred owls have displaced spotted owls from some sites in Washington (Hamer et al. 1989). Because barred owls have now been reported from about 27 different sites in California, interactions between these species will bear further study. A few hybrids between spotted and barred owls have been observed recently. Such hybridization is not uncommon between closely related species of wild birds. The extent of hybridization between these two owl species is still very limited, however, and the eventual outcome of this hybridization will take many decades or even centuries to resolve.

Diets

Spotted owls are "perch and pounce" predators (Forsman 1976), selecting an elevated perch from which they locate potential prey, either by sight or sound. When an owl detects a prey, it drops from its perch and attempts to capture the prey in its talons (the "pounce"). Spotted owls are agile, capturing prey in shrubs, trees, and on the ground. If a potential prey is in an inaccessible location or at some distance from the owl's perch, the owl may move closer before initiating its pounce. Its silent flight allows it to approach prey without being detected. In addition, spotted owls are adept at "hawking" behavior-capturing flying prey, primarily birds and insects.

Spotted owls forage primarily at night. Forsman et al. (1984) rarely observed daytime foraging by northern spotted owls, concluding that it occurred only opportunistically. On the other hand, Laymon (1991) concluded that California spotted owls in his study on the Eldorado NF, in the western Sierra Nevada, foraged regularly during the daytime when they were raising young, but not otherwise. Neal et al. (1989) reported that they often observed spotted owls-even nonbreeders-foraging for insects in the Sierra NF, taking them from bark surfaces, from

the ground, and even catching them in the air. These observations were usually in the late afternoon or early evening (Steger pers. comm.).

Marshall (1942) was the first to report on diets of the California spotted owl, based on stomach contents of two specimens and 23 regurgitated pellets gathered beneath roost trees at Whitaker Forest, Tulare County, in Sierran mixed-conifer forest with giant sequoias, at an elevation of about 5,500 feet in the western Sierra Nevada. The stomachs contained limb bones of frogs or toads, four bats (genus *Myotis*), one deer mouse, and four crickets ("probably *Gryllus*"). The pellets contained remains of 11 flying squirrels, two deer mice, and single individuals of four other mammal species, six bird species, and one June beetle. The relatively high proportions of flying squirrels and birds in this small sample are in line with several recent, more extensive studies of spotted owl diets in conifer forests of the Sierra Nevada (table 4A).

California spotted owls eat a variety of prey. For example, three samples from Sierran mixed-conifer forests produced a combined list of at least 78 different species-at least 1 amphibian, 1 lizard, 24 birds, at least 34 mammals, and at least 18 insects from a combined total of 2,716 prey items (Marshall 1942--63 prey items; Laymon 1988-1,275 prey items; Steger and Eberlein pers. comm.-1,405 prey items). In spite of this diversity, only one to five species or species-groups comprised at least 5 percent, by weight, of the owls' diets in the eight samples shown in table 4A, and at least 85 percent of the total biomass in each sample consisted of only one to four species or species-groups. Either northern flying squirrels or dusky-footed woodrats, or both, dominated prey biomass in all samples. Preliminary results from an analysis of the spotted owl's diet in the San Bernardino Mountains agree-about 80 percent of the biomass was dusky-footed woodrats, and about 10 percent consisted of medium-sized mammals like northern flying squirrels and gophers (Smith pers. comm.). The general pattern suggests a prey specialist with a search emphasis on just a few species, but which will capture and eat a wide variety of species and sizes of prey as they are encountered.

Four patterns in the results of these studies may be important: (1) Spotted owls in conifer forests of the Sierra Nevada, particularly above mid-elevation mixed-conifer forests (about 4,000-5,000 feet, depending on latitude), prey mainly on flying squirrels. (2) Owls in the mid- to lower elevations of the mixed-conifer zone and the upper part of the ponderosa pine/hardwood belt prey heavily on both flying squirrels and woodrats. (3) Both of these sets of owls consume a relatively high proportion of diurnal squirrels and/or birds, suggesting more daylight foraging than is the case for spotted owls elsewhere. And (4) spotted owls in the Sierran foothills and throughout southern California, even at high elevations, obtain 79 to 97 percent of their energy needs from woodrats. A dichotomy between flying squirrel and woodrat dominance of the diet is known for the northern spotted owl as well (review in Thomas et al. 1990, p. appendix J; Carey et al. 1992). Given the California spotted owl's diet, therefore, we need to consider ways to manage for habitats that will maintain thriving populations of flying squirrels in Sierran conifer forests and woodrats everywhere else. Although woodrats dominate owl diets in Sierran foothill riparian/hardwoods and throughout the owl's range in southern California, only about 25 percent of all California spotted owl sites are in habitats where woodrats are abundant (table 1B). The remaining 75 percent occur in Sierran conifer forests where flying squirrels are the primary prey species.

Ecological Relations

Owls and Their Prey

Common sense tells us that no animal species can survive or reproduce in areas without sufficient food, but documenting these relations by direct field studies is usually very expensive and time-consuming. For owls in general, the time needed for such studies is typically several years, or even decades, depending on the life span of the owl species studied and the kinds of prey they eat. For example, owls with diets consisting mainly of small mammals whose populations exhibit regular, cyclic "booms" and "busts" in numbers, will require longer studies to cover at least two cycles of the prey. In spite of the high demands on time and resources to complete such studies, many have been reported in the literature on owls of the world. They portray a general picture of a marked dependency of owls on the availability of their key prey species-a fact widely recognized among raptor biologists in general and owl specialists in particular.

Relations between owls and prey are manifested in a variety of ways; some species of owls are affected in several ways. A moderately extensive (but not exhaustive) search of the world's literature on owls revealed at least five common, major effects of prey availability on owl biology (table 4B): Owl reproductive rates are often positively related to prey availability. Some species of owls nest earlier when and where prey are more abundant and available. Some owl pairs do not even attempt to nest when prey are scarce. The density of breeding owls is commonly higher when and where prey species are more abundant and available. And some species of owls exhibit major movements (whole populations may shift) when prey become scarce in the area occupied.

Several studies linking prey and spotted owls have been undertaken (Thomas et al. 1990), but little evidence has been found of relations between prey abundance and the biology of spotted owls. In a study in northwestern California, Ward (1990) found that prey abundance (mainly woodrats) was low and that it varied over the landscape. The owls did not necessarily forage in stands where woodrats were most abundant, but they hunted instead in areas where the availability of prey was more predictable. The strategy suggests one of optimizing search effort. Only the study of northern spotted owls in Washington and Oregon by Carey et al. (1992) has been intensive and extensive enough to suggest relations between the owls and their prey. Owls in

Table 4B—*Review of ecological relations between owls and the relative availability of their prey. Researchers report a variety of relations, grouped here into five categories, from owl species in North America, Europe, and northern Asia.*

Species	Observed ecological relations				
	Reproductive rate positively related to prey abundance	Earlier nesting when prey are abundant	Some pairs do not nest when prey are scarce	Breeding density higher when prey are abundant	Exhibit major movements when prey are scarce
Common barn-owl	Otenni et al. 1972 Baudvin 1975, 1976 Kaus 1977 Bunn et al. 1982 Colvin & Hegdal 1985				Bunn et al. 1982
Eagle owl			Olsson 1979		
Great horned owl	Houston 1971, 1975 Adamcik et al. 1978 Rusch et al. 1972	Adamcik et al. 1978	Houston 1971, 1975 Rusch et al. 1972	Rusch et al. 1972	
Snowy owl	Portenko 1972 Bunn et al. 1982 Mikkola 1983		Bunn et al. 1982	Bent 1938 Pitelka et al. 1955 Watson 1957 Parker 1974 Wiklund & Stigh 1986	Gross 1947 Mikkola 1983
Northern hawk owl	Mikkola 1983			Mikkola 1983 Cramp 1985	Mikkola 1983 Cramp 1985
Eurasian pygmy-owl	Sonerud et al. 1972 Jussila & Mikkola 1973 Kellomäki 1977 Solheim 1984				Mikkola 1983 Cramp 1985
Great gray owl	Mikkola 1983		Mikkola 1981, 1983		Green 1969 Nero 1980 Mikkola 1983
Tawny owl	Linkola & Myllymäki 1969 Southern 1970 Petty 1987		Southern 1970 Petty 1987	Mikkola 1983 Hirons 1985	
Ural owl	Lundberg 1976, 1981 Lundberg & Westman 1984 Pietiäinen et al. 1986 Pietiäinen 1988, 1989	Linkola & Myllymäki 1969 Lundberg 1981 Lundberg & Westman 1984 Pietiäinen et al. 1986 Pietiäinen 1988, 1989	Lundberg 1981 Lundberg & Westman 1984 Pietiäinen 1988, 1989		
Long-eared owl	Hagen 1965 Linkola & Myllymäki 1969 Ziesemer 1973 Nord 1978 Mikkola 1983 Village 1985	Village 1985	Mikkola 1983 Cramp 1985	Mikkola 1983 Cramp 1985 Village 1985	Mikkola 1983
Short-eared owl	Rendall 1925 Mikkola 1983 Cramp 1985 Lockie 1955			Lockie 1955 Pitelka et al. 1955 Holzinger et al. 1973 Clark 1975 Mikkola 1983	
Boreal owl (Tengmalm's)	Linkola & Myllymäki 1969 Mikkola 1983	Mikkola 1983 Korpimäki 1987		Mikkola 1983	Mysterud 1970 Mikkola 1983 Korpimäki 1986

western hemlock forests on the Olympic Peninsula of Washington used about 4,200 acres of old forest annually; those in Douglas-fir forests in southwestern Oregon used about 2,000 acres of old forest annually; and owls in mixed-conifer forests in southwestern Oregon used about 1,120 acres of old forest annually. Estimates of the combined biomass of primary prey species taken by the owls were 5.3, 21.3, and 29.4 ounces/acre in the three forest types, respectively. Carey et al. (1992, p. 241) concluded that "Geographic variation in the areas traversed and amounts of old forest used by spotted owls reflected similar variation in the abundance and diversity of the medium-sized mammals that are the preferred prey of the owl."

Understanding Spotted Owl Habitats Through Ecological Linkages

A full understanding of why California spotted owls occur where they do, and why they do or do not reproduce well enough to maintain their populations, depends ultimately on comprehending haw various components and functions within forest and woodland ecosystems relate to the owl's ecology. Here we have attempted to interpret some of those relations in terms of the owl's key prey species, typical nest sites, and the general dynamics of forest and woodland ecosystems where California owls are known to occur and reproduce. A general graphic representation of these relations helps to envision how all the pieces fit together (fig. 4G). Assuming that presence and nesting by California spotted owls depends on the availability of a sufficient prey source, we believe that much of what is known about the owl's habitat associations can be better understood in relation to the ecology of its primary prey, especially northern flying squirrels and dusky-footed woodrats. Other key linkages relate to assuring an abundance of suitable nest sites. How does all of this relate to what we judge to be important attributes of suitable owl habitat?

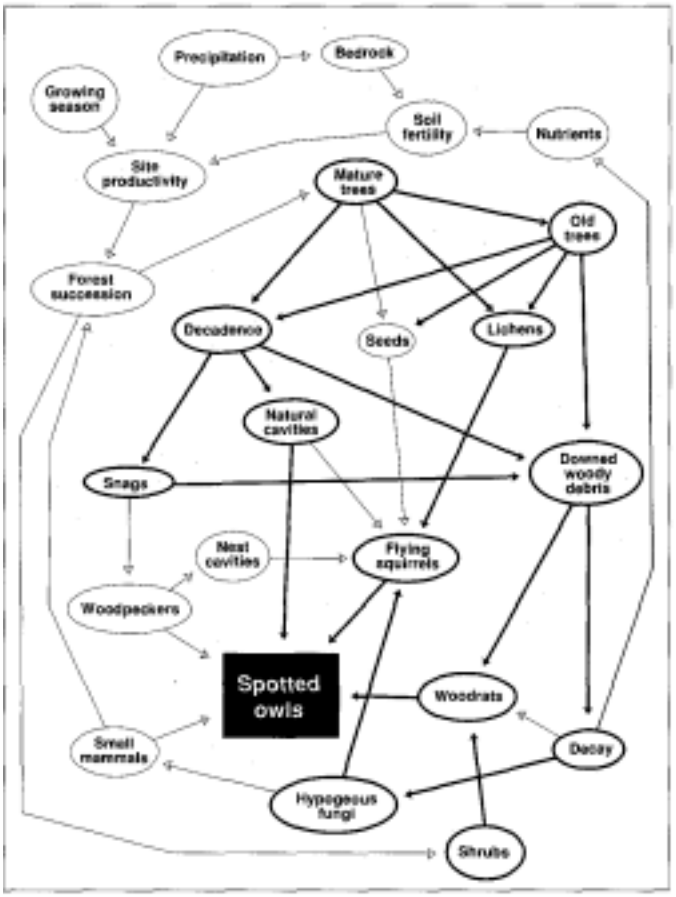

Figure 4G-Simplified, schematic representation of some important ecological linkages associated with California spotted owls.

Why Big, Old Trees?

Large, old trees are preferentially selected for nest sites by spotted owls (Chapter 5). For example, nest trees averaged larger than 40 inches in d.b.h.-much larger than the mean diameter of trees generally available. About one fifth of all nests found were in snags (dead trees) and about four fifths were in live trees. Two thirds of the nests were in large, natural cavities formed by decay at sites where branches broke off or tore out of the trunk of the tree, and another 20 percent were on broken tops of living or dead trees, or on dwarf mistletoe brooms. These conditions typically develop only after a tree is relatively old. In addition, larger trees are needed to provide large snags and longer-lasting components of dead, decaying wood on the ground, especially in the form of large logs but also in fallen limbs of various sizes.

Why Downed Woody Debris?

Functional linkages among spotted owls, their major prey species, the prey's food, and the general forest or woodland/shrub community where these linkages occur can be traced in figure 4G. Some major linkages are highlighted by broader arrows. For example, northern flying squirrels feed extensively on hypogeous (underground) fungi, especially during periods when the ground is not covered by snow. They may even cache some of these fungi to be eaten after snowfall. At least two California studies (McKeever 1960, Hall 1991) and one Oregon study (Maser et al. 1985) found that flying squirrels eat primarily fungi and lichens. Hypogeous fungi comprised the bulk of the summer diet, and the winter diet was largely arboreal lichens. The density of flying squirrels in red fir/white fir stands in the Lassen NF was strongly associated with the abundance of truffles (fruiting bodies of hypogeous fungi), and truffle abundance was strongly associated with the presence of a well-developed soil organic layer and a large volume of decaying logs (Waters and Zabel 1992). These data suggest that management practices that decrease the soil organic layer and the number of large, decaying logs will reduce the capability of a habitat to support flying squirrels, and possibly spotted owls as well.

Hypogeous fungi probably also comprise a major food source for white-footed mice (Maser et al. 1978a), an important prey species of the California spotted owl. Spores of the fungi pass unharmed through the digestive tract of these and other small mammals that consume them and are thus spread in fecal pellets over the forest floor. All hypogeous fungi are also mycorrhizal: "Mycorrhiza literally means `fungus-root' and denotes a symbiotic relationship between certain fungi and plant roots" (Maser et al. 1978b, p. 79). Trees depend on mycorrhizae for an

adequate uptake of various nutrients, and the fungi benefit by obtaining carbohydrates produced by the trees. Interestingly, the spores of hypogeous fungi are spread by the small mammals that eat them, thus completing a loop of interdependencies in forest ecosystems (fig. 4G).

As important as large, decaying logs are to functional ecosystems where spotted owls seem to thrive, logs that are positioned perpendicular to the slope of the land are most valuable. This is because they are best situated to intercept soil and water moving downslope and, as a result, to become a substantial water reservoir as they reach an advanced state of decay. Even more important is the fact that very large logs can make a vital contribution to the forest ecosystem for a longer period than they did as standing, live trees (Maser 1989). These log reservoirs provide refuges for many animal species during hot, dry parts of the year, just as they provide water to trees whose roots, aided by the symbiotic fungal mycorrhizae, have penetrated them. To ignore the role of logs in our forest ecosystems may be to lose those ecosystems in the long run.

Why Snags?

Spotted owls occasionally select snags for nest sites, either on their broken top or in natural cavites in the snags, cavities that either carried over from the live tree or were created by decay after the tree died. Among the 263 nests reported in our sample from conifer forests (table 5I), 17 percent were in snags. Snags provide the primary nesting substrate for many other cavity-nesting birds as well. Woodpeckers, which are occasionally captured and eaten by spotted owls (table 4A), excavate nesting and roosting cavities, and a variety of nonexcavating species later use the same cavities for nests or roosts. Of particular significance in the ecology of spotted owls, flying squirrels often use old woodpecker cavities for den sites. Finally, snags eventually fall and contribute to the accumulation of decaying wood on the ground. Therefore, the snag component benefits the owls both directly and indirectly in a variety of ways (trace arrows in fig. 4G).

Why Multiple Canopy Layers?

A possible ecological explanation for the prevalence of multi-layered canopies in habitats frequented by spotted owls is not clear. The structural diversity associated with these "layers" may contribute to a greater diversity of prey species. Perhaps, as Barrows and Barrows (1978) have hypothesized, the different layers provide opportunities for the owls to move up and down within the overall canopy to find the most comfortable microclimate for roosting. Or they may be important in allowing foraging owls to use perches at a variety of heights as they search for prey. On the other hand, multiple layers may be simply a covariate of some other component of the owl's habitat that is vital, such as the owl's prey.

Why Dense Canopies?

Among the most consistent habitat relations found for spotted owls is their greater use than expected of stands having 40 percent or greater (foraging) and 70 percent or greater (nesting and roosting) total canopy cover (Chapters 5 and 6). Like the owl's association with multiple canopy layers, however, possible reasons for this are not readily apparent. It may relate to one or more of the following: (1) Denser stands tend to be cooler and, as proposed by Barrows (1981), they would allow the owls a wider range of choices for locating thermally comfortable roosts. (2) Denser stands provide more concealing cover, where the owls may be able to nest and roost with less chance of discovery by potential predators. It may be no coincidence that their plumage is speckled, as this pattern would tend to camouflage them during the daytime in a forest full of sunflecks. (3) In conifer forests, where flying squirrels dominate the owls' diet, prey may be more abundant and available in denser forest stands (see Chapter 10). This would not necessarily account for the same observed relation between canopy cover and owl habitat use in areas where woodrats dominate the diet, however, because woodrats tend to be most abundant in relatively dense stands of shrubs. To benefit owls, these must be intermingled with, or adjacent to, the hardwood stands where the owls roost and nest.

Why Differences in Home-Range Size?

In general, the largest home ranges of California spotted owls occur where flying squirrels comprise the majority of the owl's diet and the smallest home ranges occur where woodrats dominate. Home ranges of spotted owls in conifer forests of the Sierra NF are several times larger than home ranges <10 airline miles away, in foothill riparian/hardwood forests (Neat et al. 1990). Owls in the conifer forest prey mainly on flying squirrels, but those in the low-elevation hardwood stands prey almost exclusively on woodrats (table 4A).

The importance of these prey to the ecology of spotted owls has been emphasized by the bolder connecting links in figure 4G. Although only one study of spotted owls has shown a clear connection between prey abundance and areas used by the owls (Carey et al. 1992), we strongly suspect that the approximately 10-fold difference in observed home-range sizes of California spotted owls results primarily from regional differences in diet. Apart from common sense and the study by Carey et al., our strongest scientific support for this contention is the degree to which densities and reproductive activities of owl species throughout the world-at least those that have been studied well enough to establish the relations-are influenced by the availability of their prey (table 4B). Not only are woodrat populations denser than flying squirrel populations, often by at least 10-fold (Chapter 10), but also woodrats weigh nearly twice as much as flying squirrels.

Why Do Most Pairs of Owls Not Nest Every Year?

Spotted owls exhibit marked yearly variation in the proportion of pairs that nest. This has ranged from essentially no pairs to nearly all pairs nesting. For example, from as low as 11 percent to as high as 70 percent of owl pairs in the Eldorado demographic study have nested in different years (R. J. Gutiérrez, pers. observ.). On the other hand, Franklin et al. (1990) reported little variation in the proportions of pairs nesting during a 6-year study in northwestern California. Much annual variation has also been observed in nesting success (proportion of pairs nesting that also fledge young) from year to year and from region to region, ranging from as low as 0 to as high as 100 percent (Forsman et al. 1984, Gutiérrez et al. 1984, Thomas et al. 1990, Lutz 1992, LaHaye et al. 1992).

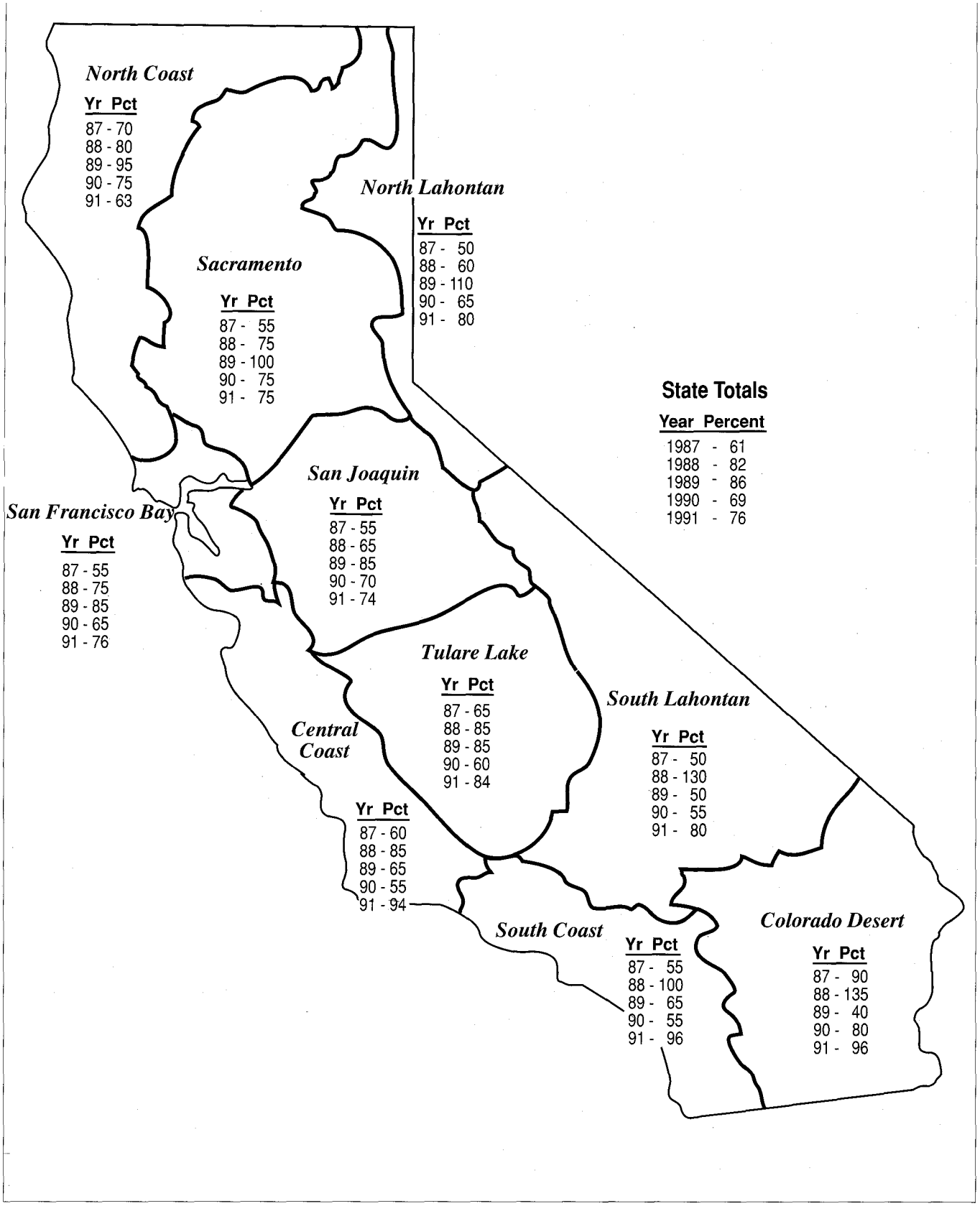

Figure 4H-Percentages of mean annual precipitation in California from 1987 through 1991, by water year (1 October through 30 September) and hydrologic region (California Department of Water Resources 1991).

Surveys of California spotted owls have been used to determine distribution, density, and other measures of "status" (see tables 3A, 3B, 3F, and 3H-J). These counts overestimate the functional owl population, however, because pairs do not occupy all sites in all years, occupied sites do not always support pairs, and each pair does not breed every year. A compilation of results from sites occupied for 4 consecutive years, adjusted to represent 50 known sites where owls defended a territory in any one of the 4 years (G. I. Gould, Jr., pers. observ.), suggests that only about 41 sites would be occupied in a given year, 34 would be occupied by pairs, and only 11 of those would produce young. Over the 4-year period, owls at 20 sites, usually the most consistently occupied, would produce 90 percent of the young.

For many owl species, failure to breed in some years has been shown to result from low prey availability (table 4B). As for home-range size, even lacking definitive studies of spotted owls, we strongly suspect that the local prey base largely determines whether a given pair of owls attempts to nest in a given year, and whether it succeeds if it does make an attempt. Drought may be a corollary here. Nearly all of the detailed studies of the California spotted owl, upon which this report is based, have been done during an ongoing drought that began in 1987 (fig. 4H). A variety of scenarios might occur. For example, drought has been observed to depress woodrat populations or not to affect them (Chapter 10), so the drought may or may not have lowered reproduction among the owls. Mild winters accompanying the drought may have increased the survival rates of the owls or the flying squirrels, or both. We cannot reach conclusions about these or other options. All we can do is acknowledge the attendant uncertainty.

Conclusions

California spotted owls share many attributes of their natural history with the northern spotted owl. Yet our knowledge of the California spotted owl's biology is meager relative to its more famous northern relative. For example, we are not yet able to set clear bounds on the range of habitats that are capabable of supporting self-sustaining populations of the California subspecies (Chapter 8). And we are not likely to be able to do this until the owls have been studied thoroughly during both wet and dry climatic cycles. Our only good estimate of juvenile survival rate for the subspecies is based on the population in the San Bernardino Mountains (Chapter 8), although we estimate that about 75 percent of all California spotted owl pairs occur in the Sierra Nevada, where habitat change (by logging) is of greatest concern. Similarly, with the exception of the San Bernardino Mountain study, estimates of age-class survival and fecundity schedules are lacking or are imprecise. No studies are available that relate California spotted owl populations to populations of their prey species. Finally, we know little about the factors important in the biology of the owl's primary prey species. The work of Waters and Zabel (1992) on flying squirrels in the Lassen NF is exemplary in that regard. Their work needs to be replicated elsewhere, and equally comprehensive studies of woodrat ecology need to be undertaken.

The general lack of information about nearly all phases of the California spotted owl's biology and ecological relations leads to high uncertainty about its present status. Because of this uncertainty, we recommend continuation of basic ecological studies and prudent forest management-following practices that will maintain future options.

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Chapter 5

Habitat Relations of the California Spotted Owl

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The California spotted owl's distribution spans a latitudinal range similar in extent to that of the northern spotted owl (Johnsgard 1988). It occurs at higher elevations than the northern subspecies, however, and portions of the overall population exist in "island" subpopulations on isolated mountain ranges in southern California (Gutiérrez and Pritchard 1990). It also occurs within sight of the Los Angeles Basin, with one of the largest human populations in North America. Grinnell and Miller (1944) first recognized that California spotted owls occupy a variety of forest types. The extent of this variety has been documented by Laymon (1988), Bias (1989), Neal et al. (1989), Call (1990), Call et al. (1991), LaHaye et al. (1992a), and Bias and Gutiérrez (1992). In this chapter we summarize the patterns of habitat variation and habitat use across most of the range of the California spotted owl.

Study Areas and Methods

Sierra Nevada

Six major studies have described habitat relations of California spotted owls in four general areas spanning the length of the Sierra Nevada (fig. 5A). From north to south, these four study areas were: (1) The Lassen Study Area (Zabel pers. comm.), which included primarily high-elevation (5,500-7,200 feet) forests of red fir and white fir (Rundel et al. 1977) and secondarily some lower-elevation habitats dominated by pines and Sierran mixed-conifer forests (see color photos 5-1 and 5-4 at the end of this chapter). The area was a mosaic of selectively logged, clearcut, and uncut stands (old-growth). (2) The Tahoe Study Area (Call 1990) was primarily in mid-elevation mixed-conifer forest (Rundel et al. 1977) at 2,200-5,200 feet. The past history of logging there resulted in a diverse patchwork of different stand ages, types, and densities. (3) The Eldorado Study Area (Laymon 1988, Bias 1989, Lutz 1992) extended from low- and mid-elevation mixed-conifer forest to higher-elevation fir forest (1;000-7,400 feet) (color photos 5-11, 5-12, and 5-18). Logging history has varied there because of the pattern of land ownership-about 40 percent of the land was in private industrial forests that occupied alternate sections in a "checkerboard" pattern with federal lands (Bias and Gutiérrez 1992). Laymon's study included winter observations of migrant owls that moved from their higher-elevation nesting habitats to foothill riparian/hardwood forests as low as 1,100 feet. These latter sites should not be construed as representative of owl sites in the Sierran conifer zone. (4) The Sierra Study Area, in the Sierra National Forest (NF) (Verner et al. 1991), included two distinct habitat types-one dominated by mixed-conifer forest at elevations ranging from about 4,500 to 7,500 feet, the other dominated by hardwoods in oak-pine woodlands and relatively dense riparian/hardwood forests at elevations from about 1,000 to 3,500 feet. Only this study area included breeding populations both in high-elevation conifer forests and riparian/hardwood forests at low elevations (color photos 5-21 and 5-22).

Southern California

Several habitat studies have been done on isolated mountain ranges in southern California (fig. 5A). Here we discuss only one major study area-the San Bernardino, which encompassed almost the entire owl population in the San Bernardino Mountains (LaHaye et al. 1992b). It was the largest of the isolated "island" populations of spotted owls in California. The San Bernardino Study Area included numerous habitat types (see Thorne 1977) because it ranged in elevation from 2,500 to about 9,000 feet (color photos 5-34 to 5-37).

The habitat of two isolated populations studied by Gutiérrez and Pritchard (1990), on-Mount San Jacinto and Palomar Mountain (fig. 5A) (color photos 5-39 to 5-42, and 5-44), had lower diversity than the San Bernardino Study Area and involved much smaller owl populations. Barrows (1980) reported observations at five roost sites of pairs or individuals on four mountains in southern California. In addition to these investigations, qualitative assessments of habitat have been made by U.S. Department of Agriculture, Forest Service (FS) biologists from the various NFs in southern California, but especially from the Los Padres NF (Sandburg and Winter 1989) (color photos 5-29 to 5-32, and 5-38). Observations of owls by forest biologists were part of their normal duties, and did not include designation of specific study area boundaries.

Photo Series

A set of color photographs of California spotted owl habitat from throughout the subspecies' range augments our text descriptions of habitats. These photographs, presented as a set at the end of this chapter, were taken from June to September 1991 during field trips by the Technical Assessment Team. The purpose of the trips was to become directly familiar with the full range of variation in the habitat occupied by this owl.

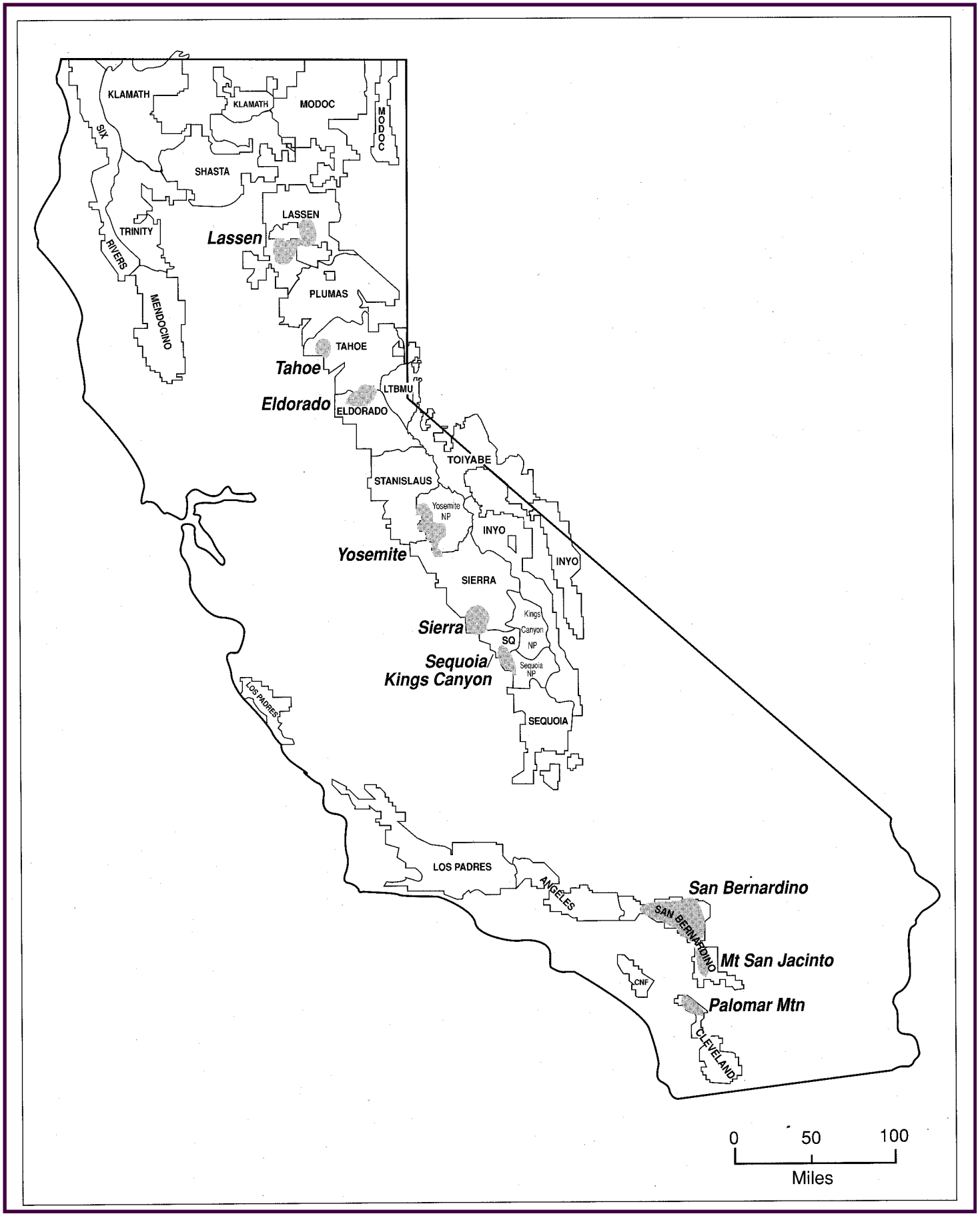

Figure 5A-Locations of radio-tracking and demographic study areas for California spotted owls.

Conifer Forests of the Sierra Nevada and Southern California

Patterns of Habitat Use at a Landscape Scale

California spotted owls use forested habitats almost exclusively (color photos 5-1 to 5-48). Only one record is available of a pair nesting in a tree not closely surrounded by a stand of other trees. That pair nested in a residual snag in a clearcut on the Sierra NF, although relatively dense stands of oaks were within 160 feet of the nest and the young moved there shortly after they left the nest (Yamanaka pers. comm.). Spotted owls have occasionally foraged in relatively open areas, such as shrubfields, meadows, or plantations, but this is exceptional. Call (1990), for example, found such habitats to be used significantly less than expected, based on availability in the Tahoe Study Area. We included these observations only to illustrate that California spotted owls occasionally occur in habitats that do not meet all their life history requirements (that is, they are unsuitable). It is important to note that one cannot infer suitability from the occasional presence of owls in a habitat.

Data at a Landscape Scale

Each of the seven Sierra Nevada NFs provided the following information on detected owl nests (n = 148): (1) timber type and size of the stand in which the nest was located, based on verified database mapping in their Land Management Plans (LMPs); (2) the same information as in (1) for each stand polygon that bordered the nest stand and was in a timber type used for foraging, roosting, or nesting; and (3) a map of the nest and adjacent stands. Stands bordering nest stands were primarily M2G, M3N, M4N, M3G, M4G, R3N, R4N, R3G, and R4G (codes for timber strata are defined in table 1C and in Appendix B). The estimated number of acres in habitat types listed in table 5A were based on the most recent FS inventory data (Fiske, pers. comm.).

Selective Use of Forest Types

Based only on those habitat types in which nests had been observed and verified, we found a significant difference between habitats selected for nesting stands and the overall distribution of available habitats in Sierran NFs (table 5A, fig. 5B). A 95-percent Bonferroni interval test (see Neu et al. 1974, Byers and Steinhorst 1984) on the forest types contributing to this difference (table 5A) showed that, based on availability of different forest stand types, spotted owls in the Sierra Nevada nested more than expected in mixed-conifer stands with medium- to large-sized trees [24 to 36+ inches in diameter at breast height (d.b.h.)], stands with a wide range of tree sizes overall (5 to 60+ inches in d.b.h.), and medium (40-69 percent) (stand type M4N) to high (70-100 percent) total canopy cover (stand type M4G). Forty-five percent of all nest stands in Sierran conifer forests, however, were in the M4N and M4G habitat types. All other habitat types that we evaluated were used equal to or less than their proportional availability (table 5A).

Table 5A-*Distribution of California spotted owl nest habitat types compared with proportions of available habitats in the Sierra Nevada.*

Habitat Type[1]	Sample size	95 percent Bonferroni interval Lower	Point estimate	Upper	Available	Result
M2G[2]	2	0	0.0135	0.0390	0.0209	U = A[3]
M3P	10	0.0121	0.0676	0.1231	0.2369	U < A
M3N,G	44	0.1962	0.2973	0.3984	0.2501	U = A
M4P	10	0.0121	0.0676	0.1231	0.1418	U < A
M4N,G	67	0.3426	0.4527	0.5628	0.2005	U > A
R3P	2	0	0.0135	0.0390	0.0448	U < A
R3N,G	3	0	0.0203	0.0514	0.0522	U < A
R4N,G	10	0.0121	0.0676	0.1231	0.0464	U = A
Total	**148**					

[1] See figure 5B for distribution of habitat types that were signficantly different (x^2 = 79.9, df = 7, P < 0.05) between used and available types.

[2] Habitat codes correspond to FS timber strata labels: M = mixed-conifer, R = red fir; 2 = pole-sized trees (<12 inches in d.b.h.), 3 = small sawtimber (trees 12-24 inches in d.b.h.), 4 = medium and large sawtimber (24-40 and >40 inhces in d.b.h.); G = 70+ percent canopy cover, N = 40-69 percent canopy cover; P = 0-39 percent canopy cover.

[3] U = A; current evidence does not indicate a difference between use and availability.
U < A; used less than expected.
U > A; used greater than expected.

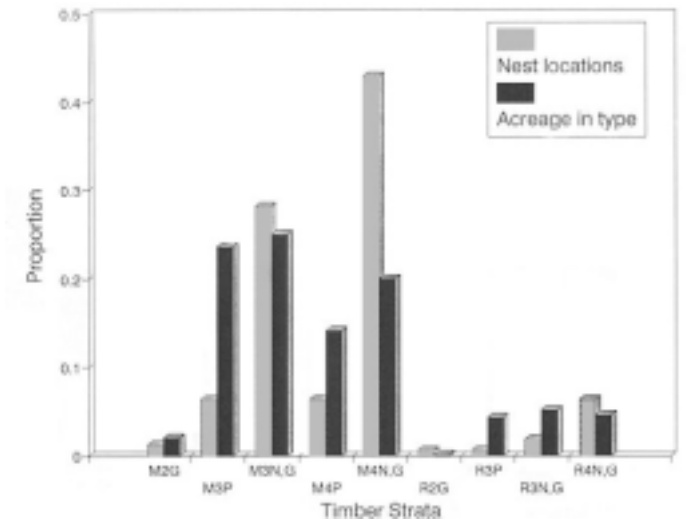

Figure 5B-Nest locations (*n* = 148) and proportional availability of different timber strata (see Appendix B or table 5A for definitions of strata codes).

In addition to the strata listed in table 5A and figure 5B, four nests were in pure stands of ponderosa pine (one each in P3N, P4P, P3G, and P4G) and eight nests in hardwood types. Because of a lack of consistency among NFs in typing these timber strata, we could not develop reliable estimates of their acreages available, or of their associated nests. Consequently, these nests were omitted from the analysis of use-versus-availablity presented in table 5A. Ponderosa pine types commonly include hardwood components, but these are not considered in timber inventories. As a result, a site with ponderosa pines in the overstory and an understory of hardwoods would be judged by its stratum label to be unsuitable for nesting (and possibly even for foraging) by the owls, even though that may not be the case. Although we lack the needed data to perform rigorous statistical tests, it is our firm biological understanding that pine stands with high canopy closure and a significant hardwood component are excellent owl habitat. Not only do they have all of the necessary structural components, but also they are in an elevational zone where the distributions of woodrats and flying squirrels overlap. The presence of a rich and diverse prey base, proper structural characteristics, and relatively mild climatic conditions may well make these sites among the highest quality owl habitat in the Sierra Nevada. We believe, therefore, that at least the P4G strata is selected for nesting by owls, in excess of its availability.

Bias and Gutiérrez (1992) found that nesting and roosting owls on the Eldorado Study Area almost exclusively used mixed-conifer stands with medium (M3G) to large (M4G) timber and at least 70 percent canopy cover (color photos 5-11 and 5-18). The M4G stands were more abundant on public than on private land in the study area, and the owls used public lands for nesting and roosting significantly more than they used private lands. Gutiérrez and Pritchard (1990) found that spotted owls on Mount San Jacinto used conifer and riparian/hardwood forests (color photos 5-41 and 5-42) significantly more than expected, based on their availability, and that owls on Palomar Mountain used primarily conifer or mixed forests of conifers and hardwoods (color photos 5-39 and 5-40).

Density of Owl Sites in Relation to Amount of Suitable Habitat

Based on intensive surveys for owls by NF personnel and others, owl densities in U.S. Geological Survey quadrangles (1:24,000; n = 49) in the zone of mid-elevation, Sierran mixed-conifer forests were significantly, but weakly, correlated with the percentage of forests having medium-sized and larger trees and high canopy closure (R^2 = 0.38, P < 0.05; fig. 5C). We interpreted these relations cautiously, however, because survey effort was not uniform among the survey units and error exists in the type mapping of mixed-conifer habitat by the FS (Call 1990, Bias and Gutiérrez 1992, G. N. Steger pers. observ.). Nevertheless, this analysis suggested that, as with nest stands, owl densities were higher in areas with a higher proportion of dense stands and large trees.

Patterns of Habitat Use at a Home-Range Scale

Here we report results of various studies that have compared attributes of sites used for nesting, roosting, and foraging with the same attributes measured at sites randomly selected from the surrounding forest. Only results of studies done in conifer forests of the Sierra Nevada and San Bernardino Mountains are reported here. Methods used to measure habitat attributes varied among the studies. Although direct statistical comparisons could not be made across all studies, we believe all methods provided objective, quantitative estimates of the attributes in local owl habitats.

All workers except Laymon (1988) used consistent methods within their studies, and workers from three study areas (Tahoe--Call 1990, Eldorado-Bias 1989, and San Bernardino--LaHaye et al. 1992a) used consistent methods among the studies. Workers from these latter three studies used a variable circular-plot design, using basal area prisms that resulted in an increasing plot size with increasing diameters of trees, an estimation procedure commonly used by foresters for estimating

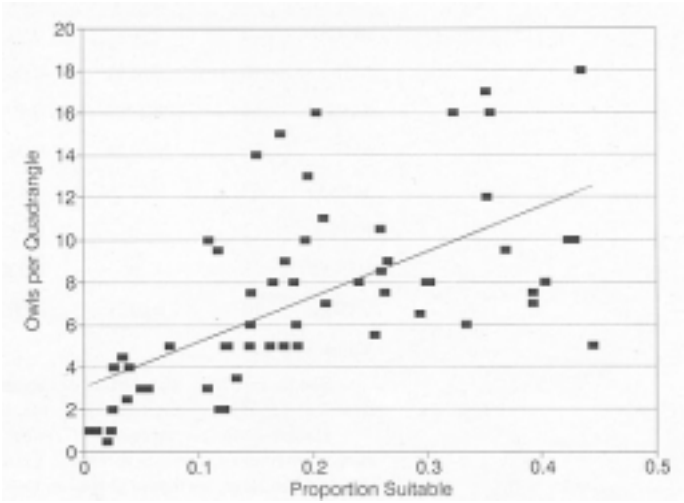

Figure 5C-Density of owl sites in the Sierra Nevada (*n*= 49) in relation to the proportion of habitat considered to be suitable for spotted owls in U.S. Geological Survey quadrangles (1:24,000).

Although our conclusions from studies in the Tahoe Study Area were basically the same as those reported by Call (1990) and Call et al. (1991), some details of our results differed slightly because we eliminated from Call's sample of random points all locations with <40 square feet per acre in basal area of softwoods. Eliminating recent clearcuts and shrubfields allowed more meaningful biological comparisons with foraging sites. In addition, we subsampled the sample of foraging sites by eliminating, at random, all but one location from each owl, or owl pair, in a given day.

In addition to studies that compared habitat attributes between random sites and sites used by owls, B. B. Bingham (pers. observ.) and Steger and Eberlein (pers. comm.) sampled nest stands in the Lassen Study Area and the Sierra Study Area, respectively, but not in comparison with random sites. In these studies, vegetation at nest sites was sampled using strip transects arranged perpendicular to one another and centered on the nest tree. Beginning 32.8 feet from the center of the nest tree, the long axes of four strip transects (32.8 by 113.7 feet-total area sampled = 0.30 acre) radiated on four sides of the nest tree along perpendicular lines through the nest tree. No vegetation data were collected within the 32.8 by 32.8 foot square centered on the nest tree.

Finally, Steger and Eberlein (pers. comm.) sampled habitats, by canopy-cover class (0-39 percent, 40-69 percent, and 70+ percent), throughout the radio-tracking portion of the Sierra Study Area, based on stratified random samples of habitat polygons in both the foothill riparian/hardwood and mixed-conifer portions of the study area. Their method used four sets of nested plots randomly located in each polygon. Plots were 16.4 by 328 feet for all trees and snags, 32.8 by 328 feet for trees >35.4 inches in d.b.h., and 65.6 by 328 feet for snags >15.7 inches in d.b.h.

Differences Among Methods

Laymon (1988), Bias (1989), and LaHaye et al. (1992a) all used tree-centered plots for the evaluation of the nest sites, but they did not center random plots on trees. This method introduced a potential bias in the comparisons between nest/roost sites and random locations. It also had the potential to bias the inferences drawn concerning stand attributes based on nest locations. Data from Call (1990), B. B. Bingham (pers. observ.), and Steger and Eberlein (pers. comm.) did not have this bias.

The magnitude of any bias introduced by centering on a large tree is related to the density of similar trees in the surrounding stand and the size of the sample plot. One way to envision the bias is to ask how likely it is that a random plot (of identical size and shape) in the same stand would sample either the nest tree or another tree having similar size and condition. We would expect samples centered on nest trees to be more strongly biased than roost locations-roosts are often in small trees in dense stands, whereas nest trees are generally larger than trees in the surrounding stand (for example, tables 5B-5D).

Based on plot size, Laymon's (1988) data may be the most biased. He used small (0.17-acre), fixed plots and all of his owl-use plots, including foraging locations, were tree-centered. Bias (1989) and LaHaye et al. (1992a) both used variable-plot methods with a basal area factor (BAF) of 20. This sampling technique has the advantage that plot size increases with the size of the nest tree. For a tree 40 inches in d.b.h., the plot size is 0.44 acres; it is nearly an acre for a 60-inch tree.

Estimating the Bias-We could not repeat these studies or obtain all the raw data for re-analysis. We could, however, estimate the probable magnitude of the statistical bias due to tree-centering and determine the extent to which it changed the inferences drawn from these analyses. For Bias (1989) and LaHaye et al. (1992a), we corrected for total basal area simply by removing the nest/roost tree. When prism sampling, overall basal area can be determined simply by counting the number of "count trees" in the plot. Each counted tree represents a certain basal area per acre, as determined by the BAF. With a BAF of 20, for instance, each tree represents 20 square feet basal area per acre (BA/acre). At nest and roost sites, Bias obtained an average of 251 and 294 square feet BA/acre, respectively (table 5B), and LaHaye et al. reported 223 and 267 square feet BA/acre for nest and roost sites, respectively (table 5C). On average, Bias and LaHaye et al. were "counting" between 11 and 15 trees in each sample plot. Removing the nest tree from the basal area calculation would remove only one tree from each plot, a reduction of 20 square feet BA/acre. This suggests a range from 203 to 274 square feet BA/acre in their nest and roost stands.

While this decrease is not large, we believe it probably exceeds the potential bias of including the nest or roost tree in the sample. For example, if the nest tree were not within the plot, most likely other trees would be. The basal area of these trees would, in part, compensate for the removal of the nest tree. To obtain better estimates of the true bias, we analyzed nest site data from B. B. Bingham (pers. observ.) and Steger and Eberlein (pers. comm.). These data were taken in the vicinity of the nest tree but did not include the nest tree. We added the nest tree and recomputed live tree and snag basal area. For Bingham's data, live tree basal area was increased by about 7 square feet BA/acre and was not significantly different from the original estimate ($P = 0.18$). Basal area for the largest diameter-class, however, was shifted by 16.4 square feet BA/acre ($P = 0.002$). Similarly, snag basal area was significantly overestimated by including the nest snag in the sample. For Steger's and Eberlein's data, live tree basal area was increased about 4 square feet/acre, not significantly different from the original estimate ($P = 0.17$). Snag basal area was increased 5 square feet/acre, not significantly different from the original estimate ($P = 0.36$).

B. B. Bingham (pers. observ.) and Steger and Eberlein (pers. comm.) used fixed plots of 0.3 acres. These plots were smaller than the plots associated with large d.b.h. classes using a BAF of 20, but not greatly so. We believe these data can be used to make reasonable inferences concerning the magnitude of bias in the results of Bias (1989) and LaHaye et al. (1992a). Laymon's (1988) plots were about half the size of those used by Bingham and by Steger and Eberlein, so the potential for bias is therefore greater.

Conclusions-Given their sampling methods, results from Bias (1989) and LaHaye et al. (1992a) should be interpreted with a number of cautions. The overall basal area figures and basal area for all trees >16 inches in d.b.h. would not be significantly

Table 5B-*Habitat characteristics (mean and percent Coefficient of Variation) of California spotted owl nest* (n *=11) and roostsites* (n = *29), and random sites (public land,* n *=328) in the Eldorado Study Area, central Sierra Nevada (Bias 1989).*

	Nest sites		Roost sites		Random sites	
	Mean	Percent CV	Mean	Percent CV	Mean	Percent CV
Physiographic attributes						
Percent slope	26.1	46.8	30.1	58.3	32.3	61.2
Elevation (feet)	4,900.0	18.6	4,561.0	14.6	4,728.3	18.1
Structural attributes						
Percent cover	89.3	16.1	95.6[a]	3.9	79.2	32.0
Basal area (square feet per acre)						
Hardwoods	38.3	69.1	43.6	60.9	61.3	138.1
Softwoods	234.4	43.8	268.4[a]	44.0	151.6	80.2
Total live	**251.0**	**25.1**	**293.7[a]**	**37.0**	**173.4**	**70.5**
Snag	52.7[a]	45.8	52.7[a]	72.8	37.0	134.2
Basal area (square feet per acre, by d.b.h. class)[1, 2]						
3.9-4.8	5.5	-	7.4	-	3.9	-
4.9-10.7	14.5	-	24.4	-	44.7	-
10.8-20.6	89.9	-	90.3	-	61.9	-
20.7-35.5	91.0	-	82.7	-	52.4	-
>35.5	110.9	-	95.1	-	42.6	-
Downed woody debris (percent cover, by diameter class in inches)						
1-11.8 inches	12.1	57.8	10.2	69.0	11.2	122.6
>11.8 inches	2.7	87.0	2.6	187.8	3.9	244.6

[a] Significantly different from the corresponding random sample, at the 0.001 level of significance (1-way ANOVA, using Scheffe test for multiple comparisons).
[1] Diameter at breast height, in inches.
[2] CVS could not be computed for these data.

Table 5C-*Habitat characteristics (mean and percent Coefficient of Variation) of California spotted owl nest* (n = *131) and roost sites* (n = *43), and random sites* (n = *296) in the San Bernardino Study Area, southern California (LaHaye et al. 1992a).*

	Nest sites		Roost sites		Random sites	
	Mean	Percent CV	Mean	Percent CV	Mean	Percent CV
Physiographic attributes						
Percent slope	51.2[a]	50.8	54.7[a]	44.6	32.3	68.8
Elevation (feet)	6,052.0[a]	20.9	6,299.2[a]	18.5	6,942.3	14.7
Structural attributes						
Percent cover	76.9[a]	21.3	83.6[a]	15.3	52.2	50.5
Basal area (in square feet per acre)						
Total live	**222.7[a]**	**41.7**	**266.7[a]**	**35.2**	**124.2**	**68.8**
Snag	21.4[a]	120.9	20.9[a]	123.3	7.8	217.3
Dead-topped trees	12.2	143.3	15.7	99.1	7.0	224.6
Hardwoods (by d.b.h. class)[1]						
0-5.9	5.2	263.0	10.5	182.8	14.8	245.2
6.0-11.8	13.1	207.1	32.7	182.3	14.8	230.3
11.9-17.7	14.4	224.6	25.7	163.9	3.5	356.0
>17.7	19.6	151.0	28.8	162.5	3.1	391.6
Total	**52.31**	**129.5**	**97.61**	**119.5**	**36.2**	**169.0**
Softwoods (by d.b.h. class)						
0-9.8	12.2	178.1	16.6	160.5	13.1	207.1
9.9-19.7	27.0	123.8	41.4	128.4	24.8	135.7
19.8-29.5	46.2	100.3	43.6	117.4	21.8	127.8
>29.5	85.4	77.1	67.1	67.7	29.2	124.1
Total	**170.4[a]**	**58.9**	**168.6[a]**	**68.5**	**88.0**	**85.1**

[a] Significantly different from the corresponding random sample, at the 0.001 level of significance (Mann-Whitney *U* test).
[1] Diameter at breast height, in inches.

Table 5D-*Habitat characteristics of California spotted owl roost sites in summer* (n =*120*), *fall* (n = *78*), *and winter* (n = *61*), *and at random sites throughout summer/fall* (n = *120*) *and winter* (n = *66*) *in the Eldorado Study Area, central Sierra Nevada (Laymon 1988). Note that all winter data were obtained in low-elevation, oak-pine forests, where the birds migrated for the winter (see Chapter 4).*

	Roost sites				Random sites					
	Summer		Fall		Summer/fall		Roost sites in winter		Random sites in winter	
	Mean	Percent CV	Mean	Percent CV	Mean	Percent CV	Mean	Percent CV	Mean	Percent CV
Physiographic attributes										
Percent slope	18.1[a]	36.3	21.1[a]	35.6	23.4	46.8	26.8[a]	36.4	19.9	30.6
Structural attributes										
Percent cover	85.8[a]	6.4	75.2	9.4	67.9	29.0	63.5[b]	12.9	29.7	32.8
Basal area (square feet per acre)										
Hardwoods	20.9	79.8	12.6[a]	106.5	26.1	146.0	18.7[b]	56.7	7.0	126.9
Softwoods	330.7[a]	21.6	259.7[a]	25.9	163.8	62.6	57.1[b]	65.1	29.2	78.8
Total live[1]	**351.6**	**-**	**272.3**	**-**	**189.9**	**-**	**75.8**	**-**	**36.2**	**-**
Snags	41.4[a]	57.6	47.5[a]	60.8	17.4	246.4	35.7[b]	168.3	19.6	63.2
Downed woody debris (tons per acre, by log diameter class)[2]										
0-3 inches	0.82	0.30	0.90	0.32	0.82	0.74	0.23[b]	0.78	0.18	0.50
>3 inches	12.16[a]	0.59	10.53	0.72	9.36	1.39	1.56[b]	1.55	0.62	1.44

[a] Significantly different from corresponding random sites in summer/fall, at the 0.05 level of significance (Student's *t* test).
[b] Significantly different from corresponding random sites in winter, at the 0.05 level of significance (Student's *t* test).
[1] The sum of softwood and hardwood basal areas. Data were not available to compute a percent Coefficient of Variation for this variable.
[2] Assumes a specific gravity of 0.4 for downed woody debris.

biased. Basal area in the largest diameter-class would, however, be overestimated, by perhaps as much as 20 square feet BA/acre. Similarly, snag basal area would be overestimated by perhaps 10 square feet BA/acre. Laymon's (1988) basal area data should be viewed with caution. For all of these studies, we have no reason to believe that estimates of canopy closure were affected by tree-centering (for example, see table 5B).

No important changes in inferences made from results of these studies were associated with these biases, although it is possible that the statistical significance of certain test results could be altered. It is important to note that in Bias (1989) and LaHaye et al. (1992a) the statistically significant basal area differences from random samples were associated most strongly with sites of roost trees, where we do not expect tree-centering to have as much impact as at nest tree sites. It is also worth noting that the statistical results presented by Call (1990), B. B. Bingham (pers. observ.), and Steger and Eberlein (pers. comm.) were not based on tree-centered plots.

Nest and Roost Sites

Physiographic Attributes-Mean elevation at nest sites in conifer forests increased -from about 5,300 feet in the northern Sierra Nevada to 6,000 feet in southern California-about coincident with low- to mid-elevation mixed-conifer zones. Nests at the highest elevations were in red fir forests in the Sierra Nevada and white fir forests in the San Bernardino Mountains. No nests have been located in subalpine forests anywhere in California.

Blakesley et al. (1992) reported that nest sites of northern spotted owls in northwestern California tended to be on steeper slopes and in the lower third of canyons. This pattern was true for the California spotted owl only in the San Bernardino Study Area (table 5C). Based on statistical methods for analyzing data from circular distributions (Zar 1984, p. 422-469), the mean aspects of nesting, roosting, and random sites were not significantly different in the San Bernardino Mountains (LaHaye et al. 1992-). Assuming equal availability of aspects, significantly more nest sites in the Sierra Nevada were located on north aspects and fewer on southwest aspects than expected (n = 148; $P < 0.001$; fig. 5D). These results should be viewed with caution, however, as we cannot evaluate the validity of the assumption that all aspects were equally available.

Roost sites used by California spotted owls were similar in structure and composition to those used for nesting, although we know less about owl roosting habitat than nesting habitat. Some spotted owls have repeatedly used the same roost sites, suggesting that they have narrow selection patterns for roosting (Barrows and Barrows 1978, Barrows 1980, Steger and Eberlein pers. comm.) or that they tend to return to familiar or favorable roosts.

Within study areas, roost and nest sites were similiar in elevation and slope (tables 5B and 5C), probably because the owls often roosted near a nest site (LaHaye et al. 1992a). All of the roosting California spotted owls found by Barrows (1980) were on north-facing slopes. Studies in the Sierra Nevada (Laymon 1988, Bias 1989) and in the San Bernardino Mountains (W. S. LaHaye pers. observ.), however, did not reveal a significant

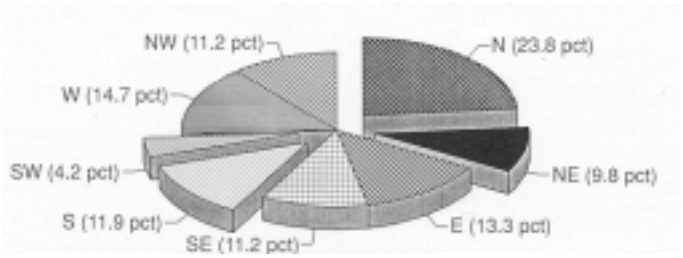

Figure 5D-Proportions of nest sites on slopes facing different directions from all nest sites located on National Forests within the range of the California spotted owl (n = 143).

difference in mean aspect between roost sites and random locations. The owls studied by Barrows (1980) were in habitats at low elevation, where the dense-canopied stands selected by the owls would be found most often on north-facing slopes.

Structural Attributes-Mean canopy cover at nest and roost sites, for the three studies that measured these variables (tables 5B-5D), was consistently higher than the canopy cover at random samples-on average, about 20 percent higher. Canopy closure at nest sites was not significantly higher than at random locations in the central Sierra Nevada (table 5B), but it was significantly higher in the San Bernardino Mountains (table 5C). Roost sites had significantly (P = 0.001) higher canopy closure than random sites in all three studies.

Mean softwood basal area was also consistently higher at nest and roost sites in all three studies. Total live tree BA/acre averaged 127 square feet greater in nest and roost stands than at random sites. As with canopy closure, measures of basal area were more often significantly different between roost sites and random sites than between nest sites and random sites (tables 5B-5D). In all cases allowing a statistical comparison, roost sites had significantly more total live tree basal area and basal area of softwoods than random locations. At nest sites, total live tree basal area and softwood basal area were consistently higher than at random sites in both studies reporting these results (tables 5B and 5C), significantly so for both attributes in the San Bernardino Study Area (table 5C).

Tree size-class data were available for nesting and roosting sites in the Eldorado NF (table 5B) and the San Bernardino NF (table 5C) and for nest sites in the Sierra and Lassen NFs (table 5E). In the Eldorado NF, nest sites averaged 111 square feet BA/acre in trees >35.5 inches in d.b.h. Nest sites in the San Bernardino NF had, on average, >85 square feet BA/acre in trees >29.5

Table 5E-*Habitat characteristics (mean and percent Coefficient of Variation) of spotted owl nest sites in the Lassen Study Area (n = 24), southern Cascade region of northern California (B. B. Bingham pers. observ.), and the Sierra Study Area (n = 11), southern Sierra Nevada (Steger and Eberlein pers. comm.).*

	Lassen Study Area		Sierra Study Area	
	Mean	Percent CV	Mean	Percent CV
Physiographic attributes				
Percent slope	25.8	51.6	7.9	66.2
Elevation (feet)	5,599.6	8.0	4,840.0	7.9
Structural attributes				
Percent cover	85.2	9.8	85.6	13.8
Live trees[1]				
Basal area (square feet per acre)				
Total	**243.8**	**36.7**	**185.8**	**73.3**
Stems per acre (d.b.h. class in inches)[2]				
5-10	93.2	72.0	96.3	73.3
11-20	60.3	50.8	35.9	43.7
21-35	17.1	73.8	16.6	57.0
>35	8.0	86.7	5.2	88.7
Stems per acre (height class in feet)				
13-25	14.8	251.7	99.0	101.9
26-39	44.3	87.1	35.0	60.1
40-53	34.2	84.4	25.1	65.3
54-79	42.4	83.4	35.0	62.3
80-105	20.8	92.3	10.4	90.9
106-131	13.2	70.6	9.2	135.3
132-157	6.7	160.1	6.4	215.2
158-183	1.8	172.0	2.1	145.2
>183	0.4	358.7	0.6	222.5
Snags				
Basal area (square feet per acre)				
Total[3]	**47.5**	**85.0**	**33.0**	**167.2**
Large[4]	21.3	119.1	19.5	131.8
Stems per acre (d.b.h class in inches)				
5-10	8.8	171.4	20.2	146.5
11-20	7.7	185.8	5.8	109.9
21-35	5.9	79.5	2.5	151.8
>35	2.8	130.8	1.2	222.0
Downed woody debris (tons per acre, by log diameter-class)[5]				
11-20 inches	3.2	103.2	2.5	78.6
21-35 inches	7.7	94.4	5.1	131.
>35 inches	11.4	100.7	13.5	128.5

[1] Only live trees with d.b.h. >4 inches.
[2] Diameter at breast height, in inches.
[3] Snags >4 inches in d.b.h., and ≥4.6 feet tall (Lassen Study Area) or ≥6.6 feet tall (Sierra Study Area).
[4] Snags ≥15 inches in d.b.h. and ≥20 feet tall.
[5] Only logs >10 inches in diameter at the large end. Assumes a specific gravity of 0.4 for downed woody debris.

inches in d.b.h. Nest sites in the Sierra and Lassen NFs averaged five and eight stems per acre >35 inches in d.b.h., respectively. These data, when combined with the analysis of nest-site preferences based on timber strata (table 5A, fig. 5B), demonstrate that a significant large-tree component is present in most owl nest stands.

At nest sites, basal areas were highest in the large-tree classes (>24 inches in d.b.h.) and decreased through each of the smaller size-classes (tables 5B and 5C). This often resulted in multi-storied nest stands dominated by larger trees with a well-developed understory (for example, color photo 5-27). The vertical stratification in these stands was not as extensive as that observed in nest stands of the northern spotted owl in northwestern California (LaHaye 1988, Solis and Gutiérrez 1990, B. B. Bingham pers. observ.).

Percent canopy cover, total live tree basal area, softwood basal area, hardwood basal area, and snag basal area were generally greater at owl roost sites than at random locations (tables 5B-5D). As at nest sites, the basal area of trees at roost sites was concentrated in the large size-classes, but with trees of all sizes resulting in multi-storied canopies.

Many of these parameters exhibited a large degree of variability, and the differences between habitat used by spotted owls and random locations may or may not have been statistically significant within a given study. The data were, however, consistent and mutually supportive among all studies. California spotted owls in these various studies chose to nest and roost in stands that were denser than average and that contained a large-tree component. Most nest sites were selected in dense mixed-conifer stands with average quadratic mean diameters of canopy trees >24 inches in d.b.h. We know of no data that contradict these findings.

Size of Activity Centers

Activity centers are areas within which owls find suitable nesting sites and several suitable roosts, and in which they do a substantial amount of their foraging. Using the sample of nest trees from conifer forests in the Sierra Nevada (n = 148), we estimated the sizes of stands containing the nest trees and the cumulative size of each nest stand plus all adjoining stands that were of a timber type used equal to or greater than its availability (table 5A). These adjoining stands may make important contributions to activity centers, because the owls have direct access to them. In some instances, nesting pairs may even spend more time in one or more of the adjoining stands than they do within the stand containing their nest.

The mean size of nest stands was 99.9 acres (SD = 114.9 acres) and the median was about 65 acres. The mean size of the nest stand plus adjacent stands was 306.7 acres (SD = 386.6 acres) and the median was about 265 acres. Numerous roosts would be available in the nesting and adjoining stands. Cumulative distribution functions for these two variables provide two important insights (fig. 5E). The majority of nest stands were smaller than 100 acres, but, in contrast, the majority of nest-plus-adjacent stands exceeded 200 acres.

Based on results of radio-tracking studies, the latter variable provides a better estimate of the size of activity centers. An estimate of the area used for foraging in an activity center may be approximated by the area that includes half of the nighttime (foraging) locations of owls during the breeding period, as estimated by the adaptive kernel method (Worton 1989). In the radio-tracking study in the Sierra NF (G. N. Steger pers. observ.), this averaged 317 acres (SD = 202; n = 9) in 1987, 296 acres (SD = 110; n = 7) in 1988, and 310 acres (SD = 127; n = 9) in 1989. These estimates were not independent from year to year, because some of the same individuals' home ranges were included in 2 or 3 of the years. In the radio-tracking study in the Lassen NF (Zabel pers. comm.), the average was 788 acres (SD = 347; n = 10) in 1989-90. In all cases, only birds with at least 20 nighttime locations were used for these estimates.

Nest Sites on Private Timberlands

Hofmann and Taylor (1992) reported general habitat conditions at 18 nest sites on industrial forest lands in the northern (n = 4), central (n = 5), and southern (n = 9) Sierra Nevada. Fourteen of the pairs nested successfully, but the report did not indicate the proportion of all owls found on private lands that nested or the proportion that fledged young. The owls nested in a variety of forest stands, ranging from sparse (5 percent) to high (86 percent) cover by multi-storied stands with large-diameter trees. Reported values of site attributes were within ranges given above for nest sites in NFs. Overall, 60-65 percent of the area within a radius of 1,000 feet of nests had "dense" canopy cover. No other structural habitat features were reported.

Taylor (1992) provided additional information on the habitat associations of owls nesting on industrial forest lands in the Sierra Nevada. Based on a sample of 28 nests, Taylor found "...a clear pattern of dominance of nest sites by medium and large d.b.h. stands..." and the data to clearly indicate "...that owls nest in areas with moderate-to-dense canopy closure" (Taylor 1992, p. 9). These results are consistent with those reported in tables 5B-5D.

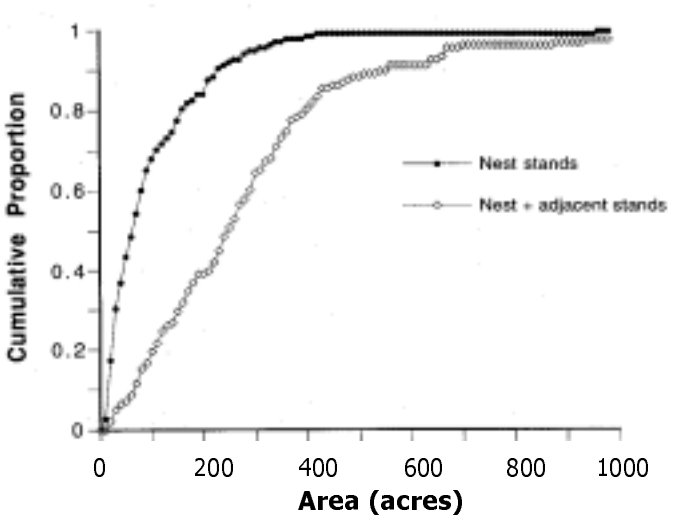

Figure 5E-Cumulative distribution of nest stands, and nest stands plus adjacent stands, arranged by size. Adjacent stands were restricted to those timber types used equal to, or greater than, their availability (n = 138).

Foraging Sites

Attributes of foraging habitats used by California spotted owls have been estimated in only two studies (Laymon 1988, Call 1990). In both studies, the range of habitat structures used by the owls was greater in foraging habitats than in nesting and roosting habitats. Laymon (1988, p. 100) concluded that the majority of spotted owl foraging locations in his Eldorado study were on sites with medium to large trees (in Laymon's classification, these were trees >24 inches in d.b.h.) and dense canopy closure (60 to 100 percent). They significantly selected for stands with trees >24 inches in d.b.h. and canopy cover of 40 to 59 percent, based on availability. On the other hand, they used stands significantly less than expected that had (1) trees in the 11- to 24-inch d.b.h. group and 60 to 100 percent cover, and (2) trees >24 inches in d.b.h. and canopy cover of 10 to 39 percent. Laymon (1988, p. 115) also reported that the owls in his study selected "foraging sites with more and larger snags."

Call (1990, p. 30) concluded that the owls in his Tahoe NF study area used clearcuts, shrubfields, and plantations significantly less than expected (P = 0.01), based on availability. They used medium timber (11-20 inches in d.b.h.) in proportion to availability (P = 0.51), and they used large timber (20-35 inches in d.b.h.) significantly more than expected (P = 0.01). In addition, the probability of an owl's using large timber was significantly greater than of its using medium timber (P = 0.003). Based on vegetation sampled at foraging locations by Call (1990, p. iv), a "discriminant function analysis indicated that the owls selected habitats with late-successional stand characteristics including mature and old-growth timber [>35 inches in d.b.h.], multiple vegetation strata, and high live timber basal area." The combined results from Laymon's and Call's studies suggest that spotted owls in these Sierran conifer forests tended to forage in stands of intermediate to older ages.

Based on three canopy-closure classes (see table 5F), owls in the Sierra Study Area used stands with 70+ percent canopy closure significantly more and stands with 0-30 percent canopy closure significantly less than expected (Verner et al. 1991; also see Chapter 6).

Physiographic Attributes-Laymon (1988) found that random sites were significantly steeper than foraging sites during both summer and fall in the Eldorado Study Area (table 5G), but Call (1990) found no difference in the Tahoe Study Area (table 5H).

Table 5F-*Structural attributes of habitats (mean and percent Coefficient of Variation, by canopy cover class) used by California spotted owls during radio-tracking studies in the mixed-conifer zone of the Sierra Study Area, southern Sierra Nevada (Steger and Eberlein, pers. comm.).*

	0-39 percent canopy cover (n =64)		40-69 percent canopy cover (n = 35)		70+ percent canopy cover (n = 21)	
	Mean	Percent CV	Mean	Percent CV	Mean	Percent CV
Percent canopy cover						
By densiometer	26.5[a]	67.6	60.0[b]	23.9	73.7[c]	14.0
By aerial photo	21.0[a]	49.9	52.9[b]	16.7	74.8[c]	6.8
Basal area (square feet per acre)						
Green trees	61.4[a]	84.2	172.2[b]	41.3	211.3[c]	20.7
Snags	4.7[a]	137.0	12.1[b]	76.3	13.9[b]	64.1
Hardwoods (by d.b.h. class)[1]						
0-4.7 inches	0.1[a]	300.0	0.3	200.0	0.6[b]	269.2
4.8-10.6 inches	0.7[a]	280.0	1.5[b]	144.1	2.0[b]	104.1
10.7-20.5 inches	1.1[a]	250.0	2.0	188.9	1.6[b]	141.0
20.6-35.4 inches	0.6	323.1	1.3	313.8	2.0	233.3
>35.5 inches	0.1	800.0	0.6	442.9	0.0	0.0
Total	**2.6[a]**	**193.3**	**5.6[b]**	**160.9**	**6.2[b]**	**109.4**
Softwoods (by d.b.h. class)[1]						
0-4.7 inches	1.7[a]	137.5	3.7[b]	107.1	4.4[b]	72.4
4.8-10.6 inches	7.2[a]	107.8	13.9[b]	70.8	21.2[c]	46.6
10.7-20.5 inches	15.4[a]	99.2	39.5[b]	45.3	54.5[c]	38.2
20.6-35.4 inches	22.6[a]	107.9	63.2[b]	60.8	74.0[b]	60.0
>35.5 inches	12.0[a]	148.0	46.3[b]	79.4	51.0[b]	75.7
Total	**59.0[a]**	**84.2**	**166.5[b]**	**43.9**	**205.2[c]**	**21.1**
Shrubs per acre	3.7[a]	325.5	18.0[b]	293.7	8.4	250.9
Downed woody debris (tons/acre, by log diameter-class)[2]						
11-20 inches	2.1[a]	88.9	3.2[b]	75.5	3.1[b]	74.2
21-35 inches	4.0[a]	102.1	4.7[b]	100.7	6.9[b]	83.7
>35 inches	3.3[a]	213.3	9.3[b]	144.7	8.2[b]	106.1

[a,b,c] Values in the same row with different alpha superscripts are different at the 0.05 level of significance (one-way ANOVA).
[1] Diameter at breast height, in inches.
[2] Assumes a specific gravity of 0.4 for downed woody debris.

Structural Attributes-Percent canopy cover, softwood basal area, total live tree basal area, snag basal area, and the amount of large, downed woody debris were generally greater at foraging than at random sites (tables 5G and 5H). Stand measurements reported for the Sierra Study Area were not related to specific foraging locations of spotted owls, so they could not be used to compare attributes at foraging locations with those at random locations. Total basal areas reported in the Sierra Study Area (table 5F) in stands with 40-69 percent and 70+ percent canopy cover were comparable to those at foraging sites reported by Call (1990) for the Tahoe Study Area and by Laymon (1988) for the Eldorado Study Area. That was not the case, however, for stands with 0-39 percent canopy cover in the Sierra Study Area. Conifers were the dominant component of basal area in all locations studied (tables 5F-5H). Point estimates for softwood, hardwood, and snag basal areas also were generally less in foraging than at roost and nest sites.

Selection Patterns of Radio-tagged Birds

Where significant patterns of habitat selection were observed among radio-tagged owls, results were consistent with those from the studies reported here. In the Lassen and Sierra Study Areas, some radio-tagged owls used denser stands and were associated with larger trees more than expected on the basis of availability. Only one bird used stands in the lowest canopy-cover class more than expected, and none did so for small tree classes (Chapter 6).

Results of Call's (1990) and Laymon's (1988) studies, reported earlier in this chapter, tend to show stronger selection for habitat attributes by foraging owls than suggested by studies reported in Chapter 6. We believe this resulted from differences between studies in their scale of measurements. Call and Laymon sampled habitats at or very near actual locations where owls foraged. Studies reported in Chapter 6, on the other hand, characterized the entire stand in which a given owl foraged, thus lacking the localized scale used by Call and Laymon.

Patterns of Habitat Use at a Stand Scale

Nest Types

All recently located nests of California spotted owls have been in trees, but some early records exist of nests found in other locations. For example, records obtained from the Western Foundation of Vertebrate Zoology (Kiff pers. comm.) included notes on 14 nests located between 1889 and 1947. Five were on cliff ledges, one was in a pigeon coop, and eight were in hardwood trees. The pigeon coop nest was composed of "manure," hay, and feathers in a deserted coop under a roof supported by four posts. This nest contained four eggs-only one of two clutches of that size ever reported for spotted owls (see Johnsgard 1988).

Quantitative information on nest trees and nest sites were provided by each of the seven NFs in the western Sierra Nevada and the four southern California NFs. This database was supplemented with identical information from four of the major study areas (Lassen--Blakesley pers. comm.; Eldorado-Moen pers. comm.; Sierra and Sequoia/Kings Canyon--G. N. Steger pers. observ.; and San Bemardino--W. S. LaHaye pers. observ.).

Table 5G-*Habitat characteristics (mean and percent Coefficient of Variation) of California spotted owl foraging locations in summer (n = 120) and fall (n = 79), and at random locations throughout summer/fall (n = 120) in the Eldorado Study Area, central Sierra Nevada (Gaymon 1988).*

	Foraging sites				Random sites in summer and fall	
	Summer		Fall			
	Mean	Percent CV	Mean	Percent CV	Mean	Percent CV
Physiographic attributes						
Percent slope	19.4[a]	90.3	17.9[a]	86.9	23.4	46.8
Structural attributes						
Percent cover	66.8	32.0	61.6	45.5	67.9	29.0
Basal area (square feet per acre)						
Hardwoods	16.6[a]	172.9	9.2[a]	275.2	26.1	146.0
Softwoods	200.4[a]	69.0	196.1	74.1	163.8	62.6
Total live[1]	**217.0**	-	**205.3**	-	**189.9**	-
Snags	23.1	216.9	28.8	208.8	17.4	246.4
Downed woody debris (tons per acre, by log diameter-class)[2]						
0-3 inches	0.80	0.75	0.83	0.82	0.82	0.74
>3 inches	11.84	1.67	13.76 [a]	1.43	9.36	1.39

[a] Significantly different from the corresponding random sites, at the 0.05 level of significance (Student's *t*-test).
[1] The sum of softwood and hardwood basal areas. Data were not available to compute a percent Coefficient of Variation for this variable.
[2] Assumes a specific gravity of 0.4 for downed woody debris.

Table 5H *Habitat characteristics (mean and percent Coefficient of Variation) of foraging* (n = *158) and random sites* (n= *256) from six California spotted owl home ranges in the Tahoe Study Area, central Sierra Nevada (Call 1990).*

	Foraging sites		Random sites	
	Mean	Percent CV	Mean	Percent CV
Physiographic attributes				
Percent slope	28.4	58.1	27.4	63.0
Elevation (feet)	3,852.0	12.5	3,888.0	13.9
Structural attributes				
Percent canopy cover	91.8[a]	12.4	85.2	47.1
Basal area (square feet per acre)				
Hardwoods	23.9	161.0	20.2	153.5
Softwoods	154 .9[a]	52.7	129.8	52.3
Total live	**178.7[a]**	**43.7**	**150.6**	**44.1**
Snags	15.3[a]	154.6	10.1	169.6
Basal area (square feet per acre, by d.b.h. class)[1]				
3.9-4.8 inches	1.6	374.5	2.2	379.2
4.9-10.7 inches	25.5	119.9	27.6	116.9
10.8-20.6 inches	52.8	79.7	51.8	86.2
20.7-35.5 inches	67.1[a]	81.1	49.5	94.7
>35.5 inches	32.1[a]	104.9	19.7	149.14
Downed woody debris (percent cover, by diameter class)				
1-11.8 inches	5.86	82.1	4.5	103.3
>11.8 inches	3.26	184.8	1.7	195.9

[a] Significantly different from the corresponding random sites, at the 0.005 level of significance (Student's *t*-test).
[b] Significantly different from the corresponding random sites, at the 0.001 level of significance (Mann-Whitney *U* test).
[1] Diameter at breast height.

Based on nest locations in trees, we recognize five nest types that are used regularly by spotted owls in the Sierra Nevada and southern California (table 5I). (1) Cavity nests (color photo 5-3) are placed in natural cavities resulting from decay, usually in the heartwood of a large, old tree. Cavities large enough for owl nests can form where large branches tear out of the trunk of the tree (side cavities). (2) Broken-topped trees and snags (color photo 5-8) may develop depressions via decay, or they may persist without much decay but still provide a broad enough surface for the owls to lay their eggs. (3) Platform nests (color photo 5-14) are those placed on remnant platforms built by other species (for example, goshawks, ravens, or tree squirrels), or on debris accumulations in densely branching structures of trees. (4) Dwarf mistletoe brooms are often dense enough that they form a suitable nest substrate. (5) "Undefined" nest types are those that do not clearly fall into types 1-4 or for which we lack data. In spite of the variety of nest types used by these owls, the nest trees are still generally larger than other trees within the same stand (see below, table 5K). The large trees most often selected for nest sites by California spotted owls also exhibited signs of old age. Forty-three percent of the nests were in large decay cavities, and another 16 percent were on broken-topped trees or snags (for example, color photo 5-8). Many other nests were placed on limb deformities that supported debris platforms.

Among 276 nests located recently, most of them in NFs in the Sierra Nevada and southern California, nest type varied markedly in different parts of the owl's range (table 5I). In particular, cavity nests dominated nest types in both northern and southern Sierran conifer forests, but platforms were most common in conifer forests of southern California, perhaps as a result of differences in the availability of nesting substrates (see LaHaye 1988). Patterns on industrial forest lands in the Sierra Nevada were similar, but with a greater proportion of platform nests. Based on a sample of 16 nests, half were cavity and half were platform type (Taylor 1992). Northern spotted owls in Oregon nested primarily in tree deformities (Forsman et al. 1984). A similar pattern was found among northern spotted owls in northwestern California (LaHaye 1988), but platform nests were more frequent in the southern part of that study area.

Forsman et al. (1984) reported that young northern spotted owls from several platform nests in Oregon left their nests several days earlier than young from cavity nests. Because they were younger and less able to climb, they spent longer on the ground than young from cavity nests. Forsman et al. speculated that, as a result, these young may have experienced higher predation while on the ground than young from cavity nests. LaHaye et al. (1992a), however, found no differences in overall nesting success among broods produced in cavity nests, broken-topped nests, or platform nests in the San Bernardino Mountains.

Table 5I-*Characteristics of nest trees used by California spotted owls, by major habitat type, based on data from all study areas except the Tahoe, and from all relevant National Forest files, 1986-1991.*

General habitat type	Number of nests	Tree condition		Nest type[1]					Nest tree	
		Alive	Snag	CA	BT	PL	MI	UN	Conifer	Hardwood
Northern Sierran Conifer	83	61	22	55	9	15	4	0	79	4
Southern Sierran Conifer	41	29	12	27	4	2	2	4	29	12
Southern California Conifer	139	128	11	33	28	78	0	0	109	30
Riparian/hardwood forests	13	13	0	5	3	5	0	0	0	13

[1]CA = cavity, BT = broken-top, PL = platform, MI = dwarf mistletoe, UN = undefined.

Table 5J-*Tree species used as nest sites by the California spotted owl, based on data from all study areas except the Tahoe, and from all relevant National Forest files, 1986-1991.*

General habitat type	White fir	Red fir	Douglas-fir	Bigcone Doug-fir	Incense-cedar	Sugar pine	Jeffrey pine	Ponderosa pine	Black oak	Live oak	White alder	Other[1]
Northern Sierran Conifer	22	9	21	0	7	16	2	8	3	0	0	1
Southern Sierran Conifer	12	5	1	0	1	2	2	5	12	0	0	1
Southern California Conifer	45	0	0	21	15	10	17	0	5	22	3	1
Riparian/hardwood forests	0	0	0	0	0	0	0	0	3	5	2	3

[1]One nest each was in giant sequoia, Coulter pine, blue oak, tanoak, cottonwood, and California sycamore.

Table 5K-*Nest stand and nest tree characteristics of California spotted owls, by general habitat type (mean ± SD), based on data from all study areas except the Tahoe, and from all relevant National Forest files, 1986-1991.*

General habitat type	Elevation (feet)	Total canopy cover (percent)	Nest tree d.b.h.[1] (inches)	Nest tree height (feet)	Nest height (feet)
Northern Sierran conifer	5,284 ± 922 *n* = 65	75.4 ± 17.2 *n* = 28	43.5 ± 14.7 *n* = 81	96.8 ± 36.7 *n* = 75	64.9 ± 25.7 *n* = 75
Southern Sierran conifer	5,750 ± 1355 *n* = 41	75.5 ± 27.4 *n* = 17	46.7 ± 19.6 *n* = 41	95.0 ± 52.7 *n* = 40	57.5 ± 31.0 *n* = 40
Southern California conifer	6,002 ± 1270 *n* = 137	79.3 ± 17.7 *n* = 131	37.0 ± 13.9 *n* = 139	87.5 ± 33.3 *n* = 139	56.5 ± 23.2 *n* = 139
Riparian/hardwood forests	2,618 ± 1271 *n* = 13	89.3 ± 10.6 *n* = 6	29.5 ± 16.6 *n* = 13	55.0 ± 23.5 *n* = 13	38.4 ± 14.0 *n* = 13

[1]Diameter at breast height.

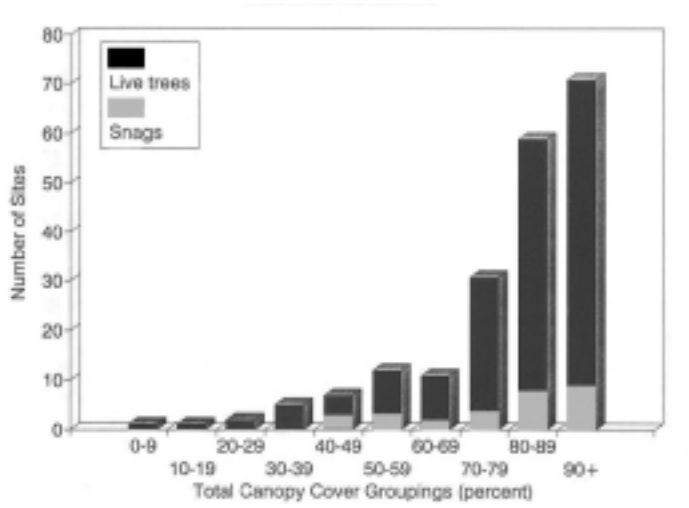

Figure 5F-Number of nest sites, by canopy-cover class; nests in snags and live trees are differentiated (*n* = 201).

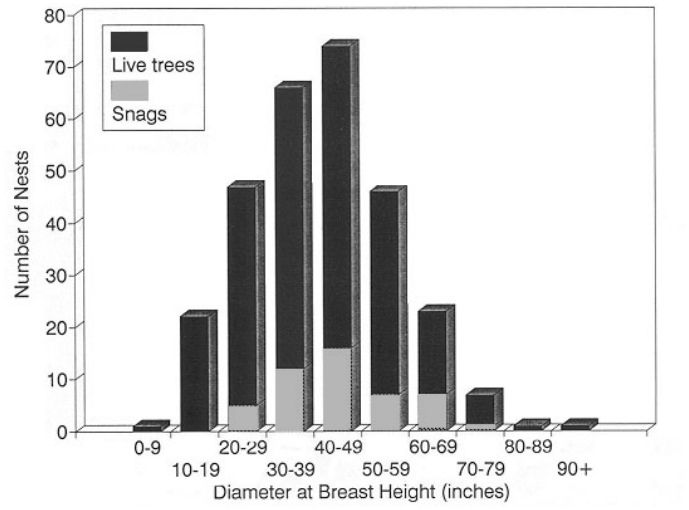

Figure 5G-Number of live trees and snags, by stem diameter-class, used for nest sites by California spotted owls (*n* = 288).

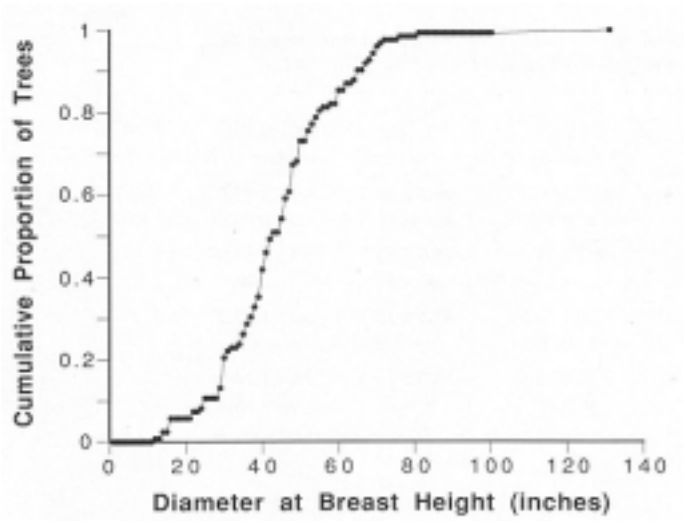

Figure 5H-Cumulative distribution of nest trees in the Sierra Nevada conifer zone, arranged by diameter at breast height (*n* = 122).

Nest Trees

Ten species of conifers and seven species of hardwoods accounted for all recent nest sites reported for California spotted owls (table 5J). Nest trees were typically in stands with high canopy cover-75.4 percent in Sierran conifer and 79.3 percent in southern California conifer forests (table 5K; see fig. 5F). These estimates compared favorably with those reported above for nest stands (tables 5B and 5C). Eighty-three percent of all nests in the conifer forests were in living trees (fig. 5G) and 82 percent were in conifers. These trees were very large, averaging about 90 feet tall (range 25-262 feet) and 41 inches in d.b.h. (range 9-81 inches), with means slightly higher in Sierran than in southern California conifer forests (table 5K). More than 75 percent of all nest trees were larger than 30 inches in d.b.h. (fig. 5H). Results from surveys of nest sites on industrial forest lands also showed that owls nested in large trees. Based on a sample of 17 nests from the Sierra Nevada conifer zone, nest tree d.b.h. averaged 41.8 inches (Taylor 1992).

The d.b.h. of nest trees in our current sample was significantly greater than that of conifers in general in the Sierra Nevada *even in 1900* (χ^2 = 167, df = 6, $P < 0.001$; fig. 5I), based on trees on plots measured by Sudworth (1900) prior to extensive logging. Interestingly, the diameter distribution of white fir trees used as nest sites by owls was not significantly different (χ^2 = 7.469, df = 5, $P > 0.10$; fig. 5J) from that of white firs measured by Sudworth. The white fir comparison is appropriate because that was the most common nest tree species used by California spotted owls (table 5J). Comparison of the sample of nest trees from Sierran conifer forests to the current diameter distribution in the M4G timber strata on the Tahoe NF also shows extensive selection for large-diameter trees (fig. 5K). To the extent that the Tahoe NF sample is representative of this timber strata in the Sierra Nevada, selection for large trees for nesting is clearly evident.

The significant inference from these results is that California spotted owls in conifer forests today are selecting nest trees from among the few remaining trees that are as large as or larger than average trees in 1900, before extensive logging began to remove the largest trees from the forest. When this pattern is coupled with the past and projected future trends of large trees in the Sierra Nevada (Chapter 13), it is reasonable to hypothesize large-diameter trees as a current or potentially limiting factor sometime in the future. That is, even if large trees are not currently limiting, we have reason to be concerned that they could soon be limiting if specific constraints on their removal are not invoked in the near-term.

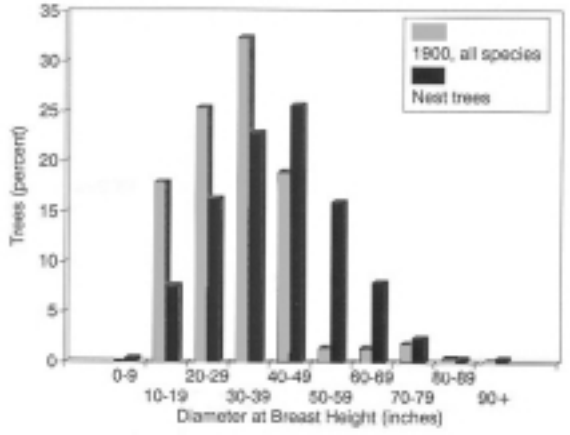

Figure 5I-Proportions of nest trees (recent) and trees available in stands in 1900 (Sudworth 1900), by stem diameter-class.

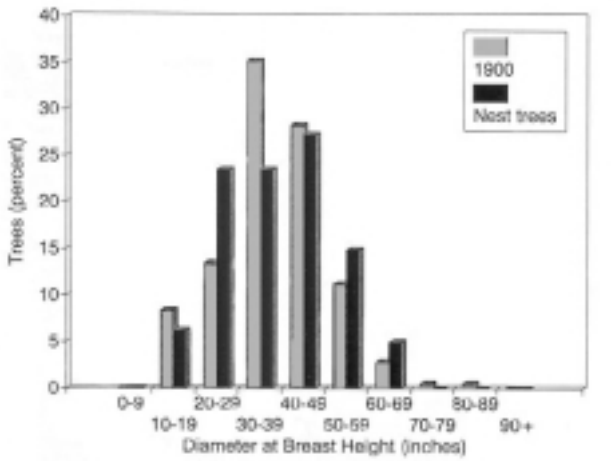

Figure 5J-Proportions of nest trees (recent) that were white firs, and white firs available in stands in 1900 (Sudworth 1900), by stem diameter-class.

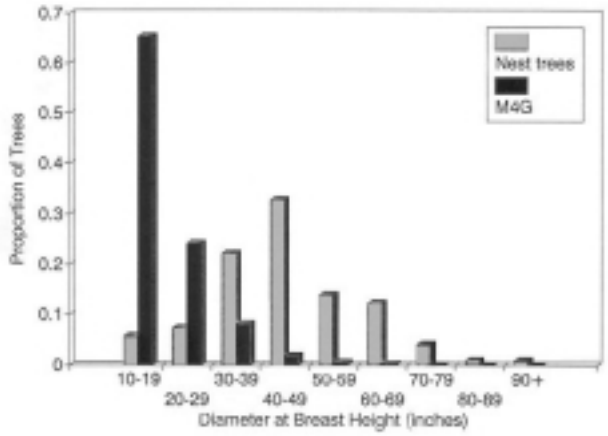

Figure 5K-Proportion of nest trees (recent) in Sierran conifer forests (*n* =122) and trees currently available in M4G stands on the Tahoe NF, by stem diameter-class.

Foothill Riparian/Hardwood Forests

Measurements of winter foraging sites and foraging stand attributes in foothill riparian/hardwood forests were available for the Eldorado Study Area (Laymon 1988) and the Sierra Study Area (Steger and Eberlein pers. comm.) (tables 5D and 5L). Because sample sizes were small, these analyses should be considered as preliminary at this time. Point estimates suggest about the same range of values for percent canopy cover as observed in the conifer forests at higher elevations (compare tables 5D, 5F, and 5L). Basal areas of green trees and snags were considerably less, and shrub density was much higher in the hardwood type than in the conifer forest. Based on Laymon (1988), and a comparison of tables 5F and 5L, together with considerable on-site experience with these habitats, we found that riparian/hardwood forests dominated by oaks tended to have less canopy layering than most sites in the Sierran mixed-conifer and ponderosa pine/hardwood types (color photos 5-23 and 5-25). Multiple layers were present, however, in the mixed-hardwood forests in southern California, where spotted owls occur in narrow riparian corridors in steep-sided canyons, as in the Los Padres NF (color photo 5-28). Tables 5D and 5L also suggest less downed woody debris in the low-elevation hardwood type, compared to conifer forests.

Nest sites in riparian/hardwood forests averaged about 2,600 feet in elevation. No pattern was evident in the types of nests found in these forests (table 5I), but the sample size was too small to establish a pattern if one existed. All of the nests located were in hardwoods that averaged 55 feet tall (range 16-98 feet) and 30 inches in d.b.h. (range 13-72 inches) (table 5K).

Collectively, these data indicate that owl habitat in the foothill/riparian forests was characterized by both lower live tree basal area and lower canopy cover than higher-elevation sites in the conifer zone. The high closure measured at nest sites in the foothill zone (table 5K) may represent a highly localized phenomenon-one uncharacteristic of stands in this area in general. Furthermore, in the foothill habitats, the average nest-tree d.b.h. was smaller (table 5K) and platform nests were more common (table 5I) than in the conifer zone. Given these contrasts, the structure of owl habitats in foothill riparian/hardwood forests appeared to be substantially different from that in mixed-conifer forests. We caution that no data exist that suggest that stand basal areas, cover classes, and nest-tree sizes used in the foothill/riparian zone would, if created in the conifer zone, provide suitable owl habitat. Indeed, owls that migrated to low-elevation sites for the winter moved back upslope and chose dense stands with large trees in the mixed-conifer forest as summer habitat (table 5D).

Table 5L-*Structural attributes of habitats (mean and percent Coefficient of Variation, by canopy cover class) used by California spotted owls during radio-tracking studies in the riparian/hardwood zone of the Sierra Study Area, southern Sierra Nevada (Steger and Eberlein pers. comm.).*

Structural Attributes	0-39 percent canopy cover (*n* = 7)		40-69 percent canopy cover (*n* = 5)		70+ percent canopy cover (*n* = 8)	
	Mean	Percent CV	Mean	Percent CV	Mean	Percent CV
Percent canopy cover						
By densiometer	36.3[a]	39.4	67.26	11.8	74.3[b]	16.3
By aerial photos	15.9[a]	66.8	59.06	11.6	80.0[c]	5.8
Basal area (square feet per acre)						
Green trees	20.0[a]	80.0	50.1[b]	51.5	65.6[b]	67.1
Snags	0.9[a]	175.0	4.1	87.2	5.0[b]	80.7
Hardwoods (by d.b.h. class)[1]						
0-4.7 inches	1.4[a]	124.2	4.6[b]	48.1	6.5[b]	91.9
4.8-10.6 inches	6.7	115.0	18.8	37.4	19.0	30.7
10.7-20.5 inches	5.9	97.8	12.9	61.5	20.0	113.7
20.6-35.4 inches	5.1	125.0	8.5	80.9	12.0	129.1
>35.5 inches	1.0	262.5	5.4	150.0	1.3	279.3
Total	**20.0[a]**	**79.4**	**50.2[b]**	**51.4**	**58.7[b]**	**65.3**
Softwoods (by d.b.h. class)[1]						
0-4.7 inches	0	0	0	0	0.1	200.0
4.8-10.6 inches	0	0	0	0	0.3	300.0
10.7-20.5 inches	0	0	0	0	2.3	219.2
20.6-35.4 inches	0	0	0	0	4.4	281.0
>35.5inches	0	0	0	0	0	0
Total	**0**	**0**	**0**	**0**	**7.0**	**258.1**
Shrubs per acre	105.0	198.8	69.0	62.5	127.0	144.4
Downed woody debris (tons per acre, by log diameter-class)[2]						
11-20 inches	0.09	264.4	0.10	223.5	0.68	164.1
21-35 inches	0		0.41	223.7	0.45	187.5
>35 inches	0		0		0	

[a,b,c] Values in the same row with different alpha superscripts are different at the 0.05 level of significance (one-way ANOVA).

[1] Diameter at breast height, in inches.

[2] Assumes a specific gravity of 0.4 for downed woody debris.

Discussion

General Patterns of Habitat Use

The first specimen of the spotted owl was collected by Xantus (1859) in the Tehachapi Mountains of southern California. This bird was likely found in the closed-canopied, riparian/hardwood forests common to the Fort Tejon region. Following this first documented sighting by Europeans, many reports of California spotted owls appeared in the literature over the next 80 years (see Grinnell and Miller 1944, Gould 1974). These reports and several nest records at the Western Foundation of Vertebrate Zoology (Kiff pers. comm.) indicated that California spotted owls in past decades used both conifer and hardwood habitats, and were found consistently in densely forested areas.

More recent observations and studies document the habitat associations of this bird throughout its range and in a quantitative fashion. These results suggest some general patterns about habitat use by California spotted owls. First, they use a broader array of habitats than used by the northern spotted owl. Second, within the general habitat types selected, they use forest patches that are complex in structure relative to what is available (for example, many trees in different diameter-classes and high canopy closure). Third, California spotted owls appear to select remnants of the older Sierran and San Bernardino conifer forests that have managed to survive 200-400 years to the present time (see table 5M). Especially for nesting and roosting, present data from several different sources suggest that most California spotted owls select dense stands with very large, presumably old trees. Fourth, although habitat attributes associated with California spotted owls at their nest and roost sites parallel those associated with northern spotted owls, foraging habitat used by the California subspecies appears to be much more variable than for its northern relative. Indeed, the considerable range in variation found in habitats used by California spotted owls is well-illustrated by the photos at the end of this chapter. In spite of this variation, however, results of studies reported in this chapter firmly establish that these owls use their forested environment in a nonrandom fashion.

Table 5M-*Core data (mean ± SD) and ages of nest trees used by California spotted owls in the San Bernardino Mountains; sample sizes are in parentheses beneath means and SDs.*

Trees	D.b.h.[1]	Tree height[2]	Nest height[2]	Core age in years	Mean percent of total radius cored
All trees	41 ± 13.0 (30)	103 ± 32.9 (30)	65 ± 4.3 (30)	230 ± 93.8 (29)	69 ± 26.4 (29)
White fir	41 ± 11.7 (14)	91 ± 25.1 (14)	65 ± 19.2 (14)	238 ± 68.2 (14)	70 ± 20.1 (14)
Sugar pine	37 ± 17.6 (3)	90 ± 31.2 (3)	53 ± 22.0 (3)	217 ± 43.1 (3)	46 ± 48.2 (3)
Jeffrey pine	40 ± 14.8 (8)	116 ± 37.9 (8)	68 ± 27.8 (8)	223 ± 143.1 (8)	78 ± 26.3 (8)
Incense-cedar	46 ± 15.8 (3)	131 ± 29.0 (3)	83 ± 27.5 (3)	193 ± 111.0 (3)	64 ± 31.4 (3)
Bigcone Douglas-fir	48 ± 16.1 (2)	115 ± 54.5 (2)	42 ± 28.3 (2)	320 ± 0.0 (1)	48 ± 0.0 (1)

[1] Diameter at breast height, in inches.
[2] Height in feet.

The association between the variable habitats used by California spotted owls and their population effects is not well understood. For example, we do not know if the birds survive and reproduce equally well in each of the many habitat types where they are found. We strongly suspect, however, that populations in some of those habitats are "sources" (reproduction exceeds replacement needs within the population, so surplus young are produced which emigrate to other areas) and populations in others are "sinks" (where reproduction is generally insufficient to replace local losses, so maintenance of the population requires immigration from other areas). We also do not know if spotted owls in the Sierra Nevada evolved in a more heterogeneous environment than was the case for northern spotted owls. Spotted owls evolving in different environments may exhibit different adaptive responses (for example, see Gutiérrez and Pritchard 1990). Although we do not yet know the answers to some of these critical questions, we infer that human-induced habitat changes (for example, from logging) may adversely affect the owls and lead to population declines.

California spotted owls in conifer forests exhibited significant overuse of M4G stands at the landscape scale. These are dense (70+ percent canopy cover) mixed-conifer forests with canopy trees averaging ≥24 inches in d.b.h. This pattern of selectivity was corroborated by comparisons with random locations of stands used for nesting, roosting, and foraging in the conifer forest. The vast majority of birds used sites with greater canopy cover, total live tree basal area, basal area of softwoods and hardwoods, and snag basal area than found at random sites. These are attributes that we would expect to find in M4G stands. Finally, selection of nest sites and nest trees by the owls further corroborates the findings from analyses at other scales of resolution. A high proportion of nest sites, especially in Sierran conifer forests, were in natural cavities or in broken-topped trees or snags. Trees used for nest sites were significantly larger and probably older than available in the general forest matrix, even in M4G stands. This pattern suggests that, currently, most nest trees are surviving remnants from forests of past centuries.

Is the Owl A Habitat Specialist?

In spite of the fact that the owl used a range of habitat conditions, we believe it should be characterized as a specialist. For example, we observed that 80 percent of all nest trees were located in stands with canopy cover of at least 70 percent. The average (and median, and modal) d.b.h. of nest trees in the Sierra Nevada was about 45 inches, but only 2 percent of all trees greater than 10 inches in d.b.h. in M4G stands on the Tahoe NF were in the 40-49 inch d.b.h. group. By specialist we mean an animal that shows a clear selection for certain habitats or habitat attributes. Two assumptions we invoked in our analyses were (1) the pattern of habitat usage we observed was not constrained by any other species, and (2) the use of a habitat type significantly in excess of its availability reflects selection. The degree to which these assumptions were met is unknown. It is possible, for example, that the California spotted owl's pattern of habitat use was influenced by competition with another raptor species. Also, the methods we used can be misleading if, for example, the preferred habitat is also the most common habitat. Regarding these two possibilities, we have no data that suggest direct competitive interactions with other raptor species, and the habitat used most commonly for nesting (M4G) is uncommon (about 20 percent, based on FS inventory data) in the Sierran landscape.

We do not claim dependence by the spotted owl upon any given habitat type or attribute. Further, we do not contend that our data, at this time, indicate that any given habitat type or attribute is "required," in the sense that its absence would lead to the owl's extinction. But we do believe that the habitat distribution patterns of the majority of owls, given the constraints of availability and possible biotic interactions, currently reflect optimal choices. If better choices were available, natural selection would act to remove those individuals making the wrong choice.

Based on our definition of a specialist and the operational manner in which we identified selection, we believe we have made the best use of the available data to craft a set of recommendations intended to secure future options for managing the

species. We have based our inferences on what the majority of the owls selected from among choices in their habitats, and assumed that these choices reflected the most important attributes to retain in future landscapes.

Recommendations

Translating all the habitat association patterns into a general characterization of nesting, roosting, and foraging stands that should be suitable for spotted owls in conifer forests is difficult. It is also risky! All too often, suggestions offered tentatively are misconstrued to be the last and definitive word on the matter. Even with these misgivings, however, we offer here some tentative estimates of stand attributes, based mainly on tables 5B-5H. Given these caveats, the tabulation below may be a fair, initial representation of the range of mean values of some attributes in suitable habitat for spotted owls in Sierran mixed-conifer forests. Most values in the tabulation generally reflect the range of means from the various studies reported in this chapter. We have combined values for nesting and roosting stands, because (1) they tend to be very similar, (2) spotted owls commonly roost within the stands that include their nests, and (3) we believe that a stand suitable for nesting would also provide conditions satisfying the roosting needs of the owls.

	Nesting and roosting stands	Foraging stands
Percent canopy cover[1]	70-95	50-90
Total live tree basal area[2]	185-350	180-220
Total snag basal area	30-55	15-30
Basal area of large snags[3]	20-30	7-17
Downed woody debris[4]	10-15	10-15

[1] Mostly in canopy ≥30 feet high, including hardwoods.
[2] Square feet per acre.
[3] Dead trees ≥15 inches in d.b.h. and ≥20 feet tall.
[4] Tons per acre.

The values for total snag basal area are high and reflect sampling of all, or nearly all, dead trees by various workers. We believe, however, that relatively small snags have little value in terms of spotted owl habitat. Snags need to be large enough to accommodate nest sites for medium to large cavity-nesting birds and den sites for flying squirrels. In addition, larger snags take longer than small snags to decompose after they have fallen. We consider snags that are at least 15 inches in d.b.h. and 20 feet tall to be near the smaller end of suitability for owl habitat. In two comparisons of total snag basal area with the basal area of "large" snags (≥15 inches in d.b.h. and ≥20 feet tall (table 5E), large snags comprised 45 percent and 59 percent of the total. Snag values in the above tabulation could be adjusted accordingly to estimate the basal area of large snags in owl habitats. This limited analysis suggests that owl nest and roost sites have from about 19 to 31 square feet basal area of large snags, and foraging sites have from 7 to 17. Because we recommended an interim approach to management for spotted owls in the Sierra Nevada (Chapter 1), one based on the concept of preserving all options for future management of spotted owls, we recommend maintaining at least 20 square feet basal area of large snags wherever possible in owl habitat. Based on current information, this standard appears to be appropriate for maintenance of suitable nesting and roosting sites. It is at the lower end of estimates for nesting and roosting sites and slightly above the upper end of estimates for foraging sites.

Estimates of the mass of downed wood in owl nesting, roosting, and foraging sites ranged from 10.5 to 24.7 tons per acre, with a mean of 17.4 and a standard deviation of 5.3. (Based on values in tables 5D-5G, and on approximations of tons/acre from values given in tables 5B and 5H.) Most of this was in pieces at least 11 inches in diameter. We believe that much of this has managed to accumulate because of effective fire suppression in Sierran conifer forests during the past 80-90 years, so these quantities probably exceed what was present during presettlement times. Fuels management specialists from R5 and from NFs in the Sierra Nevada have assured us that the fuel loads indicated by the average in owl habitats represent a significant hazard vis-à-vis the intensity of fires and the likelihood of stand-destroying fires. Consequently, we believe that a compromise is needed between fire threats and what the data indicate to be typical quantities of large logs in owl habitats. We suggest a range of 10-15 tons per acre, in the largest logs available, and believe it is inadvisable to retain logs smaller than 11 inches in diameter to attain this level. This range is at the low end of the values observed in owl habitats.

Research Considerations

Despite the considerable amount of study already done in an effort to estimate habitat-use patterns by spotted owls, we still have limited knowledge about this critical aspect of the bird's ecology. This is particularly true relative to the relations between habitat and demographic variation. This is the case largely for three reasons. First, research on this subspecies was slow in getting started, because most of the early concern was directed at the northern spotted owl. Funds available for research on the California spotted owl have not been sufficient to allow studies of their prey, or even to complete a full inventory of all habitats where the owl is likely to occur. Second, most definitive studies of the California spotted owl were initiated in 1986 or later. Coincidentally, this was when the current drought began (fig. 4H), making it impossible to determine whether observed results from owl studies should be interpreted primarily in relation to changing habitat conditions, to the drought, or both. Third, knowledge about different gradations in habitat suitability must be based on habitat-specific studies of the owl's demography--whether or not they reproduce well enough in a given habitat to equal or exceed annual mortality rates.

Demographic information on owl populations in a variety of different habitats will take many years to obtain and will depend on monitoring demographic trends through both wet and dry climatic periods. We should continue to build on existing demographic studies to attain some of the information needed, because they already have an accumulating database. We also need to consider a range of options for adding other demographic studies. In particular, we see great potential for demo-

graphic studies on lands of some of the major commercial timber companies whose forest practices differ in important ways. These are ad hoc experiments (Bias and Gutiérrez 1992) on the effects of different management regimes on the owls.

Every effort should be made to establish consistent methods, attributes to be measured, data forms, and analytical procedures to be used by all researchers on California spotted owls. Failing adoption of standard methods and so on, quantitative relations among different techniques should be developed to ease interpretation of data from different studies. Finally the efficiency and utility of different techniques should be explored to encourage adoption of a uniform protocol for basic information collection in the field.

The "Achilles heel" of wildlife management is separating correlation and causation. All analyses of habitat described in this paper are based on correlational studies. That is, we observe a particular variable, such as canopy closure, to be consistently high at owl sites relative to available sites, but we do not know if that variable is the reason why owls are present at the site. They may be there because canopy closure is usually associated with a different stand attribute, one that we have not measured and one that may be too subtle to quantify. Hence, we do not know if changes in canopy closure will consistently result in a functional response by owls inhabiting a site. The fact that we have not demonstrated cause-and-effect relations, however, does not dilute the power of these documented trends. Rather, it tempers our recommendations about managing for functional owl habitat.

Controlled experiments, in which one or more attributes are changed and subsequent functional responses of the owls are documented, are the best way to identity cause-and-effect relations. Experimentation in certain fields of science is the rule (for example, see Platt 1964). Experiments in natural ecosystems, however, are generally orders of magnitude more complicated and less controllable than experiments in fields like chemistry, physics, or molecular biology. Nevertheless, the widespread logging of forests for commodity production provides a possibility of undertaking ecological experiments on owl responses to changes in habitat. Experiments can occur at two spatial scales--the landscape (that is, a collection of owl home ranges) and the site (within a forest patch occupied by an owl or pair of owls). The critical question to be asked is: Do the changes in spatial arrangement or the structure and composition of habitats affect the owl's ability to survive and reproduce? Formulation of specific experiments should be based on empirical information generated from natural history studies (see above) and the creative application of results from modeling habitat conditions observed in natural history studies. The success of experiments in discerning alternative outcomes will determine their potential for applying a management system to a larger landscape.

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Color Photo Section

Habitat from throughout the range of the California spotted owl

5-1-Foraging habitat. Note the extensive downed wood and abundant staghorn lichen on tree trunks. Dominant trees, in order, were red fir, white fir, and Jeffrey pine; some sugar pines were present but not visible in the photo.

Habitat type: ----------Sierran Red Fir
Location: ----------Lassen National Forest
Elevation: ----------6,170 feet
Date: ----------24 June 1991
Photographer: ----------John S. Senser

5-2-Typical red fir canopy. This site was occupied by owls 5 of the 6 years surveyed, 3 of these years by pairs.

Habitat type: ----------Sierran Red Fir
Location: ----------Eldorado National Forest
Elevation: ----------6,000 feet
Date: ----------24 June 1991
Photographer: ----------John S. Senser

5-3-Probable nest tree with adult and two juvenile owls. The nest may have been the cavity in the bole of the tree, above the owls.

Habitat type: ----------Sierran Red Fir
Location: ----------Tahoe National Forest
Elevation: ----------7,000 feet
Date: ----------26 June 1991
Photographer: ----------John S. Senser

5-4-The forest floor in a foraging area showing a thick mat of decomposing organic matter. The fallen trees progress from recognizable trunks (background) to a spongy mass of organic matter (foreground).

Habitat type: ----------Sierran Red Fir
Location: ----------Lassen National Forest
Elevation: ----------6,170 feet
Date: ----------29 June 1991
Photographer: ----------John S. Senser

5-5—A foraging habitat in red and white fir showing the multi-storied nature of the stand and the presence of natural snags (left center).

Habitat type: ----------Sierran Red Fir
Location: ----------Tahoe National Forest
Elevation: ----------6,800 feet
Date: ----------26 June 1991
Photographer: ----------John S. Senser

5-6—Mixed-conifer canopy 50 feet north of a spotted owl nest site in the cavity of a giant sequoia. Trees represented here were white fir, sugar pine, and giant sequoia.

Habitat type: ----------Sierran Mixed-conifer
Location: ----------Sequoia National Park
Elevation: ----------6,200 feet
Date: ----------10 July 1991
Photographer: ----------John S. Senser

5-7-Ground litter 100 feet east of a nest tree. Observe the extensive decomposing deadwood, which may provide shelter and nurture food resources (such as hypogeous fungi) for the owl's prey.

Habitat type: ----------Sierran Mixed-conifer
Location: ----------Sequoia National Park
Elevation: ----------7,000 feet
Date: ----------10 July 1991
Photographer: ----------John S. Senser

5-8-Nest snag. Overstory canopy cover around the nest was about 30 percent, and about 40 percent in the surrounding forest. The pair at this site produced two young in 1991; they were found roosting nearby in a dense stand of ponderosa pine and incense-cedar. The area was logged for large pines during the railroad logging era of the 1920s, selectively cut in 1980, and re-entered for additional salvage logging in 1989 and 1990. Today, the forest is composed mostly of a mosaic of height classes and trees not more than 70 years old (with scattered 120-year-olds).

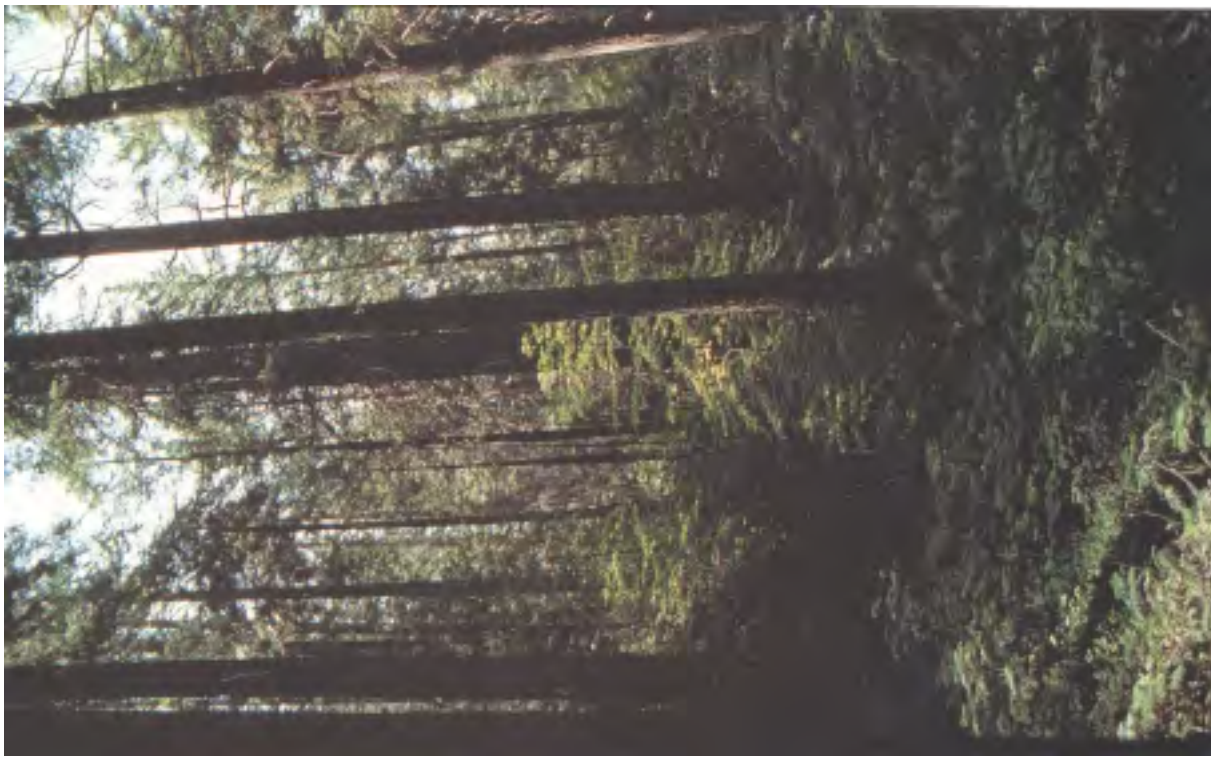
Habitat type: ----------Sierran Mixed-conifer
Location: ----------Fiberboard Timber Company
(within Stanislaus National Forest)
Elevation: ----------4,400 feet
Date: ----------8 July 1991
Photographer: ----------John S. Senser

5-9—Foraging area in a site where owl young were produced in 1990 and 1991. This site was mainly white fir with a crown closure of 70 percent and a dense understory of Pacific dogwood and California hazelnut.

Habitat type: ----------Sierran Mixed-conifer
Location: ----------Sequoia National Park
Elevation: ----------5,000 feet
Date: ----------10 July 1991
Photographer: ----------John S. Senser

5-10—Foraging habitat composed of dispersed, large ponderosa pines and a dense understory of white fir and Douglas-fir saplings and pole-sized trees. Note extensive downed wood and forest litter.

Habitat type: ----------Sierran Mixed-conifer
Location: ----------Eldorado National Forest
Elevation: ----------2,800 feet
Date: ----------24 June 1991
Photographer: ----------John S. Senser



5-11—Adult spotted owl at roost in a mixed-conifer stand of white fir and incense-cedar, with a thick understory of Pacific dogwood.

Habitat type: ---------- Sierran Mixed-conifer
Location: ---------- Eldorado National Forest
Elevation: ---------- 4,300 feet
Date: ---------- 24 June 1991
Photographer: ---------- John S. Sensor

5-12—Nest stand of mixed-conifer showing canopy of white fir, Douglas-fir, and incense-cedar. The nest cavity is about half way up the center incense-cedar. This site has high fidelity by spotted owls, with pair occupancy for the last 6 years of survey.

Habitat type: ---------- Sierran Mixed-conifer
Location: ---------- Eldorado National Forest
Elevation: ---------- 4,300 feet
Date: ---------- 24 June 1991
Photographer: ---------- John S. Sensor

5-13—Nest stand in Sierran mixed-conifer, mostly second-growth white fir and ponderosa pine. Note owl in dense foliage of white fir (upper center). This site had successful reproduction of two young in 1991.

Habitat type: ----------Sierran Mixed-conifer
Location: ----------Sierra Pacific Industries land
(within Tahoe National Forest)
Elevation: ----------4,400 feet
Date: ----------26 June 1991
Photographer: ----------John S. Senser

5-14—Nest tree (center) situated about 100 feet to the right of the view at left. The nest was found in the crotch formed by the recrowning of the broken topped white fir. Note the dense, multi-storied understory below the nest tree.

Habitat type: ----------Sierran Mixed-conifer
Location: ----------Sierra Pacific Industries land
(within Tahoe National Forest)
Elevation: ----------4,400 feet
Date: ----------26 June 1991
Photographer: ----------John S. Senser

5-15—Foraging area showing a mixture of conifers (mostly Douglas-fir) and black oak.

Habitat type: ----------Sierran Conifer/Hardwood
Location: ----------Eldorado National Forest
Elevation: ----------3,200 feet
Date: ----------25 June 1991
Photographer: ----------John S. Senser

5-16—This area was logged during the railroad logging era of the 1920s and selectively cut since. The oldest conifers are 70-120 years old. The photo shows a foraging area in a mixture of conifers (mostly white fir and sugar pine) with black oak. Note the multi-storied nature of the stand and the ground cover of broad-leaf lupine in the foreground.

Habitat type: ----------Sierran Conifer/Hardwood
Location: ----------Stanislaus National Forest
Elevation: ----------3,700 feet
Date: ----------8 July 1991
Photographer: ----------John S. Senser

5-17-Canopy typical of the Sierran Conifer/Hardwood type, showing a 60-70 percent closure of white fir and black oak.

Habitat type: ----------Sierran Conifer/Hardwood
Location: ----------Stanislaus National Forest
Elevation: ----------3,700 feet
Date: ----------8 July 1991
Photographer: ----------John S. Senser

5-18-Ground cover 30 feet west of a nest tree, showing a dense understory of bigleaf maple and conifer saplings. Note the extensive layer of needle/cone litter and presence of large downed limbs, such as the black oak limbs seen here.

Habitat type: ----------Sierran Conifer/Hardwood
Location: ----------Eldorado National Forest
Elevation: ----------4,200 feet
Date: ----------25 June 1991
Photographer: ----------John S. Senser

5-19—Black oak nest tree in 1991 (to left of group). The nest was in a cavity in one of the large limbs.

Habitat type: ---------- Sierran Conifer/Hardwood
Location: ---------- Fiberboard Timber Company (within Stanislaus National Forest)
Elevation: ---------- 4,400 feet
Date: ---------- 8 July 1991
Photographer: ---------- John S. Senser

5-20—Tanoak nest tree in 1991. Note extensive understory of young pines, Pacific madrone, and tanoak. This area has seen considerable disruption in the past 100 years. At least three fires and extensive mining have impacted this habitat.

Habitat type: ---------- Sierran Conifer/Hardwood
Location: ---------- Plumas National Forest
Elevation: ---------- 2,880 feet
Date: ---------- 20 June 1991
Photographer: ---------- John S. Senser

5-21-Overview of owl foraging habitat showing the live oaks that are typical of the area.

Habitat type: ----------Sierran Foothill Hardwood
Location: ----------Sierra National Forest
Elevation: ----------1,360 feet
Date: ----------9 July 1991
Photographer: ----------John S. Senser

5-22-Roost area in a streamside location. The photo shows dense stands of California sycamore and live oak. A roosting owl is visible on a limb in the upper-center of the photo. Nearby Cooper's hawk nests in canopies of interior live oaks provided nesting platforms in 1989 and 1990.

Habitat type: ----------Sierran Foothill Hardwood
Location: ----------Sierra National Forest
Elevation: ----------1,360 feet
Date: ----------9 July 1991
Photographer: ----------John S. Senser

5-23—Owl wintering site in interior live oak habitat. Note the abundance of downed wood. Researcher Barry Noon is examining a woodrat nest in the live oak canopy.

Habitat type: ----------Sierran Foothill Hardwood
Location: ----------Sierra National Forest
Elevation: ----------1,000 feet
Date: ----------9 July 1991
Photographer: ----------John S. Senser

5-24—Interior live oak canopy at owl wintering site. Observe woodrat nest in canopy (right center).

Habitat type: ----------Sierran Foothill Hardwood
Location: ----------Sierra National Forest
Elevation: ----------1,000 feet
Date: ----------9 July 1991
Photographer: ----------John S. Senser

5-25-Woodrat nests in owl foraging area showing distribution of nests in oak woodland.

Habitat type: ----------Sierran Foothill Hardwood
Location: ----------Sequoia National Forest
Elevation: ----------3,300 feet
Date: ----------11 July 1991
Photographer: ----------John S. Senser

5-26-Overview of a north-facing slope with typical owl habitat as it occurs in the central coastal region. The slope shows a mix of conifers (mostly coast redwood, Douglas-fir, Coulter pine, and sugar pine) and hardwoods (live oak, Pacific madrone, and California-laurel). Chamise, sagebrush, other chaparral species, yucca, and grasses are dispersed along the well-grazed, south-facing slopes.

Habitat type: ----------Central Coastal Redwood/
California-laurel
Location ----------Los Padres National Forest
Elevation: ----------3,000 feet
Date: ----------13 July 1991
Photographer: ----------John S. Senser

5-27—Overview of coastal redwoods showing multi-storied stand. The large trees here measured 46 inches in diameter at breast height and were 300-400 years old.

Habitat type: ----------Central Coastal Redwood
Location: ----------Los Padres National Forest
Elevation: ----------2,100 feet
Date: ----------13 July 1991
Photographer: ----------John S. Senser

5-28—Riparian area 300 feet downstream from a nest grove, showing the creekside California-laurel and white alder typical of these owl foraging areas.

Habitat type: ----------Riparian/Mixed Hardwood
Location: ----------Angeles National Forest
Elevation: ----------3,860 feet
Date: ----------19 August 1991
Photographer: ----------John S. Senser

5-29-Foraging area typical of riparian/hardwood habitat. The roost site is farther up-canyon (upper center of photo). The dense chaparral cover on the slopes blends with the thick white alder, live oak, and California-laurel along the stream channel, making it difficult to trace its course in the photo.

Habitat type:----------Riparian/Mixed Hardwood
Location: ----------Los Padres National Forest
Elevation: ----------2,400 feet
Date: ----------12 July 1991
Photographer: ----------John S. Senser

5-30-Roost area showing good cover composed of coast live oaks, California-laurel, and streamside white alder.

Habitat type: ----------Riparian/Mixed Hardwood
Location: ----------Los Padres National Forest
Elevation: ----------2,520 feet
Date: ----------12 July 1991
Photographer: ----------John S. Senser

5-31-Stream diversion to a reservoir for domestic use. Future water demands, especially in southern California, may have a marked negative impact on spotted owl habitat.

Habitat type:----------Riparian/Mixed Hardwood
Location: ----------Los Padres National Forest
Elevation: ----------2,250 feet
Date: ----------12 July 1991
Photographer: ----------John S. Senser

5-32-Canopy typical of riparian/mixed-hardwood habitats. Trees pictured include bigleaf maple, California-laurel, and white alder. California sycamore was also present but not visible in this photo.

Habitat type:----------Riparian/Mixed Hardwood
Location: ----------Los Padres National Forest
Elevation: ----------2,290 feet
Date: ----------12 July 1991
Photographer: ----------John S. Senser

5-33-Overview of foraging habitat showing stands of bigcone Douglas-fir and canyon live oak on the moister north-facing slopes and various species of shrubs from the chaparral community on the drier, more south-facing slopes.

Habitat type: ----------Bigcone Douglas-fir
Location: ----------Angeles National Forest
Elevation: ----------3,400 feet
Date: ----------19 August 1991
Photographer: ----------John S. Senser

5-34-Ground view 60 feet west of a nest tree. Observe the extensive dead wood, which can provide shelter for owl prey.

Habitat type: ----------Mixed-conifer/Black Oak/Live Oak
Location: ----------San Bernardino National Forest
Elevation: ----------5,920 feet
Date: ----------21 August 1991
Photographer: ----------John S. Senser

5-35-Within a nest grove. The dominant tree species here were canyon live oak, incense-cedar, white fir, and assorted pines. Canopy closure was about 75 percent.

Habitat type: ----------Mixed-conifer
Location: ----------San Bernardino National Forest
Elevation: ----------5,920 feet
Date: ----------September 1988
Photographer: ----------William S. LaHaye

5-36-Looking north from a nest tree. Note the open character of the canopy but relatively dense lower vegetative cover, composed here of curlleaf mountain mahogany. Only two of 131 nest sites and four of 134 owl territories found in the San Bernardino Mountains were in these open habitats (LaHaye et al. 1992).

Habitat type:----------Mixed-conifer with Pinyon Pine and Mountain Juniper
Location: ----------San Bernardino National Forest
Elevation: ----------8,100 feet
Date: ----------21 August 1991
Photographer: ----------John S. Senser

5-37—In the vicinity of a nest site. Tree species found here were white fir, Jeffrey pine, incense-cedar, and black oak. Canopy closure was about 70 percent.

Habitat type: ---------- Southern California Mixed-conifer
Location: ---------- San Bernardino National Forest
Elevation: ---------- 7,200 feet
Date: ---------- October 1988
Photographer: ---------- William S. LaHaye

5-38—White alder nest tree. Typical riparian/hardwood habitat providing good canopy cover.

Habitat type: ---------- Riparian/Mixed Hardwood
Location: ---------- Los Padres National Forest
Elevation: ---------- 2,500 feet
Date: ---------- 12 July 1991
Photographer: ---------- John S. Senser

5-39—This habitat burned in 1987 but has recovered quickly. Crown sprouting by the black oak (left) and bigcone Douglas-fir (right) has hastened the recovery. An owl pair was found here 2 years after the fire.

Habitat type: ---------- Bigcone Douglas-fir
Location: ---------- Cleveland National Forest
Elevation: ---------- 4,680 feet
Date: ---------- 21 August 1991
Photographer: ---------- John S. Senser

5-40—Canopy at an owl foraging area showing bigcone Douglas-fir, live oak, and black oak.

Habitat type: ---------- Bigcone Douglas-fir
Location: ---------- Cleveland National Forest
Elevation: ---------- 4,680 feet
Date: ---------- 21 August 1991
Photographer: ---------- John S. Senser

5-41—Roost area where an immature male owl was captured for banding. Vegetation shown: sugar pine, white fir, incense-cedar, live oak, and black oak.

Habitat type: ---------- Mixed-conifer/Black Oak/Live Oak
Location: ---------- San Bernardino National Forest (Mount San Jacinto)
Elevation: ---------- 5,440 feet
Date: ---------- 21 August 1991
Photographer: ---------- John S. Senser

5-42—Owl roost area showing canyon live oak (center), white fir (left), and sugar pine (background).

Habitat type: ---------- Mixed-conifer/Black Oak/Live Oak
Location: ---------- San Bernardino National Forest (Mount San Jacinto)
Elevation: ---------- 6,200 feet
Date: ---------- 21 August 1991
Photographer: ---------- John S. Senser

5-43—Owls have nested twice in this canyon live oak, once in the top of the tree and once in a cavity.

Habitat type: ---------- Mixed-conifer/Black Oak/Live Oak
Location: ---------- San Bernardino National Forest
Elevation: ---------- 5,920 feet
Date: ---------- 21 August 1991
Photographer: ---------- John S. Senser

5-44—Nest in 1991 in solitary sugar pine (center). It was a cavity nest located about two-thirds of the way up the tree. The cavity was probably created by a limb breaking away.

Habitat type: ---------- Mixed-conifer/Black Oak/Live Oak
Location: ---------- San Bernardino National Forest (Mount San Jacinto)
Elevation: ---------- 6,200 feet
Date: ---------- 21 August 1991
Photographer: ---------- John S. Senser

5-45-Overview of a hardwood ravine habitat. Note the dense hardwood stands in ravines, valleys, and on north aspects, with chaparral and grasses dominating the dryer slopes.

Habitat type: ----------Hardwood Ravines
Location: ----------Cleveland National Forest
Elevation: ----------2,100 feet
Date: ----------21 August 1991
Photographer: ----------John S. Senser

5-46-Part of the study group "hooting" their way through a beautiful stand of live oaks and grassland. Moments after this photo was taken, a male owl responded from a hardwood stand/poison oak thicket just to the left of this view.

Habitat type: ----------Hardwood Ravines
Location: ----------Cleveland National Forest
Elevation: ----------2,100 feet
Date: ----------21 August 1991
Photographer: ----------John S. Senser

5-47—Trail down Noble Canyon showing a stand of well-spaced, medium-aged live oaks. This is owl foraging habitat. A pair was found roosting nearby in a live oak with good canopy, and pellets were found along the trailside.

Habitat type: ---------- Hardwood Ravines
Location: ---------- Cleveland National Forest
Elevation: ---------- 4,640 feet
Date: ---------- 22 August 1991
Photographer: ---------- John S. Senser

5-48—Canopy typical of these hardwood ravines, showing the excellent cover provided by black and live oaks.

Habitat type: ---------- Hardwood Ravines
Location: ---------- Cleveland National Forest
Elevation: ---------- 4,640 feet
Date: ---------- 22 August 1991
Photographer: ---------- John S. Senser

Chapter 6

Home-Range Size and Habitat-Use Patterns of California Spotted Owls in the Sierra Nevada

Cynthia J. Zabel, George N. Steger, Kevin S. McKelvey, Gary P. Eberlein, Barry R. Noon, and Jared Verner

Home range is an "area utilized by an individual during its normal activities such as food gathering, mating, and caring for young" (Burt 1943), as distinguished from its territory, which is typically defended against intrusion by other individuals of the same species, except a mate or a potential mate (Nice 1941). Home ranges of neighboring individuals commonly overlap, but territories are usually more exclusive. Studies of home ranges often require attachment of radio transmitters on animals, so their movements can be monitored. Many such studies have been done on spotted owls (recent review in Thomas et al. 1990, appendix I). In this chapter we report results of two radio-tracking studies in three different study areas, one in the northern and two in the central Sierra Nevada. These data provide estimates of home-range sizes of individual males and females, and of pairs, during different periods of the annual cycle. In addition, we have compared patterns of habitat use in home ranges in relation to the different habitats available to the birds. In that sense, habitat-use information given here augments that presented in Chapter 5.

A fundamental difference exists, however, between the scales of habitat use reported here and those reported in Chapter 5. Studies in Chapter 5 examined habitat selection by owls at three scales-landscape, home-range, and stand. Stand-scale studies measured habitat attributes very near the point of an owl's activity-nesting, roosting, or foraging-and compared them with similar measurements at random locations in the surrounding forests. This was a fine-grained scale of analysis that addressed habitat attributes closely associated with an activity. Studies reported in Chapter 6 were done at a scale intermediate between the home-range and stand scales. Here we examined habitat selection at the scale of a habitat polygon (stand), a patch in the overall forest landscape that was similar enough within itself to be set apart from adjoining patches. The minimum patch size we recognized was 5 acres. For example, a meadow would be one polygon type, and an adjoining patch of forest with fairly uniform canopy closure and tree size-class would be another type. But a forest polygon could still be heterogeneous-and typically it is, with smaller subgroups of trees within it having higher canopy closure and/or larger trees than the polygon as a whole. If an owl were selecting for attributes at a scale less than the polygon size, the stand-level analyses reported in Chapter 5 would be much more likely to detect that selection than would be the results reported in this chapter. We can differentiate habitat selection only at the level of the entire polygon. Consequently, evidence of habitat selection given in this chapter is likely to be less conclusive than that given in Chapter 5.

Study Areas

Results presented here came from two study areas, one in the Sierra National Forest (NF) near the southern end of the Sierra Nevada, and the other east of Lassen National Park (NP) in the Lassen NF, at the northern end of the Sierra Nevada and the extreme southern end of the Cascade Mountains. The study area in the Sierra NF had one division in mixed-conifer forest in the Huntington quadrangle (hereafter the S-CON site) and another in foothill riparian/hardwood forests and adjoining oak-pine woodlands in the Patterson quadrangle (the S-OAK site). These were situated about 45 miles northeast of Fresno, in watersheds of the San Joaquin River and the North Fork of the Kings River. Vegetation in the S-CON site was dominated by mixed-conifer forests of white fir, Jeffrey pine, ponderosa pine, sugar pine, incense-cedar, and red fir. Elevations ranged from 5,000 to 8,000 feet. Much of the area was selectively logged from 1880 to the present, with most of the old-growth conifer trees removed. Logging within the NF and on small parcels of private land within NF boundaries is now concentrated on second-growth timber and the few remaining stands of old-growth. The S-OAK site, at elevations from 1,000 to 3,000 feet, was dominated by blue oak, interior live oak, digger pine, and various chaparral species. The Lassen NF study area (the L-CON site) was dominated by red and white fir at high elevations (5,800 to 6,600 feet) and Jeffrey, ponderosa, sugar, and lodgepole pines at lower elevations (5,000 to 5,800 feet). Selective logging has been the predominant silvicultural method used there.

Methods

Field Operations

Owls were captured with noose poles, mist nets, or fish-landing nets and fitted with backpack-mounted radio tags weighing 0.6-0.8 ounces. We attached the radio tags with cross-chest harnesses (Forsman 1983). Radio tags (AVM Instrument Co., Livermore, Calif.) had 12-inch antennae and life expectancies of 12 months. Owls tracked >1 year were recaptured and fitted with new radio tags. Owls were located by radio triangulation using the loudest-signal method (Springer 1979). At least three compass bearings were taken from known points for each owl location and plotted on 1:24,000 topographic maps. Error polygons (the area enclosed by the intersection of three or more compass bearings) at L-CON were classified as <50, <20, <5, or <2.5 acres. We attempted to obtain error polygons of <2.5 acres for all observations. At S-CON and S-OAK, we obtained additional bearings on all birds until error polygons of <2.5 acres were attained. The geometric center of each error polygon was assumed to be the owl's location. We attempted to obtain one nighttime location, by radio tracking, on each of four nights per week and one daytime location per week by direct visual observation. All nighttime observations were considered foraging locations and all daytime observations were classed as roosting locations.

Vegetation Classification

Stands of relatively homogeneous vegetation were mapped at each study site and grouped into habitat types that could be cross-classified to U.S. Department of Agriculture, Forest Service (FS) timber stand types. Black-and-white aerial photos, U.S. Geologic Survey topographic maps, large-scale color aerial photos, and 1:24,000 FS black-and-white orthophotoquads were used to define vegetation boundaries. Stands were classified according to compositional (vegetation type) and structural (diameter size-class of dominant trees and canopy-closure classes) features that could be estimated from aerial photos (table 6A). Structural classes at S-OAK differed from those at S-CON and L-CON, because most trees there were oaks with relatively small diameters at breast height (d.b.h.) when compared to conifers. We assigned each stand to two canopy-closure classes: cover by all vegetation above 7 feet (total canopy closure) and cover by only the dominant trees in the canopy (dominant canopy closure). About 70 percent of the mapped stands (polygons) in each study area were field-verified for classification accuracy. Vegetation maps were subsequently digitized, stored in a Geographic Information System (GIS), and analyzed using ARCINFO software.

Table 6A-*Vegetation classifications used in Chi-square tests of habitat selection.*

Classes	Characteristics
Tree size-classes	
Open grassland	No trees
Sapling	D.b.h. <5 inches[1]
Pole	D.b.h. 5-10 inches
Small sawtimber	D.b.h. 11-20 inches
Medium sawtimber	D.b.h. 21-35 inches
Large sawtimber	D.b.h. >35 inches
Canopy-closure classes	
Open	10 percent closure[2]
Sparse	10-19 percent
Poor	20-39 percent
Normal	40-69 percent
Good	<69 percent
Suitability as owl habitat	
Suitable	Medium or large sawtimber, canopy closure class poor or better, and total closure >69 percent
Unsuitable	All other lands

[1] Diameter at breast height of the dominant size-class, according to basal area
[2] Canopy closure based on the dominant tree size-class.

Statistical Analysis

By definition, home-range estimators assume repeated use of an area, and a random flight path does not constitute a home range. For this reason, we determined whether individual owls exhibited site fidelity prior to calculating home-range size (Spencer et al. 1990). The mean-squared distance from the center of activity (MSD) (Calhoun and Casby 1958) was used to measure site fidelity. A bird displayed site fidelity if its flight path was less than the MSD for 975 of 1,000 simulated paths. (See Spencer et al. 1990 for simulation techniques.)

Home-range size was computed using two estimators, the 100-percent minimum convex polygon (MCP) (Mohr 1947 Hayne 1949) and the 95-percent adaptive kernel (AK) (Worton 1989, Baldwin pers. comm.). Because convex polygon areas are sensitive to sample size (Jennrich and Turner 1969), we used the 95-percent AK estimates for all comparisons and statistical tests. We report 100-percent MCP estimates of home-range size to allow comparisons with other studies reported in the literature and elsewhere. The correlation coefficient between AK and MCP estimates was significant (r = 0.93, d.f. = 52, P < 0.0001). Telemetry data were partitioned into a breeding period (1 March-31 August) and a nonbreeding period (1 September-28 February Foraging (nighttime) locations were used to estimate home ranges.

The Chi-square goodness-of-fit test was used to test the hypothesis that owls used habitat types *within* their home ranges in proportion to availability (Neu et al. 1974). When this hypothesis was rejected, we used Bonferroni confidence intervals (at the P < 0.05 level) to determine which habitat types were used more or less than expected (Byers et al. 1984). Mapped polygons were classified by diameter size-class of the dominant

trees, total canopy closure, and dominant canopy closure. Chi-square analyses were performed for each of the three types of classification. In addition, the analyses were repeated after reclassifying polygons as suitable or unsuitable, based on current FS, Region 5 (R5), definitions of suitable spotted owl habitat. Suitable stands were those in which the diameter size-class of dominant trees was ≥21 inches in d.b.h., canopy closure of dominant trees was ≥20 percent, and total canopy closure was ≥70 percent.

Results

Home-Range Size

Eleven females and 10 males were radio-tracked between 26 April 1987 and 28 February 1990 at S-CON; and six females and six males were radio-tracked between 28 February 1989 and 28 February 1990 at S-OAK. Nine females and eight males were tracked between 25 May 1989 and 5 April 1990 at L-CON. Owls were monitored over periods ranging from 56 to 794 days. sampling intervals varied among owls because transmitters failed, individuals died, or owls permanently left the study areas.

Eighteen of 21 owls at S-CON, 12 of 12 at S-OAK, and 13 of 17 at L-CON passed the site-fidelity test. Owls that failed to exhibit site fidelity had few radio locations or made long movements during the breeding or nonbreeding seasons. All three birds at S-CON that failed the test were migrants that exhibited long movements (see Chapter 4).

To compare home-range sizes among sites and between seasons, we excluded owls that were tracked over a period of less than 5 months during the 6-month nonbreeding season. Our sampling frequency varied among individual owls, and 5 months was as close to complete coverage as we could achieve because of irregular sampling intervals. Estimates of home-range sizes for the nonbreeding period were calculated for 13 owls at S-CON, 5 at S-OAK, and 7 at L-CON that passed the site fidelity test and were tracked for a period of at least 150 days. The number of radio locations per season among these owls ranged from 21 to 91 ($\bar{x}$ = 58.6 ± 17.0). Home-range sizes of owls that passed the site-fidelity test and that were tracked over a period of at least 150 days were not significantly correlated with the number of radio locations. We relaxed the criteria for breeding-season estimates. Requiring a tracking period of at least 150 days, only seven owls had sufficient data to estimate a home-range size. To use a larger sample of owls, we excluded only owls with fewer than 20 radio locations within a breeding season. Fifteen of 21 owls at S-CON, 7 of 12 at S-OAK, and 9 of 15 at L-CON met this criterion. The mean number of locations among these owls as 37.6 (± 10.6) and they were tracked over an average period of 116.0 days (± 39.1, range = 56-184 days).

Home ranges were significantly larger at S-CON than at S-OAK during both seasons (table 6B). A two-way ANOVA for these two sites indicated significant effects of study site (F = 13.9, d.f. = 1, 50, $P < 0.001$) and season (F = 4.2, d.f. = 1, 50, $P < 0.05$) on AK home-range size, with an interaction effect. The interaction effect was due to larger home ranges in the nonbreeding than in the breeding season at S-CON, but home ranges at S-OAK were larger during the breeding season. The difference in home-range size between seasons at L-CON was not significant (t = 1.4, d.f. = 14, $P > 0.15$), but owls at L-CON had home-range sizes about twice those at S-CON in both seasons. Home-range sizes did not differ significantly between sexes at any site during either season.

Owls at S-CON exhibited variable behavior during the winter. Individual birds either migrated, occupied nearly the same home range in winter as in summer, enlarged their home range in winter but still used most or all of the summer home range as well, or shifted their home range for the winter but still overlapped a portion of the summer home range (Chapter 4). Among 21 owls radio-tagged at this site, six were classified as year-round residents, two as enlargers, five as shifters, five as migrants, and three as unknown. Differences in nonbreeding home-range sizes among these categories of birds were significant (F = 12.4, d.f. = 3, 17, $P < 0.001$). Shifters had the largest home ranges ($\bar{x}$ = 13,254 ± 4,984 acres), followed by enlargers ($\bar{x}$ = 5,960 ± 3,031), and residents ($\bar{x}$ = 3,302 ± 781). Only one migrant passed the site-fidelity test, and its home range was 9,146 acres.

Annual home ranges were calculated for owls that passed the site-fidelity test both seasons, were tracked over a period of at least 150 days during the nonbreeding season, and had ≥20 radio locations during the breeding season (table 6B). Owls at S-CON had significantly larger annual home ranges than those at S-OAK (t = 2.5, d.f. = 19, $P < 0.05$). As with breeding and nonbreeding home-range sizes, annual home-range sizes at L-CON were more than twice the size of those at S-CON.

Seasonal home-range sizes of pairs were calculated only when both members of pairs passed the site-fidelity test, were tracked for at least 150 days during the nonbreeding period, and had ≥20 radio locations during the breeding period (table 6B). Only one pair at L-CON met these criteria, precluding further analysis of pair home-range data. A two-way ANOVA for S-CON and S-OAK indicated no significant differences between the nonbreeding and breeding periods (F = *1.1*, d.f. = 1, 12, $P >$ 0.30), but pair home ranges were larger at S-CON than at S-OAK (F = 3.9, d.f. = 1, 12, P = 0.07). The mean proportion of home-range overlap between members of pairs did not differ significantly by study site (F = 0.3, d.f. = 1, 12, $P > 0.60$) or by season (F = 0.2, d.f. = 1, 12, $P > 0.60$). At both sites in the Sierra NF, pairs had more overlap in their areas of use during the nonbreeding period ($\bar{x}$ = 51 ± 18 percent) than during the breeding period ($\bar{x}$ = 47 ± 12 percent).

Spotted owl home ranges shifted seasonally. Overlap between breeding and nonbreeding periods, using 95-percent AKs of individual home ranges, was 34 ± 18 percent at S-CON, 54 ± 5 percent at S-OAK, and 38 ± 8 percent at L-CON.

Table 6B--*Means ($\bar{x}$) and standard deviations (SD) of home-range sizes of California spotted owls studied from 1987-1990 in the northern and central Sierra Nevada. Study sites were in conifer forest on the Lassen NF (L-CON) and in conifer forest (S-CON) and riparianlhardwood forest (S-OAK) on the Sierra NF. Estimates were determined using foraging locations and the 95-percent adaptive kernel method; 100-percent minimum convex polygon estimates of home-range sizes are in parentheses;* n = *number of individuals or pairs of owls.*

Birds	Total home-range size (acres)					
	L-CON		S-CON		S-OAK	
	$\bar{x}$ ± SD	*n*	$\bar{x}$ ± SD	*n*	$\bar{x}$ ± SD	*n*
Individual birds						
Breeding	7,061.2 ± 5,992.5 (5,422.6 ± 5,194.4)	9	2,366.8 ± 740.0 (1,798.7 ± 787.2)	24	985.0 ± 745.0 (714.6 ± 624.4)	7
Nonbreeding	11,601.0 ± 6,664.1 (14,676.7 ± 8,251.8)	7	6,834.5 ± 5,138.3 (5,943.3 ± 4,529.5)	18	661.0 ± 510.1 (761.7 ± 495.7)	5
Annual	12,473.5 ± 7,305.5 (12,927.2 ± 10,132.2)	6	5,715.1 ± 4,289.9 (5,968.8 ± 4,639.9)	16	874.1 ± 644.2 (1,042.6 ± 865.7)	5
Pairs-breeding period						
Total area	3,869.3 (3,014.4)	1	3,420.5 ± 858.1 (2,514.8 ± 873.6)	8	720.5 ± 402.9 (457.4 ± 274.4)	2
Area shared	1,869.3 (1,164.9)		1,544.5 ± 364.8 (1,027.5± 317.6)		397.9 ± 341.6 (278.6± 225.8)	
Pairs-nonbreeding period						
Total area	9,871.8 (17,292.5)	1	9,730.8 ± 10,168.0 (7,201.0 ± 6,901.2)	4	573.3 ± 271.0 (818.8 ± 251.4)	2
Area shared	1,407.9 (563.2)		4,021.2 ± 3,929.3 (3,766.0 ± 4,355.4)		321.3 ± 160.1 (297.6 ± 133.9)	
Pairs-annual						
Total area			8,253.0 ± 7,872.6 (7,709.4 ± 7,184.0)	4	778.0 ± 405.8 (875.6 ± 303.8)	2
Area shared			4,443.0 ± 4,626.1 (4,492.2 ± 4,945.2)		447.6 ± 318.9 (459.9 ± 201.3)	

Habitat Use

Habitat Composition Within Home Ranges

During the breeding season, 13 and 63 percent of the habitat types available within individual home ranges were medium and large sawtimber (≥21 inches in d.b.h.) at S-CON and L-CON, respectively (tables 6C-6E), and 91 percent of the habitat types available within owl home ranges at S-OAK were classified as old-growth. Percentages were similar during the nonbreeding season in all areas. The mean proportions of individual home ranges that were ≥40 percent dominant canopy closure varied among sites (table 6F); proportions were similar at L-CON and S-CON, but they were about two times greater at S-OAK. Proportions for ≥40 percent total canopy closure were similar among all sites. Mean percentages of home ranges that were "suitable" habitat using R5 definitions were 4 (S-CON), 27 (S-OAK), and 26 (L-CON) at the three sites during the breeding season.

Habitat-Use Patterns Within Home Ranges

Among all of the owls during the breeding season, 10 and 82 percent of the radio locations were in medium and large sawtimber at S-CON and L-CON, respectively, and 92 percent were in old-growth at S-OAK; 21, 70, and 99 percent of the locations were in these size classes at the three sites, respectively, during the nonbreeding season (tables 6C-6F). More use occurred in small than in medium and large sawtimber at S-CON 87 percent and 73 percent of the radio locations during the breeding and nonbreeding seasons, respectively. The proportions of radio locations that were in dominant canopy closure ≥40 percent were again similar at L-CON and S-CON, but nearly twice as high at S-OAK. Higher proportions of locations occurred in total canopy closure ≥40 percent, and results were similar among the sites. Use of R5 suitable habitat was low--means of radio locations in this habitat class were 4 percent (S-CON), 47 percent (L-CON), and 49 percent (S-OAK) during the breeding season (table 6F). Use was greater than availability for most site-season comparisons and definitions of suitable habitat (fig. 6A). Use of R5 suitable habitat at S-CON was equal

Table 6C *Means ($\bar{x}$) and standard deviations (SD) of areas, proportions of home ranges, and proportions* of *foraging and roosting radio locations in different tree size and canopy-closure classes for owls that passed the site fidelity test at the S-CON study site in the central Sierra Nevada. The 95-percent adaptive kernel method was used to estimate home ranges for 1987-1989 breeding and nonbreeding seasons.*

	Breeding period[1]						Nonbreeding period[1]					
	Area (acres)		Proportion of home range		Proportion of locations		Area (acres)		Proportion of home range		Proportion of locations	
Habitat type	$\bar{x}$	SD	$\bar{x}$	SD	$\bar{x}$	SD	$\bar{x}$	SD	$\bar{x}$	SD	$\bar{x}$	SD
Tree size-class d.b.h. in inches)												
No trees	9.1	35.8	0.003	0.01	0	0	736.3	1,828.5	0.058	0.14	0.031	0.08
<5	0	0	0	0	0	0	0	0	0	0	0	0
5 - 10	66.4	82.3	0.029	0.04	0.027	0.05	101.8	109.9	0.020	0.02	0.023	0.04
11 - 20	1,666.0	976.1	0.839	0.17	0.870	0.22	4,028.8	2,826.9	0.671	0.18	0.732	0.19
21 - 35	230.0	319.1	0.095	0.11	0.065	0.16	1,281.7	998.1	0.192	0.10	0.141	0.11
>35	59.0	143.8	0.032	0.08	0.038	0.08	477.5	684.4	0.054	0.07	0.073	0.12
Dominant canopy closure (percent)												
< 10	98.8	254.4	0.027	0.06	0.007	0.02	245.8	492.0	0.022	0.03	0.013	0.03
10 - 19	164.7	154.9	0.076	0.06	0.040	0.04	568.6	509.8	0.080	0.05	0.043	0.03
20-39	1,147.8	776.1	0.537	0.18	0.416	0.24	3,117.6	2,220.8	0.492	0.14	0.442	0.19
40 - 69	605.4	311.0	0.354	0.22	0.537	0.25	1,945.9	977.6	0.342	0.14	0.471	0.19
70 - 100	4.2	16.3	0.002	0.08	0	0	13.1	35.1	0.001	0	0	0
Total canopy closure (percent)												
<10	32.9	70.1	0.010	0.02	0.002	0.01	124.2	215.9	0.012	0.01	0.007	0.01
10 - 19	111.1	230.7	0.038	0.06	0.015	0.03	288.2	367.3	0.035	0.02	0.019	0.02
20 - 39	306.5	293.2	0.137	0.07	0.076	0.08	999.4	1,172.8	0.126	0.07	0.077	0.06
40 - 69	1,318.0	618.5	0.677	0.12	0.685	0.21	3,534.6	1,943.9	0.598	0.14	0.644	0.15
70 - 100	252.9	188.5	0.132	0.09	0.222	0.21	944.3	560.7	0.164	0.06	0.222	0.13

[1] Breeding period--*n* = 24 owls with a total of 1,583 locations; nonbreeding period--*n* = 18 owls with a total of 1,358 locations. An individual owl may contribute to *n* more than once if it was radio tracked during multiple breeding or nonbreeding seasons.

to or less than availability, but note the small amounts of this type available at S-CON

Nearly half of the owls at all three sites had significant Chi-square tests of habitat use for tree size-class, and nearly three-fourth of the owls had significant tests for use of canopy-closure classes. Differences in the proportion of owls that demonstrated habitat selection between the breeding and nonbreeding seasons were neither large nor consistent (fig. 6B). Fewer owls selected for tree size-class than for canopy-closure classes, and more selected for dominant canopy closure than for total canopy closure. Fewer owls had significant tests for habitat use when only foraging locations were used than when foraging and roosting locations were pooled. Summed across the three study areas (foraging and roosting locations pooled), 14 of 39 owls had significant tests for use of tree size-class, 26 owls for total canopy closure, and 29 owls for dominant canopy-closure classes during the breeding season. During nonbreeding season, 14 of 29 owls at the three study sites selected significantly for three size-class, 20 owls for total canopy closure, and 20 owls for dominant canopy-closure classes.

We tested whether owls used "suitable" habitat more than expected based on FS, R5, definitions (fig. 6A). Results were similar for L-CON and S-OAK: seven of eight birds at L-CON had significant tests during the breeding season, and four of six birds tested significant during the nonbreeding season. At S-OAK, six of seven birds and four of five birds had significant tests during the breeding and nonbreeding seasons, respectively. On the other hand, at S-CON, only four of 24 owls during the breeding season and six of 18 owls during the nonbreeding season had significant tests for use of suitable habitat.

Patterns of habitat use were weak and inconsistent among the subset of owls that passed the test of habitat selection (figs. 6C-6E). Most owls at all three sites used habitat types in proportion to their availability. Patterns were clearer and stronger for canopy closure than for tree size-class. More than half of the owls used poor cover classes less than expected and many used canopy closure ≥40 percent more than expected. Differences between dominant and total cover were minor. Patterns of selection for canopy closure did not appear to be stronger during the breeding than during the nonbreeding season. Use of tree size-class

Table 6D-*Means ($\bar{x}$) and standard deviations (SD) of areas, proportions of home ranges, and proportions* of *foraging and roosting radio locations in different tree size and canopy-closure classes for owls that passed the site fidelity test at the S-OAK study site in the central Sierra Nevada. The 95-percent adaptive kernel method was used to estimate home ranges for the 1989 breeding and nonbreeding seasons.*

	Breeding period[1]						Nonbreeding period[1]					
	Area (acres)		Proportion of home range		Proportion of locations		Area (acres)		Proportion of home range		Proportion of locations	
Habitat type	$\bar{x}$	SD	$\bar{x}$	SD	$\bar{x}$	SD	$\bar{x}$	SD	$\bar{x}$	SD	$\bar{x}$	SD
Tree size-class (d.b.h. in inches)												
No trees	6.2	10.6	0.005	0.01	0	0	0	0	0	0	0	0
<5	0	0	0	0	0	0	0	0	0	0	0	0
5-10	0	0	0	0	0	0	0	0	0	0	0	0
11 - 20	67.7	138.1	0.083	0.15	0.080	0.18	7.7	11.1	0.014	0.02	0.006	0.01
21 - 35	703.2	577.5	0.912	0.15	0.920	0.18	647.6	556.5	0.986	0.02	0.994	0.01
>35	0	0	0	0	0	0	0	0	0	0	0	0
Dominant canopy closure (percent)												
<10	26.4	55.3	0.021	0.03	0	0	52.6	76.6	0.055	0.04	0.024	0.03
10 - 19	127.9	161.3	0.132	0.14	0.081	0.09	156.6	145.7	0.210	0.16	0.108	0.09
20 - 39	102.0	167.7	0.105	0.11	0.033	0.04	125.0	244.3	0.113	0.14	0.068	0.13
40 - 69	444.8	312.7	0.542	0.23	0.494	0.36	239.6	152.2	0.391	0.10	0.378	0.17
70 - 100	69.4	32.4	0.194	0.24	0.391	0.36	81.8	39.8	0.231	0.23	0.422	0.32
Total canopy closure (percent)												
<10	26.4	55.3	0.021	0.03	0	0	52.6	76.6	0.055	0.04	0.024	0.03
10 - 19	99.0	141.5	0.093	0.09	0.069	0.08	102.8	145.7	0.112	0.08	0.060	0.06
20 - 39	76.6	80.0	0.106	0.10	0.027	0.03	113.9	86.4	0.170	0.07	0.057	0.06
40 - 69	455.0	400.4	0.501	0.27	0.416	0.30	268.5	293.9	0.347	0.11	0.385	0.23
70 - 100	114.1	49.6	0.273	0.26	0.488	0.31	117.6	43.0	0.316	0.25	0.474	0.32

[1] Breeding period--*n* = 7 owls with a total of 498 locations; nonbreeding period--*n* = 5 owls with a total of 548 locations.

showed stronger patterns at L-CON than at S-CON and S-OAK. More than half of the birds at L-CON used small sawtimber (<11 inches in d.b.h.) less than expected, and medium and large sawtimber more than expected, during the breeding season. These results were weaker during the nonbreeding season.

Discussion

Home-Range Size

Estimates of home-range size among California spotted owls are extremely variable. All available data indicate that they are smallest in habitats at relatively low elevations that are dominated by hardwoods, intermediate in size in conifer forests in the central Sierra Nevada, and largest in true fir forests in the northern Sierra Nevada.

Home-range sizes of owls in our studies at L-CON, S-CON, and S-OAK varied among areas and between seasons. The mean area used was about twice as large in the northern compared to the central Sierra Nevada, and was two to 10 times larger in high-elevation conifer forests compared to low-elevation oak woodlands in the central Sierra Nevada. Median home-range estimates for pairs of northern spotted owls were 3,000 to 5,000 acres (Thomas et al. 1990)-less than half the size of pair home ranges of California spotted owls at L-CON (12,500 acres) but about the same as the pair estimates at S-CON. California spotted owls in the foothill riparian/hardwoods and oak woodlands at S-OAK used less than 900 acres, or approximately 20-30 percent of the area used by northern spotted owls.

Two pairs of owls radio tracked in the San Bernardino Mountains used home ranges averaging more than 5,300 acres (100-percent MCP-LaHaye pers. comm.) (table 6G). Home-range sizes of pairs during the breeding period averaged 4,569 acres on the Tahoe NF (100-percent MCP, *n* = 2; Call 1990, p. 21) and 4,759 acres on the Eldorado NF [100-percent MCP, *n* = 4 (excludes two pairs with relatively few radio locations); Laymon 1988, p. 187]. These estimates, with those of 3,869 acres for the Lassen NF (*n* = 1, table 6B) and 3,421 acres for the Sierra NF (*n* = 8, table 6B), give an overall estimate of about 4,200 acres (grand mean, unweighted for sample size) for home-range sizes of owl pairs during the breeding period in Sierran conifer forests.

Table 6E-*Means ($\bar{x}$) and standard deviations (SD) of areas, proportions of home ranges, and proportions* of *foraging and roosting radio locations in different tree size and canopy-closure classes for owls that passed the site fidelity test at the L-CON study site in the northern Sierra Nevada. The 95-percent adaptive kernel method was used to estimate home ranges for breeding (1990) and nonbreeding (1989-1990) seasons.*

	Breeding period[1]						Nonbreeding period[1]					
	Area (acres)		Proportion of home range		Proportion of locations		Area (acres)		Proportion of home range		Proportion of locations	
Habitat type	$\bar{x}$	SD	$\bar{x}$	SD	$\bar{x}$	SD	$\bar{x}$	SD	$\bar{x}$	SD	$\bar{x}$	SD
Tree size-class (d.b.h.in inches)												
No trees	515.0	913.2	0.049	0.04	0	0	1,368.4	1,241.2	0.112	0.09	0.007	0.01
<5	9.9	17.5	0.001	0	0	0	39.3	38.8	0.003	0	0.002	0.01
5 - 10	207.7	332.5	0.023	0.01	0.011	0.02	608.9	383.8	0.046	0.02	0.029	0.04
11 - 20	2,659.2	3,724.8	0.300	0.15	0.172	0.11	3,502.0	2,340.1	0.247	0.12	0.261	0.12
21 - 35	1,394.8	962.3	0.251	0.10	0.298	0.15	2,755.5	1,490.4	0.224	0.10	0.220	0.05
> 35	2,371.9	2,287.2	0.377	0.12	0.519	0.17	4,644.8	2,164.0	0.368	0.09	0.480	0.10
Dominant canopy closure (percent)												
<10	1,296.3	1,797.4	0.160	0.04	0.072	0.08	2,198.5	1,469.6	0.165	0.06	0.064	0.04
10 - 19	1,598.6	2,003.9	0.204	0.04	0.142	0.07	2,859.0	1,329.1	0.223	0.05	0.131	0.13
20 - 39	2,043.2	2,230.9	0.303	0.10	0.329	0.21	3,266.3	1,415.1	0.255	0.03	0.318	0.14
40-69	1,607.0	1,461.7	0.251	0.11	0.350	0.17	2,436.2	1,439.3	0.187	0.06	0.318	0.12
70 - 100	532.8	614.3	0.076	0.03	0.108	0.08	1,294.3	840.3	0.094	0.03	0.165	0.11
Total canopy closure (percent)												
<10	679.5	1,191.5	0.067	0.05	0.033	0.06	1,088.0	985.8	0.079	0.06	0.006	0.01
10 - 19	300.8	403.4	0.041	0.02	0.012	0.02	666.9	618.7	0.048	0.04	0.013	0.01
20 - 39	1,595.1	1,983.9	0.211	0.06	0.105	0.06	1,983.2	1,359.0	0.145	0.05	0.117	0.04
40 - 69	2,038.2	2,369.7	0.263	0.09	0.204	0.16	3,268.1	1,630.2	0.257	0.08	0.185	0.11
70 - 100	2,464.3	2,063.7	0.411	0.09	0.647	0.15	5,048.4	2,205.2	0.396	0.05	0.675	0.11

[1] Breeding period--*n* = 8 owls with a total of 479 locations; nonbreeding period--*n* = 6 owls with a total of 402 locations.

The smallest estimated use areas of California spotted owls (means for pairs ranging from 98 to 243 acres) were based on kown sizes of small stringers of dense riparian/hardwoods in the Cleveland, Angeles, and Los Padres NFs (table 6G). Owls in these stringers were not radio-tagged. Perhaps some of them used more than one canyon bottom, but the Forest Biologists who made these estimates reported that, in some cases, other individuals or pairs of owls occupied the riparian stringers in adjacent canyons. Most canyon sides above the riparian zones were covered by dense chaparral. We believe it is most unlikely that the owls can use the chaparral, as it is too dense for safe or effective flight.

We strongly suspect that the large differences in home-range sizes reported here are related, at least in part, to differences in the primary prey of the owls in different localities. Consistently, California spotted owls with the smallest observed home ranges prey primarily on woodrats, but those with the largest home ranges specialize on flying squirrels. Woodrat densities generally tend to be much greater than flying squirrel densities, and woodrats weigh nearly twice as much as flying squirrels (Chapter 4). Similar relations are suggested in recent studies of northern spotted owls by Carey et al. (1992).

Habitat Selection

Here we evaluate habitat quality based on use versus availability of types (Thomas et al. 1990, appendix F). We regard as suitable those habitats selected in excess of availability by most owls. Marginal habitats are seldom or never used in excess of availability, used in proportion to availability by many owls, and used less than expected by many other owls. Habitat types used less than expected by most owls are considered to be poor in quality and are classed as unsuitable habitat.

Spotted owls in this study more consistently selected for high canopy closure than for large tree size-class. Chi-square values were consistently higher for canopy closure, and more owls had significant tests for selection of high canopy closure than for tree-size class in 18 site-season comparisons. Differences between total and dominant canopy closure were minor, but because more owls exhibited significant selection for high dominant cover than for high total cover, dominant cover may be a better measure of suitable habitat for California spotted owls.

The amount of medium and large sawtimber in individual home ranges did not appear to be a good indicator of the amount of that habitat needed to sustain California spotted owls, unlike the case for northern spotted owls (see Thomas et al. 1990). Nearly half of the California spotted owls had significant tests of

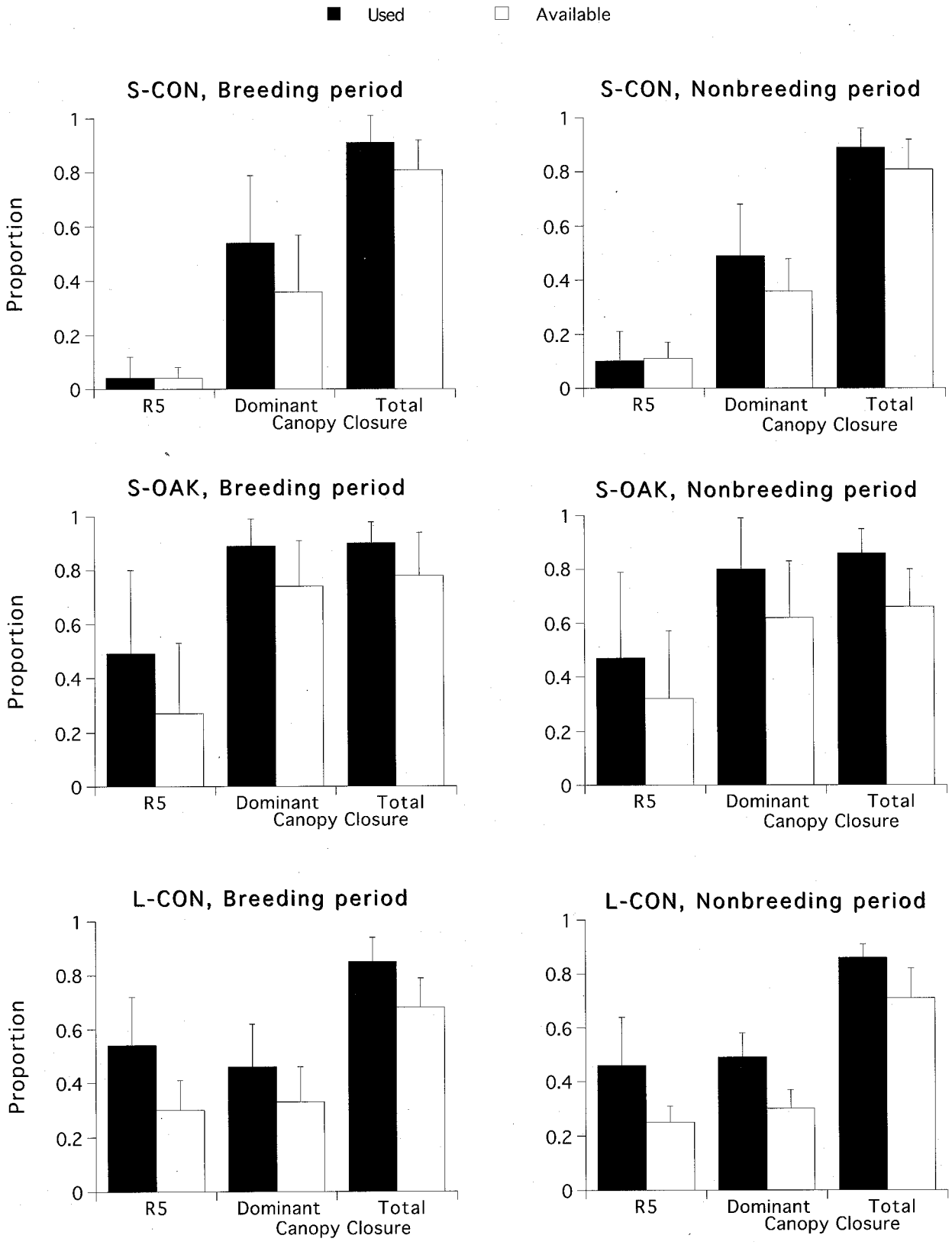


Figure 6A-Mean proportions of suitable habitat available in home ranges of California spotted owls in relation to proportions used by radio-tagged birds in different seasons and study sites. Study areas were in conifer forests of the Sierra (S-CON) and Lassen (L-CON) National Forests, and in hardwood/riparian forests of the Sierra (S-OAK) National Forest. Three categories of suitable habitat were tested: (1) R5 = Forest Service (Region 5) definition-medium or large sawtimber, dominant canopy closure poor or higher, and total closure >69 percent; (2) canopy closure of dominant trees ≥40 percent; and (3) total canopy closure ≥40 percent. Error bars are standard deviations (SD). The 95-percent adaptive kernel was used to delineate home ranges.

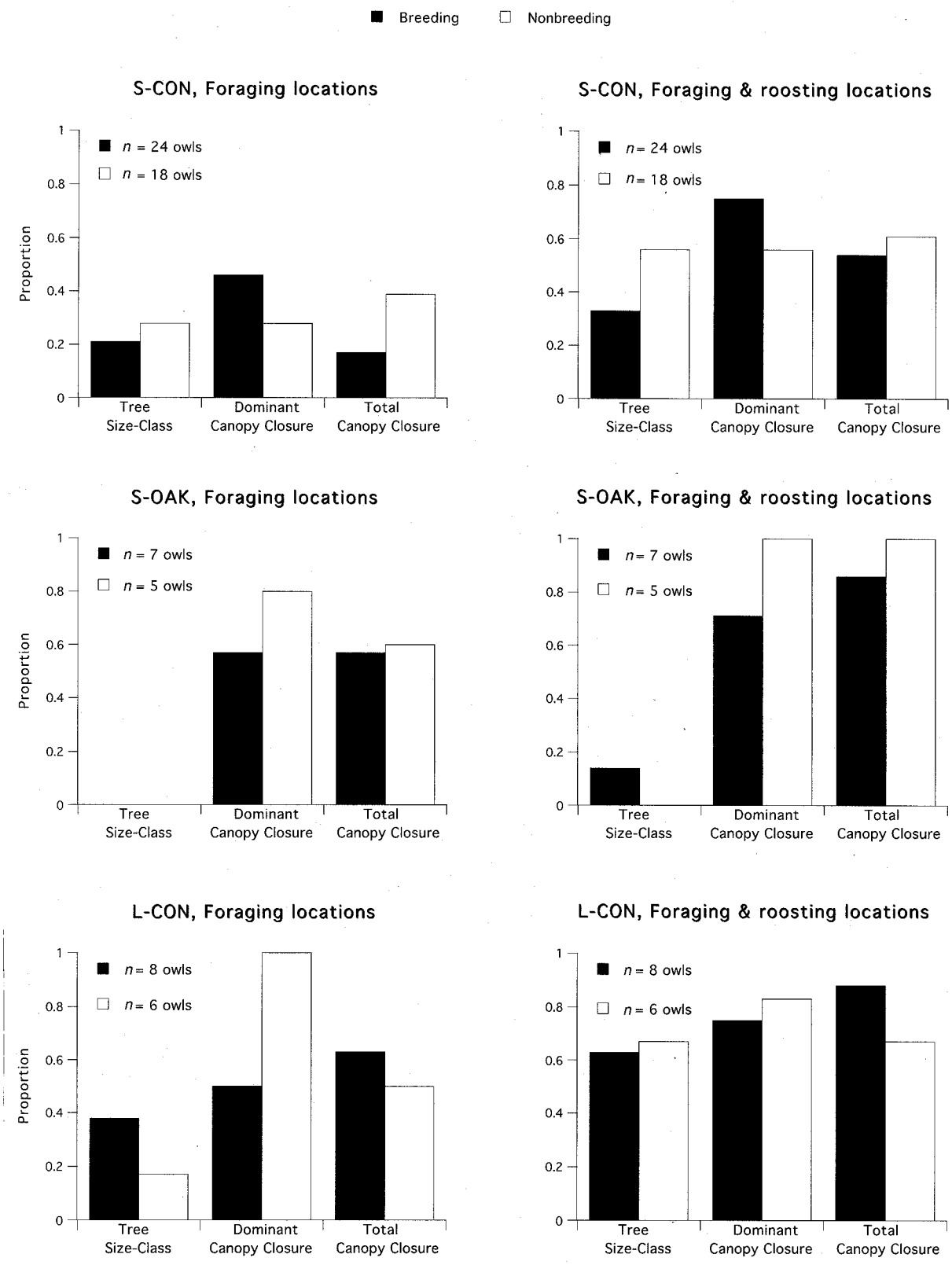


Figure 6B-The proportion of California spotted owls with significant ($P \leq 0.05$) Chi-square tests for selection of habitats based on tree size-classes, dominant canopy closure, and total canopy closure. Study areas were in conifer forests of the Sierra (S-CON) and Lassen (L-CON) National Forests, and in hardwood/riparian forests of the Sierra (S-OAK) National Forest. Tests were done separately for breeding and nonbreeding periods using foraging locations alone, and using foraging and roosting locations pooled.

selection for tree size-class, but most of them used all size classes in proportion to availability in the central Sierra Nevada. Patterns were stronger at L-CON during the breeding season, when about half of the birds used medium and large sawtimber more than expected. By contrast, old-growth was used in greater proportion than its availability, for nesting, roosting, and foraging, by most northern spotted owls in Oregon and Washington, and it was never used less than expected. Throughout their range and across all seasons, northern spotted owls consistently showed foraging and roosting patterns significantly associated with old-growth stands or mixed stands of mature and old-growth trees. Among California spotted owls, however, patterns of habitat use for tree size-class were weaker, and they were not consistent among study areas.

Canopy closure ≥40 percent was used by many California spotted owls greater than expected, by a few less than expected, and by many equal to its availability. Canopy closure ≤39 percent was used by most owls less than expected and in proportion to availability by many others. Based on these results, then, suitable habitat for California spotted owls appears to include canopy closure ≥40 percent, and habitat with ≤39 percent canopy closure is marginal to unsuitable.

The R5 definition of suitable habitat does not appear to be appropriate across the range of the California spotted owl. Most owls at L-CON (79 percent) and S-OAK (83 percent) used R5-defined suitable habitat in excess of availability. But results were quite different for owls in the conifer forest at S-CON, where this habitat type was generally not available within home ranges. At S-CON, most birds used R5-defined suitable habitat in proportion to availability, a few used it more than expected, and a few less than expected.

Habitat Selection and Population Stability

Habitat selection by owls at S-CON was generally less evident than at L-CON, even though both sites were in Sierran conifer forests. We also determined that only 13 percent of the forest in the study area at S-CON was in medium and large sawtimber, whereas the L-CON site had 63 percent of its forest in those timber size classes and several of the owls there exhibited significant selection for those timber stands. During the breeding periods of 1987, 1988, and 1989, owl crews on the Lassen and Sierra NFs monitored the occupancy status and breeding activity of owl pairs in Spotted Owl Habitat Areas (SOHAs) managed for the owls. Over that period on the Lassen NF, an absence of pairs was confirmed in 8 of 27 cases (30 percent) and breeding was confirmed in 8 of 27 cases (30 percent). During the same period on the Sierra NF, an absence of pairs in SOHAs was confirmed in 8 of 11 cases (73 percent) and breeding was confirmed in only 1 of 11 cases (9 percent). Because we lack sufficient information to determine whether California spotted owls in any part of the Sierra Nevada are reproducing at a rate that can maintain the population (Chapter 8), we cannot be certain that habitats used by owls either at L-CON or S-CON were adequate to provide for a balance between births and deaths. The data suggest, however, that the habitat available to spotted owls on the Sierra NF may be less adequate than that on the Lassen NF. Indeed, it may be that spotted owls on the Sierra NF cannot maintain their numbers, and that perhaps they are maintained in part by immigration from populations in the neighboring NPs. Note that the Sierra NF shares its northern border with Yosemite NP and its southern border with Sequoia/Kings Canyon NPs (fig. 4B).

Power of Chi-square Tests

The power of Chi-square tests of habitat selection is influenced by classification error (telemetry and/or mapping), the resolution of habitat classification, and by the number of locations available to estimate use. These factors may reduce the likelihood of detecting habitat selection when, in fact, it is occurring (type-II error-see White and Garrott 1986). In addition, the power of a test depends on the "effect size" (Cohen 1988) or, in the case of habitat selection, the degree to which differences exist between proportions of available and used habitat types. The smaller the effect size, other things being equal (significance level, desired power), the larger the sample size needed to detect selection. The small number of locations in our data could have reduced the likelihood of detecting habitat selection when it occurred. Owls with significant Chi-square tests for selection of canopy-closure classes had a mean of 72 (±23) radio locations, but owls with insignificant tests had a mean of only 57 (± 19) locations. The difference between these, sample sizes was significant (t test = 2.8, d.f. = 78, $P < 0.01$), indicating that small sample sizes may have been associated with our failure to detect habitat selection by radio-tagged owls. On the other hand, the difference between the number of locations between owls that passed ($\bar{x}$ = 69 ± 24) and failed ($\bar{x}$ = 62 ±21) tests of selection for tree size-class was not significant (t = 1.3, d.f. = 68, $P > 0.20$).

The number of radio locations approximately doubled when we pooled foraging and roosting locations. More owls had significant Chi-square tests of habitat use for the pooled data set than was the case for the foraging locations alone. The difference in Chi-square results between these two groups was apparently due primarily to differences in habitat use by foraging and roosting owls, and less so to the increase in sample size. Roost sites were more distinct from available sites than was the case for foraging sites. For example, 18 of 18 owls at S-CON used sites that had %40 percent canopy closure more than expected for roosting during the breeding period, and 83 percent had significant tests of habitat selection. Use of sites that had ≥70 percent canopy closure for roosting was similar: 16 of 18 owls had significant tests of habitat selection, and 11 of 18 owls used, these stands more than expected (G. N. Steger pers. observ.). By contrast, only 7 of 24 owls at S-CON had significant tests for use of foraging sites with dense canopy during the breeding period, and only seven owls foraged more than expected in sites with ≥40 percent canopy closure.

Effect size increases with the size of the difference between proportions of available and used habitat types, providing a useful index to identify where habitat selection is greatest. We found higher effect sizes for canopy closure than for tree size-class, and for foraging and roosting locations combined than for foraging locations alone. These results support the conclusion that the owls had differential use patterns between daytime roosting

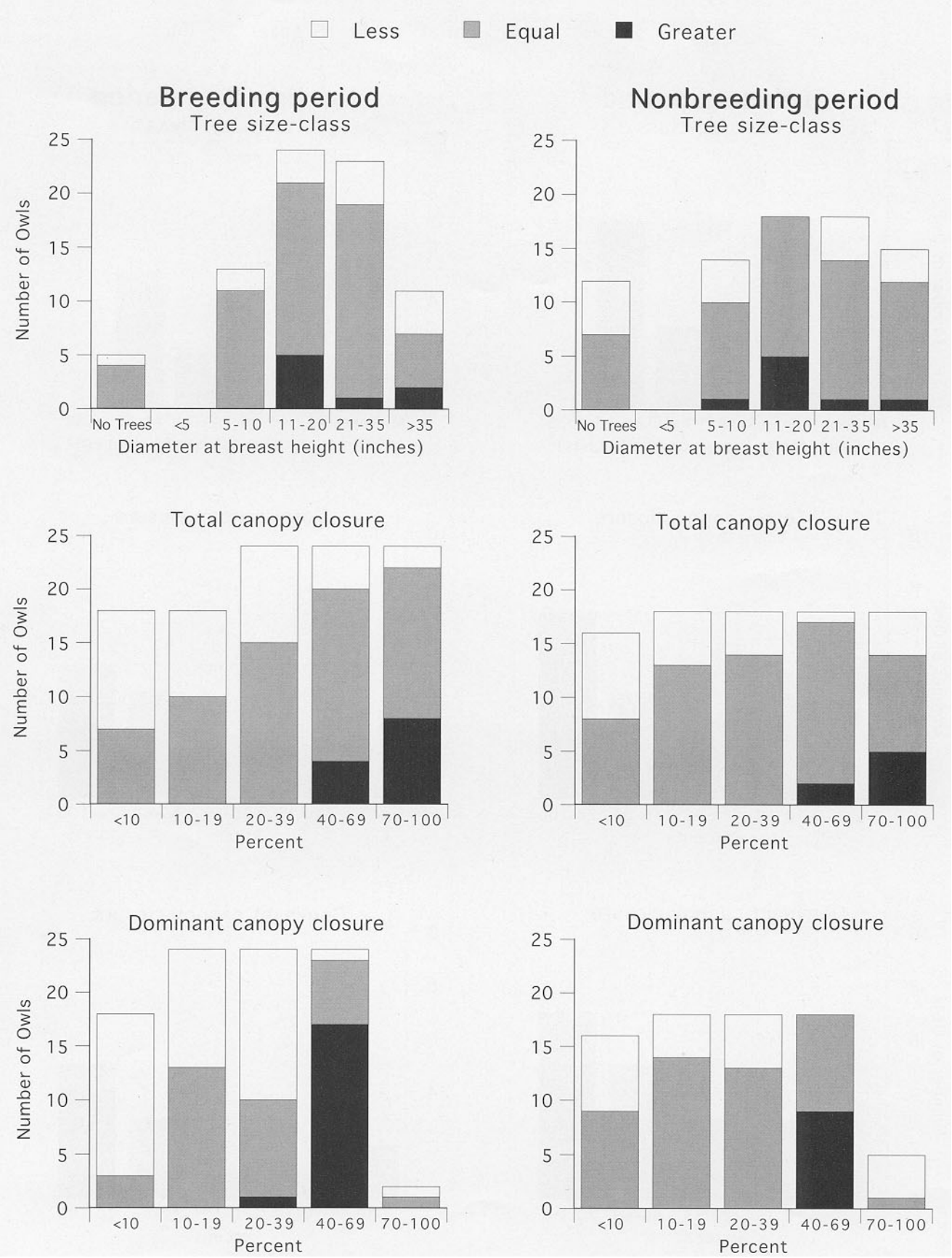


Figure 6C-The number of California spotted owls at S-CON (conifer forest study area in the Sierra National Forest) that used tree size-classes (diameter at breast height) and canopy-closure classes (percent) greater than, equal to, or less than expected during breeding and nonbreeding periods.

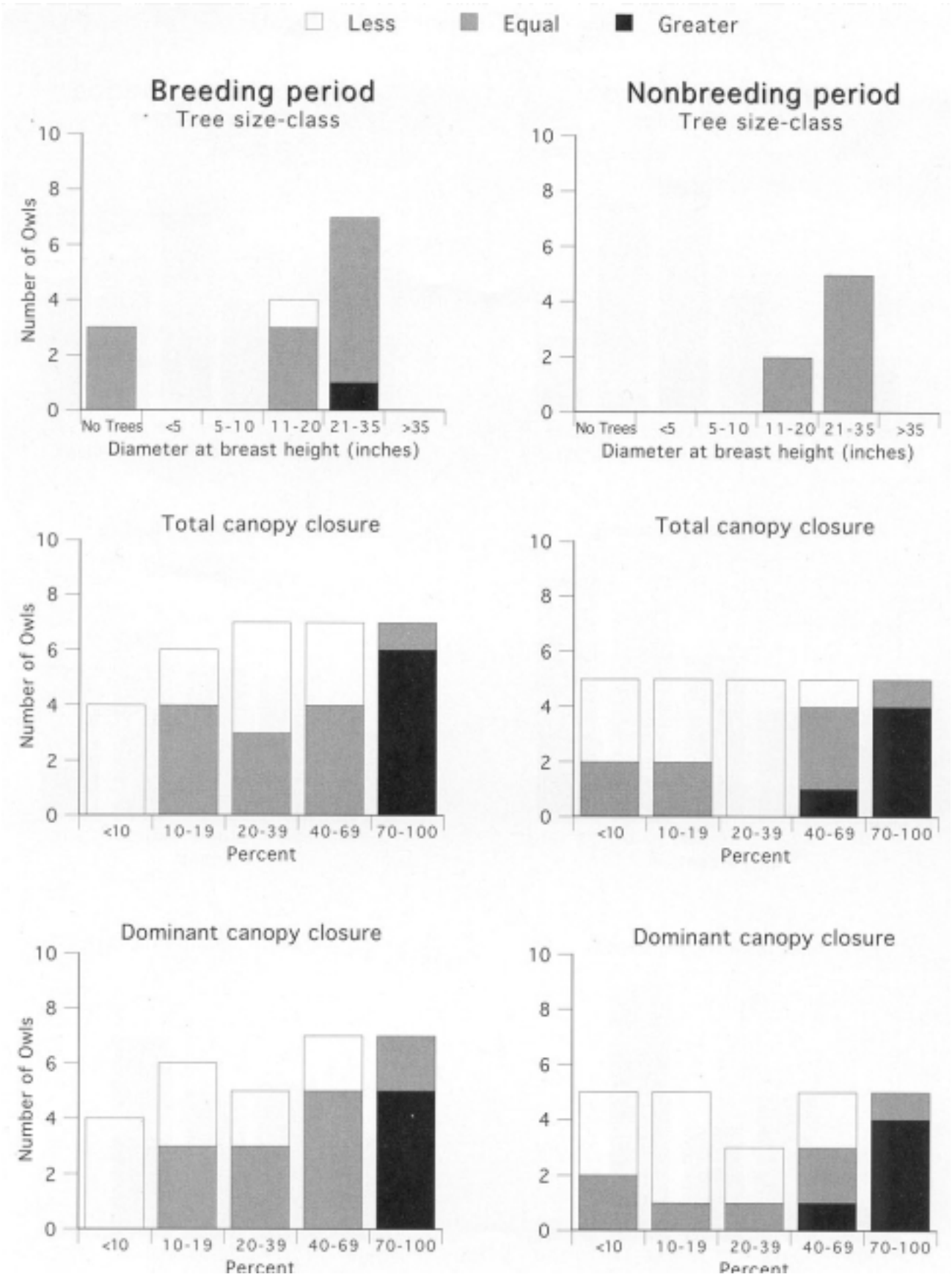


Figure 6D-The number of California spotted owls at S-OAK (riparian/hardwood forest study area in the Sierra National Forest) that used tree size-classes (diameter at breast height) and canopy-closure classes (percent) greater than, equal to, or less than expected during breeding and nonbreeding periods.

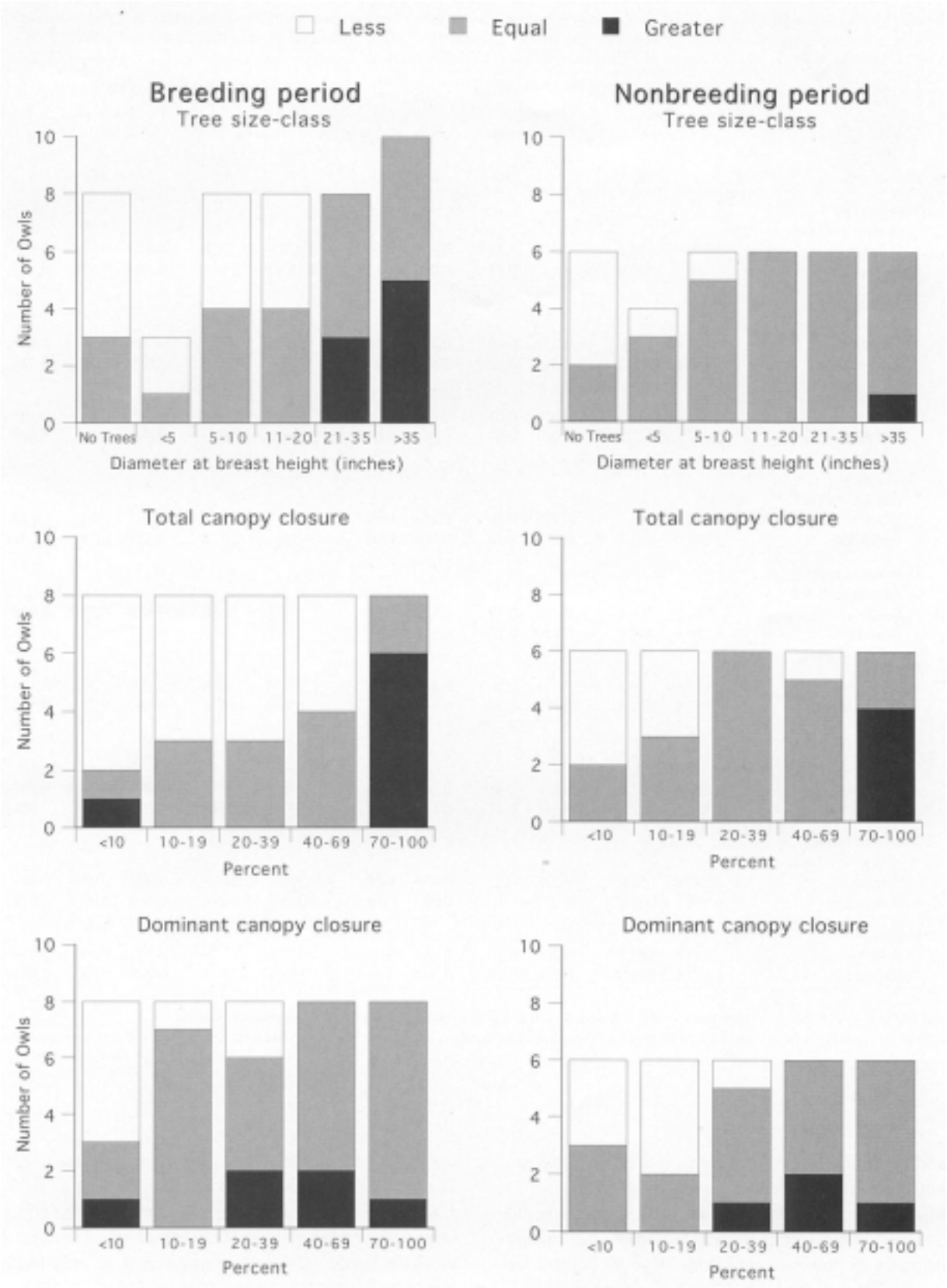


Figure 6E-The number of California spotted owls at L-CON (conifer forest study area in the Lassen National Forest) that used tree diameter-classes (diameter at breast height) and canopy-closure classes (percent) greater than, equal to, or less than expected during breeding and nonbreeding periods.

Table 6F--*Means ($\bar{x}$) and standard deviations (SD) of total area, proportions of home ranges, and proportions of foraging and roosting radio locations in suitable and unsuitable habitat for California spotted owls that passed the site fidelity test for the 1987-1990 breeding and nonbreeding period at L-CON, S-CON, and S-OAK study sites in the northern and central Sierra Nevada. The 95-percent adaptive kernel method was used to estimate home ranges (*n = *number of individual owls).*

		Breeding period[1]							Nonbreeding period[1]					
			Area (acres)		Proportion of home range		Proportion of locations			Area (acres)		Proportion of home range		Proportion of locations	
Study site	Habitat type	*n*	$\bar{x}$	SD	$\bar{x}$	SD	$\bar{x}$	SD	*n*	$\bar{x}$	SD	$\bar{x}$	SD	$\bar{x}$	SD
S-CON	Total canopy closure ≥40 pct	24							18						
	Suitable		1,570.7	734.1	0.813	0.11	0.907	0.10		4,478.9	2,378.6	0.806	0.11	0.893	0.07
	Unsuitable		450.5	540.9	0.187	0.11	0.093	0.10		1,412.1	1,734.4	0.194	0.11	0.107	0.07
	Dominant canopy closure ≥40pct	24							18						
	Suitable		609.6	308.0	0.357	0.22	0.537	0.25		1,959.0	991.5	0.361	0.12	0.487	0.19
	Unsuitable		1,411.6	1,095.7	0.643	0.22	0.463	0.25		3,932.0	3,053.7	0.639	0.12	0.513	0.19
	Region 5[2]	24							18						
	Suitable		93.6	126.5	0.039	0.05	0.037	0.08		655.8	499.9	0.105	0.06	0.105	0.11
	Unsuitable		1,927.6	1,117.4	0.961	0.05	0.963	0.08		5,256.2	3,560.3	0.895	0.06	0.895	0.11
S-OAK	Total canopy closure ≥40 pct	7							5						
	Suitable		569.1	365.8	0.779	0.16	0.904	0.08		386.1	256.4	0.663	0.14	0.859	0.09
	Unsuitable		202.0	261.1	0.221	0.16	0.096	0.08		269.2	299.4	0.337	0.14	0.141	0.09
	Dominant canopy closure ≥40 pct	7							5						
	Suitable		514.5	284.5	0.740	0.17	0.886	0.10		321.3	122.0	0.623	0.21	0.799	0.19
	Unsuitable		256.6	349.8	0.260	0.17	0.114	0.10		334.2	439.9	0.377	0.21	0.201	0.19
	Region 5[2]	7							5						
	Suitable		113.6	49.6	0.273	0.26	0.488	0.31		117.6	43.0	0.316	0.25	0.474	0.32
	Unsuitable		657.5	599.5	0.727	0.26	0.512	0.31		538.0	592.8	0.684	0.25	0.526	0.32
L-CON	Total canopy closure ≥40 pct	8							6						
	Suitable		4,502.6	4,425.3	0.679	0.11	0.851	0.09		8,316.5	3,739.6	0.709	0.12	0.864	0.05
	Unsuitable		2,575.2	3,557.8	0.321	0.11	0.149	0.09		3,737.9	2,750.8	0.291	0.12	0.136	0.05
	Dominant canopy closure ≥40 pct	8							6						
	Suitable		2,140.0	2,059.0	0.328	0.13	0.458	0.16		3,730.4	2,114.3	0.304	0.07	0.487	0.09
	Unsuitable		4,938.0	6,005.8	0.672	0.13	0.542	0.16		8,323.7	3,986.6	0.696	0.07	0.513	0.09
	Region 5[2]	8							6						
	Suitable		1,465.5	883.5	0.262	0.10	0.468	0.13		2,238.8	971.0	0.252	0.09	0.415	0.17
	Unsuitable		5,167.5	5,269.0	0.738	0.10	0.532	0.13		7,898.8	4,339.5	0.749	0.09	0.585	0.17

[1] An individual owl may contribute to *n* more than once if it was radio tracked during multiple breeding or nonbreeding periods.
[2] Region 5 definition--suitable habitat = medium or large sawtimber, dominant canopy closure poor or higher, and total closure >69 percent; unsuitable habitat=all other types.

locations and nighttime foraging locations-they were less selective among habitats when foraging than when roosting.

The small number of radio locations among our owls did not result in low power to reject the null hypothesis for canopy closure. Estimates of power ranged from 70 to 90 percent for canopy closure. We had high likelihood of detecting habitat selection for canopy closure when it occurred. Our power to detect selection for tree size-class was lower-70 percent at L-CON, 59 percent at S-CON, and 29 percent at S-OAK. Thus, even if selection for tree size-class occurred, we had low power to detect it, especially in the oak woodlands at S-OAK. The number of radio locations for canopy closure and tree size-class was the same; the differences in power were due to differences in effect size. To achieve 80 percent power at an 0.05 level of significance, with 4 degrees of freedom, given the effect size we observed for tree size-class (0.20 at S-OAK), 298 radio locations would be needed; if the effect size were 0.30, only 133 locations would be needed (see Cohen 1988, p. 258).

Effect size can also be strongly influenced by the definition of the available sampling frame. In general, the more widely defined the available frame, the greater the likelihood of demonstrating selection. By using the AK method to define the available sampling frame for each home range, we decreased the likelihood of demonstrating selection relative to a less restrictive

Table 6G *Estimated areas of use by California spotted owls that were not radio tracked. Data are tabulated by National Forest (NF),and some Ranger Districts, as minimum breeding-season estimates. Estimated areas of use were based on the sizes of drainages occupied by owls during summer surveys.*

Areas of use	Total area used (acres)		
	$\bar{x}$ x ± SD	Range	*n*
Cleveland NF			
All sites	133.4 ± 70.0	38.0 - 294.0	15
Chaparral sites	159.5 ± 85.9	38.0 - 294.0	8
Oak/Pines sites	103.6 ± 29.4	70.0 - 155.0	7
Angeles NF			
All sites	225.8 ± 148.1	37.0 - 689.0	71
Saugus Ranger District	172.6 ± 156.7	48.0 - 530.0	14
Tujunga Ranger District	235.4 ± 123.3	119.0 - 405.0	8
Arroyo Seco Ranger District	304.6 ± 144.1	37.0 - 689.0	21
Mount Baldy Ranger District	185.6 ± 134.3	46.0 - 496.0	14
Valyermo Ranger District	195.3 ± 139.7	65.0 - 600.0	14
All pairs	242.5 ± 147.4	54.0 - 600.0	38
Singles	206.5 ± 148.7	65.0 - 600.0	33
Los Padres NF			
All sites	89.3 ± 52.2	25.0 - 200.0	21
All pairs	98.4 ± 50.4	25.0 - 200.0	16
Singles	60.0 ± 51.9	25.0 - 150.0	5
San Bernardino NF[1]			
All pairs	5,329.0± 4,941.0	1,835.0 -8,823.0	2
All individuals	3,450.1± 2,504.6	674.0 -6,294.0	4

[1] Owls on the San Bernardino NF were radio tracked. Home-range estimates were determined using the 100-percent minimum convex polygon.

definition of availability based on, for example, the 100-percent MCP. This occurred because the AK algorithm tightly fits the actual distribution of points with an irregular polygon. In the limiting case with many data points, the AK could fit just the used distribution of points and exclude other habitats that truly may have been available.

Thus, failure to reject the null hypothesis (that habitat use = habitat available) in some of our tests of selection may have resulted from the effects of small samples and the use of the AK algorithm, rather than demonstrating a lack of selection. The extent to which this occurred is unknown. It is clear, however, that failure to detect habitat selection should be interpreted, for those tests with low power, in terms of a high likelihood of type-II errors. Given these limitations, it may be that confirmed selection for particular attributes (for example, canopy closure or tree size) by even a few owls should be considered strong evidence for selection in our studies. An incorrect inference would be to conclude that failure to detect significant habitat selection proves a lack of selection. For these reasons, we believe the most significant insights to spotted owl biology are provided by the habitat-use results, rather than results of tests for selection.

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Chapter 7

Patterns of Habitat Use By California Spotted Owls in Logged Forests of the Northern Sierra Nevada

Cynthia J. Zabel, Kevin S. McKelvey, and James D. Johnston

The radio-tracking study area on the Lassen National Forest (NF) reported in Chapter 6 was coincidentally an area for which we were able to locate nearly complete records of logging. It was also an area for which we had much information about the vegetation. Based on these records, we have visually examined patterns of habitat use by radio-tagged spotted owls in relation to stand histories near the geographic center of our telemetry study area. We have assumed that a low density of owl locations in an area indicated an aversion by the owls to the habitat there. Conversely, a high density of locations was interpreted to indicate selection for a particular area.

We have not attempted any statistical analyses of use vs. availability for these data, as done in Chapter 6. Logging practices were unique enough on the various study sites that we could not stratify them into meaningful categories for rigorous use-versus-availability tests. Instead, we based our evaluations of spotted owl use patterns on visual inspections of owl locations in relation to known histories of logging in stands. Such case studies may serve to enlarg;our general understanding of how the owls are affected by dift :rent stand treatments.

Study Area

The Lassen NF study area was located in the northern Sierra Nevada, east of Lassen National Park. It was dominated by red and white fir at high elevations (approximately 5,800-6,900 feet) and pine (Jeffrey, ponderosa, sugar, and lodgepole) at lower elevations (approximately 5,000-5,800 feet). The predominant silvicultural method there has been selective logging. For this chapter, we focus on the high-elevation, true fir zone. The condition of this forest in the early part of the 20th century was markedly different before logging began in the 1930s. Sierran mixed-conifer forest covered the mid-mountain slopes and red fir dominated higher elevations, except for shrub fields on the south side of Swain Mountain. The forest was dominated by large trees-average diameter at breast height (d.b.h.) of the various species was 25-34 inches for white fir, 32-35 inches for Jeffrey pine, and 28-32 inches for red fir (Boerker 1912, Evans 1919).

Methods

The cutting history within the study area was determined using records and timber sale maps from the U.S. Department of Agriculture, Forest Service (FS) and private timber companies. This information was then transferred to U.S. Geologic Survey topographic maps. Cut-unit polygons were subsequently digitized and stored in a Geographic Information System (GIS). Each cut-unit polygon contained historical information, including year of cut, type of harvest (overstory removal, group selection, thinning, sanitation, salvage, partial cut), and species removed. Radio-telemetry points from daytime roosting and nighttime foraging locations of spotted owls (Chapter 6) were overlaid onto the cut-history maps using GIS. Vegetation types (table 6A), determined from large-scale color aerial photographs and 1:24,000 black-and-white orthophotoquads, were then overlaid onto the owl telemetry points and the cut-unit maps. Vegetation polygons were classified by diameter size-class of the dominant trees (structural size class) and canopy closure class of dominant trees. For this chapter, we classified structural size class into two categories: <21 inches in d.b.h. (size classes 0-3) and ≥21 inches d.b.h. (size classes 4 and 5). Similarly, canopy closure was categorized as <40 percent cover (open, sparse, or poor) or ≥40 percent cover (normal or good). Polygons were reclassified as suitable or unsuitable spotted owl habitat based on current FS definitions. Suitable stands were those in which the diameter size-class of dominant trees was ≥21 inches, canopy closure of dominant trees was ≥20 percent, and total canopy closure was ≥70 percent.

We present three figures for each area of interest with owl radio locations overlaid on each of three vegetation types--suitable spotted owl habitat according to the FS; structural size class ≥21 inches in d.b.h.; and canopy closure ≥40 percent. Cut units and areas of owl use have been numbered in the sequence in which they are discussed in the results. For one area, we also present a 1980 orthophotograph for a visual inspection of the landscape. Timber-sale boundaries delineated on the figure do not always align with boundaries on the orthophoto. The figure represents sale maps or planned cuts, but the orthophoto depicts actual cut boundaries after logging was done. Cut units delineated on the figures are minimum representations of actual areas that were logged. Many areas were entered with light removal outside of the units we mapped, but the FS generally did not keep detailed records of such light cuts.

Results

We examined four areas located near the center of our owl home-range and habitat-use study and where much logging had occurred (fig. 7A). These areas are designated here as Griffith Hill (fig. 7B), Swain Mountain (fig. 7C), Silver Lake (fig. 7D), and Star Butte (fig. 7E). Most logged areas on Swain Mountain were little used by owls, and some heavily logged areas at Griffith Hill, Silver Lake, and Star Butte were avoided by the owls, but other logged areas were used extensively.

Griffith Hill

The Griffith Hill area was dominated by a strip of FS land approximately 3/4 of a mile wide and 2 miles long, lying between two areas of private land (figs. 7B and 7F). Canopy cover on FS land was mostly ≥40 percent. The FS land was characterized by selectively logged true fir and mixed-conifer forests. Several sites (numbers 1, 2, 3, and 4) were selectively logged in the mid-1960s by overstory removal and group selection. Private land south of this section (site 5), on the other hand, has been logged much more heavily, and canopy cover there was <40 percent. Site 5 was rarely used by the owls. Pine and fir were harvested there in 1960; in 1973 trees >24 inches were removed and the site was salvage-logged for merchantable timber; and trees of all species <20 inches in d.b.h. were thinned in the 1970s-1980s (McCrory pers. comm.). Site 5 currently has sparsely scattered trees ≥21 inches in d.b.h. in the eastern section. The adjacent private land (site 6) is owned by the same company but, according to their records, it has not been entered. The Susan River drainage, which runs through this area to the south of Lake Road (site 7), was logged by overstory removal and group selection in 1966 and 1968. It now has canopy cover ≥40 percent, but trees there are small and the site is classified as unsuitable owl habitat.

In general, spotted owl use at Griffith Hill occurred mostly on FS land. The more open private land to the north and south were used relatively little. Several owl telemetry fixes were in site 6, characterized by trees ≥21 inches in d.b.h. and a canopy closure ≥40 percent. An owl pair nested in the fir stand covering the eastern half of site 1. The owls apparently did not use the western half of site 1, which had been heavily logged and was very open. The eastern half of site 1 was "group cut" (in small areas <1 acre), and the western half was cut using overstory removal (J. D. Johnston pers. observ.).

Swain Mountain

This area covers Swain Mountain Experimental Forest (SMEF) and adjacent forests (fig. 7C). Most of SMEF lies above 5,800 feet in elevation and is dominated by forests of red and white fir. Numerous small patch cuts were made across SMEF in 1958 and from 1970 to 1972. Several stands were also selectively logged during the early 1970s. The large south-facing slope of Swain Mountain burned frequently in the past and was planted with Jeffrey pine in 1978. Today the area is dominated by a thick cover of ceanothus, chinquapin, manzanita, and small Jeffrey pines. Much of SMEF was shelterwood-logged from 1982 to 1985. Those cuts underwent intensive site preparation following logging-units were either broadcast burned or tractor-piled and burned. Most of the residual trees there today are large, old-growth firs, with densities ranging from 5 to 15 trees per acre. Several intact stands of old-growth still remain on SMEF.

Spotted owls did not use the large areas of shelterwood cuts (site 8) or the large pine plantation on the south side of Swain (site 9). Figure 7C shows that most owl locations were in habitat classified as suitable (sites 10, 11, 12, and 13), and many were in the intact old-growth stands. Most owl locations on SMEF occurred during the nonbreeding period. One owl pair had a linear home range along a road just southwest of the pine plantation (site 14). The forest along this road, and to the west of it, has been selectively logged but is still dominated by trees ≥21 inches in d.b.h. and canopy cover ≥40 percent.

Silver Lake

The Silver Lake area (fig. 7D) lies just west of the Griffith Hill area and northwest of SMEF. Its eastern part includes private land that was heavily logged in the past (fig. 7B, site 5). The area currently has a very open canopy and few stands with large trees remain. Relatively few owl locations occurred there. To the northwest and southwest were FS lands that had been selectively logged to varying degrees. Owls used this heterogeneous landscape extensively, avoiding the most open areas--sites 15, 16, and 17. Those sites formed a continuous, broad strip of land that has been logged heavily. Stands between the private land (site 5) and logged sites 15 and 17 contained suitable habitat with large trees. Cutting occurred there in small blocks, but the owls regularly used the area. Several owl locations were in high-elevation (>6,400 feet) stands that were relatively open but dominated by large-diameter firs (site 18).

Star Butte

The Star Butte area (fig. 7E) has also been selectively logged to varying degrees using overstory removal and group-selection methods. Most of this area was extensively used by spotted owls, even though much of it was not classified as suitable spotted owl habitat. The only relatively undisturbed stand of old-growth fir in the Star Butte area was used for nesting by a pair of owls in 1990 (site 19). The more heavily logged areas (site 21) and the area around Star Butte (site 22) were both used infrequently by the owls. Site 21, on private land, was logged repeatedly in the 1930s, 1940s, 1950s, and 1970s. It was logged for culls in 1980, and it has been thinned in the past 3 years (Briggs pers. comm.). Star Butte (site 22) had small pockets of large trees but was unsuitable owl habitat. It contains a 6,700-foot peak with shrubfields along its upper slopes and small firs on its lower slopes. The area southeast of Star Butte had been heavily logged and appeared to be avoided by owls.

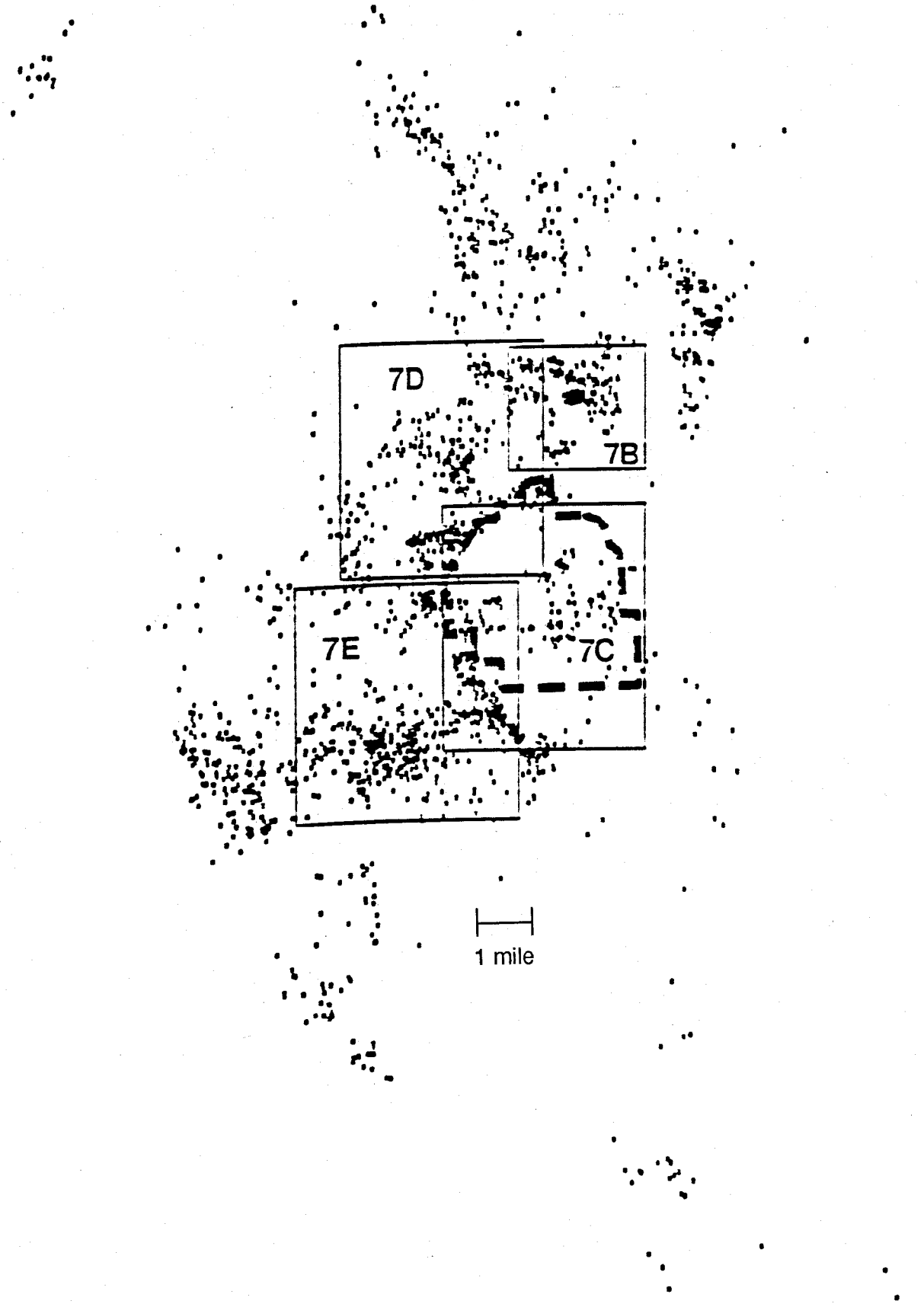

Figure 7A-Locations of study areas (7B, 7C, 7D, and 7E) on the Lassen National Forest. Radio-telemetry points from daytime roosting and nighttime foraging locations of California spotted owls are indicated. The boundary of Swain Mountain Experimental Forest is delineated as a dashed line. Study area numbers correspond to descriptive figures 7B-7E, similarly numbered.

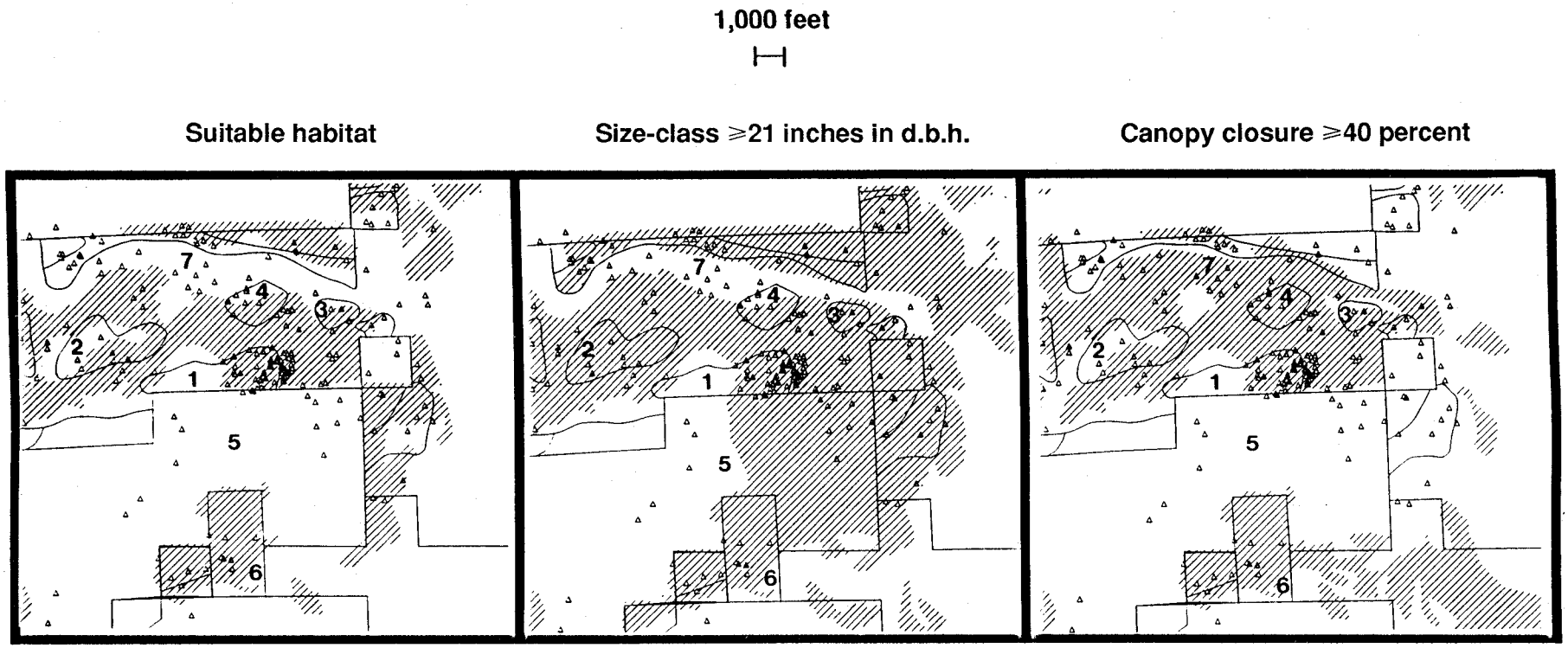

Figure 7B—Griffith Hill study area. Timber sale boundaries and section boundaries between private and National Forest lands are delineated. California spotted owl radio-telemetry locations (open triangles) are overlaid onto three vegetation types indicated by diagonal lines: (1) suitable spotted owl habitat, based on current Forest Service (Region 5) definitions; (2) stands in which diameter size-class of dominant trees was ≥21 inches; and (3) stands in which canopy cover of dominant trees was ≥40 percent. Numbers on each study area map refer to specific logging sites and areas of owl use.

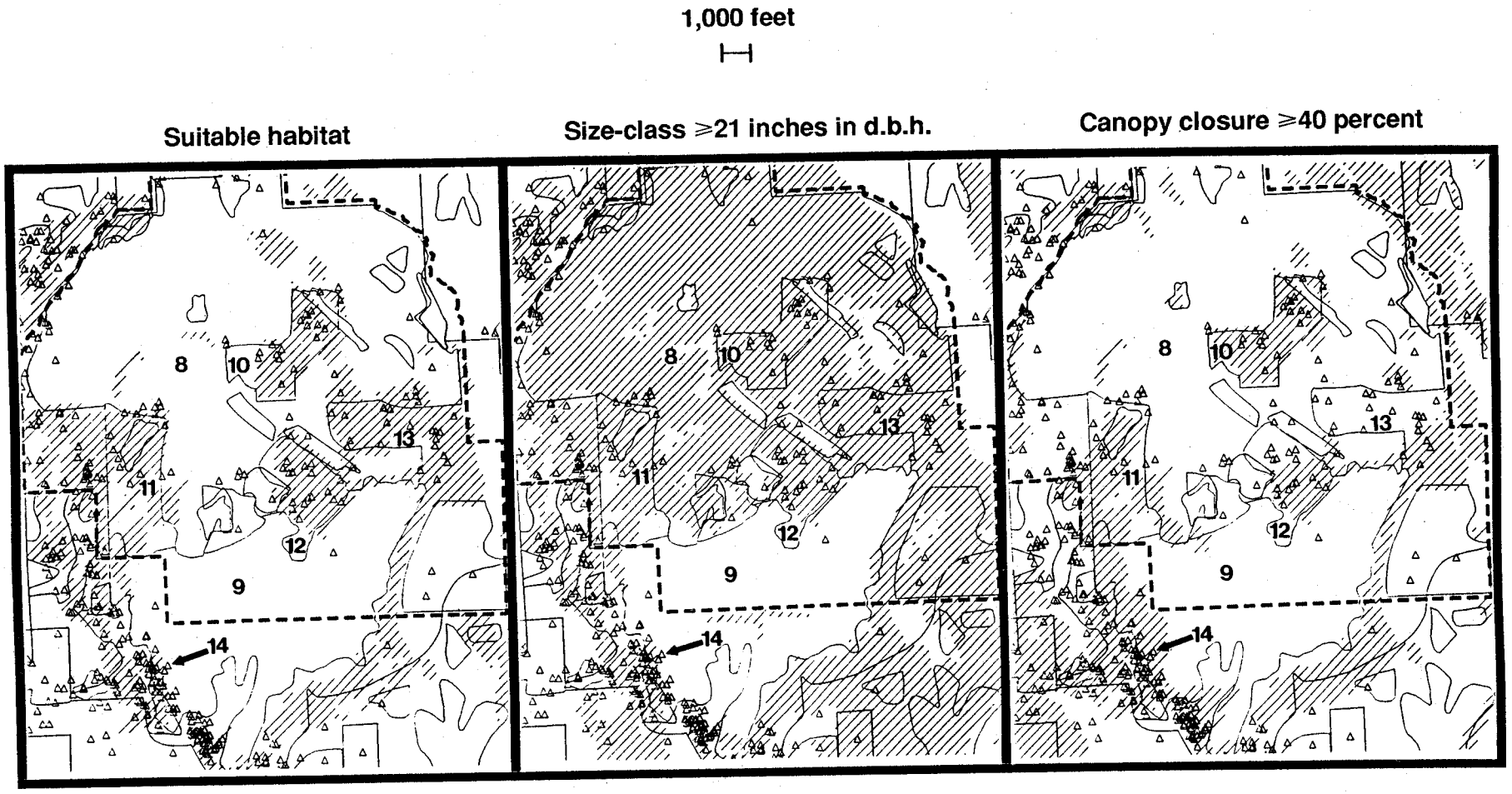

Figure 7C—Swain Mountain study area. The boundary of Swain Mountain Experimental Forest is indicated as a dashed line. Timber sale boundaries and section boundaries between private and National Forest lands are delineated. California spotted owl radio-telemetry locations are overlaid onto three vegetation types indicated by diagonal lines: (1) suitable spotted owl habitat, based on current Forest Service (Region 5) definitions; (2) stands in which diameter size-class of dominant trees was ≥21 inches; and (3) stands in which canopy cover of dominant trees was ≥40 percent. Numbers on each study area map refer to specific logging sites and areas of owl use.

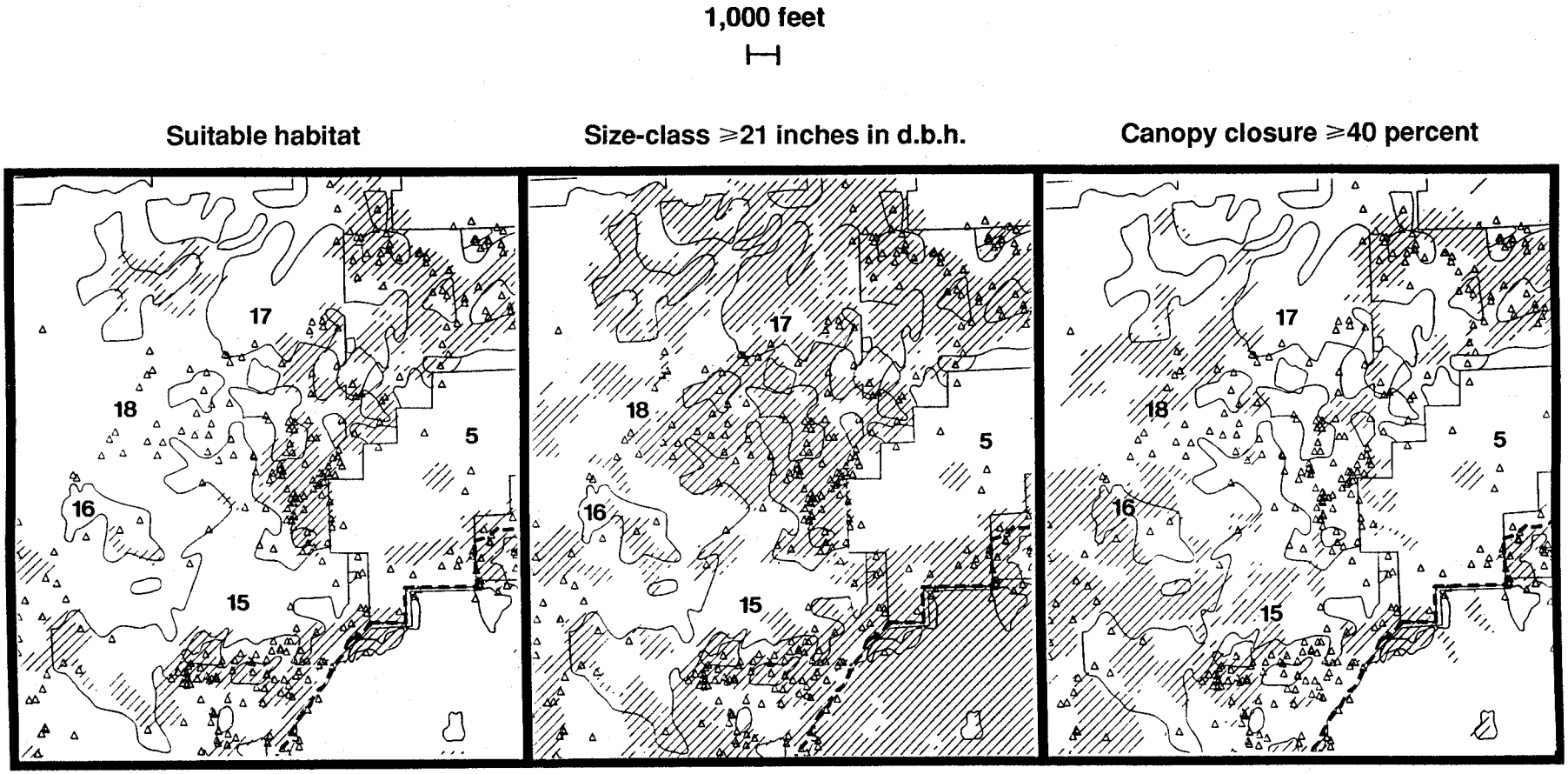

Figure 7D—Silver Lake study area. Timber sale boundaries and section boundaries between private and National Forest lands are delineated. California spotted owl radio-telemetry locations are overlaid onto three vegetation types indicated by diagonal lines: (1) suitable spotted owl habitat, based on current Forest Service (Region 5) definitions; (2) stands in which diameter size-class of dominant trees was ≥21 inches; and (3) stands in which canopy cover of dominant trees was ≥40 percent. Numbers on each study area map refer to specific logging sites and areas of owl use.

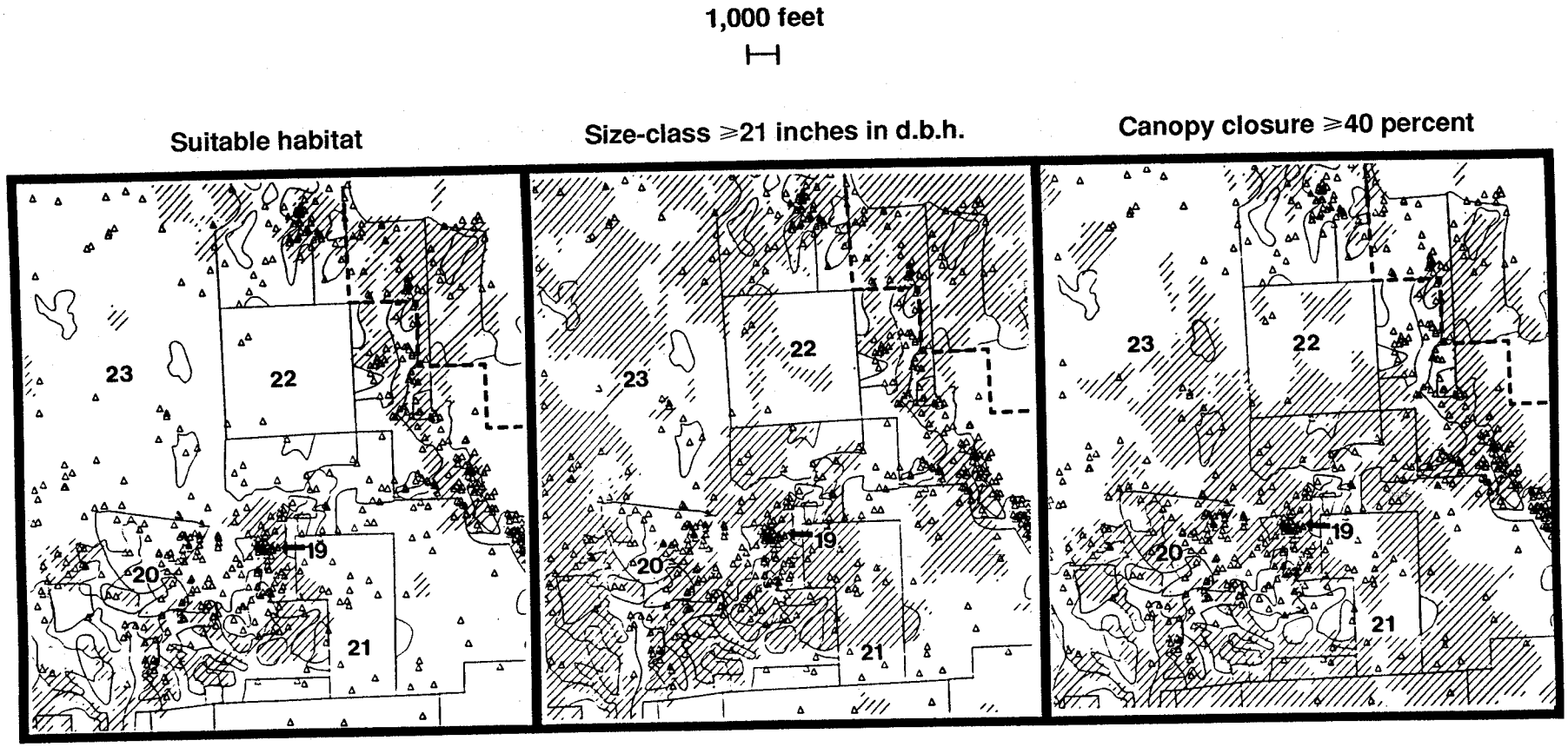

Figure 7E—Star Butte study area. Timber sale boundaries, and section boundaries between private and National Forest lands are delineated. California spotted owl radio-telemetry locations are overlaid onto three vegetation types indicated by diagonal lines: (1) suitable spotted owl habitat, based on current Forest Service (Region 5) definitions; (2) stands in which diameter size-class of dominant trees was ≥21 inches; and (3) stands in which canopy cover of dominant trees was ≥40 percent. Numbers on each study area map refer to specific logging sites and areas of owl use.

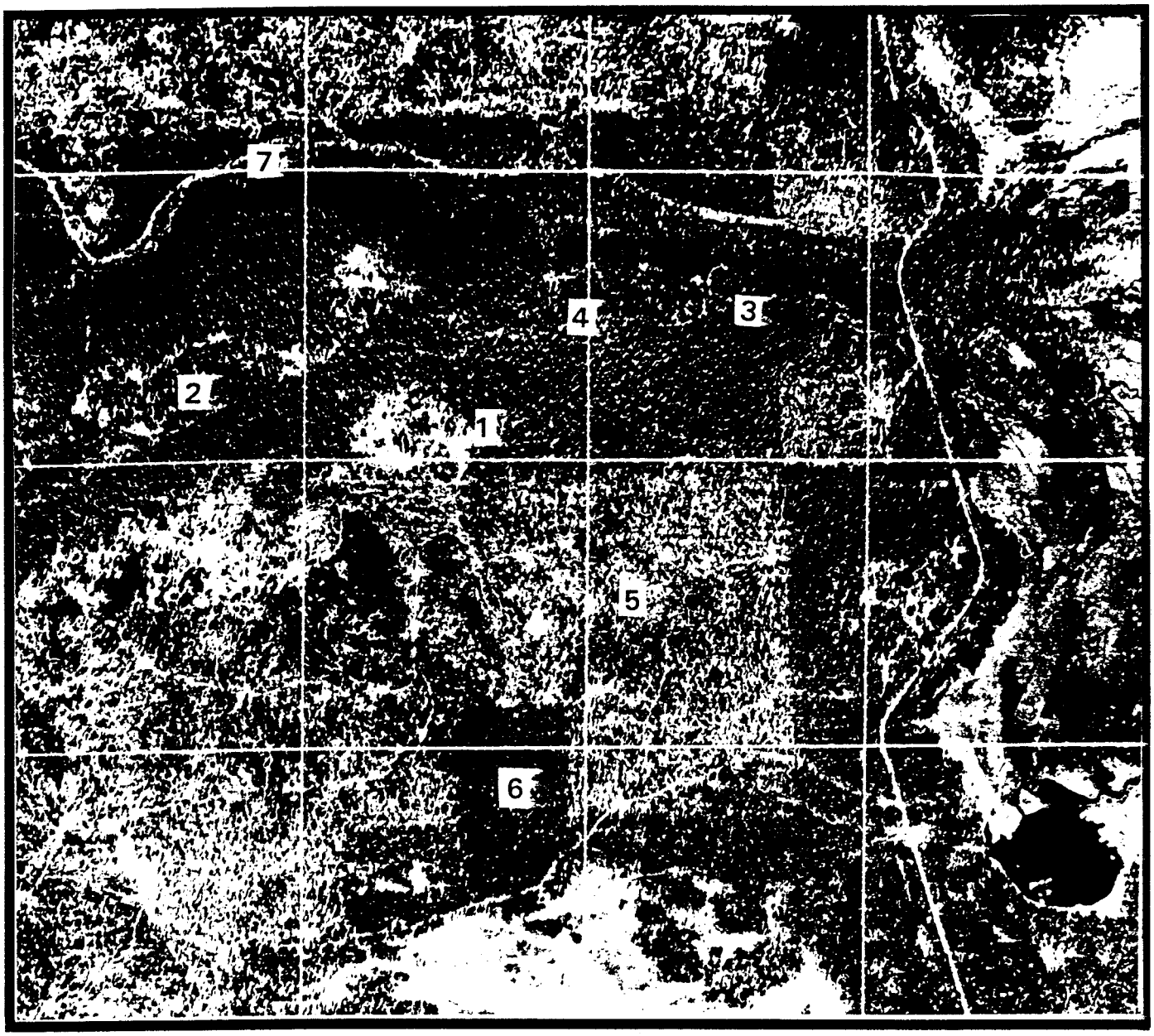

Figure 7F-Orthophotograph of Griffith Hill study area (fig. 7B). Cut units and areas used by California spotted owls are numbered in the sequence in which they are discussed in the results section of this chapter.

Site 14, near the southwest corner of SMEF, is an extension of an owl pair's linear home range referred to in the discussion of Swain Mountain. It has been selectively logged, but it was still suitable habitat and was heavily used by a pair of owls. Site 23, like site 18 (fig. 7D), is an uncut, high-elevation site that was used by owls even though it was unsuitable habitat. It also had areas of sparse, large trees where owl locations tended to occur, and pockets of high canopy cover were present.

Discussion

Decades of selective logging and wildfire on the Lassen NF have resulted in a complex and heterogeneous landscape. Unlike landscapes in the Pacific Northwest, where even-aged management has produced stands that differ primarily in stand age and size, uneven-aged management on the Lassen NF and throughout most of the Sierra Nevada has produced landscapes in which stands vary according to several factors. They vary in the number of times they have been entered for logging, the species of

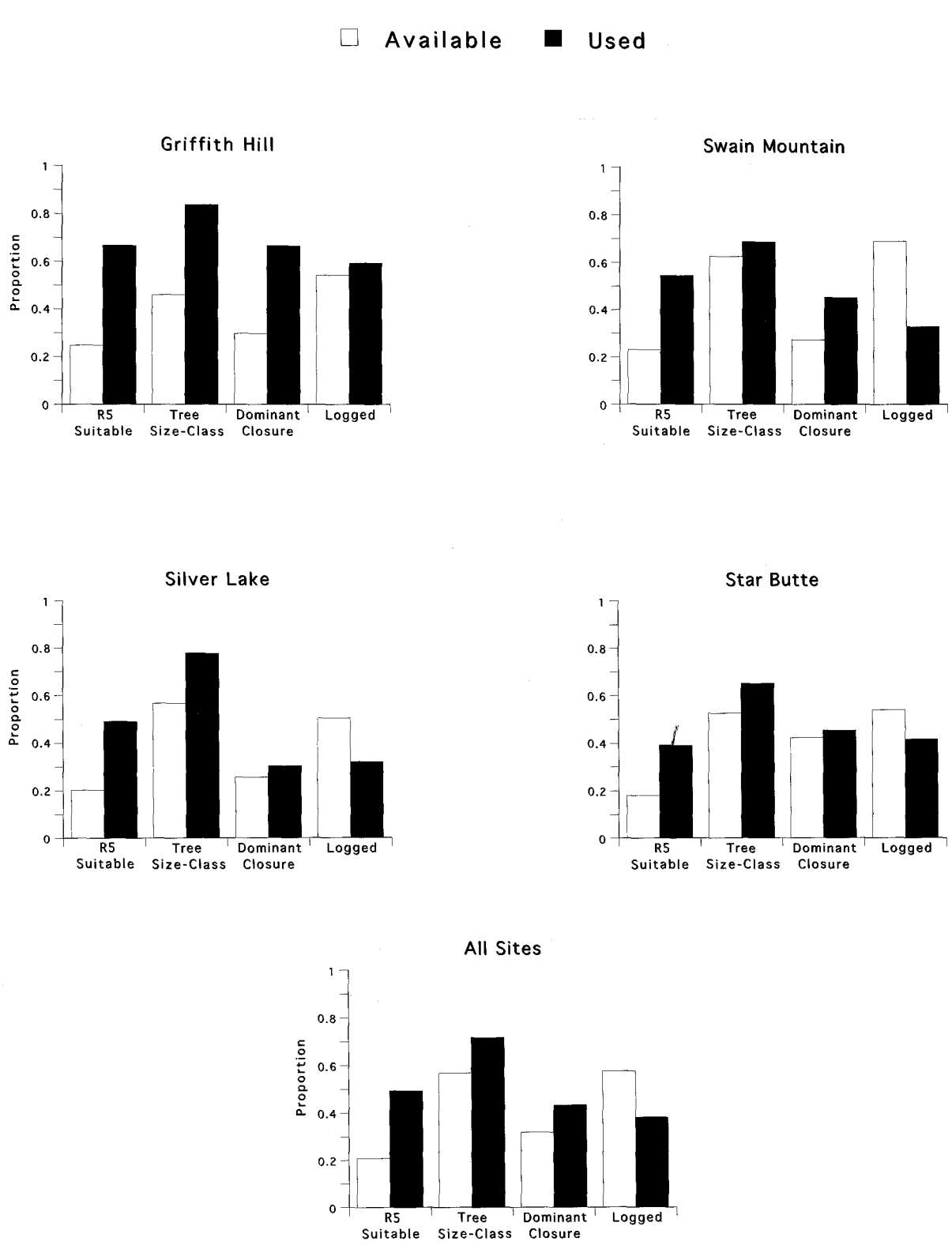

Figure 7G-Proportions of habitat types available in relation to the proportions used by radio-tagged California spotted owls at four study areas in the Lassen National Forest. Four categories of habitat were tested: (1) R5 suitable = Forest Service (Region 5) definition--medium or large sawtimber (≥21 inches in diameter at breast height), dominant canopy closure poor or higher, and total closure >69 percent; (2) structural size-class ≥21 inches in diameter at breast height; (3) dominant canopy closure ≥40 percent; and (4) logged stands.

trees taken, the diameter distribution of trees removed, and in the total volume logged. As a result, it is more difficult to compare stand structure and composition in landscapes dominated by uneven-aged management than is the case where even-aged management has occurred.

The areas we examined were predominantly logged by overstory removal and group-selection techniques in the late 1960s. It is apparent from these results that spotted owls tend to avoid altogether some forest conditions resulting from logging, but that they will use other types for foraging. Logged areas used by owls contained predominantly large trees (≥21 inches), and most of them had retained enough structure and canopy closure to be classified as suitable owl habitat (for example, site 14). Owl use of sites with large trees, dense canopy cover, and with suitable habitat (R5 definition), was greater than expected from the availability of such sites at all four study areas (fig. 7G). Some areas of low canopy cover were used where large trees were present and stands of high and low cover were interspersed (sites 2, 3, and 13). Pockets of large trees were also used when they were in areas of high canopy cover (sites 4, 20, and 21). It appears as if spotted owls will use logged sites if pockets of suitable habitat are interspersed among stands with low canopy or small trees. We cannot, however, quantify the total acreage or proportion of a site that must be in such stands before owls will use the site. These results indicate that logging by overstory removal and group selection can be compatible with spotted owl management in the red fir zone, if logged areas are small and interspersed with varying size classes and levels of canopy closure.

Use of logged sites was less than expected from the availability of such sites at three of four study areas (fig. 7G). Logged sites that were avoided by owls included large areas of sparsely distributed, big trees with low canopy cover (sites 5, 8, and 17), and large areas with dense canopy cover but small trees (sites 15 and 16). Most of the logged areas that were not used by owls had not returned to suitable owl habitat.

Spotted owls in the true fir zone used some naturally occurring sites classified as unsuitable owl habitat (see Chapter 6). These included areas at high elevations with large trees that were sparsely distributed (for example, Silver Lake site 18 and Star Butte site 23). In contrast, areas that were unsuitable habitat as a consequence of logging were often not used by owls. Examples include shelterwood-logged stands at SMEF (site 8) and private land that was heavily thinned north of Swain Mountain (site 5). Areas near site 18 and site 23 were used by owls even though they were far from the center of any concentration of owl locations. Yet, heavily logged areas (sites 5 and 8) were not used, even though they were adjacent to sites with concentrations of owl locations.

Unsuitable habitat in the Silver Lake area (site 18) was used by five individual owls during the nonbreeding period. These owls moved upslope into the higher elevations during the fall and remained there throughout the winter. Similarly, four owls used the high-elevation, uncut stands in SMEF (sites 10, 11, 12, and 13) during the fall and winter. These owls did not fly across the shelterwood-logged stands during the summer, but they did so during the winter to access uncut, old-growth stands (sites 10, 11, and 12).

This is a first attempt to determine cut patterns that spotted owls will use. Strong patterns of aversion were apparent in the data, but preference patterns were not so clear. The silvicultural prescriptions described here did not adequately convey what was removed from cut units. All the units we examined had overstory removal and group selection, yet aerial photographs indicated that different volumes of timber were removed. Some units now have dense stands of large trees, while others have sparsely distributed, large trees. A micro-scale approach, with precise measurements of stand characteristics, may be needed to better understand what logging prescriptions are compatible with spotted owls. Attributes that may have been impacted by site preparation but were not considered in the analyses presented here, such as amounts of coarse woody debris, may also be important. Such attributes may influence prey abundance and distribution, and indirectly influence use of harvested areas by spotted owls (Chapter 4).

These results indicate that cutting patterns other than clearcuts, such as heavy overstory removal, can make sites unsuitable for spotted owl foraging in the red fir zone. We do not know how these patterns may extend into Sierran mixed-conifer forests. Home-range sizes of California spotted owls were larger in the high-elevation, red fir zone (Chapter 6), which was underused for nesting (Chapter 5) compared to mixed-conifer forests. High-elevation red fir may be marginal for California spotted owls, and owls living there may be more sensitive to logging than owls in mixed-conifer forests. These results may not be applicable to other forests types. A similar study with good quantitative information on what was logged, and how, needs to be done in mixed-conifer forests.

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Chapter 8

Estimates of Demographic Parameters and Rates of Population Change

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Detailed analyses of a species' life-history structure are essential to understand its population dynamics, provide insights to effective management, and also suggest directions for future research. In this chapter, we present analyses of available demographic data on the California spotted owl, using life-history and demographic information in an approach similar to that of Mertz (1971), Nichols et al. (1980), Noon and Biles (1990), and Thomas et al. (1990, appendix L). Our objectives were (1) to characterize the life-history structure of the California spotted owl, (2) to estimate values of the demographic parameters needed to compute rates of population change, (3) to test the sensitivity of the rate of population change to each of the demographic parameters, (4) to infer which parameters may be most influenced by management decisions, and (5) to suggest future research priorities, as indicated by the demographic analyses.

Methods

Demographic studies of spotted owls were conducted at five locations for periods ranging from 2 to 6 years-Lassen National Forest (NF), Eldorado NF, Sierra NF, Sequoia/Kings Canyon National Parks (NPs), and San Bernardino NF (table 8A). Density studies were conducted at four of those sites and at three additional sites (table 8B). The territorial behavior of spotted owls allows researchers to survey their populations by listening for and eliciting vocalizations. The usual procedure is to locate owls at night, then to follow up the next day with visual confirmation and, for demographic studies, to capture and uniquely color band each bird to allow individual identification in the field without recapture. The sex of adults was determined from their vocalizations, and reproductive status was determined by a protocol in which live mice were fed to the owls and they were then observed to determine whether they eventually carried a mouse to a nest site (Forsman 1983). Captured spotted owls can be placed into one of four age-classes: juvenile ($x < 1$), first-year subadults ($1 \leq x < 2$), second-year subadults ($2 \leq x < 3$), and adults ($x \geq 3$) based on plumage characterisitcs (Moen et al. 1991). Model structure, however, seldom has been based on all four age-classes because parameter estimates do not differ among classes, or because of insufficient data. Second-year subadults and adults are often collapsed into a single age-class (see below).

Table 8A-*Summary information on the five demographic study areas.*

Location	Approximate size (square miles)	Years of marking	Total individuals marked
Lassen National Forest	500	1990-91	130
Eldorado National Forest	136	1986-91	72
Sierra National Forest	160	1990-91	82
Sequoia/Kings Canyon National Parks	130	1988-91	62
San Bernardino National Forest	730	1987-91	367

Table 8B- *Density estimates (owls per square mile) of spotted owls in California.*

Study area	Size in square miles	Crude density[1]	Reference
Northern spotted owl			
Six Rivers National Forest	113	0.609	Franklin et al. 1990a
Simpson Timber Company	94	0.990	Diller 1989
California spotted owl			
Eldorado National Forest	137	0.259	Lutz 1992
Yosemite National Park	156	0.518	Roberts et al. 1988
Sierra National Forest	160	0.526	Verner et al. 1991
Sequoia/Kings Canyon National Parks	132	0.440	Roberts 1989; Verner et al. 1991
San Bernardino National Forest	207	0.347	LaHaye et al. in press
Mount San Jacinto	67	0.466	Gutiérrez and Pritchard 1990
Palomar Mountain	13	1.657	Gutiérrez and Pritchard 1990

[1]Estimated number of owls/total study area. Much of the area included was not suitable habitat, and the proportion of unsuitable may have varied markedly from one study area to another.

Parameter Estimation

Estimates of density (owls per square mile) assumed complete enumeration of all owls within a defined area. Usually when owls were counted, they were also color-banded to minimize the likelihood of double counting. Because territorial owls tended to vocalize regularly and to be spatially restricted within their home ranges, they were more likely to be detected than

nonterritorial owls (floaters). To the extent that many floaters occurred in an area, true density may have been underestimated.

Ideally, we would use precise and accurate estimates of three classes of parameters (s_x, b_x, and a) to compute the finite population growth rate, or λ:

1. s_x = *probability* of survival from age x to $x + 1$.

Previous demographic analyses of spotted owls generally assumed that s differed for at least three age-classes-juveniles (s_0), first-year subadults (s_1), and adults (s). The adult class, defined on the basis of age at first reproduction (a = 2 years), thus included second year subadults. The juvenile stage ends at the age of 1 year for spotted owls. In our analyses we did not partition juvenile survival rate into preand postdispersal probabilities, as done by Lande (1988). The subadult stage for the northern spotted owl covers the second year of life (age 1 to age 2) and is assumed to be an age interval in which the birds typically do not breed. The adult stage was thus anything older than 2 years (Noon and Biles 1990). Ideally, survival rates of these stages can be computed directly for each population modeled, using data from that population. Using program JOLLY (Pollock et al. 1990), we could estimate juvenile survival rate (s_0) only for the San Bernardino study area, because data were insufficient for the Eldorado and Sequoia study areas. Consequently, the San Bernardino value for so was used as an approximation for the other two locations. It is similar to estimates of s_0 from several studies of northern spotted owls (Franklin 1992; USDI, FWS 1992), and λ is not especially sensitive to variations in s_0. The true value of s_0 for these sites, however, is unknown.

Data were also insufficient to compute separate estimates of s_1 and s for the Eldorado and Sequoia/Kings Canyon study areas, and these two values were statistically indistinguishable for the San Bernardino study area. Therefore, in demographic analyses reported here, we used survival estimates for only two age-classes-s_0 (juvenile) and s ("nonjuvenile," combining subadult and adult age-classes). The probability of survival to age x was thus computed as $l_x = s_0 s^{x-1}$ (by definition $l_0 = 1.0$) (table 8C).

Table 8C-*Spotted owl life history (age at first reproduction is 2 years).*

x[1]	l_x[2]	b_x[3]	$l_x b_x$[4]
0	1.0	0	0
1	s_0	0	0
2	$s_0 s_1$	b	$s_0 s_1 b$
3	$s_0 s_1 s$	b	$s_0 s_1 s b$
4	$s_0 s_1 s^2$	b	$s_0 s_1 s^2 b$
.	.	.	.
.	.	.	.
.	.	.	.
x	$s_0 s_1 s^{x-2}$	b	$s_0 s_1 s^{x-2} b$

[1] x denotes age in years.

[2] l_x denotes the probability that an individual aged 0 (a newly hatched bird) will survive to enter age class x.

[3] b_x denotes the expected number of female fledglings produced by a surviving female aged x.

[4] $l_x b_x$ denotes the net maternity function. At this time for the California spotted owl, $s_1 = s$.

2. b = fecundity, the expected number of female fledglings produced per female per year; b_x is the fecundity of a female of age x.

Fecundity values were calculated by halving the number of young fledged per territorial female, assuming an even sex ratio among fledglings. Because ages of females breeding, or attempting to breed, were seldom known, we assumed a constant reproductive rate for females of all ages: $b_x = b$ ($x \geq 2$ years).

3. a = age at first reproduction.

Apparently female spotted owls rarely breed when only 1 year old; most do not begin until at least 2 years old (Franklin 1992). Therefore, we used a = 2 years in demographic analyses reported here.

Estimates of age-specific survival rates from study areas with ≥4 years of data came from capture histories of marked birds using Program JOLLY (Pollock et al. 1990). Because some studies suggest that reproduction by spotted owls may be affected by radio transmitters attached with back-pack harnesses (Paton et al. 1991, Foster et al. 1992), estimates of survival and reproductive rates used in this demographic analysis were based solely on banded birds. To increase the precision of the estimates, we estimated the minimum number of parameters that adequately fit the data. When sufficient data were available, we tested for differences between adjacent age-classes to justify pooling of capture histories. In most cases, however, data were insufficient, so we pooled values for all individuals at least 1 year old to compute a survival rate for adults. Because the Lassen and Sierra studies have been underway for only 2 years, their data were insufficient for statistically reliable estimates of survival rates. For these sites, we simply estimated survival rates empirically, pooling data from all males and females at least 1 year old.

Analysis

Standard Lotka-Leslie methods (Leslie 1945, 1948; Lotka 1956) were applied to the estimates of vital rates (age-specific birth and death rates) to make inferences about rates of population change. In addition to assumptions identified above, we assumed (1) that reproduction was characteristic of a "birth-pulse" population-one with a single, well-defined, annual breeding period (Caughley 1977, p. 6), (2) a stable age (stage) distribution, and (3) no density dependence-a change in population density did not affect the values of the vital rates. This assumption was probably valid within the limits of the population densities modeled here. Preadult survival rate (l_2) was the probability of survival from fledging (age when leaving the nest) to age 2 and was given by the product of s_0 and s.

Estimates of all parameters needed for a completely age-specific Leslie matrix (Leslie 1945, 1948) were not available for any of the populations modeled. Often such data are limited for long-lived species, and estimates of all the age-specific parameters are impossible to attain or have large sampling variances because of small sample sizes. Repeated multiplication of imprecise estimates in fully age-specific models is likely to lead to uncontrolled error propagation (Dobson and Lyles 1989). The

Lefkovitch stage-projection matrix model (Lefkovitch 1965) is a useful approximation to an age-structured model. The dynamics of the two models are usually similar, but the Lefkovich model is more tractable (Boyce 1987). A stage is simply a category (age-class) within which birth and death rates are assumed to be constant. Consequently, estimating the population dynamics of spotted owls with a stage matrix would yield misleading conclusions only if the birds manifest an age-related decline in reproductive rate (senescence) before about 15 years old (Noon and Biles 1990). Given the current high estimates of *s*, early senescence seemed unlikely.

Our application here of the Lefkovich model uses only two stages juveniles (J) and nonjuveniles (NJ), as defined above. Time was expressed as an interbreeding interval of 1 year, and age at first reproduction was set at 2 years. Given that popula tions were based on census estimates corresponding to a period shortly after the breeding period, the Lefkovitch matrix had the following structure (details in Noon and Sauer 1992):

$$\begin{pmatrix} J_{t+1} \\ NJ_{t+1} \end{pmatrix} = \begin{pmatrix} 0 & sb \\ s_0 s & \end{pmatrix} \begin{pmatrix} J_t \\ NJ_t \end{pmatrix}$$

The location of *s* along the diagonal of the matrix reflects our assumption of constant adult survival and no senescence. The possibility of very old owls in the population had little effect on our estimate of λ assuming that adult survival was estimated, irrespective of adult age, from an unbiased sample of all adults in the population (Boyce 1987). We believe this assumption was valid for all populations modeled here.

The basic characteristic equation of the matrix is given by

$$\lambda^2 - s\lambda - s_0 sb = 0. \quad (1)$$

The dominant, real-valued solution (λ_1) is an estimate of the annual, finite rate of change of the population. Vital rates suggest an increasing population if $\lambda > 1.0$, a stable population if $\lambda = 1.0$, and a declining population if $\lambda < 1.0$. We urge caution in using the computed estimates of λ to forecast future population sizes or to infer sizes of historical populations. Lamdba estimated how the population was changing only during the period of study. Using the estimate of λ to project future population size would assume, unrealistically, that current estimates of vital rates are constant over time.

Hypothesis Tests of Lambda

We had estimates of fecundity and adult survival from three study areas and, in addition, an estimate of juvenile survival from one study. Based on these parameter estimates, and assuming s_0 to be equal at all locations, we computed λ from the Eldorado NF and Sequoia/Kings Canyon NPs in the Sierra Nevada Province, and from the San Bernardino NF in the Southern California Province. The sensitivities (partial derivatives) of λ with respect to individual life-history characteristics indicate which parameters most affect variation in population growth rate (Lande 1988, Noon and Biles 1990). In addition, sensitivities are needed to estimate the standard error of λ and to perform hypothesis tests. Sensitivities were computed by implicit differentiation of the characteristic equation (Goodman 1971, Lande 1988). Sensitivities for the two-stage Lefkovich model are:

s_0: $\partial\lambda/\partial s_0 = sb/(2\lambda - s)$;
s: $\partial\lambda/\partial s = (\lambda + s_0 b)/(2\lambda - s)$; and
b: $\partial\lambda/\partial b = s_0 s/(2\lambda - s)$.

For all areas, change in population growth rate was most sensitive to variation in adult survival rate. It was much less sensitive to variation in first-year survival rate and fecundity; sensitivity to these two parameters was about equal.

Sensitivities of λ appear in the formula that approximates the sampling variance of the estimate of λ (Lande 1988, p. 602):

$$\sigma^2_\lambda = \sum (\partial\lambda/\partial p)^2 \, \sigma^2_p \quad (2)$$

where p represents each of the parameters and σ^2_p their sampling variance. The variances of juvenile and nonjuvenile rates were estimated according to the methods of Jolly (1965) and Seber (1965). Variance of annual fecundity was based on variance among females across the years of study, divided by the appropriate sample size. For the power analyses (see below), we assumed the survival probability to have a binomial sampling distribution.

Equation (2) is based only on sampling variance, but the data include both sampling and temporal variance. Also, equation (2) neglects possible covariances among the demographic parameters and fails to account for between-year changes in vital rates. Year-to-year changes, estimated by factoring out the temporal component of variation from the total variance estimates of the vital rates and λ cannot yet be estimated for the California data.

Components of the sampling variance of λ were computed by using equation (2), based on the sensitivities and estimates of the vital rates. The standard error of λ, computed as the square root of the variance, was used to construct a confidence interval around λ For example, the 95 percent confidence interval on λ was computed as: $\lambda \pm 1.96\,\sigma_\lambda$. An estimate of λ and its standard error also allowed tests of hypotheses. Of most interest, relative to concern for the species' persistence, was whether λ was significantly <1.0. We tested the null hypothesis: H_0: $\lambda \geq 1$, versus the alternative hypothesis: H_A: $\lambda < 1$. The appropriate test statistics followed a Z-distribution, given by: $Z = |(\lambda - 1)/\sigma_\lambda|$. Tests were one-tailed with a specified probability of a type-I error = 0.05 (only a 5 percent chance of concluding a decline when none actually occurred).

Power of the Tests on Lambda

When a test fails to reject the null hypothesis (H_0, it is important to estimate the power of the test, which is the probability that H_0 will be rejected when a particular alternative hypothesis (H_A) is true. Failure to reject a false H_0 (that is, the popula-

tion is in decline) is known to statisticians as a type-II error. To estimate the power of the test when Ho was not rejected, we used a method outlined by Taylor and Gerrodette (in press). The method involves estimating two sampling distributions, one based on a specified value of λ for H_A, the other on the value of λ for H_0 ($\lambda = 1.0$). Under H_A we specified a $\lambda = 0.95$, that is, a 5 percent annual rate of population decline. This rate of decline would result in a loss of >40 percent of the population over a decade. If the two distributions are completely disjoint, the power of the test is 1.0. If the two distributions are coincident, the power is 0. Power increases as the difference between the specified value of λ and the hypothesized λ value (for example, $\lambda = 1.0$) increases, or as the variance of the distributions decreases. The probability of a type-II error (β) is estimated as a function of the overlap between these two distributions. The power of the test is then $1 - \beta$. To estimate power, we generated simulated distributions of λ under each hypothesis (H_A and H_0) based on 16,000 randomizations.

Results

Density Estimates

Estimates of crude density (number of owls/total acreage of study area) were available from seven areas within the range of the California spotted owl, four in the Sierra Nevada Province and three in the Southern California Province (table 8B). Densities varied from a high of 1.657 owls per square mile on Palomar Mountain to a low of 0.259 owls per square mile on the Eldorado NF. Overall, estimates of crude density for the California spotted owl tended to be slightly lower than those for the northern spotted owl (table 8B; see also Bart and Forsman in press).

Comparison of Demographic Study Areas

Demographic studies were done at five locations widely spaced over the range of the California spotted owl. Two studies have collected data for only 2 years, and the longest study has been in place for only 6 years (table 8D). All studies, however, are planned to continue for 3-5 more years. Some significant highlights from a comparison of the demographic attributes in the five areas (table 8D) include extensive among- and within-site variation in the proportion of nesting pairs and mean fecundity, and pronounced among-site variation in pair turnover rates (proportion of banded adults and subadults that are replaced on their territory by another bird) and nonjuvenile survival rates. Components that contributed to the observed variance in annual fecundity at a given site arose from variation in both the proportion of females nesting and in their productivity. Among-site variation in survival rates of nonjuvenile owls was particularly relevant, as even small changes in survivorship of adult females greatly affect rates of population change (Noon and Biles 1990).

Table 8D-*Summary of demographic attributes of California spotted owls.*

Attributes	Lassen National Forest	Eldorado National Forest	Sierra National Forest	San Bernardino National Forest	Sequoia/Kings Canyon National Parks
Years of banding	2	6	2	5	4
Mean proportion of pairs nesting[1]	0.52	0.31	0.65	0.59	0.51
Range of proportion of pairs nesting	0.38-0.70	0.0-1.0	0.63-0.67	0.50-0.76	0.18-0.80
Mean total fecundity[1,2]	0.48	0.94	1.02	0.59	0.53
Range of total fecundity[1,2]	0.36-0.64	0.37-1.50	0.75-1.22	0.35-0.80	0.08-1.50
Mean subadult turnover rate	0.57	0.14[3]	0.75	0.28[3]	--
Mean adult turnover rate	0.21	0.14[3]	0.19	0.28[3]	0.24
Mean empirical survival rate of subadult females	0.33	0.73	0.50	0.72[2,3]	0.80[2,3]
Mean empirical survival rate of adult females	0.84	0.73	0.74	0.72[2,3]	0.80[2,3]
Mean nonjuvenile survival	*	0.83[2,3]	*	0.75[2,3]	0.89[2,3]

[1] Weighted by yearly sample size.
[2] Males and females combined.
[3] Subadult and adult age-classes combined.
* Inadequate sample.

Hypothesis Tests on Lambda (λ)

Eldorado National Forest

This study has been underway for 6 years, with estimates of nonjuvenile survival rates based on capture histories of 72 birds >1 year old, and fecundity estimates based on reproductive performances of 66 territorial females (table 8E). The estimate of λ (equation 1) was 0.947, suggesting about a 5 percent annual rate of population decline during the period of study (1986-91). This value was not significantly <1.0 ($\alpha = 0.05$, $P = 0.1271$), so the statistical test did not reject the null hypothesis that the population is not declining (H_0: $\lambda \geq 1.0$). The test, however, had a power of only 0.30, setting the probability of a type-II error at about 0.70. The low power of the test was a result of a relatively small number of marked birds, and the large standard errors of parameter estimates (table 8E).

Sequoia/Kings Canyon National Parks

This study has been underway for 4 years, with estimates of nonjuvenile survival rates based on capture histories of 45 birds >1 year old, and fecundity estimates from the reproductive performances of 45 territorial females (table 8F). The estimate of λ was 0.969, suggesting about a 3 percent annual rate of population decline during the period of study (1988-91). As in the Eldorado study, the statistical test ($\alpha = 0.05$, $P = 0.2709$) failed to reject the null hypothesis (H_0: $\lambda \geq 1.0$). In this case, the test had a power of only 0.30, with an 70 percent probability of failing to detect a real decline of this magnitude. The very low power of the test was a consequence of the small number of marked birds and, to a lesser extent, the standard errors of parameter estimates (table 8F).

San Bernardino National Forest

This study, underway for 5 years, was unique among demographic studies of spotted owls in sampling, almost in its entirety, an insular population (LaHaye et al. 1992). It provides an estimate of juvenile survival rate of 0.296, based on capture histories of 130 owls banded shortly after fledging (table 8G). The estimate of nonjuvenile survival rate is based on capture histories of 184 birds > 1 year old, and the fecundity estimate comes from reproductive histories of 328 territorial females. Lambda was estimated at 0.827, suggesting about a 17 percent annual rate of population decline during the period of study (1987-91). The statistical test ($\alpha = 0.05$, $P \leq 0.0001$) strongly rejected the null hypothesis (H_0: $\lambda \geq 1.0$) of a nondeclining population.

Table 8E--*Estimates of the annual finite rate of population change (λ) for the California spotted owl in the Eldorado National Forest, with test statistics and P value for the test of the null hypothesis that λ ≥ 1.0 vs. λ < 1.0.*

Parameter	Estimate	Sample size	Standard error	*P*
Juvenile survival (s_0)[1]	0.296	130	0.055	--
Nonjuvenile survival (s)[2]	0.826	72	0.039	--
Fecundity (b)[3]	0.470	66	0.054	--
Population change (λ)	0.947	--	0.046	0.1271

[1] LaHaye (pers. comm.).
[2] Combined estimate for males and females, adults and subadults.
[3] Number of female young per territorial female.

Table 8F-*Estimates of the annual finite rate of population change (λ) for the California spotted owl in Sequoia/Kings Canyon National Parks, with test statistics and P value for the test of the null hypothesis that λ ≥1.0 vs. λ < 1.0.*

Parameter	Estimate	Sample size	Standard error	*P*
Juvenile survival (s_0)[1]	0.296	130	0.055	--
Nonjuvenile survival (s)[2]	0.895	45	0.047	--
Fecundity (b)[3]	0.267	45	0.059	--
Population change (λ)	0.969	--	0.051	0.2709

[1] LaHaye (pers. comm.).
[2] Combined estimate for males and females, adults and subadults.
[3] Number of female young per territorial female.

Table 8G-*Estimates of the annual finite rate* of *population change (λ) for the California spotted owl in the San Bernardino National Forest, with test statistics and P value for the test of the null hypothesis that λ ≥1.0 vs. λ < 1.0.*

Parameter	Estimate	Sample size	Standard error	*P*
Juvenile survival (s_0)	0.296	130	0.055	--
Nonjuvenile survival (s)[1]	0.747	184	0.024	--
Fecundity (b)[2]	0.297	328	0.087	--
Population change (λ)	0.827	--	0.035	0.0000

[1] Combined estimate for males and females, adults and subadults.
[2] Number of female young per territorial female.

Discussion

Owl Densities

Because we were able to estimate only crude density for most study areas at this time, interpretations of results are tentative. This is true because crude density does not adjust for the amount of unsuitable habitat in a study area. If one area has a higher proportion of unsuitable habitat than another, but the amounts are unknown, estimates of crude density for the two areas are not comparable. With this caution in mind, density estimates at least suggest some questions that need to be resolved.

The Eldorado study area is mostly forested. The apparent low density of spotted owls there may result from the fact that much of the area is in classic, alternate-section, checkerboard ownership between NF and private timberlands that have been intensively managed for timber production. For example, Bias and Gutiérrez (1992) reported that most roost sites and all nest sites in the Eldorado study area were on public lands. The private lands have not been generally clearcut, however, so owls probably forage in much of the private ownership.

Various hypotheses can be advanced to account for the apparent high density of owls on Palomar Mountain: (1) Crude density may have been overestimated. We know from other studies, for example, that density estimates of spotted owls are affected by the size of the study area, with positively biased estimates in study areas <40 square miles (Franklin et al. 1990b). Based on a regression equation and a proportional adjustment from the asymptotic density in Franklin et al. (1990b, fig. 4), the density estimate for Palomar Mountain should be adjusted downward to about 1.1 owls per square mile. But this is still higher than estimates for all other areas. (2) An extensive fire destroyed much owl habitat on Palomar Mountain in 1987, 1 year before the density survey (Gutiérrez and Pritchard 1990). Several previously occupied owl sites were lost in the fire and an unknown number of additional birds may have been displaced. As a result, densities may have increased temporarily from packing by displaced birds into remaining habitat. (3) Home-range sizes of spotted owls in much of southern California are considerably smaller than they are in conifer forests of the Sierra Nevada or in the San Bernardino Mountains (Chapter 6). Over much of the owls' distribution in southern California, however, suitable habitat tends to be concentrated in small, relatively isolated ravines and canyons; most of the intervening habitat is unsuitable. The crude density of owls there could be similar to that where home ranges are larger but where suitable habitat is more continuous. This is the case, for example, between the foothill woodland and conifer forest segments of the Sierra NF study area (Verner et al. 1991). If suitable habitat is more continuously distributed on Palomar Mountain, but owl home ranges there are relatively small (for example, because the owls specialize on woodrats as a prey source), the observed high density at Palomar could be a real difference from all other density studies of the California spotted owl.

Sources of Bias in Estimates of Lambda

Juvenile Survival

"Estimates of juvenile survival rate can be biased low if some juveniles leave the study area, survive a full year, and never return. To the extent that these three events occur, juvenile survival rate is underestimated and the estimates of λ are too low" (USDI, FWS 1992, appendix C). If emigrating juveniles do not survive their first year, or if they survive but are subsequently detected, then no bias occurs. To provide a statistically reliable estimate, we estimated s_0 using the maximum-likelihood procedure from Program JOLLY (Pollock et al. 1990) for the San Bernardino study (LaHaye pers. comm.). We believe the estimate from that study is reliable. First, it was based on a sample of 130 owls banded as fledglings. Second, the study area covers almost the entire San Bernardino Mountain Range, and the population was largely isolated from other owl populations (LaHaye et al., 1992). Consequently, the area covered by dispersing juveniles was more restricted and the entire area was surveyed each year. These factors greatly increased the likelihood of reobserving banded juveniles. Finally, the estimate of s_0 (0.296) is nearly the same as that for the five northern spotted owl study areas (s_0 = 0.311) (USDI, FWS 1992) based on longer-term studies.

Nonjuvenile Survival

As for estimates of juvenile survival, nonjuvenile survival rate would be underestimated if many banded birds permanently left a study area and survived at least 1 year. Thomas et al. (1990, appendix L) investigated this potential bias by computing the number of emigrations per bird-year in studies of radio-tagged, adult spotted owls. A bird-year was defined as one adult bird tracked for one calendar year. From radio-tracking studies near Roseburg, Oregon, only one permanent emigration occurred in >100 bird-years. Similarly, in northwestern California, one permanent emigration occurred in 60 bird-years. These findings suggest that estimates of adult survival rate for the northern spotted owl were essentially unaffected by permanent emigration from study areas. Although we lack comparable data from the California spotted owl, we have no reason to believe that permanent emigration by adults would be more common for that subspecies.

Senescence

The effects of age-related decline in reproductive potential of spotted owls have been explored by Noon and Biles (1990). Failure to account for senescent declines could result in a significant overestimate of λ. Conversely, incorporating senescence when it does not occur can result in significant underestimates of λ. We do not know the life span of spotted owls or whether fecundity remains constant through life. The high, observed

estimates of *s* would not likely arise, however, if spotted owls lived <15 years. If reproductive senescence occurs at earlier ages, the decline in λ would be increasingly pronounced.

Researchers often assume that birds do not experience senescent declines in fecundity and survival rates (Deevey 1947). An estimate of mean generation length (Caughley 1977, p. 124) without reproductive senescence and assuming *s* = 0.92, however, suggests the unlikely average age of mothers at the birth-pulse = 53 years. Given the magnitude of this estimate, we believe that senescent declines must occur in reproduction and/or adult survival rate. Invoking reproductive senescence at ages of 16 or 26 years yields more reasonable estimates of generation length (≅ 8 and ≅ 12 years, respectively), but it lowers the estimates of λ. Reproductive senescence is not likely to occur much before 16 years; rather, we would expect strong natural selection against the evolution of early senescence in a species with life-history characteristics like the spotted owl's.

Stable Stage Distribution

Calculation of λ from equation (1) assumes a stable stage distribution. If the vital rates are constant, the convergence to a stable distribution is asymptotically exponential (Caswell 1989, p. 70). If the vital rates vary stochastically, or are time-dependent, then the assumption of a stable stage distribution is invalid. At this time we have insufficient data to estimate the degree of stochasticity in the vital rates for the spotted owl, or to determine if the year-to-year differences among projection matrices represent time-dependency or simply sampling variation. In the absence of this information, we assumed mean values for the vital rates. We can, however, examine the likelihood of introducing a bias into the estimate of λ by assuming constant vital rates, and thus a stable stage distribution.

If the growth of a given population is time-dependent, then the growth of that population is described by the product of a sequence of projection matrices. In the special case of independent matrices (that is, independent environments), population growth rate is equivalent to the dominant eigenvalue (λ) of the projection matrix based on the mean values of the vital rates (Tuljapurkar 1982). Unfortunately, under stochastic conditions, the growth rate of the average population may be a misleading indicator of population stability. This occurs because the distribution of population sizes from stochastic projection matrices is approximately lognormal (Tuljapurkar and Orzack 1980). A property of lognormal distributions is that the modal or most likely population size will always be smaller than that based on mean values of the vital rates (Gerrodette et al. 1985). Under conditions of stochasticity, the realized trajectory of any single population is simply one of an infinite number of possible outcomes. Thus, the actual growth rate of any single population with stochastic vital rates is always less than or equal to the growth rate estimated from mean values of the projection matrix (Cohen et al. 1983).

The likely consequence of our assumption of a time-invariant, mean projection matrix, therefore, was to overestimate the growth rate (λ) experienced by any given population, unless the environmental variability was negligible. In general, as the environmental variability becomes small, the average growth rate of a stochastic population approaches (from below) that described by the dominant eigenvalue of the mean projection matrix (Caswell 1989, p. 222). There are some exceptions to this general rule. For example, in nonstochastic, periodic environments, Tuljapurkar (1989) found that variation can increase population growth rate if the period of the environmental oscillation is roughly equivalent to the generation length of the organism being modeled. We emphasize that this is an unlikely outcome for any climatically induced variation in the vital rates of a given species (see, for example, figs. 8A and 8B). The general observation that, in stochastic environments, a probability of extinction exists even when the mean growth rate, λ, is >1.0 (Lande and Orzack 1988) should temper any overly optimistic interpretation of λ values.

Tests on Lambda

Although the null hypothesis of a stable population was not rejected for either the Eldorado or the Sequoia/Kings Canyon study area, we could not correctly conclude that these populations were stable during the periods of study. The power of our statistical tests was disturbingly low for both areas, and there was a high likelihood of failing to detect real annual declines of 5 percent or less. The greater uncertainty that accompanied a smaller sample of banded birds and a shorter time series of capture histories is clearly illustrated by comparison with the northern spotted owl. The estimate of λ for the northern spotted owl on lands managed by the Bureau of Land Management near Roseburg, Oregon, was nearly identical to that for the Eldorado study area (λ = 0.941 vs 0.947, respectively). In the Roseburg study, however, the null hypothesis of a stable population was strongly rejected (probability of a type-I error <0.0005-USDI, FWS 1992, appendix C). In contrast to the Eldorado study, the Roseburg study was based on a larger sample of birds (589 vs 72) and a longer time series (7 years vs 6 years).

Given the high likelihood of accepting false null hypotheses of stable populations in the Sierra Nevada studies, the correct inference to draw from the statistical tests is that, at this time, we are uncertain about true trends of the Eldorado and Sequoia/Kings Canyon populations during the periods of study.

If the California spotted owl has experienced gradual declines in habitat quality in the Sierra Nevada, these effects may be subtle and, therefore, more difficult to detect than those experienced by the northern spotted owl. With the exception of the mid-1980s, very little clearcut logging was practiced in the Sierra Nevada. Even the heavy cutting that occurred on private timberlands near mills and railroad lines usually left some large trees standing that could eventually serve as nest sites in regenerating stands. In contrast, within the range of the northern spotted owl, most logging has been by clearcutting, and most of the decline in suitable owl habitat has been compressed into the interval since about 1950 (Murphy and Noon 1992). As a result, the landscape pattern for northern spotted owls is coarse-grained, with clear distinctions between suitable and unsuitable habitat. Selective logging of the largest trees from the most productive sites in the Sierra Nevada has resulted in significant changes in diameter distributions and produced a more fine-grained landscape pattern for the California spotted owl (Chapter 11).

The effects of changes in forest structure and landscape pattern on owl demographics are unknown. If changes in habitat quality accompany selective logging methods, however, it seems obvious that they would produce less pronounced declines in the vital rates than clearcut logging. As a result, only very long-term studies involving a large number of banded birds would be able to detect such effects.

We do not know the reason(s) for the significant decline of about 17 percent in numbers of territorial owls in the San Bernardino study area from 1987 to 1991. Much logging occurred there in the 1960s, but we doubt whether that disturbance can explain the current decline. A more plausible hypothesis involves either direct or indirect effects of the drought in southern California. For example, precipitation from 1987 through 1990 averaged about 60 percent below normal at a weather station at the western end of Big Bear Lake, in the San Bernardino Mountains (fig. 8A) and 67 percent of normal at the east end (fig. 8B). Rainfall in 1991 was above normal at both of these sites, but almost all of it occurred in March, after the owls would have initiated breeding. One working hypothesis is that dusky-footed woodrats, the primary prey of the owls in the San Bernardino Mountains (Chapter 4; LaHaye pers. comm.), have experienced marked population declines as a result of the drought. For example, Linsdale and Tevis (1956) and Spevak (1983) reported depressed woodrat populations in California during droughts, although Kelly (1989) failed to find a decline in woodrats during a drought at Hastings Natural History Reservation in Monterey County in the late 1980s.

If the recent drought has contributed in some way to the decline of the owl population in the San Bernardino Mountains, it suggests that the population is subject to high levels of environmentally induced variation in its demographic parameters. As the population declines, individuals may be lost from marginal habitats, where survival and reproduction are possible only during "good" times (for example, see O'Connor 1986). Individuals that survive, and even reproduce, during the decline may be those that occupy better, more stable habitats, as where more mesic conditions prevail (for example, riparian areas). Such refuges would be particularly important to the species' long-term persistence, and any destabilization of them-by logging, water diversion, depression in ground water levels, or excessive development of recreational activities-could pose a significant threat to the species' survival.

Future Research Needs

Based on a three-stage model, estimates of parameter sensitivities from all three study areas suggest that λ values were most sensitive to estimates of adult survival rate (s), distantly followed by first- and second-year survival rates (s_0, s_1) and fecundity (b) (fig. 8C). The sensitivity coefficient associated with age at first reproduction was small (Noon and Biles 1990). The much steeper slope for adult (≥2 years) survival rate demonstrates the importance of precise estimates of adult survival to produce precise estimates of λ. Introducing senescence at age 16 increases the slopes for fecundity and prereproductive survival rates, but s is still most important (fig. 8D). For a fixed recapture probability, more precise estimates of s can be attained only by having a larger sample of banded birds.

A comparison of figures 8C and 8D indicates that it may be important to know whether spotted owls exhibit senescent decline in fecundity or survival. Noon and Biles (1990) showed that estimates of population growth rate (λ) were strongly influenced by the age at which reproductive senescence was assumed. Without detailed information on reproductive histories of marked individuals, insights into senescent declines in the owl's vital rates cannot be detected.

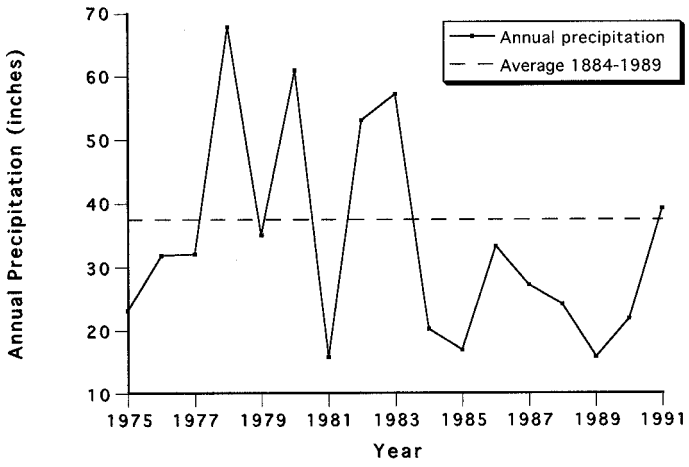

Figure 8A-Annual precipitation (inches) from 1975-91 as measured at the western end of Big Bear Valley, in the San Bernardino Mountains (Lundy pers. comm.).

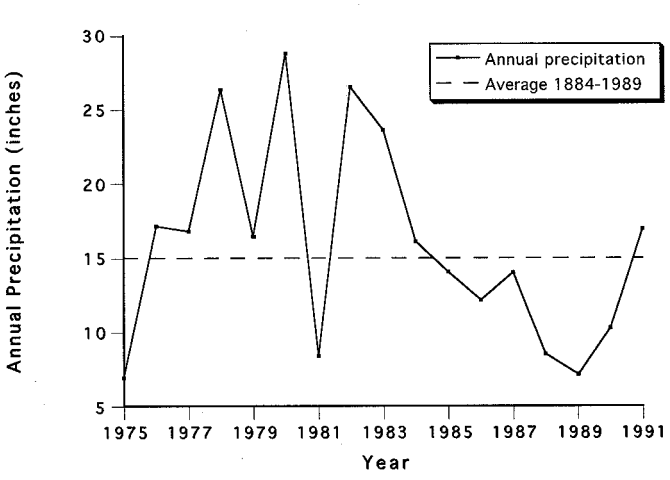

Figure 8B-Annual precipitation (inches) from 1975-91 as measured at Big Bear City, in the San Bernardino Mountains, 7 miles east of the weather station for results reported in figure 8A (Lundy pers. comm.)

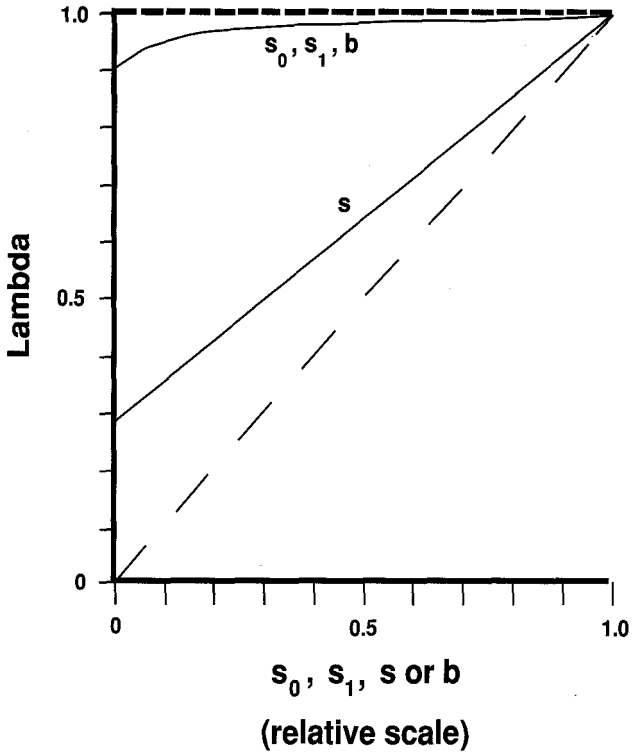

Figure 8C-Population growth rate (lambda) for a stage-structured model of the California spotted owl. The figure shows the effects on lambda (λ) of a proportional decline in a specific demographic rate, with all others held constant. Empirical estimates of mean survival rate have been scaled by 1/ λ to yield an initial starting point of λ = 1.0 on the abscissa.

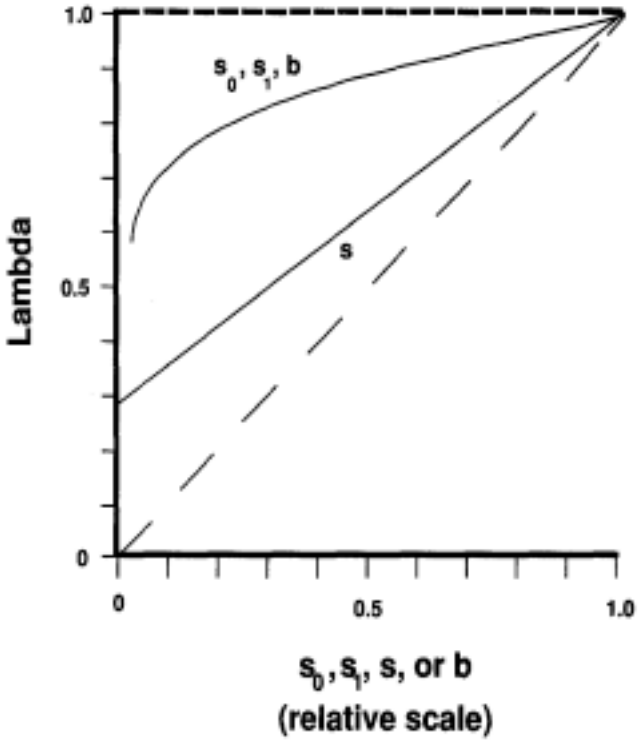

Figure 8D-Population growth rate (lambda) for an age-structured model of the California spotted owl.. The figure shows the effects on lambda (λ) of a proportional decline in a specific demographic rate, with all others held constant. Empirical estimates of mean survival rate have been scaled by 1/ λ to yield an initial starting point of λ = 1.0 on the abscissa.

Two sources of information are relevant to a species' rate of population change (λ). One is the sensitivity of λ to variation in the vital rates as reflected in coefficients of parameter sensitivity. The other concerns those life-history attributes that show the most natural variation. Variation in population growth rate (λ) may be more closely associated with attributes that are naturally more variable than with attributes that are less variable but to which growth rate is mathematically more sensitive. We cannot yet estimate the magnitude of natural variation in demographic parameters of California spotted owls. Estimates that confound sampling error and true annual variation from the five demographic study areas (table 8D), however, indicate that fecundity exhibits the greatest annual variation. Fecundity combines two important components: productivity per breeding female and the proportion of females ≥2 years of age that breed. The latter is particularly variable (table 8D).

Factors contributing to the low and variable reproductive rates of spotted owls also need investigation. We do not know whether the extensive annual variation in reproductive success is due to variable resource levels (prey base), variable climatic conditions, or some combination. Nor do we know whether reproductive rates or adult survival rates can be increased by direct management for prey populations; this is also an important research question.

Finally, as suitable spotted owl habitat becomes more fragmented, it will become increasingly important to estimate dispersal capabilities of California spotted owls (Chapter 4) and to identify factors that affect survival during dispersal. This includes influences on the survival of juvenile birds dispersing from their natal territories, as well as adult birds displaced by habitat loss.

Management Implications

Implications of the demographic results for management involve decisions that may differentially affect adult and preadult birds. The life-history pattern of the spotted owl suggests that it must have evolved in an environment stable with respect to adult survivorship. The much greater sensitivity of λ to variation in adult than preadult survival rates indicates strong natural selection to maintain low adult mortality rates. Further, the low fecundity rate suggests that recruitment may always have been variable. In spite of this, high adult survivorship has allowed the

spotted owl to persist through long periods of low reproductive output. A consequence of this trade-off is of great concern when considering management for spotted owls. Namely, low fecundity precludes rapid recovery from a population decline. Any management action that lowers adult survival rate, particularly when coupled with a reduction in population size, markedly increases the likelihood of local extinction.

Although λ is relatively insensitive to changes in s_0 and b (figs. 8C and 8D), we cannot infer that these attributes are unimportant when developing management plans. Adult survival rate is relatively high and may not be amenable to further increases. Assuming no reduction in adult survival rate, increasing first year survival or fecundity by direct management activity may be the most feasible way to increase the growth rate of spotted owl populations. For example, certain silvicultural prescriptions may increase the availability of the owl's preferred prey and somewhat ameliorate the otherwise negative effects of logging. But these prescriptions are still unknown and untested.

Given the spotted owl's life history structure, an evaluation of management decisions in terms of persistence likelihoods are possible only when viewed over the long-term (50-100 years). With a high adult survival rate and an apparently long life span, the Spotted Owl may be able to persist over the short-term even in the face of extensive reduction in the amount of its suitable habitat. Thus, significant time lags may occur in responses of spotted owl populations to declining environmental carrying capacity. By themselves, therefore, short-term survey results, even those including observations of breeding owls, are insufficient to allow inferences about population viability.

Rapid rates of population decline in either deterministic or stochastic analyses are not surprising when the finite rate of increase (λ) is <1.0. Leslie-Lefkovitch projection matrices and life table models yield simple exponential models of population growth or decline (see discussion in Noon and Sauer, 1992). For this reason, it is inappropriate to use estimates of λ to project future population size without strict qualifications. Most natural populations presumably demonstrate density-dependence in one or more life history parameters. Many examples exist of bird species shown to exhibit density-dependent effects on vital rates. These include the gray partridge (Blank et al. 1967), the mallard (Hill 1984), the tawny owl (Southern 1970), and the European sparrowhawk (Newton 1988). No empirical data for spotted owls presently indicate a relation between population density and values of vital rates. Nevertheless, on the basis of a simple nonspatial model, Boyce (1987) argued that spotted owl populations at low densities should exhibit density-dependent increases in survival and reproduction that could stabilize the populations. Very different inferences are drawn, however, from models that include the additional reality of spatial structure, such as the uncertainties of successful dispersal and mate finding in spatially structured populations. Lande (1987) and Lamberson et al. (in press) found that owls at low population densities may experience negative effects of low densities that further depress survival and fecundity. In fact, their models indicate that if population densities are very low, or the amount of suitable habitat is greatly reduced, a threshold point exists beyond which the owl populations collapse to extinction.

We believe there are implications for the management of California spotted owls. Future management activities, for example, must not increase the mean nearest-neighbor distances among suitable pair sites. Subtle factors that uniformly decrease habitat quality, or increase fragmentation, will act to reduce population density and incrementally increase the uncertainties associated with successful dispersal and mate-finding. Habitat-induced changes in vital rates, such as declines in first-year survival and in the proportion of breeding females, will lead to declines in population growth rate. If suitable habitat is allowed to decline and become fragmented, as for the northern spotted owl, the uncertainty of successful dispersal will become progressively more relevant to the subspecies' long-term population dynamics and likelihood of persistence. Should this pattern ensue for the California spotted owl, then the most effective way to assure its long-term persistence may be to create a connected network of habitat conservation areas (HCAs) as was proposed for the northern subspecies (Thomas et al. 1990). Large HCAs provide stable areas of high population density that promote a balance between pair turnover and colonization of pair sites, either through internal recruitment of dispersing juveniles or the emigration of owls from neighboring HCAs. Implementing such a strategy, however, would risk an increasing threat of stand-destroying fires in areas maintained primarily for the owls.

Finally, it is important to recognize that rates of population change (λ) and the values of the owl's vital rates are ultimately determined by habitat quality at both local and landscape scales. For example, habitat quality at the scale of the home range may determine the survival and birth rates for an individual pair of owls. At a larger scale, the number of suitable pair sites and their spatial arrangement may determine the persistence of local populations. And, at a regional scale, providing habitat for a large number of local populations distributed widely across the landscape will increase overall persistence of the subspecies by decreasing the likelihood of populations simultaneously experiencing negative environmental effects. Thus, to ensure stable owl populations in the Sierra Nevada and Southern California Provinces will require specific management prescriptions, implemented at local to regional scales, to retain the amount and spatial pattern of habitat that will provide for a long-term balance between birth and death rates.

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Chapter 9

Stability Properties of the Spotted Owl Metapopulation in Southern California

Barry R. Noon and Kevin S. McKelvey

Spotted owls in the Southern California Province have an insular population structure characterized by large (about 200 pair sites) to small (about 2-4 pair sites) local populations distributed among discrete mountain ranges (fig. 9A, table 9A). The distribution of habitat "islands" is discontinuous across the landscape, reflecting natural discontinuities in vegetation structure and composition, in topographic conditions, and in the effects of extensive human-induced habitat disturbance and fragmentation. Lowland areas surrounding these mountain ranges are primarily desert scrub and chaparral habitats that are unsuitable for spotted owls. Relatively narrow gaps between populations, like the 6-mile separation at Cajon Pass, between the San Gabriel and San Bernardino populations (fig. 9A), are probably not complete barriers to dispersing owls. Longer separations, however, such as that of about 30 miles through the Los Angeles Basin, between populations in the San Bernardino and Santa Ana Mountains (fig. 9A), may present significant survival risks to dispersing owls such that successful colonization is very unlikely. The degree to which these gaps act to severely reduce or eliminate demographic rescue between populations is unknown. To date, however, no banded spotted owl has been located within any population outside that of its origin (LaHaye pers. comm.). The most significant gaps between owl populations are discussed in table 3K and shown on a distribution map in that chapter (fig. 3A).

Even within many of the mountain ranges, the distributions of habitat and owl sites are discontinuous. For example, in the Cleveland and Los Padres National Forests (NFs), most suitable spotted owl habitat is patchily distributed because it is resticted to deeply dissected canyons dominated by oaks and surrounded

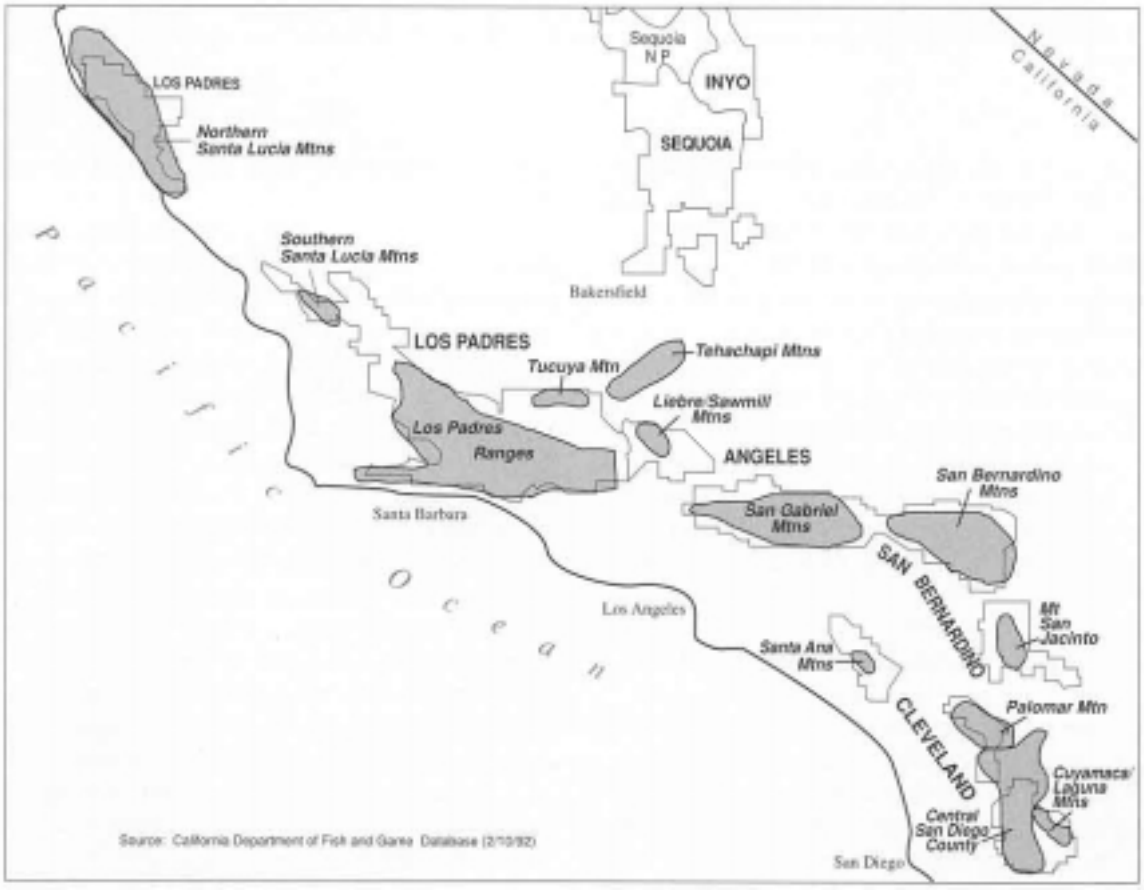


Figure 9A-"Island" populations that comprise the southern California metapopulation of spotted owls. Estimated numbers of owl sites for each "island" are given in table 9A.

Table 9A-*Owl sites,[1] pairs and status of pairs on these sites, and nearest neighbor distances of California spotted owl populations in southern California (from Stephenson 1991 and Chapter 3). Compare values tabled here with the locations of these areas, shown in figure 9A.*

Area	Owl sites (all years)	Pairs since 1987	Breeding since 1987	Potential population[2] (no. sites)	Nearest neighbor distances[3]
San Diego Ranges	37	18	6	76	18 - 33 miles
Palomar Mountain	(18)				
Central San Diego County	(9)				
Cuyamaca/Laguna Mountains	(10)				
Santa Ana Mountains	2	1	-	12	30 - 40 miles
San Jacinto Ranges	20	16	9	29	11 - 18 miles
San Bernardino Mountains	124	114	66	125	6 - 11 miles
San Gabriel Mountains	54	22	5	95	6 - 20 miles
Liebre/Sawmill Mountains	14	10	2	20	12 - 20 miles
Tehachapi Mountains	4	0	-	12	unknown
Tecuya Mountain area	5	3	-	10	9 - 12 miles
Los Padres Ranges	65	32	17	100	8 - 12 miles
So. Santa Lucia Mountains	12	6	2	19	32 - 45 miles
No. Santa Lucia Mountains	39	22	1	80	45 miles
Southern Monterey	(14)				
Northern Monterey	(25)				
Total	**376**	**244**	**108**	**578**	

[1] See glossary in Appendix B for a definition of "owl site."
[2] If each site were assumed capable of supporting a pair, the total population would be the number of sites times 2.
[3] Where two distance values are shown (that is, 12-20 miles), they represent the distances to the two closest neighboring populations.

by unsuitable chaparral habitat. Thus, many of these populations have an insular structure at both landscape and local scales. The present modeling study was prompted by the need for a better understanding of the potential effects on population persistence of isolation between subpopulations, and changes in habitat continuity within otherwise continuous habitat islands.

Although spotted owl records in southern California exist from the early part of this century (Stephens 1902, Clay 1911), careful population studies are recent. LaHaye et al. (1992) have studied the demography of the owl population in the San Bernardino Mountains, and Gutiérrez and Pritchard (1990) reported on surveys done on Mt. San Jacinto and Palomar Mountain. In addition, infrequent surveys in NF lands provide a cumulative record of spotted owl locations outside of these study areas (Gould et al. 1987, Stephenson 1991).

The largest population occupies the San Bernardino Mountains (about 124 owl sites), with considerably smaller populations in the other ranges (table 3H). The cumulative total number of known owl sites within the southern California "archipelago" is estimated at 376 (table 9A), with an approximate population of 300-350 pairs at any point in time. The population trend is known for only one location. During the interval 1987-91, the resident, territorial population in the San Bernardino Mountain study area declined by about 17 percent per year (LaHaye et al. 1992; Chapter 8). If this rate of decline were to continue, the territorial population would decline by 50 percent in about 4 years.

Based on theory and limited empirical data (reviewed in Gilpin and Hanski 1991), we believe the ultimate stability of this metapopulation will depend upon several factors. These include the persistence of one or more populations large enough to escape the negative effects of demographic and environmental stochasticity, and with demographic characteristics resulting in a production of excess individuals to serve as potential colonists for other local populations. Many of the small, isolated populations that occur in southern California are probably maintained by occasional immigration from these more productive source areas (see Pulliam 1988 and Howe et al. 1991 for a discussion of source-sink dynamics). In addition, given a high likelihood of significant environmental variation (for example, wildfires, prolonged periods of drought, or rapid urbanization) at least two source populations will be needed, and they should be sufficiently separated to minimize the likelihood of their simultaneously experiencing negative perturbations.

The human population in southern California continues to expand into the forested mountain habitats of the spotted owl. In the San Bernardino Mountains, for example, the human population has grown from about 19,000 in 1970 to over 40,000 in 1992, with 5 million annual visitors (Dib and Griffone 1991). Accompanying this growth is a reduction in the quality and

amount of forested habitat for spotted owls-a consequence of urbanization, highways and smaller roads, and recreational developments. Although we lack earlier estimates of spotted owl population sizes or densities, we nonetheless consider it likely that spotted owls have declined in both number and distribution from historic levels.

Given the metapopulation structure of the southern California spotted owl population, recent declines within the largest and most contiguous population in the region, and significant threats to loss of suitable habitat due to rapid human population growth, we believe that a specific conservation strategy is warranted for the subspecies in this part of its range.

This chapter has two main purposes: to explore, in a general sense, the stability properties of the southern California metapopulation structure, and to make specific recommendations for conservation of the subspecies in this part of its range. Toward this end, we make frequent reference to pertinent population theory and use results of simulation models to explore conservation alternatives. Our goal was not to estimate extinction likelihoods-we believe it is premature to conduct such analyses at this time. Currently, the only estimate of population change from this region suggests a rapid decline in the territorial population (Chapter 8). Under a strict assumption of constancy in the vital rates, projecting forward at this rate shows a rapid decline to extinction. Until more is known about natural fluctuations in vital rates of populations, however, such projections are unwarranted.

Rather, our goal was to explore the geometry of the metapopulation, including both habitat and owls, to gain insights into what spatial arrangement of habitat would minimize future extinction risks. In this chapter we present the results of our efforts to integrate, in the form of computer simulation models, the species demography with variations in the amount, distribution, and quality of owl habitat. The computer simulation models were developed specifically to aid the development of a conservation plan for spotted owls (Thomas et al. 1990, appendix M; Lamberson et al. in press; McKelvey et al. in press). We used the results of computer simulations to test basic principles of reserve design (Murphy and Noon 1992) and to provide guidance about the necessary spatial design of a reserve system implemented on real landscapes.

Methods

Parameter estimates and model structure were based on information from the study of marked populations (LaHaye et al. 1992; Chapter 8). Owls were captured during the breeding season, aged, sexed, and individually marked. Reproductive status was determined for all individuals using methods outlined by Forsman (1983). Young were counted after fledging had occurred (that is, after they left the nest). Individuals were initially placed into four age classes (juvenile, first-year subadult, second-year subadult, adult) according to criteria developed by Moen et al. (1991). Because of similarity in survival rates, first- and second-year subadults were pooled with adults and collapsed into a single stage. Annual survival rates for banded juveniles, subadults, and adults were calculated using Jolly-Seber capture-recapture models for open populations (Jolly 1965, Seber 1965) using program JOLLY (Pollock et al. 1990).

The estimate of fecundity combines two important components-the number of females fledged per nest and the proportion of females ≥2 years of age that breed. Thus, "adult" refers to ages subsequent to the second year of life. Fecundity was estimated each year as the mean number of young fledged per pair, assuming a 1:1 sex ratio at birth. Within the adult age class, survival rate was assumed to be constant, and we assumed no reproductive senescence. For our simulation models, we divided the population into three stages juveniles, subadults, and adults. Time was expressed on an interbirth interval of 1 year, and we assumed an age at first reproduction of 2 years (that is, birds just beginning their third year of life).

Lambda (λ), the estimated annual, finite rate of population change from the San Bernardino study was 0.827 (table 8G), indicating that the territorial population there was in precipitous decline. Because λ represents a simple exponential rate of change, using the vital rates estimated from this study to project future populations would be a trivial exercise. All populations would decline exponentially regardless of the amount and distribution of suitable habitat. To evaluate possible effects of variation in landscape geometry, we initially adjusted the survival rates by multiplying them by $1/\lambda$ to yield a λ=1.0 in suitable habitat. A11 demographic rates were again slightly increased to allow for the possibility of a 2 percent annual rate of population growth (λ = 1.02). This scaling of the survival rates allowed for a growing (source) population in suitable habitat. Differences in model results based on the landscape model (see below) would, therefore, reflect the effect of differences in distribution and amount of suitable habitat, and not an assumption of depressed demographic rates. Based on current field studies (Chapter 8), however, the adjustments we made to the demographic rates for suitable habitat were optimistic.

Dynamic Projection Models

No natural population is exposed to purely deterministic forces. Thus, population dynamics of the spotted owl should be examined relative to both demographic and environmental stochasticity. Further, simple deterministic analyses are also limited in that they provide no insight into the dynamics of mobile populations in real landscapes. That is, they incorporate no information on the movement behavior of animals in heterogeneous environments and the uncertainties of finding suitable habitat and mates. Failure to account for the spatial component

of both animal locations and their habitat distributions ignores the covariance between demographic rates and habitat variation.

A conservation strategy for any species is ultimately described by a map that integrates information on the species' distribution; the distribution of current and potentially suitable habitat; and economic, political, and legal constraints (Thomas et al. 1990; Murphy and Noon 1992). To develop a general set of conservation recommendations for the southern populations of the California spotted owl, we needed insights into how the landscape-scale arrangement of owls and their habitat affected their population dynamics. The data available to us lacked detail and were imprecise (see Chapter 3). As a result, we could explore the effects of landscape geometry and variation in the distribution of habitat types only in a nonspecific way, and make general recommendations about the significance of different components of the landscape.

To provide a framework to guide the conservation evaluation of the California spotted owl, we drew general inferences from several simulation models incorporating various degrees of spatial information. Our approach, which investigated the effects of variable dispersal efficiencies on the population dynamics of territorial animals occupying heterogeneous landscapes, had its foundation in previous work by Lande (1987, 1988). Lande's model was based on a hypothetical species with a monogamous, territorial breeding system and with obligate juvenile dispersal from the natal area. This model was directly applicable to the life history structure of the spotted owl.

Nonexplicit Spatial Models

In the following, we briefly review the structure and assumptions of two models used to assist in the design of a reserve strategy for the northern spotted owl (see Thomas et al. 1990, appendix M). We do not discuss these models exhaustively but simply make reference to results from those models that are most applicable to the conservation of spotted owls in southern California. Additional details can be found in Thomas et al. (1990, appendix M), Lamberson et al. (in press) and McKelvey et al. (in press).

The Individual-Territory Model

Model Description

This model (Lamberson et al. in press) extended that of Lande (1987) by relaxing the assumption of demographic equilibrium and allowing the simulated landscape to be dynamic. Life history was expressed as a three-stage, two-sex projection model. The model assumes that all newly fledged juveniles disperse, and that adult birds who experience loss of their territory (for example, due to logging) also disperse. Lande's model allowed some likelihood of a juvenile's inheriting its natal territory. Based on the settling patterns of owls first banded as juveniles, however, inheritance of the natal site is a very rare event. Our model focuses on a landscape with a fixed spatial extent and with a fixed number of potential territories (or "sites"). Sites were either suitable for survival, mate attraction, and reproduction, or they were unsuitable. Only the suitable sites were capable of being occupied. The key response variable in our model is the occupancy rate of sites by pairs. As in Lande's model, this model lacks realism because of the global nature of juvenile and adult search-all cells had an equal likelihood of being sampled.

The search process was simulated as sampling with replacement. The key equation describing search success in our model (see Lande 1987) was

$$\Pr(\text{success}) = 1 - (1 - \text{unoccupied suitable sites/total sites})^{m}, \quad (1)$$

where m is the number of sites that can be searched prior to mortality (additional equations describing the model dynamics are given in Lamberson et al. [in press]).

A nesting pair will annually produce young (according to a deterministic or stochastic likelihood), and these will disperse at the end of the season, the males seeking an unoccupied site and the females seeking a site occupied by a solitary male. Dispersal success is density-dependent, calculated by assuming random search of accessible sites. Search capabilities, together with the occupancy ratio of searched sites, determines the bird's potential for successful dispersal (consistent with Lande 1987).

Relevant Model Results

The most significant conclusions from Lande (1987) and Lamberson et al. (in press) are (1) that the occupancy of suitable habitat declines with a declining proportion of the landscape that is suitable habitat (fig. 9B), and (2) that if the amount of suitable habitat declines below some threshold value, the population will become extinct (fig. 9C, curve A). That is, because of uncertain-

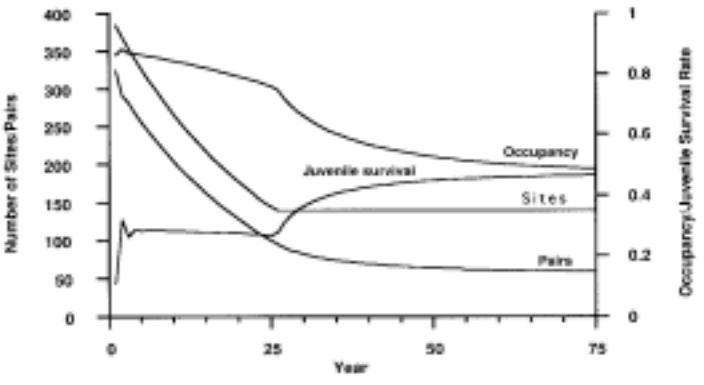


Figure 9B-Trend in the number of pairs of spotted owls, number of sites, site occupancy by pairs, and juvenile survival rate based on a 75-year simulation. The simulation assumed that 4 percent of the suitable owl habitat was lost per year until 14 percent remained, and that juvenile owls could search 20 sites.

ties associated with search and mate finding, a species can be critically habitat-limited even in the presence of suitable but unoccupied habitat.

New findings, beyond those reported by Lande (1987), resulted from the model of Lamberson et al. (in press), because of its dynamic and nonequilibrium nature. First, survival probability, as a function of the percent of suitable habitat, is affected by environmental variation. Once again the deterministic case shows a stairstep function, with the jump from 0 to 1 occurring at the threshold point (fig. 9C, curve A). Adding environmental variance makes the extinction threshold less abrupt (fig. 9C, curves B and C). Second, in a scenario involving incremental loss of suitable habitat (for example, by logging), the crowding of older owls into remaining suitable habitat is likely to produce temporarily high occupancy rates-much higher than expected under long-term stable conditions (fig. 9B). Thus, predicting long-term population status from short-term occupancy data can be very misleading.

The Territory-Cluster Model

The primary limitation of the individual-territory model was the global nature of search. In reality, organisms search locally and are primarily influenced by the local nature of the landscape rather than its global condition. The basis of the territory-cluster model (Thomas et al. 1990, appendix M; Lamberson and Noon 1992) is a fixed, rectangular array of circular clusters containing a variable number of owl sites (territories). Every site within a cluster, assumed to be of identical size, was either suitable or unsuitable (defined as in the individual-territory model). Clusters could be either totally or partially suitable-the carrying capacity of a cluster equalled the number of suitable sites. For a given simulation, all clusters were the same size (that is, they contained the same number of sites). As in the individual-territory model and Lande (1987), the response variable was the proportion of suitable sites occupied at any point in time.

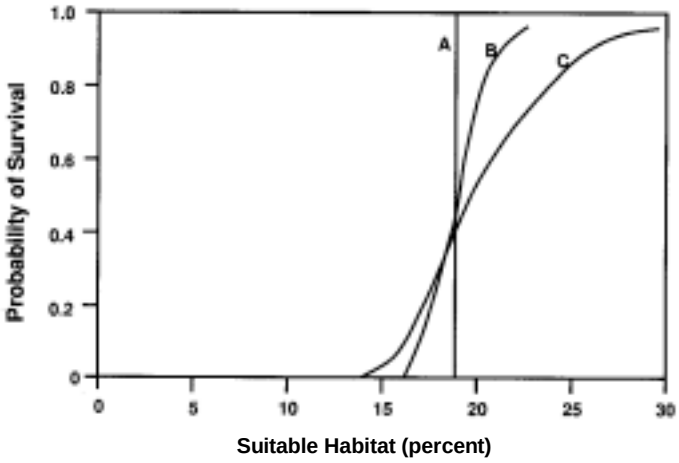


Figure 9C-The 250-year survival probability in relation to the percentage of suitable sites in the landscape. Curves A, B, and C represent the conditions of no, low, and high environmental variability, respectively.

The matrix between clusters was assumed to be entirely unsuitable for owl sites. Assuming a constant percentage of the habitat as potentially suitable Habitat and restricting the habitat to clusters had two important consequences: (1) as cluster size increased, the distance between adjacent clusters increased predictably (fig. 9D); and (2) the dispersal angle between adjacent clusters (see fig. 9E), and the probability of selecting this angle, were independent of cluster size.

The landscape simulated by the model had a "wrap-around" structure to exclude possible anomalous results that might arise from edge effects. The clusters on the right side of the grid were treated within the model just as though they were immediately to the left of those on the left side of the grid. The top and bottom rows of clusters were treated in a similar manner.

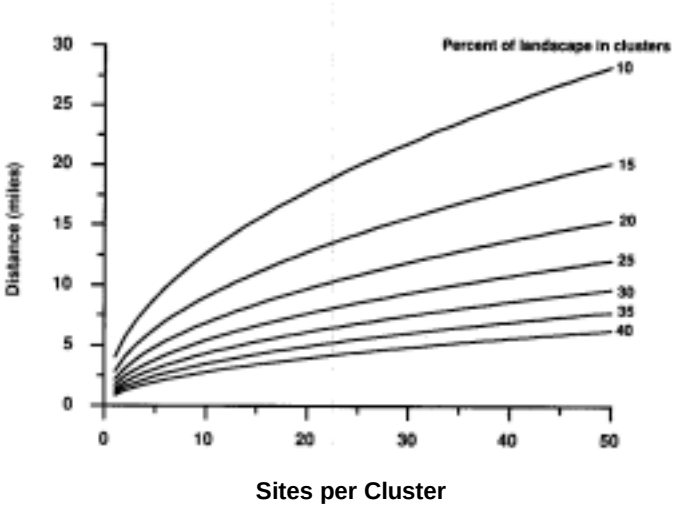
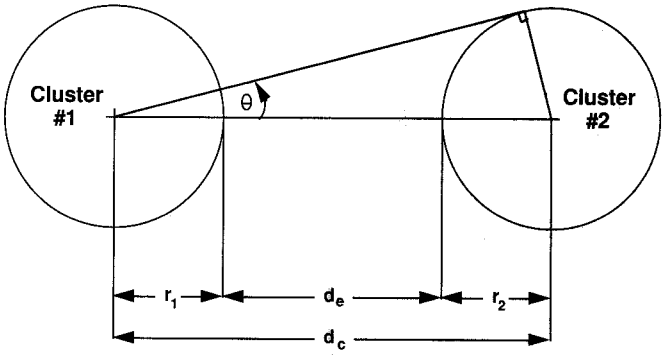


Figure 9D-Nearest-neighbor distance between clusters in relation to cluster size. Each curve represents a different percentage of the landscape assumed to be suitable habitat and located in the clusters.



P_r (disperse from Cluster 1 to Cluster 2) = 2θ/360

$$\theta = \arctan \frac{r_2}{\sqrt{d_c^2 - r_2^2}}$$

Figure 9E-Method of estimating the angle of intersection between two adjacent clusters in the cluster model. The probability of dispersing in the correct direction is a function of the combined angles of intersection of the six neighboring clusters.

The life history was expressed as a three-stage, female-only projection model. Initial values of the vital rates were based on table 8G, and survival rates were scaled by multiplying by 1/0.827 to provide for a stable local population in suitable habitat. Based on observations of recently fledged young near the nest site (Marcot and Holthausen 1987), a predispersal survival component of 0.6 was assumed for the juvenile survival rate. The dispersal component of first year survival arose from properties of search efficiency and landscape pattern, thus allowing the possibility of a growing population. Fecundity was treated stochastically, based on good years and bad years for reproduction, with expected values equal to field data (table 8G). We assumed complete spatial autocorrelation for the reproductive pulses.

Dispersal Dynamics

As in Doak's (1989) model, our model distinguished between dispersal within and among clusters. All clusters were equally accessible in Doak's model, but we introduced the additional reality that search was spatially constrained and was, therefore, affected by the status of neighboring clusters. Within-cluster dispersal in our model was identical to the individual-territory model, with each dispersing owl allowed to sample with replacement a given number, *m*, of sites within the cluster (equation 1). To determine the allocation of search effort within a cluster, we assumed a random walk from a random starting point. By simulation, we estimated the expected number of steps taken by a dispersing bird before it crossed the boundary of a circular cluster. The assumption was that an owl could traverse one site in a single time step. Based on 10,000 simulations of circular clusters of various sizes, and regressing the number of steps taken before crossing the circle, we estimated the following relationship:

$$\text{Expected}(m) = 0.41 * \text{number of sites in the cluster.} \quad (2)$$

For clusters with 20 sites, for example, an average of eight sites were searched within clusters before crossing the boundary into the matrix between clusters. The total number of searches across all clusters (m = 22) was based on the upper bound of the 90th percentile of the maximum dispersal distance of 56 radio-tagged juvenile spotted owls (Thomas et al. 1990, p. 305) and the assumption that each site had a diameter of about 2 miles.

If a dispersing juvenile did not find a suitable site within its natal cluster (based on a fixed number of searches), it was forced to disperse between clusters. Between-cluster dispersal was modeled as a straight-line path moving away from the natal cluster at a random azimuth. Two sources of mortality were encountered. First, the bird must move in a direction that would intersect a neighboring cluster. The probability of intersection for each adjacent cluster was governed by the following equation (see fig. 9E):

$$\text{Probability(disperse from cluster 1 to cluster 2)} = 2\theta/360 \quad (3)$$

$$\text{where } \theta = \text{arctangent}\left(r_2 / \sqrt{d_c^2 - r_2^2}\right)$$

Second, if a correct direction was chosen, the likelihood of successful travel to the neighboring cluster lying a distance d miles away (measured edge-to-edge) was modeled by a declining exponential,

$$\Pr(\text{survive to } d) = \exp(-kd) \quad (4)$$

The value of k was estimated by arranging the maximum straight-line distances attained by the 56 radio-tagged juvenile owls in rank order, then regressing the natural log of the cumulative proportion represented by that distance (dependent variable) on the associated distance and forcing the regression through 0 (r^2 = 0.97) (see fig. 4F). Because search begins in the natal cluster and moves through adjacent clusters, the search success in this model, as in nature, is a function of the condition of the landscape near to the bird's natal site.

Model Parallels to the Southern California Metapopulation

The structure of the cluster model crudely approximates aspects of the southern California spotted owl habitat distribution (fig. 9A). Clusters can be considered analagous to local habitat islands, and gaps between local populations are analagous to the matrix-areas that allow dispersal (with inevitable survival risks) but no reproduction. Model results allowed us to make general inferences to (1) the relation between cluster size and local population stability, (2) the effects of variable spacing among clusters on mean pair occupancy, and (3) the most efficient ways to allocate lands to a reserve design.

Relevant Model Results

Because the number of combinations of model parameters is immense, many sensitivity analyses were done (table 9B). The most significant result, however, was based on the relation between mean pair occupancy and cluster size. For a simulation with 60 percent of the sites suitable within a cluster, occupancy did not stabilize until clusters held at least 15 sites (fig. 9F).

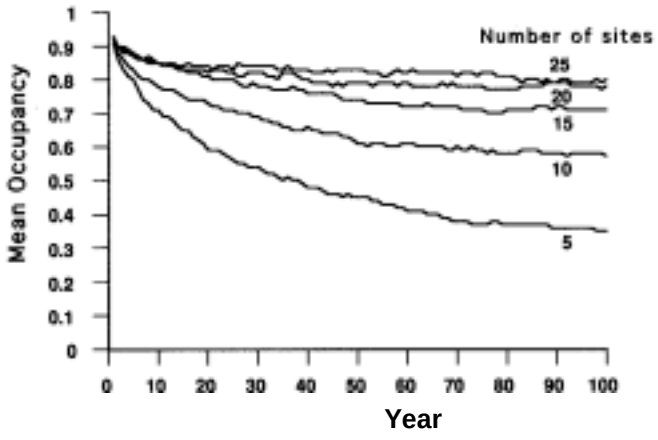


Figure 9F-Mean proportion of cluster occupied in relation to time, based on a 100-year simulation. The number of sites per cluster varied from 5 to 25, and 60 percent were assumed suitable; 35 percent of the landscape was in clusters.

Clusters of 15 sites stabilized at about 70 percent occupancy, while clusters of >20 sites stabilized at about 80 percent, a figure representing nearly full occupancy given adult survival rates. Further increases in cluster size had little effect on occupancy. As the number of suitable sites within a cluster increased, the marginal difference in occupancy among clusters of different sizes became less pronounced.

Based on the relation between the landscape fraction within clusters (habitat islands) and cluster spacing (fig. 9D), different levels of allocation to a reserve system can be viewed in terms of the distance between clusters. We found mean occupancy rate to be strongly affected by increased spacing between clusters for cluster sizes <20 sites (fig. 9G). In contrast, clusters with >25 sites showed minimal distance effects beyond separations of about 20 miles (fig. 9G). Adding low levels of environmental variation in survival rates lowered occupancy rates about 7 percent and suggested slightly larger cluster sizes for the same level of occupancy (fig. 9H).

An alternative approach to choosing an optimal cluster size is to estimate the expected number of owls occupying a fixed amount of suitable habitat. Based on mean occupancies at 100 years from fig. 9F, the efficiency of land use is clearly higher for larger clusters (fig. 9I).

Inferences to Reserve Design from the Nonexplicit Spatial Models

Results from these models suggest that providing for clusters of territories should increase the persistence likelihood of spotted owls, primarily by facilitating juvenile dispersal (compare Doak 1989). If habitat becomes too diffuse at a local scale, populations there will experience extinction events and require recruitment from larger source areas for recolonization (the "rescue effect"). Given assumptions of the cluster model (≥60 percent of sites suitable, moderate connectivity among adjacent clusters), clusters with >20 sites should provide for locally stable populations in the absence of catastophic disturbance. Adding moderate levels of environmental variation in the survival rates, however, raises the desired minimum cluster size to about 25 sites.

Once clusters reach about 35-45 sites, they attain high levels of local stability and become relatively independent of the distance to their nearest neighbor. Within the structure of our model, this occurred because almost all dispersing juveniles found suitable sites within their natal cluster. Given a fixed number of total searches (m = 22), and the allocation of within cluster search following equation 2, all search is expended within

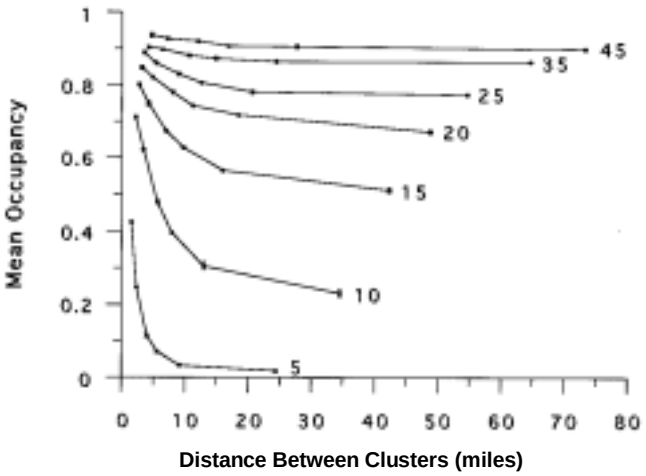


Figure 9G-Mean proportion of clusters occupied as a function of the distance between clusters. The number of sites per cluster varied from 5 to 45, and 60 percent were assumed to be suitable.

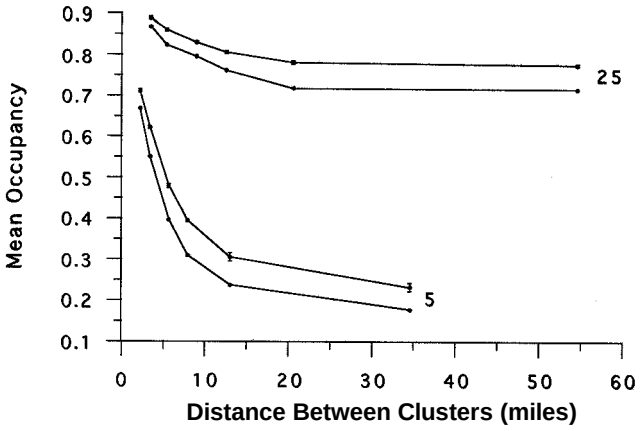


Figure 9H-Mean proportion of clusters occupied as a function of distance between clusters. The number of sites per cluster was either 5 or 25, and 60 percent were assumed to be suitable. The lower curve of each pair represents simulations including environmental variation in survival rates.

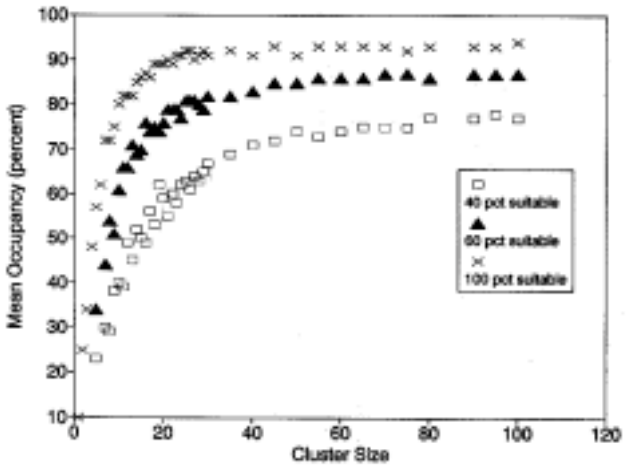


Figure 9I-Steady-state mean occupancy rate in relation to cluster size. The curves represent 40, 60, and 100 percent of the sites within each cluster as suitable habitat.

Table 9B--*Qualitative results of sensitivity analyses for the territory cluster model.*

Factor varied	Sensitivity[1]
Within-cluster search efficiency	Low for large clusters; high for small clusters
Resistance to between-cluster dispersal	Low for large clusters; high for small clusters
Search time outside of natal cluster	Low to moderate for large clusters; high for small clusters
Initial population size	Low if population was in large clusters; high if population was in small clus ters

[1] Measured in terms of reduction in mean pair occupancy.

the natal cluster when cluster size equals 54 sites. At this point in our model, all clusters are acting as independent subpopulations.

Comparing these general model inferences to estimates of the number of sites in various habitat islands in the Southern California Province (table 9A) provides some significant insights. Based on current estimates of owl sites, many of these habitat islands have <25 sites, are isolated by >10 miles, and are therefore expected to be very unstable. That is, they will be subject to extinction events because of both demographic and environmental variation, or act as sink areas (Pulliam 1988). As such, their occupancy status will depend largely upon immigration from neighboring habitat islands. The possible dependence of these populations on immigration from larger source populations parallels results for insular populations of acorn woodpeckers in the southwestern United States (Stacey and Taper 1992), and red-cockaded woodpeckers in the southern Appalachian mountains (Conner pers. comm.).

The cluster model had several optimistic assumptions. Most important were that (1) no uncertainty was associated with mate finding, (2) only low levels of environmental variation in vital rates were simulated, and (3) clusters were assumed to be circular, thus minimizing the perimeter:area ratio. A circular shape (1) maximizes the density of suitable habitat and, given our within-cluster search algorithm, suggests very high search efficiencies; and (2) it affects the estimate of the probability of leaving the natal cluster in an appropriate direction. For both stability of mean occupancy and to achieve a specified occupancy rate, relaxing these assumptions would generally require larger cluster sizes.

A Spatially Explicit Landscape Model

The landscape model links an organism's survival and reproduction explicitly to its current habitat location. In reality, habitats range in quality from those that support demographic rates resulting in a net gain of births over deaths (source areas) to those that yield a net loss (sink areas). The latter habitats would be unoccupied in the absence of immigration from source areas. As Pulliam (1988) has argued, it may be that habitat-specific demographic rates are more important than age-specific rates to a species' long-term population dynamics. In this model, a population's rates of survival and fecundity will vary based on landscape configuration and the distribution of habitat types. The model, a two-sex, single-organism simulator, assumes that each organism must search the landscape to find new territories and mates. Each organism is born, moves, attempts to find a mate and breed, and dies. This format allows the behavior of each individual to be simulated by following a series of probabilistic rules.

Male and female behavior in this model is similar to that in the territory-cluster model. Males search for territories to occupy. If they find a suitable nest site, they stop moving and become territorial. The likelihood of settling in a given site is a function of the habitat quality of that site. Males remain on their selected site until they die or the site becomes unsuitable for nesting. If the site becomes unsuitable, the males become nonterritorial and reinitiate search. Females are born and disperse from the natal site to seek unpaired, territorial males. When they find a territorial male, they obligately pair. Once paired, females remain on site until they die or the site becomes unsuitable for nesting.

Paired individuals split up when one member of the pair dies, or the site becomes unsuitable for nesting. If the female dies, the male remains territorial and stays on site. If the male dies, the female has no site fidelity and will initiate search for a new mate. If the site becomes unsuitable for nesting, both members search independently for a new site. The movement of females after loss of their mate is supported by field data. In general, females move more often then males, occasionally leaving sites to search for new mates even when their previous mates are still alive.

In the landscape model, by contrast with the previous two models, if a juvenile fails to locate an unoccupied, suitable site it does not die-rather, it becomes a floater. As a consequence, search efficiency has less of a direct effect on juvenile survival rate, but a strong effect on the dynamic movement between the reproductive and nonreproductive stages. To the extent that search inefficiency prevents pair formation, fecundity declines and λ decreases accordingly.

Demographics

All demographic parameters are linked to site quality. Individual mortality and fecundity are determined by the quality of the site occupied at the beginning of each time-step. In keeping with the stage-structured approach, risks are assumed to be constant within a stage over the course of a year. The year is divided into *i* time-steps, and the risk per step for an owl in stage-class *j* occupying habitat type *k* is defined as the *i*th root of the yearly risk for class *j* and habitat type *k*.

In the model analyses described below, we allow a maximum of three habitat types: (1) suitable habitat with associated vital rates from table 8G, initially scaled by $1/\lambda$ to provide for a stable or growing population; (2) sink habitat with reproduction and survival below that needed for a stable population; and (3) unsuitable habitat that allows survival at reduced rates, but no reproduction. The model structure will support additional categories of habitat quality, but available data do not support this degree of resolution.

Movement

The map is divided into a fixed array of grid cells, each representing one territory-sized unit. The grid is hexagonal to allow more realistic movement. The rate of movement depends on the size of the grid cell and the number of time-steps per year. Individual moves are restricted to adjacent cells. The mobile classes of the owl (nonterritorial males and females) have an opportunity to move at each time-step. To ensure that certain birds or areas of the map are not given preferential access to open territories or mates, the order of movement is fully randomized at each time-step.

In its simplest implementation, movement is a random walk. The model, however, allows owls to search with "intelligence"; that is, they may favor movement through good habitat and avoid poor habitat. Similarly, females may move obligately to known territorial males, and nonterritorial males may be averse to crossing into defended territories. This intelligent behavior is modeled by giving the owls absolute knowledge of the quality of the cell they occupy and partial knowledge of adjacent cells. They have no knowledge of more distant parts of the landscape. This knowledge takes the form of a series of switches and weighting factors that condition the probability of movement (table 9C).

Three boundary conditions can be specified at the map edges: absorbing, reflecting, and wrap-around. In addition, internal reflecting zones can be created by specifying a land type for which the owls show complete aversion.

Fledglings

Fledglings are defined for model purposes as young that survive to disperse. We assume both good and bad years for fledging and complete correlation in reproductive pulses among populations. If it is a good year, then the pair produces fledglings according to a beta random variable ranging from zero to the maximum clutch size. Two levels occur at which variability can affect the number of fledglings. If the area under the beta distribution is concentrated around the mean clutch size, the population will pulse based on the frequency of good years. When a good year occurs, all pairs at all sites will produce at about the mean number of fledglings. If the probability of a good year is 1.0, variability in the number of fledglings will occur on an individual-territory basis and will depend on the parameters of the beta distribution. Both parameters are linked explicitly to habitat quality and the stage-class of the pair. Because this is a two-sex model, the sex ratio of fledglings is also adjustable.

Relevant Inferences to the Southern California Metapopulation

Effects of Cluster Shape

The cluster model assumed circular clusters, but the landscape models allowed us to closely specify the shapes of clusters

Table 9C -*A summary* of *factors that can affect an individual's movement in the landscape model.*

Factor	Based on	Sex	Form
Becomes territorial	Habitat quality/occupancy	M	Probabilistic switch
Aversion	Habitat quality	M/F	Weighted probability
Site fidelity	Habitat quality	M/F	Weighted probability
Linear propensity	Behavior	M/F	Weighted probability
Territorial aversion	Occupancy	M	Weighted probability
Female finds male (current cell)	Occupancy	F	Absolute switch
Female finds male (adjacent cell)	Occupancy	F	Probabilistic switch
Global boundary	-	M/F	

(habitat islands). To compare general model results between the two models, the landscape model was used to project population trends from a number of hypothetical landscapes with an identical number of suitable sites (McKelvey et al. in press). Other than suitable habitat configuration, there were no differences in the initial values of any model parameters. The map boundaries were wrap-around so that the exact location of the habitat within the map frame was unimportant. In these simulations, only two habitat qualities were simulated: habitat suitable ($\lambda = 1.0$) and unsuitable for nesting. The movement parameters deviated only slightly from a random walk-birds were twice as likely to choose suitable habitat, males treated occupied habitats identical to unsuitable habitat, and birds were twice as likely to move in the same direction as to choose a different direction.

Model results parallel the territory-cluster model, showing that a clustering of suitable habitat is both more efficient in terms of mean population level and more stable in terms of lowered extinction probabilities than is a random structure. We found, however, that the shape of the cluster had an important effect on its stability properties and mean occupancy rates. A cluster with a low ratio of edge to area supported a larger population and was more stable than continuous clusters of identical area but with greater irregularity (compare figs. 9J and 9K). A high edge-to-area ratio had a negative impact on demographic stability: the rate of decline in a large, highly irregular cluster was similar to the decline rate of the dispersed cluster system, but it had a lower extinction likelihood.

Source-Sink Dynamics

Previous results demonstrated the impact of reserve shape when each landscape cell was either suitable or unsuitable for breeding. In that case, the breeding population was limited entirely to the suitable habitat. In a landscape containing a gradient of habitat qualities, source locations would produce an excess of individuals, and sink locations would absorb some of the dispersing juveniles from the sources. Consequently, when a possibility exists of nesting in sink locations, populations will occur exterior to the source habitat areas even though vital rates in the sinks do not allow for a self-supporting population (see similar conclusion in Buechner 1987, p. 71). The presence of sink areas adjacent to habitat clusters may adversely affect the stability properties of the clusters. In our simulations, the mean population size of the entire landscape was higher in the source-sink system, but the mean occupancy of the reserve clusters was lower and the variability among the population size trajectories increased with time.

In summary, the landscape model demonstrated that the shape of clusters is nearly as important as their size. As a result, the size of irregularly shaped clusters must be larger to maintain the same mean occupancy rate compared to clusters more circular in shape. Further, model results indicate a possibility that in landscapes exhibiting a gradient of habitat qualities, the presence of sink habitats adjacent to reserves may have opposing effects. Overall population size is increased but projected population sizes are more variable. In terms of persistence likelihoods, however, we believe that increases in population size associated with increases in the amount of sink habitat should more than compensate for any negative effects associated with increased variability in the sizes of populations within clusters.

Application of the Landscape Model to the Southern California Metapopulation

Constructing the Map

The map, which characterized in a spatially explicit fashion the distribution of owl populations and their habitat islands in southern California, was based on the 1986-91 cumulative spotted owl survey data done primarily on public land (Chapter 3; Stephenson 1991). Each township (6-x-6 miles) in the Southern California Province was characterized according to the estimated number of owl sites it contained (fig. 4C). The collection of sections with owl sites defined the habitat islands and corresponded closely to locations listed in table 9A and shown in figure 9A. Thus, owl locations at a scale of 36 square-mile sections defined the location of suitable owl habitat. Each section, representing about 23,000 acres, was represented by nine hexagonal grid cells. This produced grid cells of about 2,500 acres, roughly corresponding to the size of individual spotted owl home ranges during the breeding season in mixed-conifer forests of the Sierra Nevada (table 6B). If a section had >9 sites, the extra sites were added to an adjacent section. The initial map, as it appears at the beginning of a simulation, is shown in figure 9L.

Imposing a fixed grid-cell size on a species with geographically variable area requirements is problematic. The number of owl sites will be underestimated in those parts of the species' range where its area requirements are smaller. For those habitats in southern California where home ranges are apparently the smallest (riparian/hardwood areas; table 6G), we examined the distribution and spacing among known owl sites. Most were separated by large areas of chaparral, making it unlikely that a single grid cell would contain two or more home ranges. In some cases where a single cell could contain two or more owl sites, we have probably underestimated the number of sites.

Initializing the Map

The map was initialized, in terms of owl pairs, using the estimated number of suitable sites per township (36 square miles) (see fig. 4C). If a township, for example, was estimated to contain six pair sites, then six sites (grid cells) were randomly selected from among the nine sites representing that township on the map. Each simulation was initialized with about 360 pairs of spotted owls.

For most simulations we used only two habitat types--suitable and unsuitable. Suitable habitats were characterized by a λ, slightly >1.0. Unsuitable habitats (the landscape matrix)

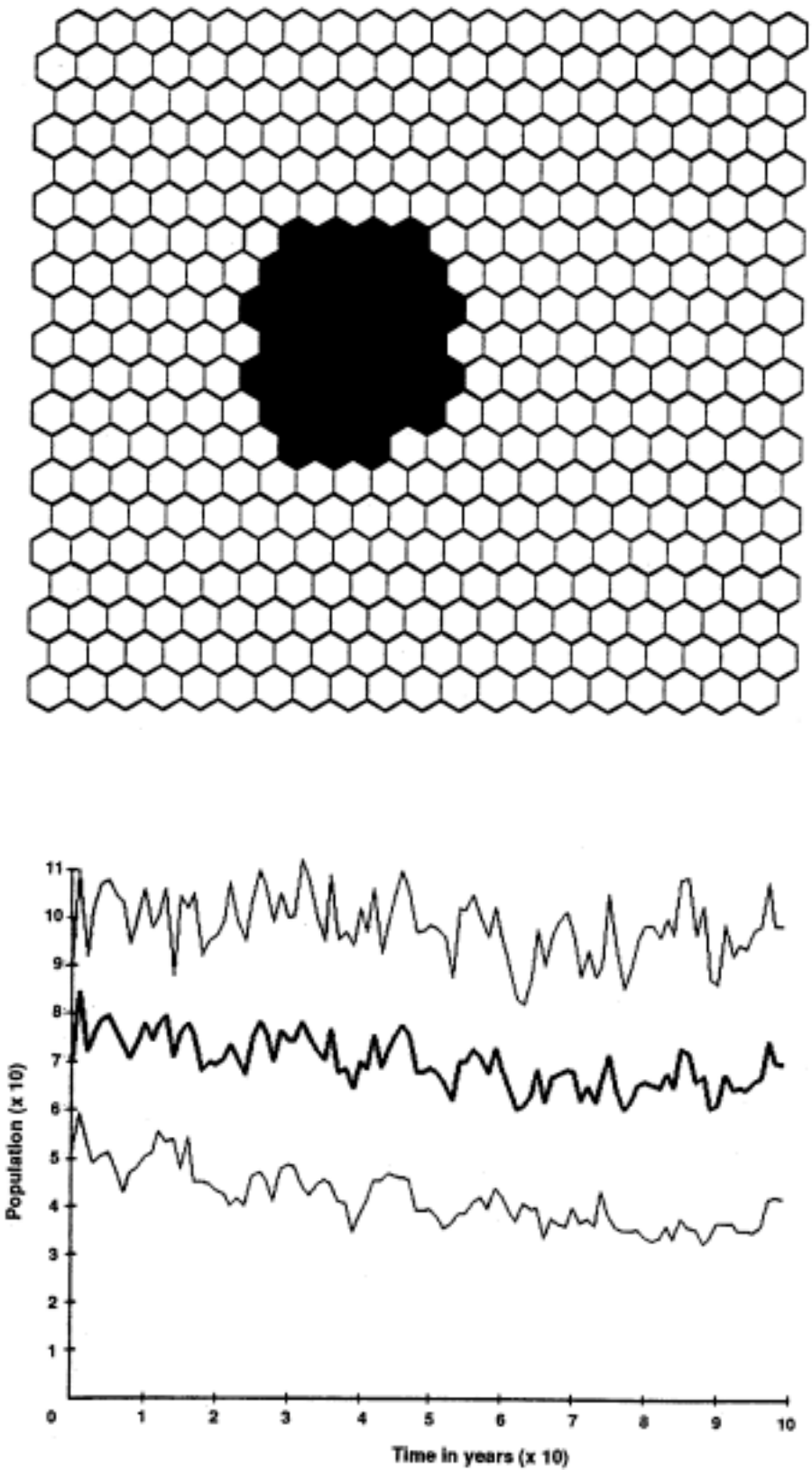


Figure 9J-Landscape model simulation showing simulated landscape with suitable habitat arrayed in one large, regular block. Results are based on 30 simulations. The heavy line represents the mean population, the thin lines are one standard deviation from the mean.

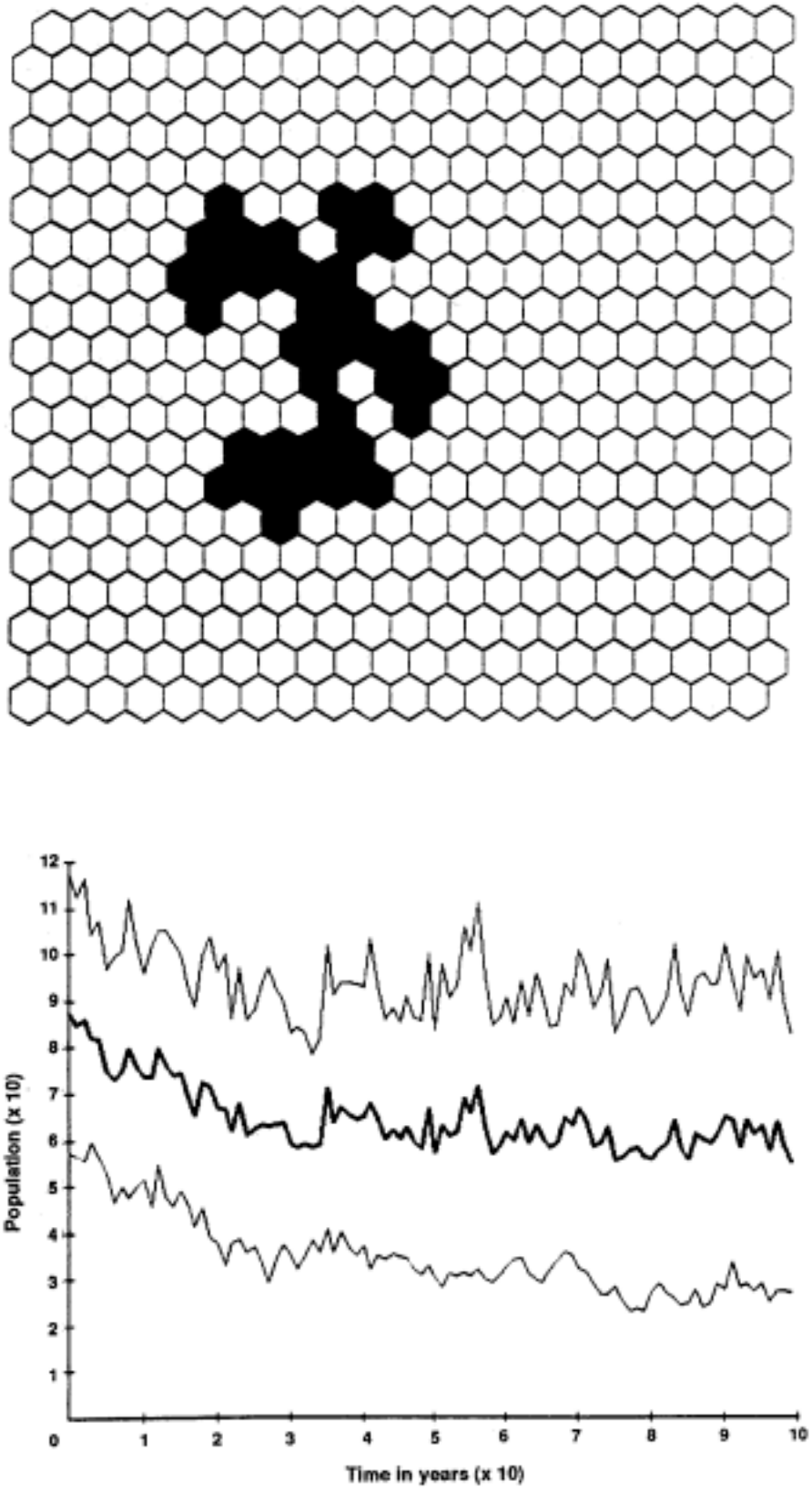


Figure 9K-Landscape model simulation showing simulated landscape with suitable habitat arrayed in one large, irregular block. Results are based on 30 simulations. The heavy line represents the mean population, the thin lines are one standard deviation from the mean.

Figure 9L-The southern California metapopulation "map" used as the initial condition for subsequent simulations based on the landscape model. In this map showing the initial condition, hexagonal cells defining the "islands" were assumed to be suitable habitat. Areas outside of the islands (the matrix) were unsuitable.

were characterized in different ways according to expected survival rates (table 9D), but these sites never supported reproduction. Sink habitat was introduced in a third set of simulations; it had an assumed $\lambda_s = 0.80$.

Simulations

All simulations assumed stochastic fecundity rates, expressing both within- and among-year variation (see above). Survival rates only expressed within-year variation based on binomial sampling probabilities. All owls experienced similar pulses in reproduction-that is, we assumed complete spatial autocorrelation within the metapopulation. Simulations represented 150-year projections and were based on 50 replications. Various assumptions were made about the search capabilities of dispersing juveniles and the degree to which the matrix surrounding habitat islands could support owl survival (table 9D). In general, birds were twice as likely to move to a suitable cell than an unsuitable cell. This had the effect of making it less likely to leave an area of clustered, suitable habitat and more likely to be attracted to such an area. The map was static-after setting initial conditions, there were no changes in the amount or distribution of habitat-for all simulations.

Each suitable site was assumed to contain a pair of owls at the initiation of each simulation. Therefore, the population was effectively above its carrying capacity at time zero (figs. 9L-9P). Even under optimum conditions, a suitable site would have an expected pair occupancy rate <1.0 because of random mortality events. As a result, each simulation showed an initial population decline. Comparisons of results based on population trajectories should be made over the last 100 years of each simulation.

Interpreting Simulation Results

Results of simulations should not be interpreted as estimates of extinction likelihoods. We believe it is premature to make reliable estimates of extinction likelihoods at this time, as too many uncertainties exist about the long-term values of the vital rates and the dispersal capabilities of juvenile owls. For example, we do not known whether gaps between adjacent habitat islands are total or only partial barriers to dispersal. The most relevant output from the simulations are the maps, which summarize mean occupancy rates for each cell over the 150-year simulation interval. In general, areas of the landscape with very high occupancy rates represent potential source areas. In contrast, areas of the landscape with low occupancy rates represent sink areas. Interpreting the model results in a visual and spatially explicit way allows insights into areas of the landscape that are particularly vulnerable to local extinction events, as well as areas that represent sources for immigrants to other local populations.

Results

All simulations were initialized according to the spatial pattern of suitable habitat shown in fig. 9L. Suitable habitat supported demographic rates, on average, that yielded a λ slightly >1.0. Differences among the simulations reflect different assumptions about the survival risks experienced by owls moving

Table 9D-*Values of the demographic rates in suitable habitat and in the matrix for different model simulations. Risks to dispersing birds and dispersal capability were varied among the different simulations.*

		Simulation						
	Suitable					Source	Source/sink	
Demographic rates	habitat	A	B	C	D	reduction	Matrix	Sink
Juvenile survival	0.358	0.20	0.20	0.18	0.01	0.18	0.18	0.30
Subadult survival	0.903	0.70	0.70	0.45	0.01	0.45	0.45	0.75
Adult survival	0.903	0.80	0.80	0.45	0.01	0.45	0.45	0.75
Fecundity	0.279	0	0	0	0	0	0	0.175
Dispersal capability		22	44	22	22	22	22	22

through the matrix among the habitat islands. Because dispersal abilities are largely unknown, we bracketed a range of possible responses, ranging from very optimistic to an assumption of almost complete isolation of local populations (see table 9D). None of the simulations assumed any absolute barriers to dispersal in any direction, with the exception of the Pacific Ocean, which acted as a reflecting barrier.

Simulations A and B

In these simulations we made optimistic assumptions about the survival risks experienced by dispersing birds. Survival rates were only slightly depressed from values experienced in suitable habitat (table 9D). Simulation A suggested a relatively stable metapopulation structure with areas of high occupancy concentrated in the San Gabriel-San Bernardino Mountain complex (fig. 9M). Smaller and more isolated subpopulations, such as Tecuya Mountain, the South Santa Lucia Mountains, and Palomar Mountain (fig. 9A), had significantly lower mean occupancy rates, indicating frequent turnover within sites with subsequent recolonization at irregular intervals. In general, the lower the mean occupancy rate of a site, the longer the interval to recolonization after a turnover event.

Parameter values for simulation B were identical to A, except that we doubled the search capabilities of dispersing owls (table 9D) and the equilibrium population was about 15 percent higher than observed in simulation A. Results were similar except that occupancy rates were elevated overall, most significantly in the smaller but isolated clusters (for example, in the Los Padres Ranges of Ventura and Santa Barbara counties, and on Mount San Jacinto) (fig. 9A). Thus, sites were being recolonized at a greater rate.

Simulation C: Increasing Dispersal Costs

Assumptions made in the previous simulations about risks to movement in the matrix were very optimistic. In this simulation we relaxed those assumptions somewhat, and assumed that survival rates in the unsuitable matrix habitat were half those in suitable habitat (table 9D). Results indicated that small, remote subpopulations had occupancy rates in suitable sites of only 20-40 percent (fig. 9N). That is, suitable sites in these habitat islands are unoccupied 60-80 percent of the time. Occupancy rates in the San Gabriel-San Bernardino complex remained high because, having many tightly clustered owl sites, they were effectively immune to costs of dispersal through matrix habitats. Total population size was reduced by about 30 percent, compared to simulation A, but appeared to reach an equilibrium within the last three decades of the simulation (fig. 9N).

Simulation D: Population Isolation

In this simulation, we set movement costs in the matrix very high so that all but the closest clusters were effectively isolated from each other. The effects were dramatic. Overall population size was reduced by about 40 percent, and the population size did not equilibrate until the ninth decade (fig. 9O). High per-site occupancy rates were restricted to relatively large clusters (>40 sites) and with mostly contiguous sites (fig. 9O). In areas with a low density of suitable sites, even habitat islands with about 40 sites, such as the Palomar Mountain/central San Diego County/ Cuyamaca/Laguna Mountains complex (fig. 9A), were unstable and had very low occupancy rates (<15 percent). All local populations between the western part of the San Gabriel Mountains and the San Rafael wilderness (Las Padres NF) experienced frequent local extinction events (fig. 9O). The San Gabriel/ San Bernardino complex remained the most stable locus of high occupancy within the metapopulation.

Simulation E: Source Reduction

The San Gabriel/San Bernardino complex consistently had the highest occupancy rates and was the key source population for immigrants into other areas of the metapopulation. Therefore, we wanted to investigate its resilience to disturbance and the effect that such disturbance would have on the stability of the rest of the metapopulation. To simulate this scenario, we randomly changed 1/3 of the suitable sites within this complex to unsuitable sites and assumed moderate survival costs to movement through the matrix (table 9D).

The effect of the simulated decline in habitat within the largest population was pronounced. The overall size of the metapopulation was markedly reduced, and an equilibrium size had not been attained even after 150 years (fig. 9P). Comparing figures 9P and 9N suggests that loss of habitat within the largest source population would greatly reduce occupancy rates through

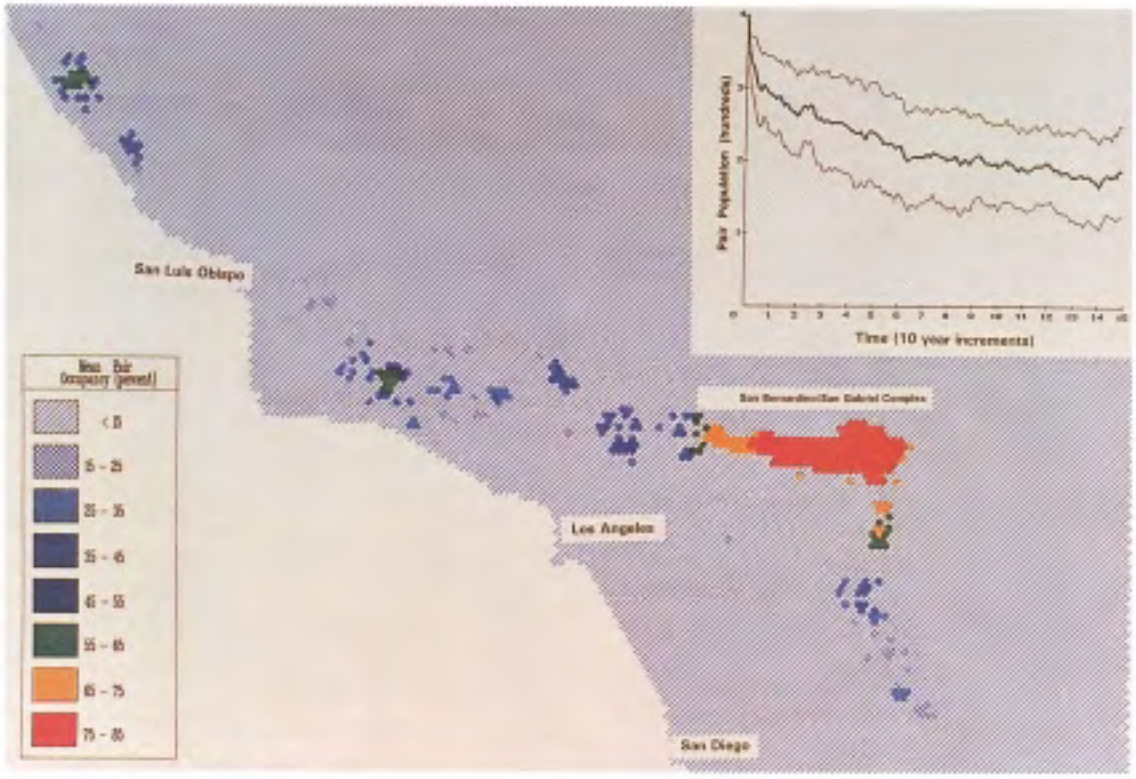


Figure 9M-Landscape model simulation A, showing mean (±1 standard deviation)150-year trajectory of the metapopulation (inset) and the mean pair occupancy rate of habitat cells (from fig. 9L) averaged across the time interval and based on 50 simulations (parameter values used in the simulation are described in table 9D).

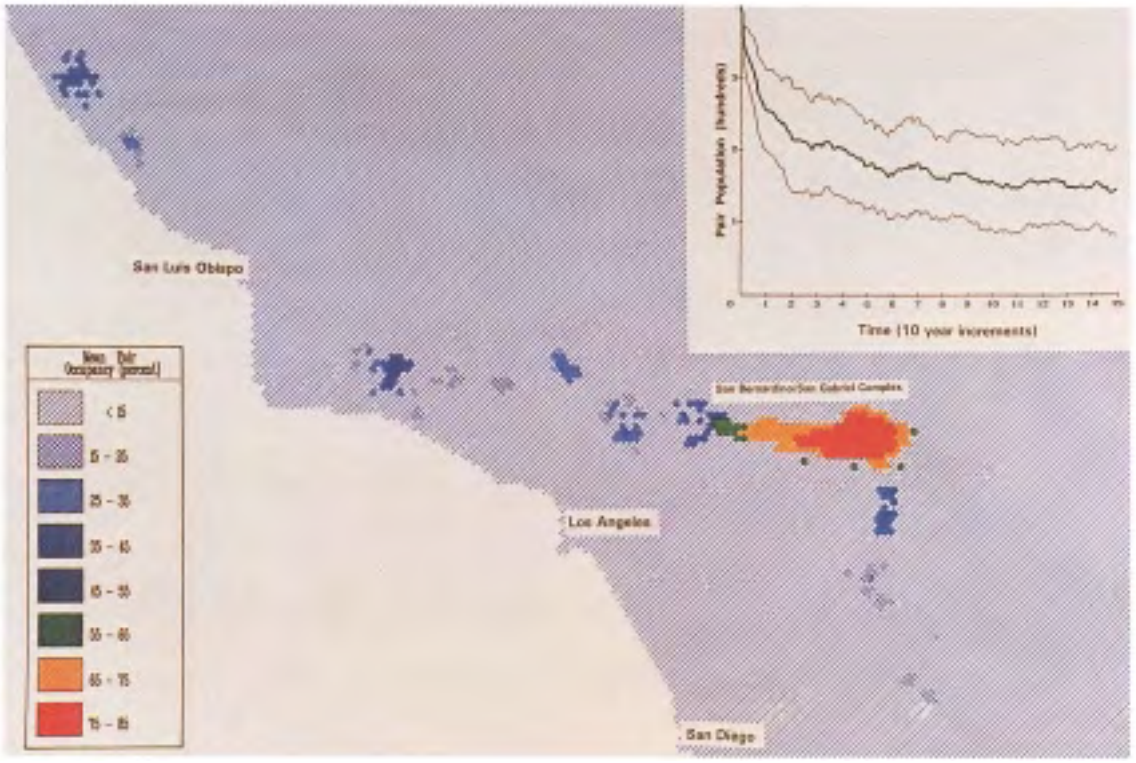


Figure 9N-Landscape model simulation C, showing mean (±1 standard deviation) 150-year trajectory of the metapopulation (inset) and the mean pair occupancy rate of habitat cells (from fig. 9L) averaged across the time interval and based on 50 simulations (parameter values used in the simulation are described in table 9D).

out the metapopulation. In addition, the small local populations of owls immediately to the west of the complex had gone extinct or had occupancy rates less than 20 percent. Interestingly, the overall size trajectory for the metapopulation in this simulation showed a steeper decline than that for isolation (simulation D) (fig. 9O). That is, decreasing the net production of potential colonists from the major source population within the metapopulation appeared to have more adverse effects than increasing the degree of isolation among local populations. Collectively, these results suggest that, to a large extent, the persistence of much of the southern California metapopulation relies upon maintaining the habitat integrity of the San Gabriel/San Bernardino habitat complex.

Simulation F: Source-Sink Effects

For this simulation we randomly changed 50 percent of the suitable (that is, source) habitat (λ = 1.02) within the entire metapopulation (fig. 9L) to sink habitat (λ = 0.80). This simulation thus represented both a source reduction and the introduction of sink habitat. Sink habitat, unlike matrix habitat, supported both survival and reproduction, but at nonreplacement rates (table 9D). We assumed limited ability by the owls to discriminate between source and sink habitats-searching birds were only 10 percent less likely to settle in sink habitat. Simulation results suggested a dramatic, exponential decline to metapopulation extinction within about 100 years (fig. 9Q). Average occupancy rates over the interval were >15 percent only for the San Gabriel/San Bernardino complex. Even this habitat island was unstable, however, and could not sustain its population over the long-term. Given this level of source reduction (50 percent), even greatly increasing the owl's ability to discriminate source from sink habitats did not stabilize the population.

Discussion

Simulation results suggested that the San Gabriel/San Bernardino owl population plays a pivotal role in maintaining the southern California metapopulation. Unfortunately, the resident, territorial population of spotted owls in the San Bernardino Mountains has declined precipitously since 1987 (LaHaye et al. in press; Chapter 8). If the territorial population is in some sort of dynamic balance with a nonterritorial (floater) population, then these sorts of declines may be accommodated over the short-term and pose no long-term threat (see Franklin 1992). If these trends also characterize the other local populations, however, and were to persist for another 5-10 years, we believe the persistence of the entire metapopulation would be at risk.

Several key factors remain unknown. For example, we do not know if these trends characterize the other local populations. If the decline in the territorial population in the San Bernardino Mountains is a response to region-wide, environmentally induced variation, then other local populations may be responding in a synchronous fashion. The degree of environmental correlation within the metapopulation is also unknown. Regional rainfall patterns, however, suggest that the degree of correlation may be high (figs. 8A and 8B). The effects of environmental correlation on persistence among populations depends upon their life histories, including diet switching and changes in prey availability (for example, Horton and Wright 1944, Vogl 1967). Modeling efforts by Harrison and Quinn (1989) suggest that even strong environmental correlation in extinction risks will not have a major effect on persistence time for large vertebrates, except when local populations become very small-but see a counter argument in Stacey and Taper (1992). Our models all assumed a complete correlation among populations in their response to environmentally induced variation in fecundity.

Persistence in metapopulations also depends critically on dispersal capabilities, distances between local populations, and risks involved in moving between habitat islands. The persistence of small, local populations with high turnover rates depends upon rescue by colonists from other populations in the metapopulation. This, too, is an area involving much uncertainty. The dispersal capabilities of California spotted owls and how they move through heterogeneous landscapes are mostly unknown.

Given the uncertainties regarding synchrony of extinction risks among local populations, whether the declines in the size of the territorial population will continue into the future, and the dispersal capabilities of juvenile owls, we believe it is premature to estimate extinction likelihoods. Simple application of the current estimates of the vital rates for the San Bernardino population (table 8G), for example, would show a rapid collapse to extinction. Our approach has been to gain general insights into the management of owl habitat in terms of its quality, amount, and geometry. We did this by viewing population dynamics as emergent reflections of landscape pattern and the distribution of habitat types. The landscape model was particularly valuable because it allowed us to gain insights into the dynamics of individual populations related to specific locations on the landscape.

Simulation results suggest that, in those parts of the species' range where suitable habitat constitutes only a small fraction of the landscape, populations are unstable and have low occupancy rates. The pattern is improved if the metapopulation contains a large source population. This result parallels the individual-territory model and predictions from Lande's (1987) modeling. That is, when the amount of suitable habitat becomes too small a percentage of the landscape, thresholds are encountered and populations may decline to extinction (fig. 9O). This occurs despite the continued presence of suitable habitat at these locations.

The general predictions from the cluster model were also demonstrated by the landscape model. Specifically, when clusters (habitat islands) became too small, or suitable habitat too diffuse, occupancy rates dropped precipitously. Assuming moderate to strong risks to dispersing birds, only those clusters with more than 40 sites and largely contiguous habitat showed high occupancy rates (figs. 9M and 9N). For example, the isolated sites on the western slope of the San Gabriel Mountains dropped to low occupancy rates when dispersal costs were high (fig. 9O).

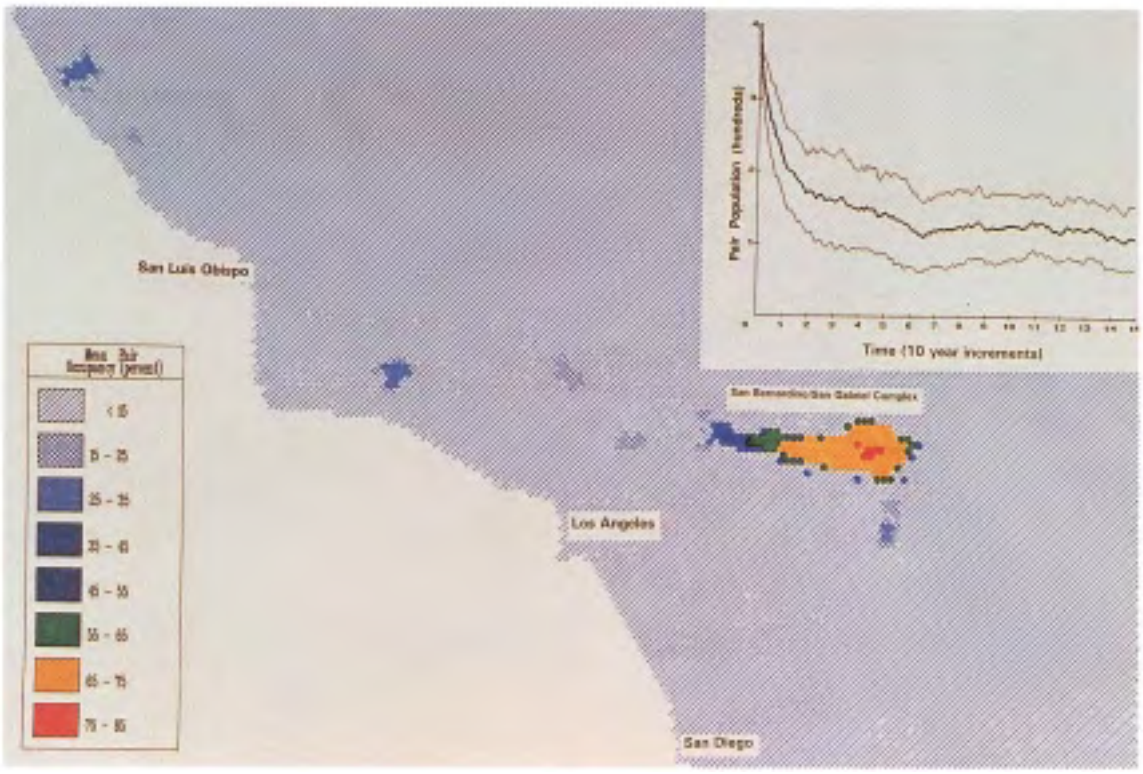


Figure 9O-Landscape model simulation D, showing mean(± 1 standard deviation) 150-year trajectory of the metapopulation (inset) and the mean pair occupancy rate of habitat cells (from fig. 9L) averaged across the time interval and based on 50 simulations (parameter values used in the simulation are described in table 9D).

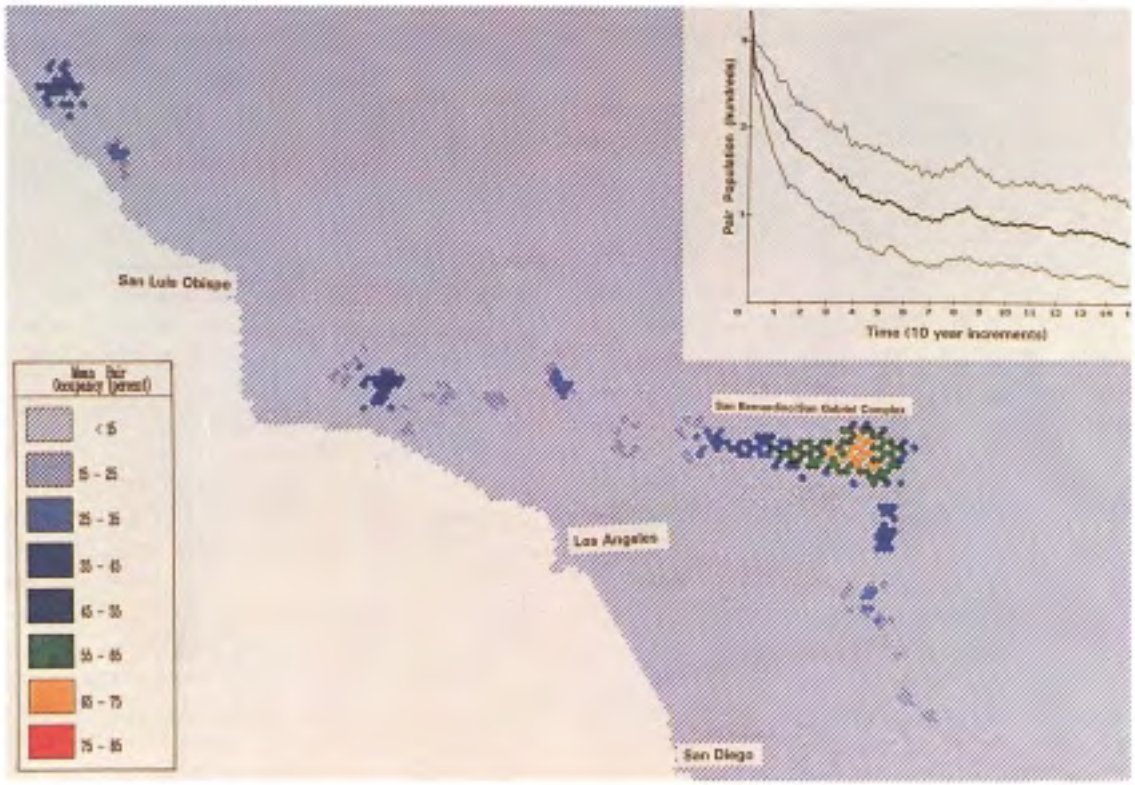


Figure 9P-Landscape model "source reduction" simulation, showing mean (± 1 standard deviation) 150-year trajectory of the metapopulation (inset) and the mean pair occupancy rate of habitat cells (from fig. 9L) averaged across the time interval and based on 50 simulations (parameter values used in the simulation are described in table 9D).

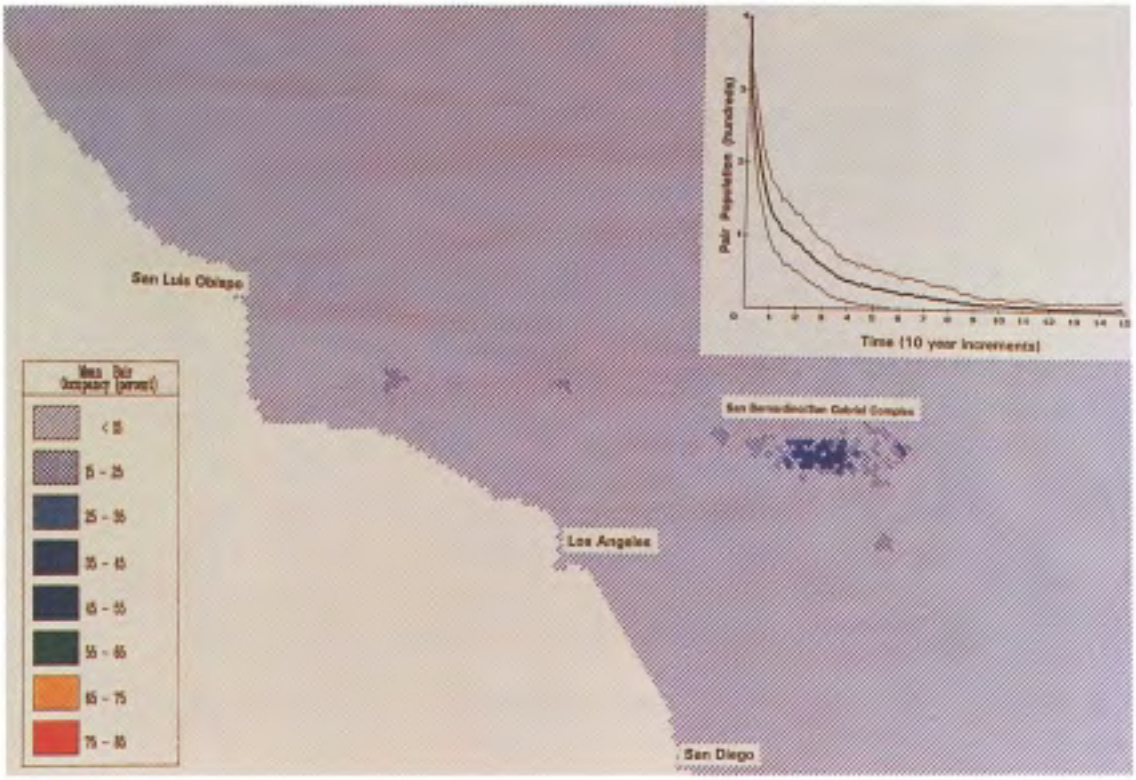


Figure 9Q-Landscape model "source/sink" simulation showing mean (±1 standard deviation) 150-year trajectory of the metapopulation (inset) and the mean pair occupancy rate of habitat cells (from fig. 9L) averaged across the time interval and based on 50 simulations (parameter values used in the simulation are described in table 9D).

The simulations also illustrated the interaction between size and spacing (fig. 9G). The islands near the San Gabriel/San Bernardino complex retained moderate occupancy rates even though they were small and dispersal risks were high (for example, the San Jacinto Mountains, 11 miles from the southern San Bernardino Mountains). In contrast, the population occupying the Los Padres Ranges, >30 miles from the western edge of the San Gabriel Mountains, declined to <40 percent mean occupancy even though this habitat island supports at least 65 pair sites. In general, the largest clusters with the shortest nearest-neighbor distances (table 9A) were the most stable and had the highest occupancy rates.

A consistent finding from the simulations, and predictable from our simpler models, was the significance of the San Gabriel/ San Bernardino population to the dynamics of the entire metapopulation. Simulated declines in the amount of suitable habitat in this complex lowered occupancy rates throughout the entire metapopulation (fig. 9P).

Population declines were particularly pronounced when half of the source habitat was changed to sink habitat and the owl's ability to discriminate among these habitats was limited (fig. 9Q). As the ability to discriminate source from sink habitats increased, the rate of decline of the population became less pronounced, but with a 50 percent reduction in source habitat no positive equilibrium was attained. When selection is imperfect, some owls may settle in sink habitat and reduce the occupancy rate in source habitat. The result is a decline in population size, often with no positive equilibrium. This finding is consistent with results reported by Pulliam and Danielson (1991) based on a different model formulation.

In some situations the presence of sink habitat may contrib.- ute to metapopulation size (Pulliam and Danielson 1991, Howe et al. 1991). Whether sink habitat acts to enhance metapopulation persistence depends critically on the owls ability to discriminate between source and sink habitats. If some owls that would otherwise settle in source habitat, are attracted to, and settle in, sink habitat then the effects can be negative. The extent to which spotted owls can discriminate among habitat types in terms of their expected birth and death rates is unknown. It is unlikely, however, that habitat selection is perfect. Because search is finite, population trend ultimately depends upon the amount and distribution of source habitat, even when selection among source and sink habitats is perfect.

In the case of the California spotted owl, the effects of landscape pattern on survival during dispersal may induce high levels of both spatial and temporal variation in juvenile survival rate. If habitat becomes more fragmented, the uncertainty of successful juvenile dispersal will become progressively more relevant to the likelihood of persistence. Even in a diffuse system with many suitable territories, pair occupancy will be low because of low recolonization rates. As a result, in a highly fragmented system, positive density-dependent growth rates usually associated with low population densities are unlikely. The effects of changes in landscape pattern on demographics are particularly significant if losses occur disproportionately in source habitat (fig. 9P).

Habitat-induced population declines also occur at the scale of the individual pair site or territory. Territories, the basic unit for our models, can be thought of as small islands, each having a maximum of one reproducing pair. They are similar to islands in that (1) they have spatial dimension-they occupy a certain area of the landscape; (2) they have some level of habitat quality; and (3) when they experience local extinction (one or both members of the pair either dies or emigrates), they must be recolonized through immigration from outside the territory or by an existing, nonterritorial floater within the territory.

The concept of territories as individual islands, with habitat quality explicitly defined by the expected values for birth and death rates, is key to understanding the dynamics of the spatial models. In all of the spatial models, search for suitable habitat is a sampling process. In the individual-territory model, the landscape is searched randomly and search success depends on the average density of suitable sites on the map. In the territory-cluster model, random search is confined to the clusters, which vary in the number and adjacency of suitable sites. Search success in this model depends primarily on the density of suitable territories within the cluster and secondarily upon the density of clusters in the landscape. In the landscape model, search success is defined at each time-step and for each owl by the density of suitable habitat in the territories immediately adjacent to the cell ("territory") currently occupied. When three or more habitat types occur, each cell on the map is not only a location, but, in terms of search success, a habitat-quality state with specific transition probabilities controlling movement into alternate states.

In a spatial model with search, a system composed of territorial clusters is more stable than a diffuse system because clusters produce regions where search efficiency is maximized. Circular clusters are the most stable because the density of suitable habitat is locally maximized. All other geometric forms will have lower search efficiency when compared with a circular cluster, unless clusters have strongly reflecting boundaries. In a cluster with a sufficient number of suitable territories, a population can recover from low occupancy because search efficiency will remain high. The key to stable populations within clusters is that they contain a sufficient number of high quality (= suitable) sites ($E[\lambda] \geq 1.0$) to support population large enough to avoid local extinction due to stochastic demographic events. Surprisingly, it is possible that the presence of marginal or sink habitat may actually reduce population size even though some individuals may breed in these habitats (Pulliam and Danielson 1991, McKelvey et al. in press).

Management Recommendations

Our recommendations for the persistence of spotted owls in the Southern California Province focus on the dynamics of its habitat at two spatial scales. First is the landscape scale. The arrangement of owls and owl habitat across the landscape shows that most of the population is concentrated in the San Gabriel/ San Bernardino Mountains complex. Every effort should be made to keep this population intact by maintaining the amount and spatial connectivity of suitable habitat there. Current demographic estimates suggest that the resident, territorial population is in significant decline. This population needs to be closely monitored for the foreseeable future, and attempts must be made to better understand the causes of the decline.

Other smaller, local populations do not have the potential to provide a large number of colonists. These populations are important, however, in diminishing the risk that local populations would simultaneously experience adverse impacts (Den Boer 1968, 1981). Advantages are often gained by distributing populations widely across an extensive geographic area (Quinn and Hastings 1987, Gilpin 1990)-the degree of environmental correlation among local populations is reduced, as is the likelihood of simultaneous extinction events (see discussion in Stacey and Taper 1992).

Local populations will continue to function as part of a larger metapopulation only if they remain connected through dispersal. If local populations become increasingly isolated by reduction in the sizes of habitat islands or by the creation of barriers to dispersal, occupancy rates decline because of a decline in the rate of demographic rescue, and the likelihood of extinction increases (table 3K; see discussion of problem areas in Chapter 3). Small, isolated populations will be the first to be lost to extinction, but even the largest, most continuous populations will experience increased risks if the overall size and spatial extent of the metapopulation is decreased.

Options to decrease population isolation through management efforts are severely limited in southern California. Because the current metapopulation structure is largely the natural expression of vegetation patterns resulting from edaphic, topographic, and climatic constraints, little opportunity exists to enhance dispersal habitat between subpopulations. The obvious goal, therefore, is to avoid creating additional barriers to dispersal beyond those not amenable to management.

The second level of concern is at the scale of the individual territory. It may be that the greatest threat to persistence of spotted owl populations is a subtle but continual decline in habitat quality (that is, a gradual conversion of source to sink habitat), on a site-by-site basis. As discussed in Chapter 8, subtle declines in λ will be difficult to detect except in the largest and longest-term demographic studies. Pulliam (1988) and Pulliam and Danielson (1991) concluded that knowledge of habitat-specific

demographic rates is ultimately needed for the effective management of wild populations. We agree. We must be able to target for preservation those habitats needed today for the species' persistence, and learn how to manage for such habitats in the future. Only by understanding the relations between demographic rates and the structure and composition of vegetation at the stand level can we be certain of maintaining habitat that provides for a stable or growing population.

Both scales of research and management-landscape and territory-are equally important, and both must be pursued to address the persistence requirements of spotted owls in southern California.

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Chapter 10

General Biology of Major Prey Species of the California Spotted Owl

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Full understanding of the habitat relations of California spotted owls depends, in part, on knowledge of the habitat relations of their primary prey species. For example, the northern flying squirrel is the primary prey of the owl in conifer forests of the Sierra Nevada, comprising as much as 61 to 77 percent of the total biomass eaten in some localities and seasons (table 4A). The dusky-footed woodrat is the primary prey in lower-elevation forests and woodlands of the Sierra Nevada and throughout all habitats in southern California, making up 74-94 percent of the diet, by weight, in various areas. Current evidence indicates that suitable nest sites and the most common foods of northern flying squirrels are usually found together in mature and older forests, which may help us understand why spotted owls forage more often in such forests. Woodrats are typically associated with shrubfields, especially those dominated by thick-leaved, evergreen species. Spotted owls in the Sierran foothills and in southern California commonly occur in forests and woodlands with a light to moderate shrub understory, or that adjoin more extensive stands of chaparral. In addition, radio-tracking studies of spotted owls in the Sierra NF have shown that their home ranges in Sierran mixed-conifer forests are measured in thousands of acres, but those in foothill riparian/hardwoods are measured in hundreds of acres (Neal et al. 1990). This difference is probably related, at least in part, to the facts (1) that woodrat densities are generally several times higher than flying squirrel densities and (2) that woodrats weigh nearly twice as much as flying squirrels.

Here, to expand a general understanding of spotted owl ecology, we present brief biological descriptions of several species of small to mid-sized mammals that most commonly occur in diets of the California spotted owl (see Chapter 4).

Dusky-Footed Woodrat

Distribution and Habitat

Dusky-footed woodrats occur in the Pacific Coast region from the Oregon side of the Columbia River to northern Baja California. Within the range of the California spotted owl, they inhabit coastal, piedmont, and montane chaparral and forest communities. Evergreen or live oaks and other thick-leaved shrubs are important habitat components throughout this woodrat's geographic range (see color photo 5-29). They are most numerous where shrub cover is dense, and least abundant in open areas (Fitch 1947). They are one of few small mammal species of chaparral habitats that flourish in old, dense stands (Quinn 1990).

Habitats that are unsuited or poorly suited for dusky-footed woodrats include open grasslands or fallow, weedy ground; sparsely wooded forests; woodlands solely of conifers or with little shrub understory; and pure stands of chamise, manzanita, or ceanothus (Linsdale and Tevis 1951).

In the Sierra Nevada, this woodrat occurs generally below 5,000 feet in elevation (lower in the north-about 3,300 feet at Mt. Lassen and 4,000 feet in Yosemite National Park (NP), and higher to the south-rare at 6,000-6,500 feet in the Kern River drainage). It occupies foothill riparian/hardwoods in the northern San Joaquin Valley. The highest capture rates of woodrats in the foothills of the west-central Sierra Nevada were in chaparral, woodland, and forest communities with a mix of overstory trees and shrubs (table 10A). These results appear to agree with those of Sakai and Noon (1992a), who indicate that dusky-footed woodrats in northwestern California are most abundant in brushy stands of sapling/early-aged poletimber. In the southern Sierra Nevada (Kern County), in a chaparral community of ceanothus and interior live oak between 2,560 and 3,200 feet in elevation, woodrats were most often trapped around patches of rock gooseberries, and their nests were common where gooseberry thickets encircled rock outcrops or dead snags (Lawrence 1966).

In the San Bernardino Mountains, the dusky-footed woodrat occurs on both the Pacific and desert slopes, ranging from about 1,600 feet on the Pacific slope and 3,800 feet on the desert slope up to at least 8,000 feet on both sides, where it is the primary prey species of the spotted owl (LaHaye pers. comm.). Grinnell (1908) found most nests in California scrub oak and pinyon associations and few along willow-lined canyons. They occur in big sagebrush/pinyon-juniper woodlands in the New York-Providence mountain chain in eastern San Bernardino County.

In the San Gabriel Mountains, dusky-footed woodrats occur on both the Pacific and desert slopes, exhibiting the same elevational distribution as in the San Bernardino Mountains. In the coastal sage belt, they are restricted to areas close to intermittent streams supporting tall shrubs or small trees. Nests are built mostly of white sage in isolated clumps of lemonade sumac. Population densities -generally are low in this community (M'Closkey 1972). Higher numbers are found in adjacent canyons on densely vegetated slopes. At higher elevations on the desert side, favored spots for nests are thickets of chokecherries, mountain whitethorn, and currants. In the pinyon-juniper woodlands, both conifer species were used for nest sites; but Califor-

Table l0A-*Captures of small mammals in snap traps (Museum Specials and Victor rat traps) in various habitats and seral stages in the western Sierra Nevada, California, based on sampling in Amador, Calaveras, Mariposa, Nevada, Placer, and Tuolumne counties. Values are captures per trap night*[1] *(adapted from Williams and Johnson 1979).*

Habitat and Seral stage	Species captured				
	Dusky-footed woodrat	Brush mouse	California mouse	Deer mouse	Pinyon mouse
Annual grassland	0	0	0	0.0910	0
Chaparral					
Grass/forb	0	0	0	0.2340	0
Light shrub	0.0039	0.0133	0	0.0261	0.0011
Dense shrub	0.0098	0.0031	0	0.016	0.0004
Oak/digger pine					
Seral	0.0007	0	0	0.0074	0
Mature	0.0052	0.0319	0.0007	0.0059	0
Ponderosa pine					
Seral	0.0011	0.0015	0	0	0.0011
Mature	0.0007	0	0	0.0020	0
Mixed-conifer					
Seral	0.0048	0.0045	0	0.0003	0.0003
Mature	0.0030	0.0052	0	0.0015	0
Riparian/hardwood					
Low elevation	0.0044	0.0044	0	0.0022	0.0011
Mid-elevation	0	0	0	0.0007	0

[1] Data from 33 transects; total trap nights = 19,824.

nia scrub oak seemed to be preferred wherever it occurred. They sometimes build no visible nests where talus is available (Vaughan 1954), although careful examination usually reveals clipped branches adjacent to crevice or tunnel entrances (Sakai and Noon 1992a).

In central coastal areas, dusky-footed woodrats appear to prefer closed woods on drier sites, including a high percentage of live oaks with a mixed shrub understory (California coffeeberry and poison oak are the most prevalent shrubs). North-facing slopes meet these conditions best in the area around Hastings Natural History Reservation (hereafter, Hastings Reservation) at about 1,500-2,500 feet in elevation, where intermittent streams with willows also provide high-quality habitat (Linsdale and Tevis 1951). Overhead branches and downed logs often provide woodrats with a means of traveling above ground level; this appears to be an important structural component of the habitat for some populations (as at Hastings Reservation) but not for others.

Woodrats radio-tagged by Sakai and Noon (1992b) sometimes moved in the evenings as far as 165 feet into old-growth forests adjoining their home ranges in shrublands. Sakai and Noon did not determine how long these woodrats remained in the old-growth, or what they did there, but generally they were back in their nests in the shrublands by the following morning. Two radio-tagged woodrats dispersed through old-growth forest from their natal home range into another shrubfield, in one case a distance of at least 650 feet. Such movements by woodrats would make them more available as prey for species like spotted owls that frequent these older forests.

Patterns of Abundance

Reported densities of dusky-footed woodrats range "from just a few animals to >40 per acre in early pole-timber stages, to perhaps 0.4 to 1.2 per acre in large saw timber and old growth" (Thomas et al. 1990, p. 207). In a corridor of habitat measuring approximately 100 by 1400 feet along an intermittent stream, Linsdale and Tevis (1951) trapped about 30 different individuals per month in one year and about 66 per month in another. These results suggest woodrat "densities" of about 9.3 and 20.6/acre-more than a two-fold difference between years. Densities in undisturbed habitats ranged from 2.1/acre in open woodlands of canyon live oaks and scattered Pacific madrones in the Santa Cruz Mountains, Santa Clara, County (Merritt 1974), to 18.3/acre in a riparian/hardwood forest of red alders, willows, and elderberries in coastal Sonoma County (Wallen 1982, Carraway and Verts 1991). Farther inland in Sonoma County, densities were 8.1/acre in late summer and 5.7/acre in winter in an undisturbed, riparian deciduous woodland dominated by red alder, California boxelder, and willows (Cranford 1977). In a study on the San Dimas Experimental Forest in the San Gabriel Mountains (Horton and Wright 1944), mean densities of woodrat houses were 4.6/acre in an area primarily of chaparral and oak woodland, 1-4/acre in

chamise chaparral, 10/acre in riparian/hardwood communities, and 10/acre in unburned oak/chaparral and mixed chaparral above 4500 feet; a golden oak woodland with nearly complete canopy cover and almost no shrub understory had almost no woodrats. Chew et al. (1959) found 16 dead woodrats per acre in a burned canyon bottom dominated by oaks and California sycamores in south-coastal California.

Various studies have reported effects of habitat change on densities of dusky-footed woodrats. Woodrats declined significantly during a prolonged drought in the Santa Monica Mountains, Los Angeles County (Spevak 1983), and Linsdale and Tevis (1951) reported depressed numbers during a drought at Hastings Reservation. On the other hand, Kelly (1989) reported a dramatic population increase during a serious drought at Hastings Reservation in 1988. He attributed this to a large acorn crop in the autumn of 1987, possibly augmented by mild weather conditions. Removal of poison oak from the understory depressed population density in the Berkeley Hills, Alameda County (Vestal 1938); flood, browsing, and trampling of the understory by ungulates reduced woodrat numbers at Hastings Reservation (Linsdale and Tevis 1956). Following complete removal of shrubs from study plots in chaparral cover in coastal dunes near Morro Bay, San Luis Obispo County, a woodrat population declined sharply in the first 2 years following treatment and disappeared entirely by the third year. Areas undisturbed by fire had higher densities of woodrats than burned areas (Lee 1963, Gambs and Holland 1988). Studies by Wirtz et al. (1988), in an area of montane chaparral that burned in southern California, established that preburn densities of woodrats had not yet been reached 4 years after the burn. Postburn densities were higher in areas of light and normal burn than in areas with hot burns where all plant material was destroyed.

A suspected outbreak of plague in 1966-67 decimated woodrat populations in foothills of the southern Sierra Nevada, the Tehachapi Mountains, and the Coast Range (Murray and Barnes 1969).

Cranford (1977) reported significantly larger home ranges for males than females (0.59 vs 0.48 acre) in a riparian woodland bordered by grasslands and surrounded by redwood forest. Kelly (1989) found the same situation in riparian/hardwoods in Monterey County. Sakai and Noon (1992b) found a similar difference, though not statistically significant, among woodrats in shrubfields dominated by brushy tanoaks with an overstory of Douglas-fir in northwestern California. Depending on the spacing of nest clusters (color photo 5-25), females often shared portions of the same home range; consequently home ranges of breeding males can overlap those of several females.

Diet

The herbivorous dusky-footed woodrat apparently obtains most or all of its water from its food. It eats parts of a wide variety of plant species, but the water-rich leaves of thick-leaved shrubs found throughout the woodrat's range are probably the most important source of food. The bulk of the diet consists of leaves and the terminal shoots of twigs, with seasonally important food sources consisting of flowers, fruits (nuts, seeds, fleshy fruits, and so on) and fungi. Bark, wood, and other organic materials are also eaten occasionally. Fruits, fungi, and leaves are often cached within nests.

Linsdale and Tevis (1951) found that acorns and fruits of California coffeeberry were most numerous in caches examined at Hastings Reservation. Leaves and other parts of coast and canyon live oaks, California blackberry, chamise, California coffeeberry, buckbrush, and Jim brush were the major plants eaten. Somewhat less common in the diet were valley, blue, and black oaks; California wild rose; toyon; poison oak; Pacific madrone; and mountain whitethom. Parts of 56 other plant species were consumed (amounting to about 10 percent of the total diet), while 470 plant species (87 percent of the flora at Hastings Reservation) were not found in the diet of this woodrat.

In Joshua Tree National Monument, about 75 percent of the material in food caches in nests .consisted of shrub live oak and about 25 percent was California juniper (Cameron 1971). These proportions were the same even where the dusky-footed woodrat occurred together with the desert woodrat. The main foods in southern California coastal sage communities were lemonade sumac (fruit, seeds, vegetative parts), California buckwheat (vegetative parts), white sage (seeds, flowers, vegetative parts), and California scrub oak (leaves, fruits) (Meserve 1974).

Weights

Specimens from the western Sierra Nevada ranged in weight from 7.2 to 8.6 ounces (Grinnell and Storer 1924). Winter and summer weights in samples from foothill areas in San Diego County averaged 7.7 ± 0.7 and 6.5 ± 0.4 ounces, respectively (Stallone 1979). Sakai and Noon (1992b) reported a mean weight of 7.8 ± 0.14 ounces for a pooled sample of both sexes and all ages (n = 366) in Humboldt County. Adult males there averaged 10.7 ± 0.14 ounces (n = 101), and adult females averaged 8.5 ± 0.09 ounces (n = 133). At Hastings Reservation (Linsdale and Tevis 1951), adult males averaged 8.8 ounces (range 7.1-10.6) and adult females averaged 8.4 ounces (6.4-12.5). These rodents exhibit marked individual and seasonal variation in weight (table 10B). Immature woodrats weighing <5.3 ounces were trapped

Table 10B-*Weights (mean and range in ounces) of all ages of male dusky footed woodrats captured each month during a year at Hastings Natural History Reservation, Monterey County, California (adapted from Linsdale and Tevis 1951).*

Month	*n*	Mean	Range
January	68	8.9	7.0 - 12.0
February	67	9.3	4.9 -13.6
March	94	9.2	5.4 - 13.0
April	106	9.0	2.6 - 13.3
May	77	8.5	3.2 - 13.2
June	83	7.8	2.7 - 11.6
July	97	7.0	1.9 - 11.3
August	54	7.1	1.9 - 11.4
September	92	7.9	3.2 - 13.3
October	58	8.0	3.5 - 11.3
November	66	8.6	3.5 - 12.7
December	91	9.0	3.7 - 12.9

only between April and September. Immatures weighing from 3.5 to 7.0 ounces were trapped in all months but were taken most often in June and July.

Nests

Nests of sticks and other woody debris are typically located on the ground, occasionally in trees (color photo 5-23) or dense shrubs where support for the structure is available, and sometimes in rock crevices and abandoned human structures. Linsdale and Tevis (1951) summarized nest locations at Hastings Reservation as follows:

Most often	Bases of coast live oaks, California coffeeberry, willows, poison oak, California buckeye, California-laurel (bay).
Less often	Against logs, in rock outcrops (probably be cause of a lack of appropriate rocks or insuffi cient cover plants in areas studied-rocks are important in the San Gabriel Mountains and the southern Sierra Nevada), hollow cavities in trees (perhaps because of rarity and difficulty of de tecting such nests), and among limbs of trees (trees with the right configuration of large and small branches to support nests may be pre ferred over the ground).

The structure of the plant community where nests were located at Hastings Reservation was described by Linsdale and Tevis (1951) as a mixed woodland with a mosaic of dense shrubs and trees, forming a complete and complex (multilayered) canopy:

Most often	Closed woodlands consisting predominately of coast live oaks (59 percent; $n = 100$).
Less often	Dense shrubs (28 percent), especially where California coffeeberry and poison oak were most abundant.
Rare (<10 pct)	Lone coast live oak trees (5 percent); live oak savanna (8 percent) (blue oak and valley oak savannas were not used for nests).

Nests are an important part of woodrat population dynamics. Nest clusters, occupied by related individuals, are common in favored habitats. Females, unlike males, stay in or near their natal area throughout their life, where related females breed in the same vicinity, living close together in kin clusters but in separate houses (Kelly 1989). In addition, individuals tend to cluster in favored habitat patches; consequently, such favored areas tend to become "crowded" over time (Linsdale and Tevis 1951). Vogl (1967) reported one adult per nest, but Sakai and Noon (1992a) have occasionally captured two adults per nest in northwestern California.

Reproduction and Development

Linsdale and Tevis (1951) found that 70 percent of the woodrats in their study area at Hastings Reservation survived less than 1 year, 27 percent survived 2 years, and 3 percent survived at least 3 years. Reproduction occurred in all months at Hastings, with the fewest pregnancies in December and the most in February. The number of juveniles appearing outside the nest was greatest in July and least (0) in January and February. Females were polyestrous, producing one to five litters per year, with one to four young per litter (mean about 2.5).

Forest Management

Fires, shrub removal, logging, and other human and natural disturbances generally reduce the suitability of woodrat habitat. Selective cutting of trees that opens the canopy and promotes growth of shrubby understory probably enhances habitat after several years, as do other logging techniques that promote successional stages with a complex mix of over- and understory trees and shrubs (Hooven 1959). The short-term effect, however, probably would be to reduce habitat suitability for woodrats. Although studies by Sakai and Noon (1992b) indicate that woodrats sometimes move from shrubfields into the edges of old-growth forests, it cannot be argued that logging to create openings would result in a net benefit for spotted owls in the conifer zone of the Sierra Nevada. First, available data from radio-tracking studies indicate that spotted owls seldom forage in shrubfields (Neal et al. 1989, Sisco 1990, Solis and Gutiérrez 1990, Zabel et al. 1992); and second, dusky-footed woodrats are generally uncommon as high as the mixed-conifer zone in the Sierra Nevada, where most logging currently occurs. Flying squirrels are the dietary staple of spotted owls in forests at these higher elevations, so logging there is more likely to have a negative effect on owl prey (via flying squirrels) than a positive one (via woodrats).

In forests below the Sierran mixed-conifer zone, small-scale logging operations might benefit spotted owls by enhancing woodrat populations. Although this needs further study, smaller sales might benefit spotted owls if done in areas adjacent to forested stands where the owls are known to forage. In such cases, woodrats that occasionally wander from their shrubby home ranges into the adjoining forest could become available as prey for spotted owls.

Woodrats do not survive fire well, especially very hot burns (Wirtz et al. 1988), and they are slow to recolonize burned areas (Longhurst 1978, Wirtz et al. 1988). Consequently, aggressive fuels management programs in chaparral country can benefit woodrat populations, especially in southern California where home ranges of owls in riparian/hardwood forests are closely surrounded by thick stands of chaparral (Chapter 5).

Northern Flying Squirrel

Distribution and Habitat

The northern flying squirrel is a medium-sized, nocturnal rodent that nests in trees in a great variety of forest communities over a broad, continental distribution. In California they occur in the North Coast, Klamath, southern Cascade, Sierra Nevada, and

Transverse Ranges. They are distributed throughout forested regions of the Sierra Nevada but apparently are more common in the mixed-conifer and red fir forests of the Pacific Slope than in the drier forests of the east slope. They are generally found above about 4,000 feet elevation in the Yosemite region and down to about 3,000 feet or lower in the northern Sierra Nevada, and in protected canyons and on north-facing slopes farther south. A single record from Chico is probably exceptional, but it suggests that flying squirrels may sometimes occur near the floor of the Central Valley in riparian/hardwood forests. Isolated populations also occur in the San Bernardino and San Jacinto mountains and probably in the San Gabriel Mountains of southern California.

Unfortunately, little published information is available on habitat associations or population levels of flying squirrels within the range of the California spotted owl. In the Sierra Nevada, common tree species associated with flying squirrels are black oak, white fir, and red fir. In the Lassen area, McKeever (1960) found flying squirrels in stands of ponderosa pine, lodgepole pine, and mixed stands of red and white fir. According to Waters and Zabel (1992), populations of flying squirrels have been located in second-growth stands of white fir at high elevation (about 6,300 feet) in the Lassen NF (color photo 5-1). These squirrels often travel and forage on the ground, so elements of the forest understory also are probably important in determining the suitability of their habitat.

In the San Bernardino Mountains, flying squirrels occur in mixed-conifer forests between about 5,200 and 7,500 feet in elevation (color photo 5-35). White fir and black oak are the principal tree species associated with these squirrels in the San Bemardinos (Grinnell 1908, 1933; Williams 1986). On a ridge south of Big Bear Lake, Summer (1927) caught 22 flying squirrels over the course of several months-all in white firs.

Stand size was an important attribute of suitable flying squirrel habitat in mature mixed-evergreen forests dominated by Douglas-fir on the Six Rivers NF. Northern flying squirrels were found in 60-80 percent of stands larger than 50 acres, on about 15 percent of stands of 25-50 acres, and on <10 percent of stands smaller than 15 acres (Rosenberg and Raphael 1986).

Sites with northern flying squirrels in isolated populations in the southern Appalachians varied markedly in plant community structure and composition (Payne et al. 1989). Occupied sites were commonly on north-facing slopes or in montane islands of conifer forests with cooler, mesic environments. Density of overstory trees varied from 364 to 1336 per acre; density of snags ranged from 11 to 138 per acre; and understory cover ranged from 35 to 86 percent. In a study of the southern flying squirrel in central Virginia, Sonenshine and Levy (1981) concluded that areas with few shrubs or vines as ground cover were unsuitable as habitat. An oak or oak-associated canopy with an understory of dense shrubs was optimal habitat. Presence of the squirrels was strongly correlated with shrub density. Although major differences exist in the distribution and habitats of northern and southern flying squirrels, the study by Sonenshine and Levy suggests that understory may be as important as tree canopy in determining habitat suitability.

Although Doyle (1990) captured similar numbers of flying squirrels in riparian and upland habitats, she concluded that riparian habitats were, nonetheless, superior to upland sites for flying squirrels. Waters and Zabel (1992) have found relatively high densities of flying squirrels in forest stands on the Lassen NF that are not near running water.

Patterns of Abundance

No published data are available on population densities, age structure, or reproduction in the Sierra Nevada or the mountains of southern California. A summary of most available literature indicated that "typical squirrel densities reported for mature and old-growth forests are 0.4 to 1.2 animals per acre" (Thomas et al. 1990, p. 205). Carey et al. (1992) found that flying squirrel density in southwestern Oregon was significantly greater in old-growth Douglas-fir stands (mean density = 0.8/acre) than in managed second-growth stands (mean = 0.4/acre). On the other hand, Rosenberg and Anthony (in press) failed to show significant differences between flying squirrel densities in old-growth (mean = 0.9/acre) and second-growth Douglas-fir stands (mean = 0.8/acre). Waters and Zabel (1992) found that average flying squirrel density was about 43 percent higher in late-seral red fir/white fir stands on the Lassen NF (range = 0.7-1.5/acre) than in red fir/white fir stands that were about 100 years old (range = 0.6-1.0/per acre). They have also found that flying squirrel density is strongly associated with the abundance of truffles-fruiting bodies of underground (hypogeous) fungi.

Diet

The diet of northern flying squirrels, at least as determined in California studies, consists primarily of truffles and arboreal lichens (McKeever 1960, Hall 1991, Waters and Zabel 1992), although they are known to eat a variety of other foods including seeds, nuts, insects, bird eggs and nestlings, and tree sap (Wells-Gosling and Heaney 1984). Maser et al. (1985) found that 90 percent or more of foods eaten in Oregon were fungi and lichens-hypogeous fungi accounted for more than 80 percent of the summer diet, and lichens comprised more than 50 percent of the diet year-round in northeastern Oregon. At Sagehen Creek, in the eastern Sierra Nevada, Hall (1991) found that spores of hypogeous fungi were the most common items found in feces and stomach samples year-round, but suspected that samples taken during deep snow cover indicated that the squirrels may store hypogeous fungi for consumption during winter months. Lichens and gill fungi were most prevalent during periods when snow covered the ground at Sagehen Creek. Hall considered arboreal lichens to be a very important winter food source for flying squirrels in areas with much snowfall (also see McKeever 1960). From studies of captive-reared animals, Laurance and Reynolds (1984) determined that winter diets consisting almost wholly of lichens may be more a matter of necessity than of preference for northern flying squirels. The captives selected pine seeds over lichens, moss, algae, and cones and branch tips from ponderosa pine.

Weights

Size varies significantly in a north-south cline along the Pacific Coast (Wells-Gosling and Heaney 1984), with the largest individuals in Alaska and British Columbia and the smallest in California. Weights of flying squirrels captured in Yosemite NP ranged from 3.62 to 5.76 ounces (Grinnell and Storer 1924). Juveniles captured in August and September in the Lassen NF averaged 2.89 ounces, and adults averaged 4.34 ounces (Waters and Zabel 1992). In a study by Witt (1991) in Douglas County, Oregon, the mean weight of adults captured between September 1983 and June 1984 was 4.7 ± 0.1 ounces (range = 3.7-6.5 ounces, n = 164). Generally the mean weight of adults was highest in January (mean = 5.0 ounces), dropping steadily to April, remaining stable from April through August (mean = 4.4 ounces), and increasing again through December.

Nests

Northern flying squirrels use several den sites; Carey (1991) found individuals in Oregon that used as many as seven. Two types of nests or dens are common-those located among branches of trees (for example, stick nests built by birds or other tree squirrels, clumps of dwarf mistletoe, and moss), and those located in natural cavities in trees and snags or abandoned woodpecker holes (Wells-Gosling and Heaney 1984). In Oregon, live conifers with cavity nests averaged 49 inches in d.b.h.; snags with cavity nests averaged 35 inches in d.b.h. (Carey 1991). Nests in such cavities are probably important in areas with cold winters (Cowan 1936, Weigl 1978), although Waters and Zabel (1992) have found populations of flying squirrels in high-elevation (about 6,300 feet) stands of second-growth white fir where few snags or cavities occurred. We do not know how commonly flying squirrels build their own nests.

Reproduction and Development

Litters commonly consist of two to four young, rarely one to six (Wells-Gosling and Heaney 1984). In Yosemite NP, females with two to four embryos were found in June (Grinnell and Storer 1924). Young are born between mid-June and mid-August in Oregon (Carey 1991). Weaning occurs at an age of about 60 days. Carey reported that young in an Oregon study were not weaned until mid-October to mid-November; they either dispersed in autumn or spent the winter in the nest with their mother. Young can walk and begin to leave the nest when about 40 days old. Most yearling females did not breed, and about 25 percent of the adult females did not breed in a given year. Although several authors have suggested that more than one litter is produced per year (Grinnell and Storer 1924, Witt 1991), a single litter is probably more common, at least throughout the Sierra Nevada (Waters and Zabel 1992). In the Sierra Nevada, two "half-grown" young were captured on 31 October, and a "quarter-grown" young was found on 16 September (Grinnell and Storer 1924, p. 214).

Forest Management

Habitat features that most strongly influence flying squirrel abundance include: sufficient trees to enable efficient locomotion; nest and den site substrates (cavity-bearing trees and snags), and truffle and arboreal lichen biomass. Although flying squirrels can glide at least 155 feet (Mowrey and Zasada 1984, J. R. Waters pers. observ.), forestry practices that create openings wider than about 120 feet probably have a negative effect on flying squirrel locomotion. Tree height is also important. Flying squirrels cannot glide as far from small trees as they can from tall ones.

As cavities provide important nest and den sites, efforts should be made to leave cavity-bearing trees and snags. In areas lacking potential nest sites, it may be possible to increase flying squirrel populations by adding nest boxes.

Truffles and arboreal lichens are the most important food types for flying squirrels throughout California and in the Pacific Northwest. Arboreal lichens are especially important as a winter food resource. Forest practices that reduce truffle and lichen biomass will probably negatively impact flying squirrel abundance. Ongoing research by Waters and Zabel (1992) indicates that truffle biomass is strongly associated with the presence of a well-developed soil organic layer and the volume of decaying logs (color photos 5-7, 5-18, and 5-34). Forest practices that negatively impact those parameters, such as broadcast burning and bulldozer piling after logging (Harvey et al. 1980), will reduce the capability of the forest to sustain flying squirrels. Data from Waters and Zabel (1992) also show that arboreal lichens (in the genera *Letharia* and *Bryoria)* commonly eaten by flying squirrels are much more abundant in older red fir/white fir forests than in younger forests.

Management of conifer forests in the Sierra Nevada for flying squirrels should emphasize retention of large snags and older trees, and nonintensive site-preparation techniques.

Pocket Gophers

Distribution and Habitat

Two species of pocket gophers occur within the main geographic range of the California spotted owl. Mountain pocket gophers range from the Mt. Shasta Region southward in the Sierra Nevada to at least the northern boundary of Tulare County (Hall 1981). They generally occur from above 6,900 feet in the Sierra NF (5,600 feet in the Stanislaus NF and Yosemite NP) to slightly above timberline (Grinnell and Storer 1924; D. F. Williams, pers. observ.). They are found throughout subalpine areas of both Sequoia and Kings Canyon NPs (Graber, pers. comm.), generally at elevations above 8,500 or 9,000 feet that are not frequented by spotted owls. They are most common in deeper, drier soils around meadow margins, but they occur everywhere

except on bare rock and within closed-canopied, mature and older forests with little or no herbaceous ground cover (Ingles 1952).

Southwestern pocket gophers occur in the western Sierra Nevada at elevations below the mountain pocket gopher, and in the lowlands, mountains, and deserts of western and southern California and northern Baja California. They probably range to timberline in the southern Sierra Nevada, from Tulare County southward. Distribution records of pocket gophers above 6,900 feet in the southern Sierra Nevada are unavailable, although one or the other species surely is found there (Hall 1981). Southwestern pocket gophers are most common on open ground with well-drained soils supporting grasses and forbs, but they can be found everywhere except on bare rock and in closed-canopied, mature and older forests.

Great Basin pocket gophers occur on the eastern slopes of the Sierra Nevada and on the Modoc Plateau. We do not discuss them in detail here because they probably occur mostly outside the breeding range of the California spotted owl, and because features of their population dynamics, habitat, and diet that are of importance to spotted owls probably do not differ from those of other pocket gophers. Generally, the ranges of these three species of pocket gophers do not overlap.

Patterns of Abundance

Mean density of mountain pocket gophers in favored meadow habitats was estimated at 10/acre in autumn over a 4-year period (Ingles 1952). The lowest estimates were in summer and autumn 1950 (4/acre), the highest in summer 1949 (19/acre). Biomass of mountain pocket gophers fluctuated from a low of 27.7 ounces/acre in spring 1948 to a high of 46.3 ounces/acre in summer 1949; this had dropped to an estimated 11.8 ounces/acre by the following summer.

In favored habitat at the San Joaquin Experimental Range (SJER), Madera County, the density of breeding adult southwestern pocket gophers averaged about 2.0/acre over five breeding seasons. Numbers of young produced by these adults averaged 2.3/acre over four breeding seasons (estimates from figures in Howard and Childs 1959, p. 340). Near Bass Lake, Madera County, in a Sierran mixed-conifer forest (about 4,500 feet), the density on a plot that included cutover forest and meadows was 4.6/acre, but Storer et al. (1944) believed this to be only half or less of the actual population.

General Life History Features

Pocket gophers are solitary and territorial, normally not ranging beyond the boundaries of their territories. They are most active early in the morning and late in the day, near sundown; at the highest elevations, most activities occur in late afternoon and evening. They are fossorial creatures, digging and living in underground tunnels, and creating many shallow, foraging tunnels about 5 inches below ground level. Their burrow entrances are plugged with dirt except when the gophers are pushing dirt from excavations to the surface, foraging on plants around the burrow entrance, or searching for mates. During excavation and while foraging on plants at the surface, they usually expose no more than the anterior half of their body at the burrow entrance.

Most burrowing activities occur during the cooler, wetter months in western California. At lower elevations, little or no burrowing occurs during the dry summer period, when gophers retreat to their few, deeper tunnels and plug the shallow ones. They may subsist mainly or entirely on cached food during this period. At higher elevations, when snow covers the ground, pocket gophers come to the surface and burrow through the snow to reach food plants, often packing these tunnels with dirt from underground excavations.

Burrow systems of neighbors typically are discrete. Any interconnections that may be accidently established apparently are kept plugged with dirt. Hearing may play a role in preventing encroachment by neighbors (Ingles 1952).

Soil, plant cover, and seasonal flooding are the principal factors determining habitat suitability and density of these pocket gophers. Areas with waterlogged soil and sites of seasonal flooding are unsuitable as permanent habitat. At SJER, at an elevation of about 1,000-2,000 feet in the western foothills of the Sierra Nevada, the strongest correlation with abundance of pocket gophers was soil depth (Howard and Childs 1959). Gophers were not found living in soils shallower that about 12 inches, and were most abundant in soils at least 24 inches deep. Areas with the deepest soils showed the highest above-ground productivity of herbaceous plants.

Mean weights of female pocket gophers were greater in sites with deep soils compared to sites with shallow soils, but differences were not statistically significant. Pocket gophers living in irrigated fields are significantly larger and heavier than their genetically identical neighbors in natural communities (Howard and Childs 1959, Patton and Brylski 1987). Areas supporting an abundance of grasses and forbs, especially species forming underground rhizomes, corms, tubers, bulbs, and other storage organs, provide the greatest habitat values for food. Areas with dense or complete canopy cover of woody shrubs and trees provide the poorest habitats for pocket gophers.

Diet

Pocket gophers eat a variety of plants, favoring herbaceous over woody material. Food not immediately consumed is cached in underground larders. Much of the information on diet comes from examination of these caches. Most species of grasses and forbs known to occur in a foothill oak-pine savanna at SJER were found in caches of southwestern pocket gophers. Seeds, tubers, bulbs, rhizomes, and acorns also were found in the caches (Howard and Childs 1959). Mountain pocket gophers near Huntington Lake, on the Sierra NF, also ate a wide variety of plants. During snowless months, caches of corms and roots of meadow bitterroot and golden brodiaea were found in caches. In winter, mountain pocket gophers cached mountain whitethorn leaves in snow tunnels, and the parts of willow stems covered with snow were frequently gnawed (Ingles 1952).

Weights

Microgeographic, seasonal, and annual variations occur in weights of adult pocket gophers. Season, sexual activity, and habitat quality have major influences on size and mass of adults (Howard and Childs 1959, Daly and Patton 1986, Patton and Brylski 1987). Mean weights of mountain pocket gophers in a Sierra Nevada meadow ranged from 2.2 (lowest summer average) to 3.1 ounces (highest spring average). Nonbreeding animals in autumn averaged from 2.2 to 3.0 ounces in different years (Ingles 1952). Weights of southwestern pocket gophers at SJER varied as follows (Howard and Childs 1959, fig. 11).

Females 8-10 months of age--mean = 2.2 ounces (range 1.8-2.6).

Females 20-22 months of age--mean = 2.6 ounces (range 2.2-3.1).

Males 8-10 months of age--mean = 3.2 ounces (range 2.3-8.8).

Males 20-22 months of age--mean = 4.3 ounces (range 3.9-4.7).

Mean weights of trapped animals were highest in spring and lowest in summer and autumn.

At Hastings Reservation, modal weights of trapped males were between 4.0 and 4.4 ounces, with a range of about 2.1 (juveniles) to 7.7 ounces (largest adults). Modal weights of trapped females were between 3.2 and 3.9 ounces, with a range from about 1.9 (juveniles) to 4.7 ounces (largest adults) (Daly and Patton 1986, fig. 3).

Reproduction and Development

Mountain pocket gophers begin breeding in May or June and young are born in June to August. Only one litter of three or four young per year is the norm. From about mid-July to early September, young disperse over the ground surface until a suitable site is found (Ingles 1952). Often burrow systems established by dispersers are in marginal or unsuitable habitats, such as shallow, sterile, granitic soils, or in small plots of higher ground surrounded by waterlogged soil. Some adults and young of the previous year apparently disperse in winter through snow tunnels. Dispersing adults are predominately males.

Based on studies by Howard and Childs (1959), southwestern pocket gophers at SJER commenced breeding in January, considerably earlier than is the case with the mountain pocket gopher. Most females were first pregnant the last 2 weeks of February; mean litter size there was 4.6. The young dispersed from March to May, although both young and adults occasionally moved over the ground at other periods of the year. Females born in January sometimes produced litters in April or early May of the same year. Most females produced only one litter per year, but a few had two. Between 50 and 75 percent of the females in January 1950-1954 were young of the previous breeding season (9-11 months old).

In a mixed-conifer forest at an elevation of about 4,500 feet, near Bass Lake, Madera County, scanty data suggest that young are born in early July and that some females may have two litters, similar to populations of this same species at lower elevations (Storer et al. 1944).

In a montane woodland community at Hastings Reservation, southwestern pocket gophers began breeding after onset of the winter rainy season, usually by January (Daly and Patton 1986). The breeding population was composed of animals at least 7-8 months old. Most females probably had only a single litter.

The breeding season of southwestern pocket gophers in the San Bernardino Mountains, at an elevation of about 7,500 feet near Bear Lake, is probably similar to that of mountain pocket gophers in the Sierra Nevada (Grinnell 1908).

Estimated survival of southwestern pocket gophers to 1 year of age ranged from about 5 to 40 percent for males and 15 to 50 percent for females between 1949 and 1953 (Howard and Childs 1959). Less is known about mountain pocket gophers, but 34 percent of the individuals in autumn populations in the Sierra NF were young of the year, and little turnover was detected in the spring breeding populations of 1949 and 1950 (Ingles 1952).

Forest Management

Generally, actions that tend to benefit pocket gophers would tend to lessen overall habitat suitability for spotted owls, so we would not recommend any active management to increase the amount of suitable habitat for gophers. Natural and man-made openings in the forest will undoubtedly occur with sufficient regularity to assure that these burrowing mammals will continue to be available as prey for California spotted owls.

White-Footed Mice

Distribution and Habitat

Five species of white-footed mice (genus *Peromyscus*) occur within the range of the California spotted owl. Indeed, white-footed mice are nearly ubiquitous in terrestrial habitats and often one or another species in this group is the most abundant small mammal. They exhibit considerable geographic variation in habitat associations, so results of studies on a given species in one locality should not be too broadly applied. Because of its marginal occurrence with the California spotted owl, we do not include the cactus mouse in this review.

Brush Mouse

Brush mice range throughout most of the area inhabited by California spotted owls, although they are absent from most of the inner coastal ranges (Diablo Range) of central California south of Suisun Bay and north of the Transverse Ranges in Kern and Santa Barbara Counties. They are relatively scarce above 3,500 feet in the northern portion of the western Sierra Nevada (Grinnell et al. 1930), but may occur higher in chaparral and other shrub associations on south-facing slopes (Jameson 1951). They occur up to about 5,100 feet at the level of the Sierra NF. On the Pacific slopes of the San Gabriel Mountains, brush mice

occur mainly between 1,600 and 6,000 feet, where they show decided preferences for rocky sites in oak woodlands, riparian/hardwood communities, and mixed-species chaparral (Vaughan 1954). Brush mice climb readily and are often seen or captured in trees. They are not known to hibernate or to enter torpor.

Brush mice may construct nests in hollows in trees or in ground burrows. They are closely associated with oaks and rocky sites. At Pinnacles National Monument in the Gabilan Range, Monterey County, brush mice comprised only 5 percent of the white-footed mice captured in a complex mix of woodland, chaparral, and grassland communities. They were significantly associated with poison oak and medium-sized rocks (10-50 inches), and they showed a significant negative association with grass (Fellers and Arnold 1988). Elsewhere they are typically the most common white-footed mouse where rocks and oaks occur together in oak woodlands and forest communities below the mixed-conifer zone. In the central Sierra Nevada (Yosemite NP), oaks and proximity to water were commonly associated with brush mice (Grinnell and Storer 1924). Other researchers have not verified a dependence on surface water; possibly exposed rocks in canyon bottoms and shrubby growth along streams provide suitable habitat in otherwise inhospitable surroundings. At SJER, an area with no permanent streams, brush mice were the most common species of white-footed mouse, preferring rocky areas sheltered by oaks (Quast 1954). They were also the most common species in the La Panza Range of San Luis Obispo County, with nearly equal abundance in blue oak woodland, mixed chaparral (chamise, ceanothus, and scrub live oak), and the ecotone between these communities along canyon bottoms (Murray 1957).

California Mouse

California mice occupy chaparral and woodland communities in western California and northern Baja California, south of San Francisco Bay on the Coast, and from Mariposa County southward in the Sierra Nevada foothills. Their elevational distribution in the Sierra Nevada is generally from the lower half of the ponderosa pine forest downslope to the mid-elevation, oak-pine woodlands and chaparral. Elevational limits in the mountains of southern California are generally below about 4,900 feet, with an exceptional record at 7,900 feet in the San Jacinto Mountains (Grinnell 1933). California mice climb readily and are frequently captured in traps set in shrubs and trees (Meserve 1976a, 1977). They may become torpid on a diurnal cycle when deprived of food (Hudson 1967).

California mice have more specialized habitat requirements than brush and pinyon mice, preferring broadleaved woodlands and mixed chaparral and being more limited in their elevational and latitudinal distributions. Within their geographic range, they are closely associated with the distribution of both dusky-footed woodrats and California-laurel (bay), although both associates occur much farther north than California mice (Merritt 1974). Plant communities inhabited include valley foothill hardwood and oak-pine woodlands, various chaparral associations, and riparian deciduous. Within preferred habitat, California mice are often the most abundant small mammal species. At Pinnacles National Monument, California mice accounted for 10 percent of all captures of white-footed mice. They were absent from areas of extensive grass and large patches of chamise chaparral. Variables most strongly associated with the presence of this species were hollyleaf cherry, medium-sized rocks, and Chinese nests (a wildflower) (Fellers and Arnold 1988). They are among the commonest rodent species in mixed-chaparral communities in the San Gabriel Mountains below about 4,900 feet (Vaughan 1954, Wirtz et al. 1988). In coastal sage communities, they are generally limited to thickets of large shrubs and small trees in riparian/hardwood stands (Vaughan 1954). M'Closkey (1972) captured only six residents in coastal sage scrub and their mean duration on plots was less than half that of cactus and deer mice. He believed their occurrence on the study plot was due to previous flooding of their preferred habitat along washes where trees and large shrubs were found.

California mice often nest in abandoned or occupied stick nests of dusky-footed woodrats. They also may nest in hollows in trees, snags, or logs, and they construct stick nests of their own, often under fallen logs and smaller downed woody material (Merritt 1978). They apparently do not burrow readily; many researchers have proposed that their distribution and abundance are limited by availability of suitable nesting sites (Merritt 1974, 1978).

Deer Mouse

Deer mice occur throughout the range of the California spotted owl, and in most plant communities, from marshes and grasslands at or below sea level, through woodlands and forests, to above timberline in the mountains. Within this broad area, however, they are generally common only in riparian/hardwood and grassland communities at lower elevations, and riparian, forest, and meadow communities from the mid-elevation mixed-conifer zone upslope through lodgepole and subalpine pine forests. Deer mice probably are the most terrestrial of the white-footed mice considered here (King 1968; Meserve 1976a, 1977). Meserve (1977) seldom found them in shrubs or trees in a southern California community of coastal sage, even though they can climb readily and are taken in traps set in brush and trees. Torpor under natural conditions is unknown for deer mice.

Deer mice typically nest in ground burrows, hollow logs, or talus. Nests are less frequently located in hollows of trees and snags. They are generally much less common than brush and pinyon mice in ponderosa pine, oak-pine woodlands, foothill and montane hardwood forests, and chaparral on the western slopes of the Sierra Nevada (for example, tables l0A and l0C; Quast 1954), in the coast ranges, and in mountains of southern California. Within these communities, they are most often found in riparian deciduous associations, wet and dry meadows, and grass/forb seral stages. In the northern Sierra Nevada, deer mice were significantly more abundant in forested than in shrub stages of mixed-conifer forest (Jameson 1951). In coastal woodland and chaparral communities, deer mice are uncommon and usually associated closely with riparian/hardwood communities or large openings dominated by annual grasses and forbs. At Pinnacles National Monument, deer mice comprised 20 percent of the white-footed mice captured in a complex of grassland, oak, pine, and chaparral communities. Most captures were on burned

Table 10C-*Captures of small rodents that may be prey of California spotted owls, by successional stage (after Verner and Boss 1980)1 in forest communities of the western Sierra Nevada, Sierra NF (D. F. Williams pers. observ.). Total adjusted sampling effort was 18,200 trap days (one trap day = one pitfall trap set for 24 hours). Trapping was simultaneous in all forests and successional stages. Values are actual captures, except "catch rate," which is the number captured per trap day. Captures were standardized to represent equal sampling effort in the various habitat types. (Most habitat types/stages were sampled on two transects of 10 traps each, set for 7 days in 1980 and 28 days in 1982. LTB in ponderosa pine, GF in mixed-conifer, and LTC in red fir forests were sampled only on single transects, so numbers of actual captures there were doubled.)*

Forest community and mammal species	Habitat type/stage									Total	Catch rate
	GF	SSS	PMA	PMB	PMC	LTA	LTB	LTC	RH		
Ponderosa pine											
Southwestern pocket gopher	1	1	2	0	0	2	0	--	1	7	0.0013
Deer mouse	12	0	0	0	1	1	2	--	1	11	0.0020
Brush mouse	3	2	3	0	0	1	8	--	10	27	0.0048
Pinyon mouse	0	6	4	6	13	13	0	--	0	42	0.0075
California vole	2	0	0	0	1	0	0	--	1	4	0.0007
Total	**18**	**9**	**9**	**6**	**15**	**17**	**10**	**--**	**13**	**91**	**0.0188**
Mixed-conifer											
Southwestern pocket gopher	0	0	1	1	0	0	0	0	0	2	0.0003
Deer mouse	2	21	14	3	6	7	12	11	29	105	0.0167
Brush mouse	0	0	0	0	1	0	0	1	2	4	0.0006
Pinyon mouse	0	0	1	2	0	0	0	0	0	3	0.0005
Long-tailed vole	0	12	4	1	0	0	1	0	7	25	0.0040
Total	**2**	**33**	**20**	**7**	**7**	**7**	**13**	**12**	**38**	**138**	**0.0221**
Red Fir											
Mountain pocket gopher	6	1	1	0	0	0	0	2	4	15	0.0024
Deer mouse	40	30	9	15	12	14	15	10	42	187	0.0300
Long-tailed vole	5	6	0	5	1	1	5	0	40	63	0.0100
Total	**51**	**37**	**10**	**20**	**13**	**15**	**20**	**12**	**86**	**265**	**0.0424**

[1] GF = grass/forb; SSS = shrub/seedling/sapling; PMA = pole-medium tree with <40 percent canopy cover; PMB = pole-medium tree with 40-69 percent canopy cover; PMC = pole-medium tree with >69 percent canopy cover; LTA = large tree with <40 percent canopy cover; LTB = large tree with 40-69 percent canopy cover; LTC = large tree with >69 percent canopy cover; RH = riparian/hardwood community in corresponding forest zone.

areas and in a grassy field. Variables positively associated with their occurrence were chamise and bird's foot trefoil (together), and yerba-santa. Percent cover of oak leaf litter was negatively associated with deer mice (Fellers and Arnold 1988).

In the San Bernardino Mountains, brush mice outnumbered deer mice on mixed-conifer plots at elevations between 5,800 and 7,000 feet, but deer mice were more abundant on mixed-conifer plots at 7,600 feet (Kolb and White 1974). Grinnell (1908) found deer mice common only in big sagebrush on the desert slopes and high ridges, and in montane forests above 6,900 feet. Deer mice were not captured by Spevak (1983) at four sites in the Santa Monica Mountains, Los Angeles County, in chaparral, riparian, and coastal sage associations. Yet Price and Kramer (1984) caught small numbers in a variety of microhabitats in a coastal sage community in Riverside County. M'Closkey (1972) also captured deer mice in a coastal sage community in Orange County and noted that they were the most general in habitat preference, being found along the moisture gradient from grasslands to woodlands. In mixed montane-chaparral communities of the Pacific slopes of the San Gabriel Mountains, deer mice were absent from chaparral that had not been burned for several years but were present on all burned plots, with peak numbers occurring 2 years after burns (Wirtz et al. 1988).

Pinyon Mouse

Pinyon mice also occur throughout the area inhabited by California spotted owls, but generally range below the mixed-conifer forests on the western slopes of the Sierra Nevada. They are associated with oak-pine woodlands and chaparral communities, usually with one or more species of conifers such as juniper, pinyon pine, or digger pine. They are less common in ponderosa pine habitats, where they most often occur on hotter, drier slopes in association with chaparral or in more mature stages of forest. In southern California they are generally uncommon or only locally distributed on the Pacific slopes of the mountains. Vaughan (1954) found none on the Pacific side of the San Gabriel Mountains. In the San Bernardino Mountains, Grinnell (1908) captured them only at two localities on the Pacific side. One was a south-facing slope at 6,500 feet vegetated with Coulter pine, chamise, deer brush, curlleaf mountain mahogany, and California scrub oak-plants typical of the upper-elevation chaparral of the Pacific side, and pinyon pine and western serviceberry-plants more typical of the desert side. The other was a south-facing slope where pinyon mice were taken between 5,100 and 5,500 feet among a mix of plants of upper-elevation chaparral and lower-elevation forest (ponderosa pine, white fir, and black and canyon live oaks). Chaparral plants

predominated. Pinyon mice readily climb and are frequently taken in traps set in shrubs and pygmy conifers (for example, juniper, pinyon pine, digger pine, Coulter pine).

Pinyon mice nest in ground burrows or hollows in trees. They apparently do not become torpid. In the central coastal chaparral, woodland, and forest communities, they are common wherever shrub or tree cover is found, especially with one or more species of pygmy conifers or dense stands of chamise or ceanothus chaparral (or a mix of these and other shrubs). Pinyon mice were the most abundant small mammal trapped in chamise chaparral at Hastings Reservation (Bradford 1976). At Pinnacles National Monument, pinyon mice accounted for about 66 percent of the white-footed mice captured in a variety of oak, pine, grass, and chaparral associations. They were found in all community types but grassland. Large rocks and various shrub species were significantly associated with occurrence of pinyon mice. Grasses and forbs indicated the poorest habitats (Fellers and Arnold 1988). In the Sierra Nevada, they are mostly limited to areas with dense brush or tree cover below about 4,600 feet, and are usually abundant only where oaks do not dominate. At SJER, pinyon mice were commonly associated with moderate to dense stands of brush, particularly buckbrush, and rocks. Likewise, in the southern Sierra Nevada (Kern County), pinyon mice preferred stands of buckbrush and rock outcrops (Lawrence 1966). In the La Panza Range of San Luis Obispo County, they were more than four times as common in a chaparral community of chamise, buckbrush, and coast live oaks as they were in a blue oak/digger pine woodland (Murray 1957). None was taken in chaparral communities in over a decade of studies on the San Dimas Experimental Forest, on the Pacific slope of the San Gabriel Mountains (Wirtz et al. 1988).

Patterns of Abundance

Results of trapping suggest some differences in habitat affinities of white-footed mice in the western Sierra Nevada (tables l0A and lOC). Deer mice were captured in most habitat types and seral stages, exhibiting apparent specialization at low elevations (where brush and pinyon mice co-occur) in sites dominated by grasses and forbs. Their habitat associations increase markedly with increasing elevation to the point that they are ubiquitous in the red fir zone, where no other species of white-footed mice occur. Pinyon mice were generally confined to sites with shrubs, mixtures of shrubs and small trees, or shrubs and widely scattered trees in all habitats sampled except the oak/digger pine type, yet other studies (Quast 1954, Block et al. 1988) found them to be common in this woodland type, where they were associated with shrubs. Brush mice were relatively uncommon in most habitats, except those at lower elevations that had large trees in the canopy. California mice were essentially missing from the sample, although study sites were either too far north for this species or generally in habitat types where we would not expect to find them.

Any interpretation of habitat use reported in tables 10A and 10C should note differences in elevation and forest composition. Sierran mixed-conifer sites reported in table 10A, for example, were mostly on north-facing slopes of canyons 2,000-3,900 feet in elevation, where Douglas-fir occurred with ponderosa pine, sugar pine, incense-cedar, or black oak. Studies reported in table IOC were farther south, at elevations of 5,200-6,500 feet. Douglas-fir was rare there, and most sites had white fir mixed with the other species listed above.

Densities of white-footed mice within the range of the California spotted owl generally fluctuate between lows in December and January to highs in July and August. At higher elevations in mixed-conifer and fir forests, annual peaks in densities may be delayed into August or September. Densities of different species vary from <1 to >30 mice/acre. Various density estimates have been reported in the literature; these are summarized below (animals/acre), but readers should be mindful of the problems with estimating densities of small mammals and the variety of methods used.

Brush mice-1.0-15.3 (Zeiner et al. 1990); 3.0-15.2 (Sierran mixed-conifer, Bass Lake area, Storer et al. 1944); 1.3 (Lake Tahoe area, Storer et al. 1944).

California mice-31.2 (xeric chaparral, central California, Merritt 1974); 37.2 (mesic oak-laurel forest, central California, Merritt 1974); 0.1-0.8 and <0.8 (southern California coastal-sage scrub, MacMillen 1964 and M'Closkey 1972, respectively).

Deer mice-4.0-10.0 (White et al. 1980); 4.9-14.2 (mixed-conifer forest,Sierra Nevada, Bass Lake area, Storer et al. 1944); 19.1 (Lake Tahoe area, Storer et al. 1944), <0.4-1.6 (southern California coastal sage, M'Closkey 1972).

Pinyon mice-1.0 (oak-laurel forest, central California, Merritt 1974); 34.8 (xeric chaparral, Merritt 1974).

General Life History Features

White-footed mice are nocturnal and active throughout the year. Some species become torpid under food or water deprivation, but others do not. They nest in ground burrows, talus, hollow logs, and in hollows in trees. They readily climb in brush and trees (scansorial). Arboreal tendencies differ among species, however, with brush and California mice being the most scansorial of the species occurring in California, and deer mice the least. White-footed mice are not highly territorial except near their nest, but territoriality differs among species. The California mouse is the most territorial species, living in male-female pairs with nearly nonoverlapping home ranges (Ribble and Salvioni 1990).

Diet

White-footed mice are omnivorous, feeding on seeds, fruits, fungi, flowers, foliage, insects and other arthropods, carrion, and other animal matter (Zeiner et al. 1990). Specific studies suggest that the four species considered here are largely opportunistic in choice of diet, although differences are seen where species' ranges overlap (for example, Jameson 1952; Meserve 1976a, 1976b). Insects (especially larvae and pupae), seeds, fruits, and fungi probably comprise the bulk of their diets. California mice

eat large quantities of California-laurel seeds, the thick, hard coats of which cannot be cracked by pinyon mice (Merritt 1974). In a coastal sage community, California mice ate mostly shrub fruits, seeds, and flowers and smaller quantities of grass seeds (Meserve 1976a).

Reproduction and Development

Reproduction varies geographically, altitudinally, and annually. Females appear to be seasonally polyestrous, with most births occurring between March and October, but some females may be pregnant in any month. The most prolonged reproductive seasons are found in populations at or near sea level and on the lower slopes of coastal ranges. The shortest reproductive seasons occur at the highest elevations in montane communities.

The breeding season of brush mice peaks in April and May; a secondary peak in June to August seems to depend upon the previous crop of acorns. Litters average three to four young; females probably average near two litters per year, although they can have four. Females born in spring can breed in the summer of their first year.

Although California mice may breed year-round in coastal areas, most breed between March and September. Litter size averages two to three (MacMillen 1964, Merritt 1978), with up to three to four litters per year. Females born early in the year breed late in the reproductive season of the same year, although California mice mature more slowly than the other white-footed mice considered here.

Deer mice may breed year-round, depending upon climate, but most reproduce between March and October. Litters are l arger at higher elevations and latitudes, but probably average four to six for populations within the range of the California spotted owl. Numbers of embryos for 46 females from the Sierra NF, most captured between mid-June and mid-August in mixed-conifer and red fir forests, averaged 5.2 ± 1.43 (range = 2-9). Mean litter size for 11 females in a southern California coastal-sage community was 4.3 ± 1.3 (MacMillen 1964). Females may have two to four litters during the breeding season-fewer at higher elevations and latitudes. Young born in spring breed later in the same summer or autumn.

Pinyon mice breed mainly from May to September, averaging two to three young per litter. Females may breed when 3 months old.

Little information is available on dispersal by these species within the geographic range of the California spotted owl. Dispersal probably commences soon after weaning, but individuals may leave their natal homes over a protracted period, depending upon circumstances such as survival of the mother, population density, and food abundance. Time to weaning varies geographically and by species. For brush and deer mice, weaning probably averages about 25 days (range of reported values, 22-37 days, summarized by Zeiner et al. 1990). California mice are weaned in an average of 35 days, although some litters may not be weaned until 44 days (McCabe and Blanchard 1950, Merritt 1974). Clark (1938) reported 50 days as the period before weaning in pinyon mice, although other studies found considerably shorter periods-about 25 (McCabe and Blanchard 1950) or 30 days (Douglas 1969).

Weights

The deer mouse is the smallest of the four species considered here. Adults (excluding pregnant females) weigh about 0.53-0.91 ounces (Layne 1968); the mean for a Sierra Nevada sample was 0.70 ± 0.01 ounces, *n* = 144. Grinnell and Storer (1924) listed a range of 0.45-0.74 ounces for deer mice caught in the central Sierra Nevada.

Adult brush mice ranged in weight from about 0.77 to 1.19 ounces in the Yosemite region (Grinnell and Storer 1924). The mean of a mixed-age sample of brush mice in the Sierra NF varied from about 0.74 to 0.95 ounces (table 1013).

Breeding adult pinyon mice from central coastal California averaged 1.19 ± 0.11 ounces (Merritt 1974). The range of weights in the Yosemite region was 0.82-1.44 ounces (Grinnell and Storer 1924). Samples of breeding adults from the Sierra NF averaged about 0.98-1.09 ounces.

California mice are the largest of the white-footed mice in California. Most reported adult weights range from about 1.33-1.75 ounces (Grinnell and Storer 1924, Layne 1968, Jameson and Peters 1988). Merritt (1974) reported mean weights of breeding adults as 2.0 ± 0.28 ounces in central coastal California. A population mean for all ages and sexes captured year-round in a coastal-sage community in southern California was 1.20 ounces (MacMillen 1964).

Table l0D-*Variation in weights (in ounces, mean ± SD, with range and sample size below) of three species of white footed mice during summer (June-August, Sierra National Forest, Fresno County) and winter (January, San Joaquin Experimental Range) (D. F. Williams pers. observ.).*

Season	Sample	Brush mouse	Deer mouse	Pinyon mouse
Summer	Adults	0.99 ± 0.11	0.74 ± 0.13	1.00 ± 0.07
		(0.74 - 1.33)	(0.46 - 1.12)	(0.77 - 1.30)
		n = 39	*n* = 208	*n* = 31
	Young	0.51 ± 0.08	0.43 ± 0.09	0.54 ± 0.12
		(0.41 - 0.63)	(0.21 - 0.56)	(0.39 - 0.77)
		n = 5	*n* = 113	*n* = 12
	Pooled	0.93 ± 0.18	0.63 ± 0.19	0.87 ± 0.24
		(0.42 - 1.33)	(0.21 - 1.12)	(0.39 - 1.30)
		n = 44	*n* = 321	*n* = 43
Winter	Adults	0.78 ± 0.07	0.54 ± 0.07	0.90 ± 0.13
		(0.67 - 0.95)	(0.39 - 0.70)	(0.70 - 1.09)
		n = 31	*n* = 14	*n* = 9
	Young	0.61 ± 0.03	0.49 ± 0.07	0.57 ± 0.08
		(0.56 - 0.67)	(0.35 - 0.60)	(0.49 - 0.67)
		n = 12	*n* = 13	*n* = 5
	Pooled	0.73 ± 0.10	0.51 ± 0.08	0.78 ± 0.20
		(0.56 - 0.95)	(0.35 - 0.70)	(0.45 - 1.09)
		n = 43	*n* = 27	*n* = 14

Management

Clearcutting or similar tree harvest and brush thinning or removal generally result in increased numbers of deer mice. Wildfires and controlled burns that reduce shrubs and small trees and increase cover of grasses and forbs also enhance populations of deer mice in woodland, forest, and chaparral communities (Jameson 1951, Quast 1954, Lawrence 1966, Spevak 1983, Fellers and Arnold 1988, Wirtz et al. 1988) (also see table 10C). On the other hand, numbers of other species of white-footed mice in lower-elevation mixed-conifer, ponderosa pine, oak-pine woodland, and various hardwood and chaparral communities would be reduced or eliminated by clearcutting, brush removal, or fire. Management that promotes increased abundance of oaks would increase numbers of brush mice. In the San Gabriel Mountains, in mixed-chaparral communities on the San Dimas Experimental Forest, brush mice were rare on plots in chaparral that had not been burned for 28 years, but increased in abundance after burns. Brush mice increased to six times their preburn density on areas with normal burns and 14 times on areas with hot burns. Brush mice recolonized burned areas sooner than California mice (Wirtz et al. 1988). In coastal northern California (Hopland Field Station, Univ. of California), both brush and pinyon mice were adversely affected by converting chaparral to grassland, but positively affected by converting old, decadent chaparral to young- and intermediate-aged stands (Longhurst 1978). California mice were the only common *Peromyscus* in the mature montane chaparral at San Dimas Experimental Forest. They were the slowest of the white-footed mice to recolonize mixed montane-chaparral communities in the San Gabriel Mountains after burns. Captures after bums were greater on normal burns than hot burns, and postfire densities were generally greater than preburn densities (Wirtz et al. 1988). Management that promotes increased cover and vertical complexity of chaparral and woodlands, increased abundance of California-laurel and dusky-footed woodrats, and increased numbers of potential nests would enhance populations of California mice.

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Chapter 11

Historical Perspectives on Forests of the Sierra Nevada and the Transverse Ranges of Southern California: Forest Conditions at the Turn of the Century

Kevin S. McKelvey and James D. Johnston

Preface

Let me say a word of thanks to the members of the forestry force who acted as my escort. I wish to thank other gentlemen also, but particularly the members of the forestry force. l am, as you gentlemen probably know, exceedingly interested in the question of forest preservation. I think our people are growing more and more to understand that in reference to the forests and the wild creatures of the wilderness our aim should be not to destroy them simply for the selfish pleasure of one generation, but to keep them for our children and our children's children. 1 wish you, the Forest Rangers and also all the others, to protect the game and wild creatures and of course in California, where the water supply is a matter of such vital moment, the preservation of the forests for the merely utilitarian side is of the utmost, of the highest possible consequence; and there are no members of our body politic who are doing better work than those who are engaged in the preservation of the forests, keeping nature as it is for the sake of its use and of its beauty.

Theodore Roosevelt, 9 May 1903.

The Sierra Nevada has been impacted by western civilization for more than 150 years and heavily impacted for at least the past 100 years. Impacts include mining, logging, the grazing by both sheep and cattle, and changes in fire patterns-notably fire suppression in the twentieth century. Site-specific data from the 1800s are scattered and not comprehensive, but several events occurred around the turn of the century that led to reasonably detailed and quantitative accounts of the condition of the land and forests. General Grant, Sequoia, and Yosemite National Parks (NPs) were established in 1890. Forest reserves were set aside between 1891 and 1909 and renamed as National Forests (NFs) in 1907. After creation of the forest reserve system, the United States Geologic Survey (USGS) initiated the first systematic surveys of the forest reserves as part of a series of annual reports. For a brief period, from about 1897 to 1902, these surveys were very thorough and often included maps of topography, timber volume, logging intensity, and species distribution. Surveys covering most of what is now the Eldorado and Stanislaus NFs and Yosemite NP were published in 1900 (Fitch 1900a, 1900b; Marshall 1900; Sudworth 1900a). Similar inventories were done by Leiberg (1902), mainly in what is now the Tahoe and Plumas NFs. Additional information concerning what are now the Sierra and Sequoia NFs and Sequoia/Kings Canyon NPs was obtained by analyzing Sudworth's (1900b) unpublished field notes.

Areas in southern California were also surveyed around the turn of the century. Leiberg (1899a, 1899b, 1899c) examined the San Jacinto, San Bernardino, and San Gabriel reserves in 1897. The San Jacinto Quadrangle was reexamined in 1900 and Barnard (1900) produced a 30-minute topographic map (fig. 11A).

This chapter is largely an analysis of these USGS survey efforts, with ancillary data from other sources. The men involved with the surveys were professionals whose job it was to assess the condition of the newly created reserves. Their studies appear to be reliable and accurate, providing quantitative assessments of forest stands that are of great historic interest and importance today.

Sierran Forests at the Turn of the Century

Nonaboriginal Human Impacts

Logging in the Middle and Southern Sierra Nevada

Logging was used mainly to support local markets, including the growing towns and communities of the Sacramento and San Joaquin Valleys (Ayers 1958). All major towns were associated with mines, and nearly all timber cut supported the mines-for housing employees, timbers to keep tunnels from collapsing, processing ore, and transporting processed ore to market by rail (Sudworth 1900a). "Large mines" consumed between 2,000 and 3,500 cords annually (fig. 11B). Fuel needs of stamp mills-machines or mills for pulverizing ore-were impressive. The Empire Mine, for instance, had a 30-stamp mill that consumed 11 cords of wood in a 10-hour period (Bohakel 1968) or, assuming constant operation, 9,600 cords a year.

Most logging before 1900 occurred at low elevations on lands adjacent to mines, because wagons were the chief means for transporting timber (Sudworth 1900a, Leiberg 1902) (fig. 11C). Sudworth mapped cut-over and partially cut regions (fig. 11D, table 11A). With the exception of a large area of cutting that extended up the American River, Forest Service (FS) lands and many higher-elevation private lands had not been logged (fig. 11E). Laudenslayer and Darr (1990) provided an analysis of cutting during that period by the Michigan-California Timber Company.

The partially cut lands, especially those more distant from Placerville, were largely exploited for the shake market (Sudworth

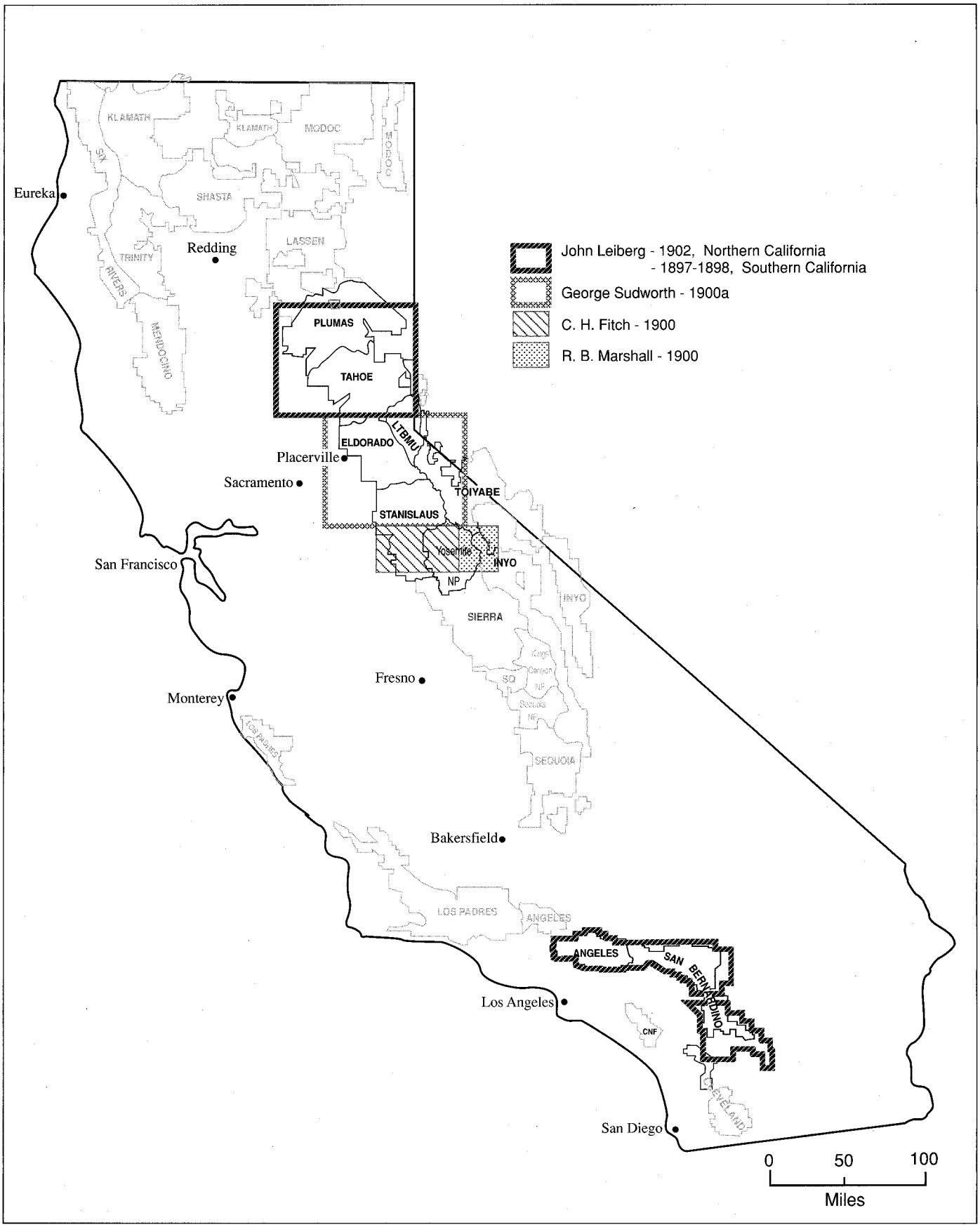

Figure 11A--Areas surveyed by Leiberg (1899a, 1899b, 1899c, 1902), Marshall (1900), Fitch (1900a, 1900b), and Sudworth (1900a).

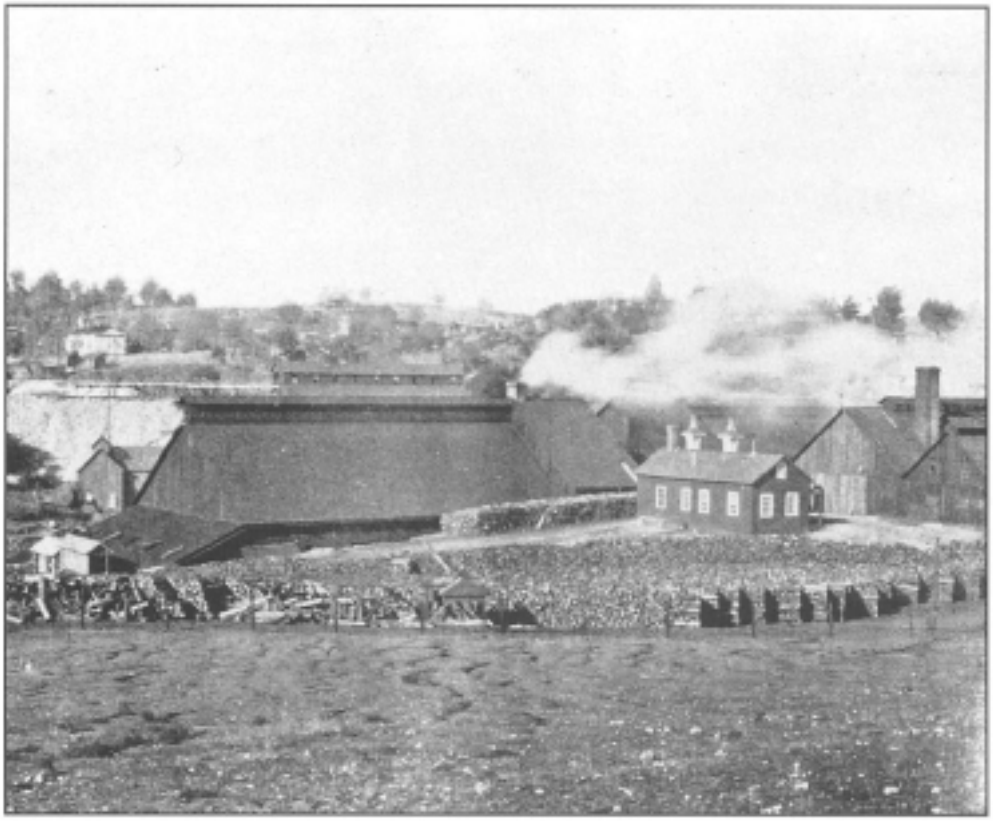

Figure 11B-Large mining plant at Angels Camp, where great quantities of yellow pine cord wood were consumed. Thousands of cords of this 4-foot cordwood were needed to keep each mill going throughout the year. Hundreds of mills operated up and down the Sierra Nevada during this era, processing ore for gold and other minerals. Wood also was the primary fuel for heating and cooking in homes and businesses, as well as providing energy to run the steam engines, which powered winches, sawmills, and locomotives.

Location: -------In foothills just below the Stanislaus National Forest, central Sierra Nevada.
Elevation:-------About 2,000 feet
Date: ----------Probably 1899
Source:---------Sudworth 1990a
Photographer: -----Unknown

Figure 11C--A common method of hauling yellow pine logs to mills was by horse and wagon. Before railroads entered the area, transportation of raw logs and lumber had definite limitations. Mills, which remained close to the timber source, tended to be smaller and more mobile. When the local timber was used up, the mill was disassembled and moved to another area.

Location:-------Stanislaus National Forest, central Sierra Nevada
Elevation: ----About 4,000 feet
Date: ----------Probably 1899
Source: -------Sudworth 1990a
Photographer: ----Unknown

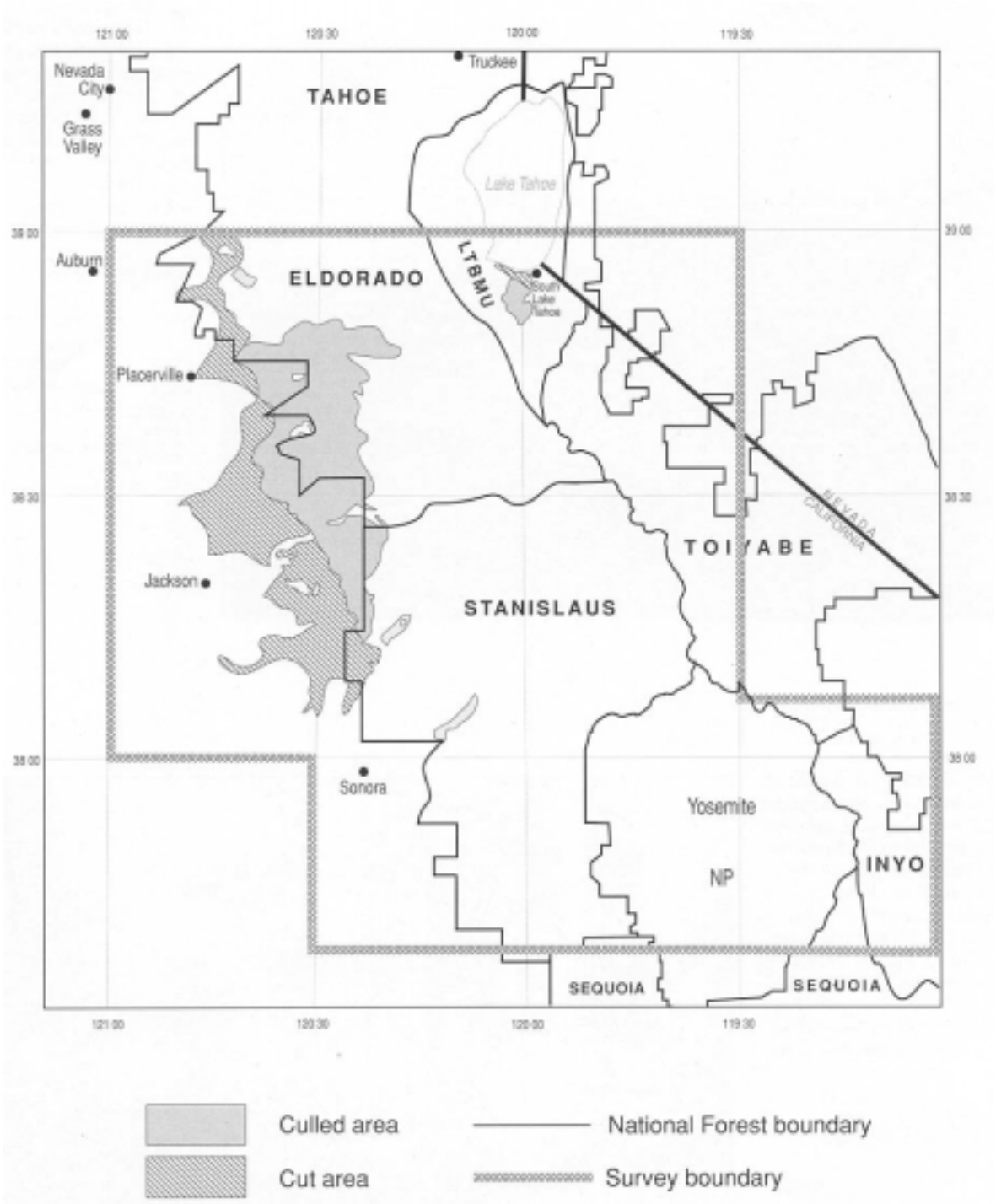

Figure 11D--Areas of logging activity from maps by Marshall (1900), Fitch (1900a), and Sudworth (1900a). Culled areas were selectively logged. Most of the cutting in this area was associated with the town of Placerville.

Table 11A--*Areas sampled by Sudworth in the Sierra Nevada at the turn of this century (Sudworth 1900a) (see figs. 11A and 11D).*

Areas	Area (square miles)		
	Logged	Culled[1]	Virgin[2]
Thirty-minute quadrangles			
Placerville	122	162	152
Jackson	175	18	0
Pyramid Peak	0	148	642
Big Trees	89	104	564
Markleeville	0	0	322
Dardanelles	0	0	659
Forest Reserves			
Stanislaus	0	0	641
Tahoe	0	3	130
Total	**386**	**435**	**3,190**
Percent of total	**10**	**Il**	**79**

[1] Culled areas were selectively logged.
[2] Lands listed as grazing or nonforest were omitted.

1900a). Shakes were the most valuable product at the time, maintaining a market value well above dimension lumber into the twentieth century. On the Stanislaus NF in 1912, for instance, shake prices were $5.00 to $7.50 per thousand (Graves 1912), approximately the same price reported by Sudworth.. Shakes were produced only from the choicest sugar pines, and only from select portions of the bole-no more than 40 percent, according to Sudworth. For this reason, shake cutting always resulted in partial removal of standing timber, and it always left much waste. Following a similar pattern, giant sequoias were split to produce grape-stakes (fig. 11F).

Logging in the Northern Sierra Nevada

Ore deposits extended into higher elevations in the northern Sierra Nevada than in the middle and southern parts. Consequently, placer and hard-rock mining and logging were more extensive there than to the south. In particular, areas north of Nevada City and the Truckee Basin were heavily cut (fig. 11G). Again, access was key and the presence of the Southern Pacific Railroad allowed transportation to more distant markets. Lake

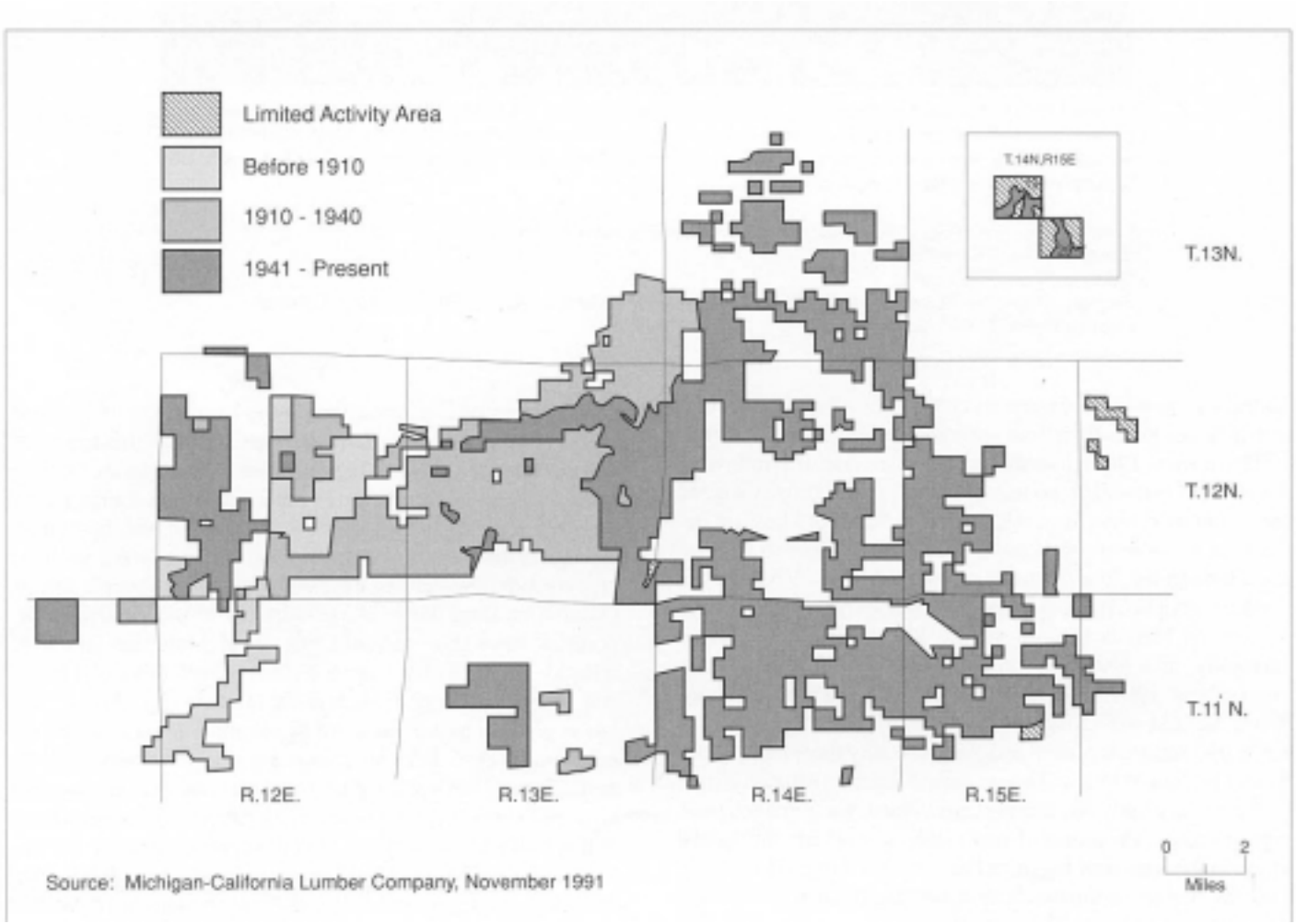

Figure 11E--Chronology of cutting on lands of the Michigan-California Timber Company. These lands lie within the area surveyed by Sudworth in 1900. Cutting prior to 1910 occurred within a very limited acreage.

Figure 11F--This ancient giant sequoia, named the Mark Twain Tree in 1888, sprouted in 550 A.D.; it was 1,341 years old and 90 feet around the base at the time of this photo. Smith Comstock erected a sawmill just 250 yards west of this tree. Giant sequoia wood made poor lumber, so it was split into grapestakes (center) and posts (left) to supply California's rapidly expanding vineyards.

Location: ----------Big Stump, Sequoia/Kings Canyon National Parks
Elevation: ----------5,760 feet
Date: ----------1891
Source: ----------Steve Anderson Collection, Hume Lake Ranger District, Sequoia National Forest
Photographer: -------C. C. Curtis

Tahoe also provided convenient access, allowing large quantities of timber to be taken from areas adjacent to the lake (Leiberg 1902, McKeon 1984). In addition, a 4-mile-wide strip following the railroad between Reno and Sacramento was heavily logged for locomotive fuel (fig. 11G; Palmer 1992). Gold-bearing deposits at mid-elevations (Clark 1966) caused mines to be scattered throughout forests of the region. The Yuba River Basin, north of Nevada City, was logged to supply large mines at Grass Valley and Nevada City (elevations 2,400 and 2,600 feet, respectively) as well as at Sierra City (elevation 4,200 feet).

Leiberg (1902) reported that 1,386,890 acres in the northern Sierra Nevada were logged between 1850 and 1902, and that 2,337,930 acres were uncut. Logging intensity there varied from 5 to 99 percent of total volume removed. Leiberg estimated that, on the average, only 50 percent of the volume was removed from logged stands. He provided two means to evaluate the spatial extent and intensity of logging. The maps used to prepare figure 11G gave volume estimates, both in the "culled" areas and in areas that were not entered. Those maps were supported by detailed written descriptions of the forest on a drainage-by-drainage basis.

Analysis of cutting patterns in the North and Middle Forks of the Feather River, for instance, clearly shows that most cutting occurred at elevations below current FS boundaries. Oroville was the primary destination of lumber from these drainages, and the only method for transporting the timber was by wagon, restricting the trip to 40 miles or less (Leiberg 1902). Most cut areas reported by Leiberg were within 20 miles, straight-line, of Oroville or along lower slopes adjacent to the Central Valley north of there. For example, Big Bend Mountain (about 15 miles) was heavily cut over and Chino Creek (about 20 miles) was reportedly logged. According to Lefberg (1902, p. 58), however, in an area of about 15 square miles immediately north of Chino Creek "...lies a block of heavy forest, the heaviest in the basin. It is of ,the yellow-pine type, but contains an unusually large proportion of sugar pine... Both the yellow and sugar pine in this heavy block of timber are of exceptionally large size and of old growth. Much of the sugar pine runs above 5 feet basal diameter, with clear trunks 40 to 60 feet in height." This block of timber was clearly desirable but just beyond reach of the wagon-based logging of 1902. For this reason, cutting in these

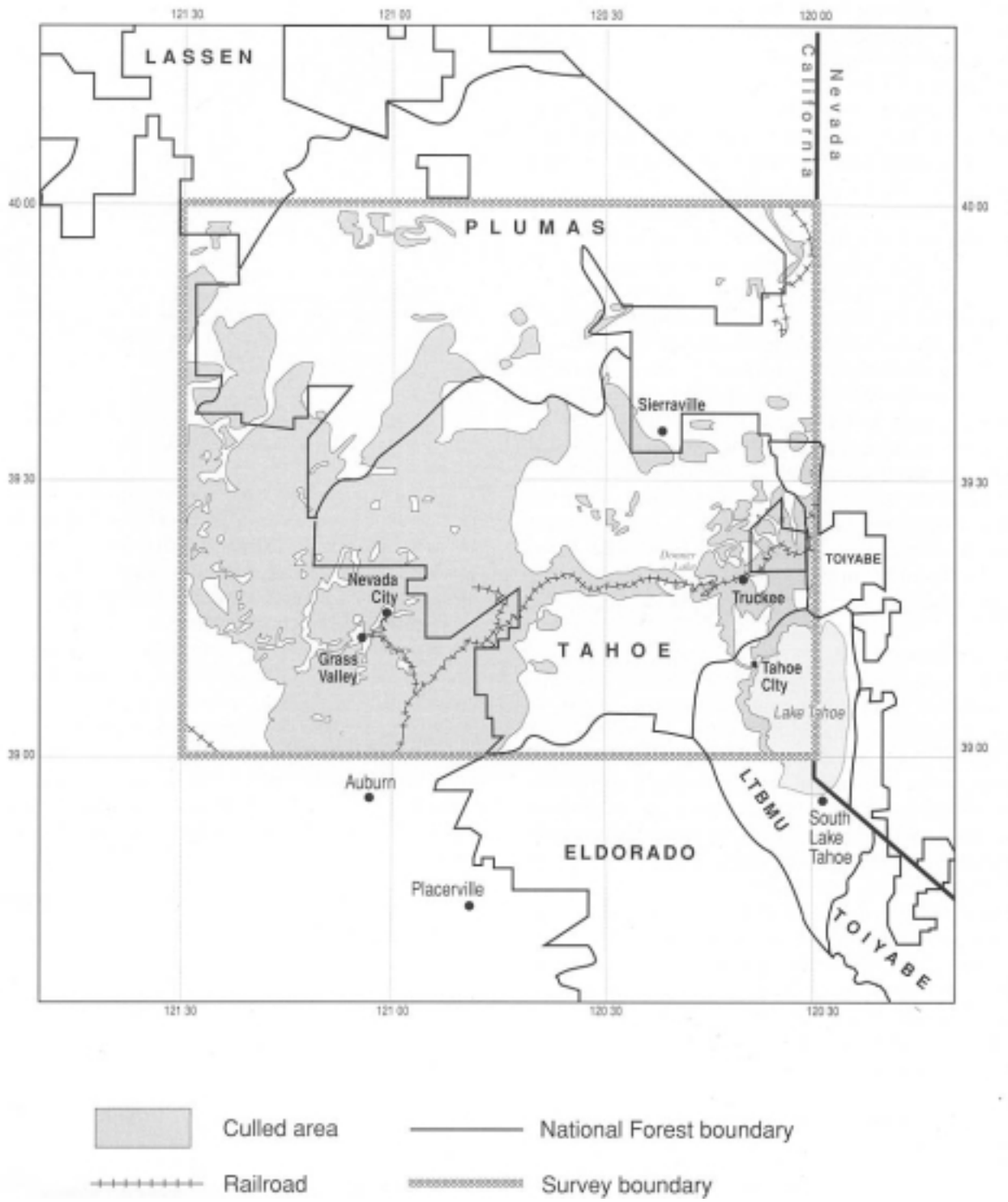

Figure 11G--Areas of logging activity from maps by Leiberg (1902). Leiberg did not, as did Sudworth (1900a), differentiate between cut-over lands and culled lands. In many areas cutting appears to have been very light.

drainages did not extend far into what is now the Plumas NF (fig. 11G). Areas of NF land that were entered tended to be at extreme limits of the transportation capabilities and would therefore have been subjected primarily to high-grading of sugar pines. This assertion is supported by an inventory done by the Plumas NF in 1910, which estimated that 870,506 acres of the Plumas were in a forested condition but only 11,983 acres (1.3 percent) had been "cut over" (Moore 1913).

On the other hand, 57 percent of the Yuba river drainage was described as being cut. In areas adjacent to towns or major rivers, Leiberg stated that most trees were removed. On other lands, cutting was much more selective.

Results of inventories by Leiberg and Sudworth, supported by the Plumas NF plan of 1913 and records of the Michigan-California Timber Company, show that cutting at the turn of the century was spatially limited to areas near population centers and major transportion routes. With notable exceptions of the Truckee Basin, Yuba River Basin, and lands immediately adjacent to the Southern Pacific Railroad, logging occurred at low elevations with relatively little within NF boundaries in the Sierra Nevada prior to the turn of this century. Limited by transportation capabilities, much of the logging on what are now NF lands was reduced to light high-grading of the most valuable trees. The NF most heavily impacted was the Tahoe. There the railroad, combined with mining at higher elevations, caused significant logging in what is now FS land. Even in the Tahoe NF, however, about half of the forest had not been entered at the turn of the century.

Grazing by Sheep

Unlike logging, which impacted limited acreage in the Sierra Nevada prior to 1900, the entire Sierran range appears to have been intensely overgrazed for decades, beginning in the early 1860s when a severe drought killed most of the cattle in California (Vankat 1970, Ratliff 1985, Ewing et al. 1988). According to Ratliff, not only did the drought cause a shift from cattle to sheep, but it also initiated the practice of summer grazing in alpine meadows of the Sierra Nevada (fig. 11H). In 1862, California ranges supported 3 million sheep, about 40 percent of which grazed the Central Valley. Grazing peaked in 1876, when more than 6 million sheep grazed state-wide (Ratliff 1985, Ewing et al. 1988). Sheep grazing was still intense in 1900, when an estimated 200,000 animals grazed during summer and fall in the Sierra Reserve (Vankat 1970). Descriptions of the impact of grazing on vegetation are particularly intense in much of the literature of that period:

> *There are practically no grasses or other herbaceous plants. The forest floor is clean. The writer can attest the inconvenience of this total lack of grass forage for in traveling over nearly 3,000,000 acres not a single day's feed for saddle and pack animals was secured on the open range... Barrenness is, however, not an original sin. From a study of long-protected forest land in the same region and from the statements of old settlers, it is evident that formerly there was an abundance of perennial forage grasses throughout the forests of this territory... It would seem that this bare condition of the surface in the open range has been produced only through years of excessive grazing by millions of sheep--a constant overstocking of the range* (Sudworth 1900a, p. 554-555).

> *The trampling of thousands of sheep pastured on these slopes during the summer and fall reduces the soil, to a depth of 6 or 8 inches, to the consistency of dust. Rain washes this dust into creeks and rivers, and heavy winds lift it up and carry it away* (Leiberg 1902, p. 15, concerning the red fir type).

> *The great obstacle to the explorer is not the danger of crag or chasm, but the starvation threatening his animals, through the destruction of the fine natural meadow pasturage by sheep* (Russell Dudley 1898, professor of botany, as quoted by Vankat 1970, p. 20).

> *The soil being denuded of grass is broken up by thousands of sheep tracks, and when the rains come this loose soil is washed down the mountainsides into the valleys, covering up the swamps and meadows, destroying these natural reservoirs* (1894 report by Acting Superintendent of Sequoia and General Grant NPs, as quoted by Vankat 1970, p. 20).

> *The Kern River drainage was ...almost impassable to the traveler, to such an extent is every living thing eaten off the face of the earth and trampled underfoot by the hundreds of thousands of sheep which each year roam over that territory* (1893 report by Acting Superintendent of Sequoia and General Grant NPs, as quoted by Vankat 1970, p. 29).

> *Clean surface; sheep grazed and burned. No reproduction. 10,000 feet elevation* (Sudworth 1900b, p. 10).

The last quote above, referring to an area at the headwaters of the Kings River, now in Sequoia/Kings Canyon NPs, was typical of site-specific examples in Sudworth's notes. The seasonal migration of sheep from the Central Valley up to alpine meadows in mid-summer meant that even very remote locations experienced the impact of overgrazing.

Recurrent themes typify the writings of different observers. Grazing at an intensity that produced significant soil erosion was noted in both the northern and southern Sierra. Removal of all grass was repeatedly mentioned in the context of travel being inconvenient because pack animals could not graze. In many cases, this was contrasted with the contention that grasses were abundant in forests prior to grazing. Although we suspect that many early writers harbored an anti-sheep bias, the numbers of sheep mentioned casually (hundreds of thousands, millions) appear to be accurate.

Burning by Sheep Herders

Sheep herders also burned extensively to encourage growth of grasses and forbs and to remove fuel and young trees from the forest floor. All accounts mention this, but we cannot be certain about the extent to which sheep-related fires contributed to overall fire frequency. John Muir, writing in 1877, felt that 90 percent of fires were caused by sheep herders, but his estimate was probably exaggerated (Vankat 1970). It is clear, however, that the pattern and intent of fires set by sheep herders differed from those set by Native Americans. The intent was to improve grazing on high-altitude pasturage and to remove obstacles that impeded movement by sheep. Consequently, sheep herders gave special attention to burning large, downed fuels (Sudworth 1900a, Vankat 1970) and to burning mesic areas to stimulate forage production.

We consider it likely that this intensity of grazing, combined with repeated burning by sheep herders, had a severe impact on herbaceous vegetation and on patterns of forest regeneration in the

Figure 11H--Sheep grazing in the Sierra Nevada.

Location: ----------Northside of Crabtree Meadow, Sequoia National Park
Elevation: ----------10,400 feet
Date: ----------29 July 1890
Source:----------Vankat (1970) Photographer: -----Unknown

Sierra Nevada. In the absence of competing vegetation, regeneration was rapid and dense when sheep and fires ignited by sheep herders were no longer prevalent in montane forests. According to Leiberg (1902, p. 15), such areas were common

> *...varying from 1 acre to 3 or 4 acres, scattered along the ridges from Webber Peak to the Rubicon River, on which the grass and weeds have been so thoroughly eaten out that even the sheep have abandoned them. On such tracts, left undisturbed for four or five years, Shasta firs [red fir] cover the ground to the number of 10,000 to 15,000 trees to the acre.*

Leiberg (1902, p. 43) also reported that stands freed from burning for 15 years

> *...may be seen in the Mohawk Valley, on areas in the central portions of the basin of the West Fork of Feather River and in the northern portion of the Truckee Basin. These sapling stands, composed of yellow pine, red [Douglas-] and white fir, and incense cedar, singly or combined, are so dense that a man can with difficulty force his way through.*

Sudworth (1900a, p. 553) found a "general lack of herbaceous growth and irregular reproduction of timber species [and a] general absence of small-sized timber intermediate between seedlings and the large timber" in unfenced forests. In "fenced and otherwise protected forests," he found "uniform abundance of herbaceous growth," "plentiful reproduction of timber species," and "presence of intermediate sizes of small timber."

Vankat (1970) measured the ages of numerous trees in Sequoia NP, finding that a major regeneration pulse occurred at approximately the time sheep were removed from the Park (fig. 11I). Vankat also found that particular areas (for example, meadows) and species (for example, big sagebrush) had not recovered from grazing by the late 1960s. We can reasonably infer that the intensity of sheep grazing for nearly 40 years in the Sierra Nevada impacted stand structure and regeneration patterns, producing lasting changes in mixed communities of grasses, forbs, and shrubs.

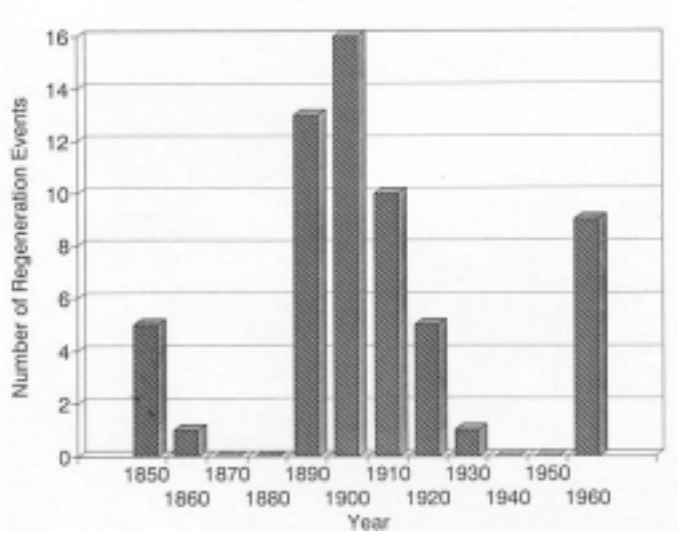

Figure 11I--Periods of significant regeneration on sites within Sequoia National Park. This graph was generated by combining tables found in the appendices of Vankat (1970).

Stand Structure

The best data on stand structures at the turn of this century came from a set of 1/4-acre plots measured by Sudworth (1900a, 1900b). Data from 22 plots were presented in his formal document (1900a) for the USGS on the Stanislaus and Tahoe reserves, and data from 26 additional plots were included in his notes on the Sierra Reserve (1900b). Here we report analyses of all plots in the USGS report but only 20 of the 26 plots in Sudworth's notes. Four of those not analyzed were in groves of giant sequoias (Sudworth was particularly interested in the big trees), and two were at high elevation and contained large components of foxtail pine. These plots represented uncommon forest types and were not considered of general interest. Sudworth did not describe the methods he used to select plots, but their primary purpose was to support the maps he created. His maps, a standard product in USGS surveys of that period, subdivided the entire area surveyed (about 3,000,000 acres) into subunits based on similarity in timber volumes. Sudworth often referred to his plots as being "representative" of a particular area. He probably used scattered plots to calibrate ocular estimates. He reported only trees 11 inches or more in diameter at breast height (d.b.h.) in the USGS report and only 12 inches or more in d.b.h. in his notes. He mentioned regeneration in his notes, but the meaning of the term was not quantified.

Several uncertainties are associated with analyses of data from the turn of the century. In particular, estimates of volume per acre, either at the stand level or derived from plot data, should be viewed with caution. At a stand level, volumes were calculated using scaling rules based on the limits of merchantability. Because small trees (for some species defined as trees <16 in d.b.h.) and tops were not used, and because saw kerfs were wider than today, the volume reported on a per-acre basis in 1900 would, therefore, be considerably less than if the same acreage were cruised today. This underestimation (by current standards) was significant. For the San Jacinto Reserve, for instance, Leiberg (1899a, p. 356) estimated the total volume at 98 million board feet (MMBF). He noted, however, that "The sawmills in the reserve... handle the timber in the most economical manner possible, utilizing the trees far up in the crown, where the diameter dwindles to 8 inches or less. Worked up in this manner, the quantity of available merchantable timber would amount to at least 200,000,000 feet..."--a full doubling of the volume estimate.

Volume estimates based on the plots could be derived directly from the data, but this too is risky because the criteria used for plot selection are unknown, and volume appears to have been very heterogeneously distributed in the forest. Fitch (1900a) noted that volume averaged 80-140 thousand board feet (MBF) per acre in selected areas of the Yosemite Quadrangle, but the overall average was between 30 and 40 MBF. Given the small number of plots available for analysis, coupled with the highly variable stocking levels present at the time, use of volume statistics derived from plot data to infer volume-per-acre for the forest system is not justified. For this reason, we have not used volume estimates to compare current and historical forest conditions. Instead we have used the proportions of stems in particular diameter classes, or the proportions of basal area by species.

Diameter Distribution

Stands described by Sudworth (1900a) were very large and very old. The average yellow pine, for instance, was reportedly 150-180 feet tall, 3-4 feet in d.b.h., and 250-350 years old. Although Sudworth did not measure trees less than 11 inches in d.b.h., available evidence indicates that trees in those smaller classes were uncommon, though patches of very small regeneration appear to have been present, based on photos and text in Sudworth's report and on discussion by Leiberg (1902) of regeneration following removal of sheep. Most stems exceeded 25 inches in d.b.h., and many extremely large specimens were measured (fig. 11J). Of the major timber species, sugar pine, Douglas-fir, and white fir occurred only as very large trees (fig. 11K). Sugar pines were a minor stand component, but most of them were in the very large diameter classes. A comparison of that distribution with the largest diameter stands in Sierran for-

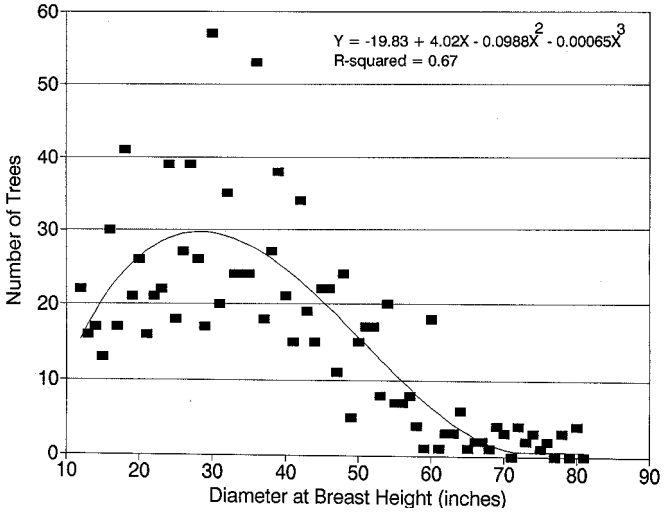

Figure 11J--Distribution of trees in forests of the Sierra Nevada in 1900. All species were lumped by diameter class and all of the plot information (Sudworth 1900a, 1900b) was combined. Many of the trees with diameters at breast height <15 inches were lodgepole pines.

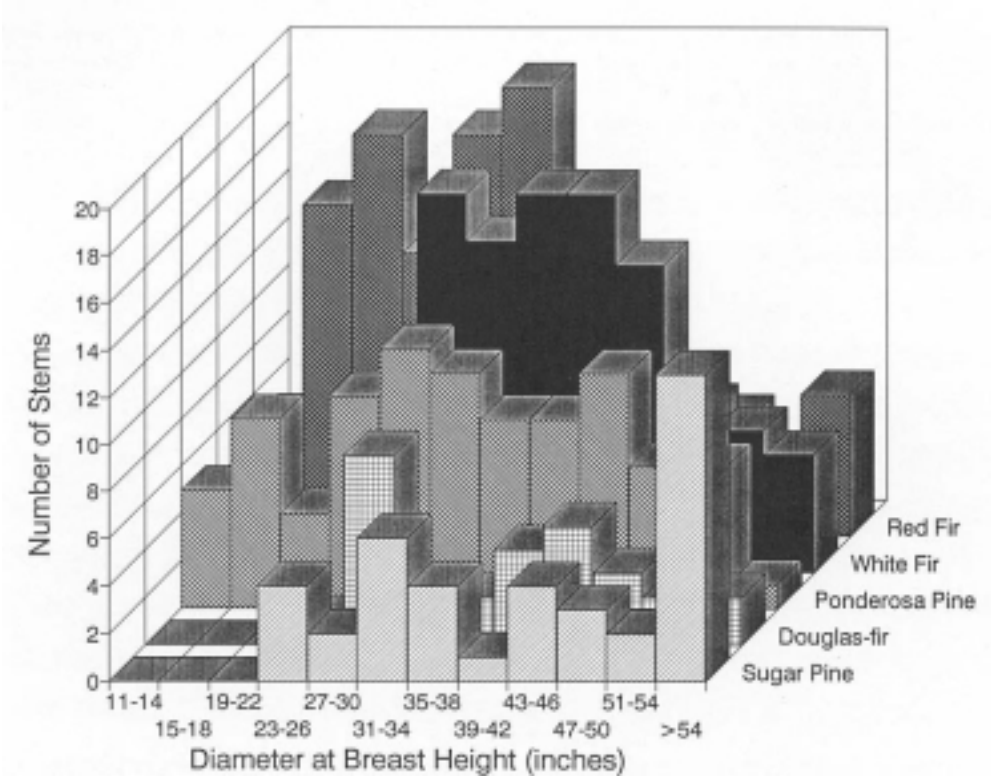

Figure 11K--Diameter distribution of trees in the Sierra Nevada, by species, for published plot data (Sudworth 1900a). Sugar pine, Douglas-fir, and white fir were present only in very large diameter classes.

ests today shows that far more of the stand basal area in the forests of 1900 was concentrated in very large trees (fig. 11L).

Species Composition

Species composition was apparently mixed at the turn of the century, with all major timber species represented. White fir and incense-cedar were widely distributed and present in large numbers (table 11B, fig. 11M). Pines did not dominate the forests, either in number or in volume. Volume estimates by species at about the turn of the century, available from several sources (table 11C), supported the plot-level data of Sudworth (1900a, 1900b). Note that many estimates made at that time underestimated the volume in true fir, because those trees were not considered merchantable unless they were at least 16 inches in d.b.h., whereas pines were merchantable when 12 inches or more in d.b.h. (Leiberg 1902). For his part, Sudworth did not give forest-wide volume estimates, but noted that the elevational range of white fir was between 3,800 and 7,500 feet, and that it formed 30-45 percent of the stand in areas where it was most abundant.

When compared with the current species composition in Sierran forests, the composition at the turn of the century was reasonably similar (compare fig. 11N and table 11C). Comparing the forest-wide estimates made by the Plumas NF in 1913 (Moore 1913) with current estimates from mixed-conifer timber strata (timber strata codes are defined in table 1C and in Appendix B), it appears that true fir and incense-cedar have increased and that pines have decreased (fig. 11O). This is probably an overestimate of the shift, however, because other strata, such as

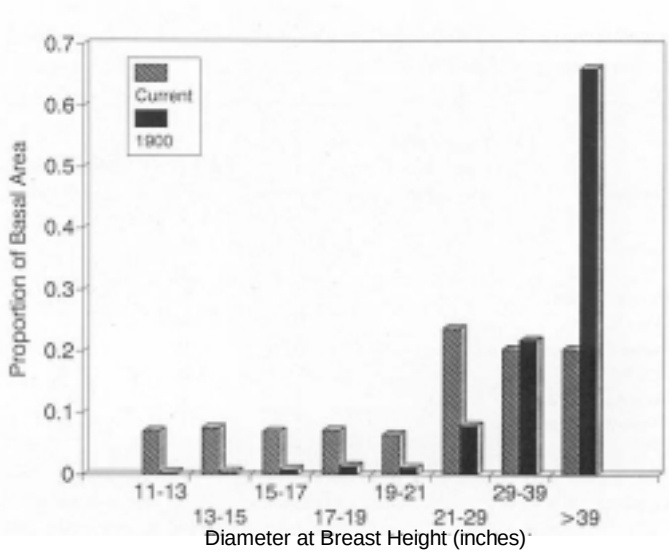

Figure 11L--Basal-area distributions of trees in forests of the Sierra Nevada for 1900 and current stands. The 1900 distribution was based on information presented in figure 11J; the current distribution was based on Forest Service Region 5 inventory data from timber strata for the largest size-classes (4, 5, and 6).

Table 11B—*Species composition matrix (stems per quarter acre) for Sierran forests in 1900 (data from Sudworth (1900a). Timber strata are our professional judgments about which current classes Sudworth's plots fit (E = eastside pine; M = mixed-conifer; P = ponderosa pine; W = white fir; R = red fir; L = lodgepole pine).*

Plot	Sugar pine	Ponderosa pine	Western white pine	Lodge-pole pine	Jeffrey pine	Incense-cedar	White fir	Red fir	Douglas-fir	Black oak	Mountain hemlock	Total	Timber strata
1					6		15					21	E
2	2	2				11	3					18	M
3		19				4						23	P
4	16					2	5					23	M
5		8				12				7		27	P
6							20	11				31	W
7				14								14	L
8	4					4	8					16	M
9								47				47	R
10	2				1	3	20	4				30	M
11					9							9	E
12			11					41			15	67	R
13					10		8					18	E
14	4				3	5	4					16	M
15	2					2	6		13			23	M
16			4	28				16				48	R
17	3	4				3	15		2			27	M
18	4	19				6				1		30	P
19		4				2			7	2		15	M
20	1	17				9				1		28	P
21		13				5						18	P
22	1					5	3		12			21	M
Total	**39**	**86**	**15**	**42**	**29**	**73**	**107**	**119**	**34**	**11**	**15**	**570**	
Percent	**6.8**	**15.1**	**2.6**	**7.4**	**5.1**	**12.8**	**18.8**	**20.9**	**6.0**	**1.9**	**2.6**		
Frequency	**0.46**	**0.36**	**0.09**	**0.09**	**0.23**	**0.64**	**0.50**	**0.23**	**0.18**	**0.18**	**0.05**		

Table 11C-*Estimates of the proportional volumes of conifers at various times and locations in the Sierra Nevada.*

Species	Yellow pine[1] type, turn of this century	Shasta fir type, turn of this century	Plumas NF, 1913	M4G strata,[2] 1980-1990
Sugar pine	20	0	16	12
Yellow pine	38	21	39	15
Incense-cedar	0	0	29	13
Douglas-fir	21	0	14	16
White fir	19	0	24	44
Red fir	12	75	18	0
Western white pine	0	3	0	0
Mountain hemlock	0	2	0	0

[1] Yellow pine and Shasta fir types from Leiberg (1902). These data were for standing "mill timber" cruised using "Michigan practice"-trees >8 inches in d.b.h. and having ≥10 feet of clear lumber in the trunk. Both incense-cedar and lodgepole pine were listed as being present in the stands, but they were not included in the mill estimates of timber volume. "Yellow pine" is either Jeffrey or ponderosa pine.

[2] Values shown for M4G strata were averaged over all Sierran National Forests. M4G strata were mixed-conifer stands, with trees ≥24 inches in diameter at breast height, and >69 percent canopy closure (see table 1C).

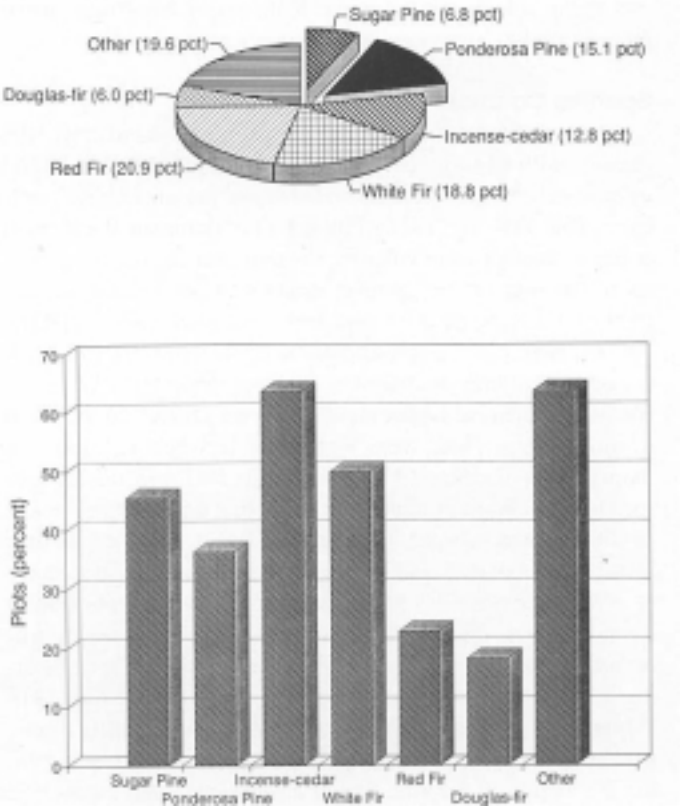

Figure 11M-Proportions of individuals and frequencies of occurrence among plots of tree species, based on plot data from Sudworth (1900a).

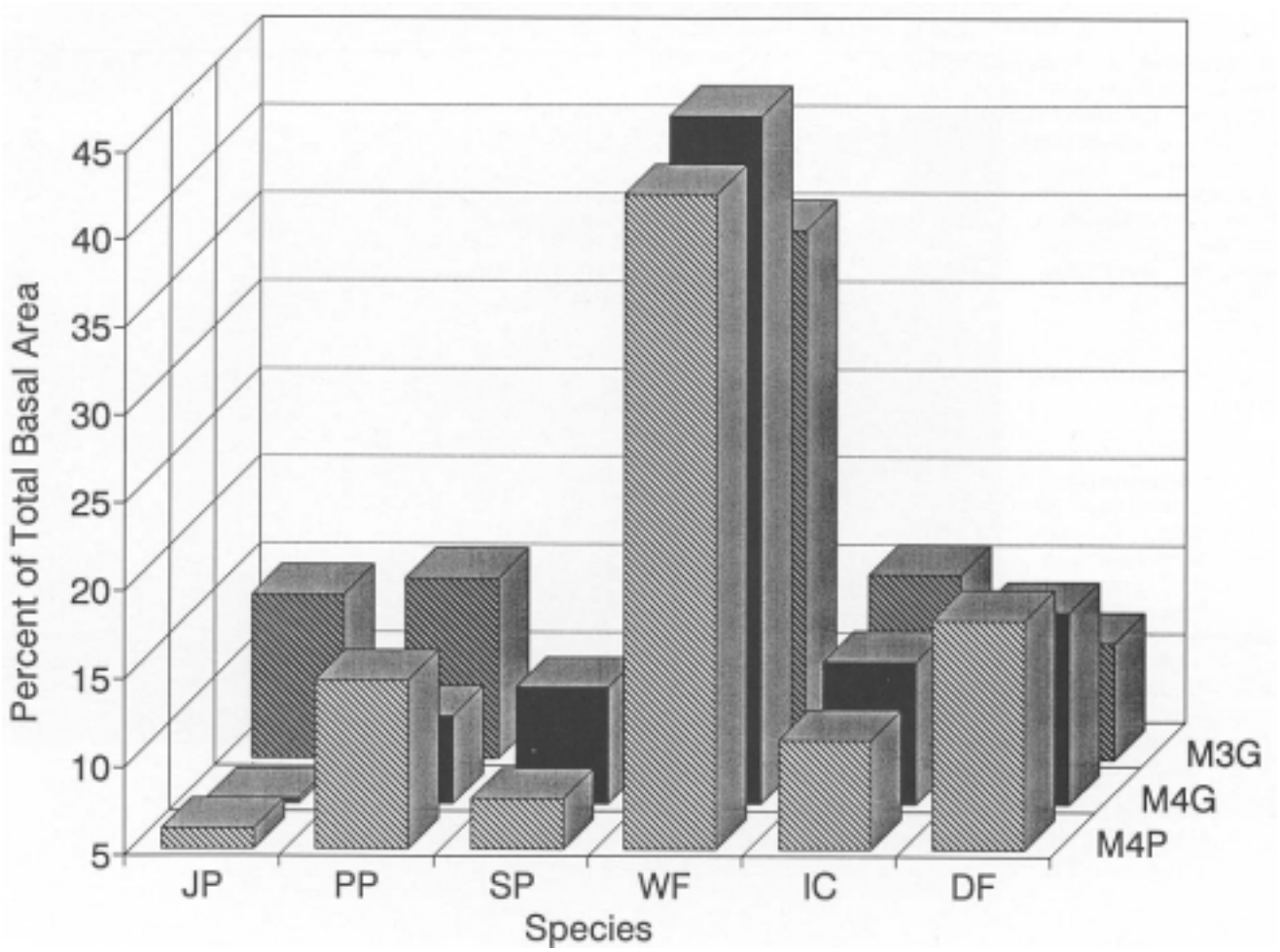

Figure 11N--Species composition (1980-1990) in the most widespread mixed-conifer strata (JP =Jeffrey pine, PP = ponderosa pine, SP = sugar pine, WF = white fir, IC = incense-cedar, and DF = Douglas-fir). For the strata labels, M = mixed-conifer forest, "3" means that the dominant tree diameter-class lies between 12 and 24 inches; "4"indicates that it lies between 24 and 40 inches. "P" indicates poor stocking--canopy closure 0-39 percent; "G" indicates good stocking-canopy closure >69 percent. These data were derived from Forest Service Region 5 inventory data.

the ponderosa pine type, have far fewer firs and a greater percentage of yellow pine. It is reasonable, however, to infer from these data that the proportion of fir (basal area or volume) has increased by perhaps 10-20 percent, while the proportion of yellow and sugar pines has decreased by a similar amount. We are surprised that this trend has not been stronger, given the preference for logging yellow and sugar pine and the expected successional patterns of the forest. The stand structure at the turn of the century was often quite open, and became more scattered subsequent to heavy logging (figs. 11P and 11Q). These open stand conditions may have favored pine regeneration and helped to produce the species composition we see today (figs. 11R and 11S). Compare figures 11P and 11Q with figures 11R and 11S to observe these changes. The trend toward the more shade-tolerant fir will be enhanced by selective removal of other species, by fire suppression, and by maintenance of the very dense stand conditions that exist in many areas of the Sierra Nevada today. The trend will, to a certain extent, be counteracted by infestations of the fir engraver beetle, to which these stands appear to be very susceptible.

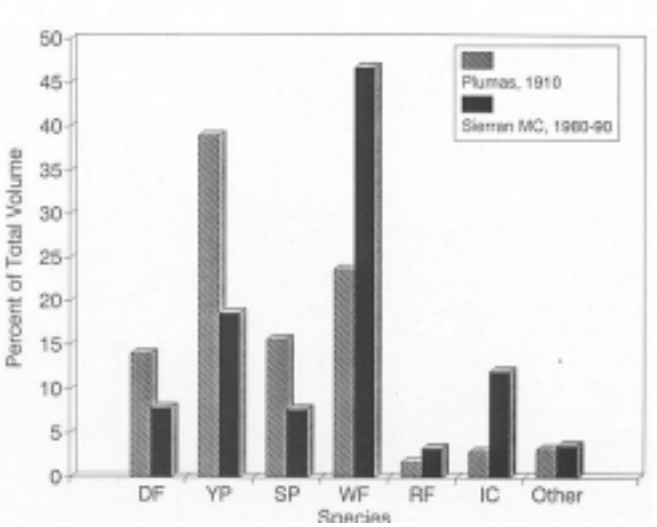

Figure 11O--Volume estimates, by species, in the Plumas National Forest in 1910 (Moore 1913) and from current inventory data. Mixed-conifer (MC) strata M3G, M4P, and M4G were combined for this analysis. See figure 11 N for species codes and a description of the timber strata classifications.

Figure 11P--Left half of two-photo historic panorama. Between 1924 and 1930, this area was owned and intensively logged by the Yosemite Lumber Company, then either sold to or exchanged with the Stanislaus National Forest. Typical of railroad logging days, about 70 percent of the timber was removed and about 30 percent left. An ample number of snags, cull logs, tops, and limbs were left scattered to decay naturally.

Location: ----Looking west from the railroad grade, 1 mile south of Camp 16, into Moss Creek Canyon, Stanislaus National Forest
Elevation:-----6,257 feet
Date: ----------1930
Source: -----USDA Forest Service, Regional Photo Archives, San Francisco, CA
Photographer: ---Unknown

Figure 11Q-Right half of two-photo historic panorama. This photo was labeled "old" cutting (1929) on the left background, and "new" cutting (1930) on the right foreground. Note the area left-center (arrows) where soils were intensively impacted by skidding. Today this area still has mostly brush and young black oaks (fig. 11S). Other areas, where some residual conifers were left and skidding had less impact, show a more rapid natural regeneration.

Location: --Looking northwest from the railroad grade over an unnamed tributary to Moss Creek, Stanislaus National Forest
Elevation: --6,257 feet
Date: --------1930
Source:------USDA Forest Service, Regional Photo Archives, San Francisco, CA
Photographer: -Unknown

Figure 11R-Left half of 1991 comparative photo. Today the area shown in figure 11P shows a dense mixed-conifer forest of white fir, ponderosa pine, incense-cedar, sugar pine, and scattered black oaks. This regeneration is all natural. It has been classified as owl foraging habitat.

Location: ----Same as previous historic photo (fig. 11P), but looking more tothe right.
Elevation: -----6,257 feet
Date: ----------December 1991
Photographer: ----John S. Senser

Figure 11S-Right half of 1991 comparative photo. Arrows denote the same general areas seen in figure 11Q. Crane Flat Lookout (on the upper right peak) and the railroad grade are hidden by dense second growth. The light vegetation on the background slopes and left foreground is black oak in autumn foliage. Insect kills dominate the patch of gray conifers.

Location: ----Almost the exact perspective as figure 11Q
Elevation: ----6,257 feet
Date: ----------December 1991
Photographer: ----John S. Senser

Cutting History in the Sierra Nevada

The rate of volume removal, in general terms, serves as an index of the level of logging disturbance on the land. We developed a cutting history for the Sierra Nevada from 1869-1990 (fig. 11T). This was based largely on county records from 1947-1990 available from the California Department of Forestry and Fire Protection (1947-78) and the California State Board of Equalization (1979-90), and from statewide totals by species prior to 1947 (May 1953). Prior to 1947, therefore, we assumed that all volume generated by species common in the Sierra Nevada was taken only from the Sierra Nevada. That species group included ponderosa and sugar pines, incense-cedar, and white fir. Volume estimates from the early period were probably inaccurate for several reasons. The assumption that the state's entire harvest of sugar and ponderosa pine came from the Sierra Nevada would tend to bias these estimates high. On the other hand, the volume estimates do not accurately account for fuelwood, shake production, and extensive wastage left in the woods (May 1953, Laudenslayer and Darr 1990); all of those factors would tend to bias the volume estimate low. We do not know the extent to which these contrasting biases would tend to offset each other.

By 1913, logging contracts were similar to those used today by the FS. Maximum stump height was 18 inches, and the merchantable top was set at 8-10 inches in diameter. The planned rotation period in the Plumas NF was set at 200 years, and the maximum cut was set at 132 MMBF (Moore 1913). Local use of wood for fuel apparently declined in the early part of the twentieth century. The proposed cut for the Stanislaus NF in 1912 allocated only 164 MBF for "free use" (Graves 1912). Because of these restrictions, the market volume after 1910 probably reflected the actual cut reasonably well.

Logging in the Sierra Nevada increased until about 1950, with a significant dip during the Great Depression. Logging levels declined slightly after 1950, remained fairly constant until the 1982 recession, then increased again to the point that 1990 levels were near the historic peak. This pattern differs from that in north-coastal California, where the rate of logging increased dramatically after World War 11 and then declined (fig. 11U).

Prescriptions used to cut timber in the Sierra Nevada have also differed from those of the coast. Logging in the Sierra Nevada prior to the 1980s seldom used a clearcutting prescription. If a tree had no market value, it was simply left standing. Even through the 1970s, when a policy shift toward clearcutting occurred, it accounted for most of the volume taken only from 1983 to 1987 (fig. 11V). By the end of the decade, cutting was increasingly concentrated in salvage operations (fig. 11W). Because early cutting, even the relatively heavy cutting done on private lands, seldom involved clearcuts (figs. 11P-11S), disturbance patterns in the Sierra Nevada are very different today from those that have characterized the habitat of the northern spotted owl. In most of the lands occupied by the northern spotted owl, heavy clearcutting in recent years has generated a patchwork of uncut "old growth" and new plantations-a spatially heterogeneous system. In the Sierra Nevada, virtually all stands have been entered and trees have been selectively removed. Both private (Laudenslayer and Darr 1990) and public owners tended to apply similar harvest rules on large blocks of land. Because tree removal has targeted larger stems, and because these large trees appear to have been unevenly distributed on the landscape, forming groves (Fitch 1900b), it is likely that their removal caused a decrease rather than an increase in landscape-level forest heterogeneity.

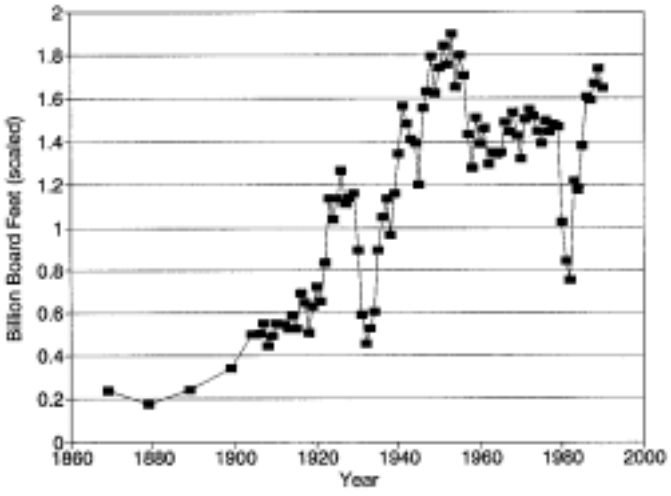

Figure 11T-Market volume of timber from the Sierra Nevada. Volume before 1947 was based on data supplied by May (1953); volumes for 1947-1990 were based on records kept by the California Department of Forestry and Fire Protection (1947-78) and the California State Board of Equalization (1979-90).

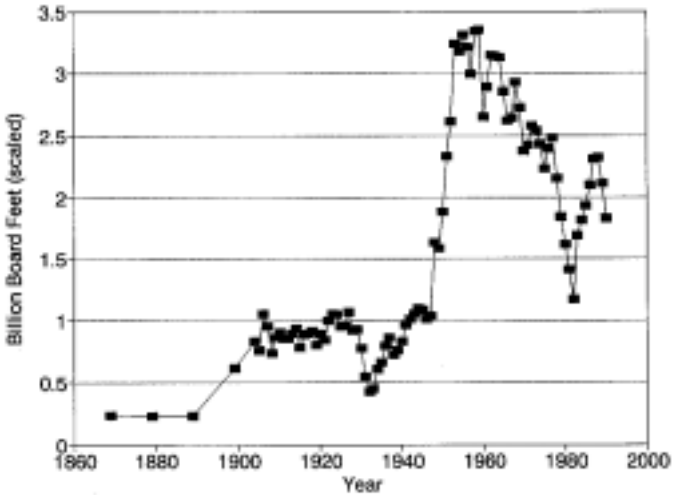

Figure 11U-Market volume of timber from California's North Coast. Volumes were derived from the same sources as those in figure 11T. Volume before 1947 was based on state-wide totals, assuming that all redwood and Douglas-fir came from coastal forests.

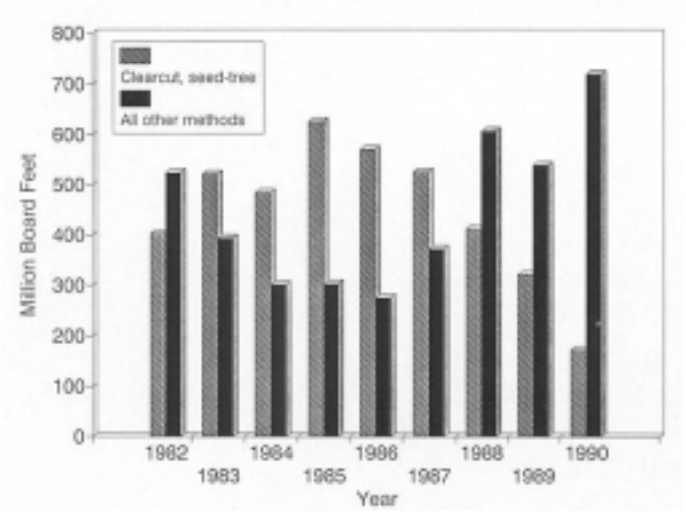

Figure 11V-Logging patterns by prescription for National Forests in the Sierra Nevada, 1982-1990 (from sold-sale records, Forest Service Region 5).

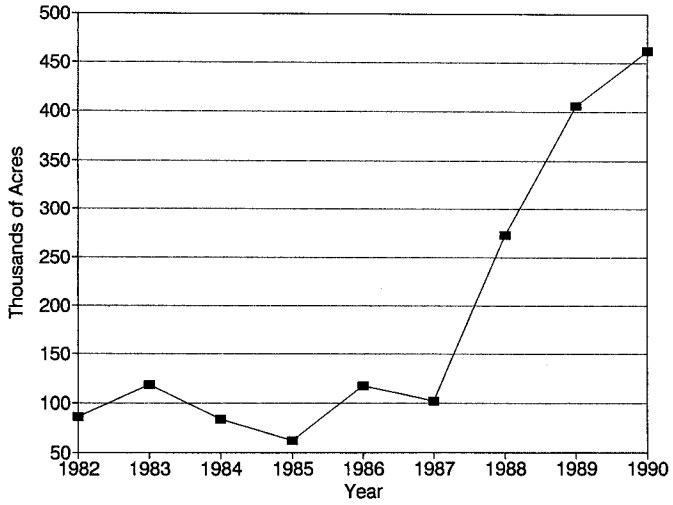

Figure 11W-Acres entered for sanitation-salvage logging on National Forests in the Sierra Nevada, 1982-1990 (from sold-sale records, Forest Service Region 5).

Discussion of Sierran Forest Conditions

Because grazing and burning occurred simultaneously and in the same areas, we cannot separate their effects. As Sudworth (1900a) noted, however, destruction of a perennial grass community did not likely result from fire alone. The ability of intense grazing to interfere with regeneration is well known, and was documented by both Sudworth (1900a) and Leiberg (1902). The bare soils prevalent at the turn of the century probably provided an excellent seed bed for abundant tree regeneration, a process discussed by both Sudworth and Leiberg and supported by Vankat (1970). The pattern of burning by Native Americans probably differed from that of sheep herders, because their goals differed. Both groups sought short-tern and long-term alteration of the forest. Native Americans probably used fire to herd game and to improve wild food crops (Vankat 1970, Lewis 1973, Anderson 1991). Sheep herders, on the other hand, sought to improve grazing and to remove obstacles to the passage of sheep.

We do not expect, therefore, that the forest described at the turn of the century was in any sense pristine. Although most current FS lands were uncut then, the forest floor and regeneration structure were impacted repeatedly by intense grazing. Moreover, even if that forest were relatively untouched, it would not necessarily have looked like a pristine forest that would exist today. Many of the trees in older forests in 1900 were established in the 1600s or before, and grew during a period characterized by extended droughts. The periods from 1750 to 1820 and from 1860 to 1880 were very dry in California (fig. 11X) (Fritts and Gordon 1980, Fritts 1991). The forest that Sudworth (1900a) described was largely established before those droughts began.

Drought, combined with grazing and fire, created a forest dominated by very large, old trees and with very little ground cover. We believe the forests described at the turn of this century were less heterogeneous than the forests influenced by aboriginal and lightning fires. The latter were probably typified by heavily stocked areas on more mesic sites, more trees in intermediate size-classes, and more large-diameter logs and other woody materials on the ground (sheep herders specifically targeted large woody debris for burning).

Cutting in the Sierra Nevada increased steadily over time, reaching a peak after World War II. Since then, with the exception of the 1982 recession, cutting has remained at fairly constant levels. The pattern of partial cutting that typically removed only the largest and oldest trees from a stand, coupled with abundant regeneration that followed removal of sheep from the forests and the initiation of fire suppression, resulted in a shift in diameter distribution of trees between the forests of 1900 and 1990. Available evidence suggests that species composition, measured as basal area or volume, has not yet been substantially altered by these practices, but observation suggests that much of the current regeneration consists of true fir and incense-cedar.

The mixed-conifer zone of the Sierra Nevada, therefore, has few or no stands remaining that can be described as natural or pristine. To various degrees, the forest system has been changed from one dominated by large, old, widely spaced trees to one characterized by dense, fairly even-aged stands in which most of the larger trees are 80-100 years old. This forest appears to be unstable. It is highly susceptible to drought-induced mortality, as competition for water weakens trees on drier sites. It is impacted by massive bark beetle infestations. And it is very flammable (Chapter 12). Its trajectory into the future is largely unknown, but stand structure can be expected to change markedly over the next 100 years.

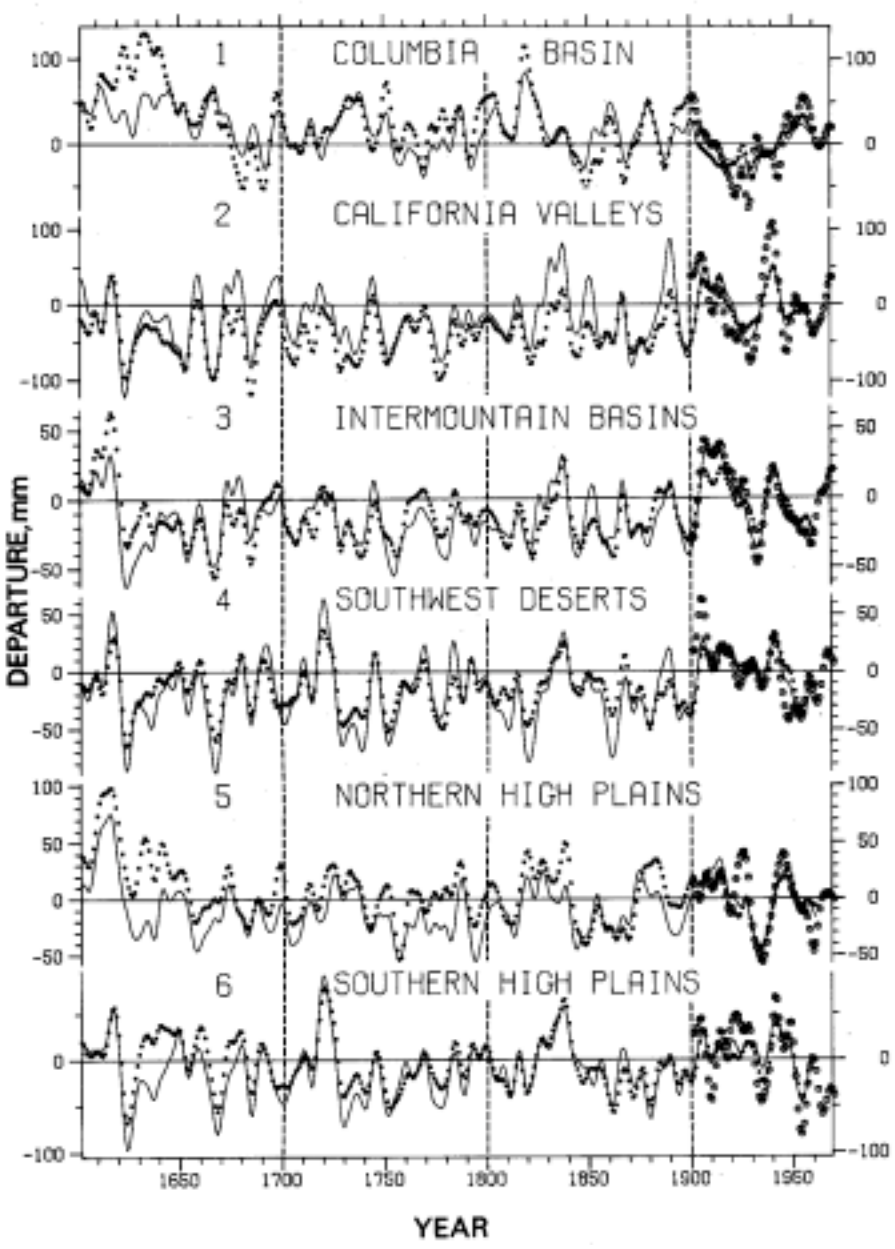

Figure 11X-Patterns of precipitation in the western United States from 1600 to 1970 (Fritts 1991, figure 7.4), based on tree-ring analyses. The solid line is based on data from the western United States, the small dots are based on data from a larger grid covering the entire United States, and the large dots in the twentieth century are based on measured precipitation data.

Southern California Forests at the Turn of the Century

The Forest Reserve system in southern California consisted in 1897 of the San Bernardino, San Gabriel, San Jacinto, and Trabuco Canyon reserves. Today, the San Bernardino NF includes parts of the San Bernardino, San Jacinto, and San Gabriel (eastern edge) reserves. The Angeles NF contains most of the San Gabriel Reserve, and the Trabuco Canyon Reserve, which covered a portion of the Santa Ana Mountains, has been largely incorporated into the Cleveland NF. Leiberg (1899x, 1899b, 1899c) surveyed the first three reserves in 1897, and Bamard (1900) resurveyed the 30-minute San Jacinto Quadrangle in 1900 and provided a map similar to those created by Sudworth and Leiberg for the Sierra Nevada.

Surveys included acreage outside of current FS boundaries. The San Bernardino and San Jacinto reserves, for instance, included many areas that are now privately owned, managed by the Bureau of Land Management, or incorporated into Indian Reservations. For this reason, total acreages are larger and the proportions of reserves listed in a nonforested condition are greater than would be indicated by current inventories. Most of the timbered acreage has, however, been retained by the FS, so statistics associated with forested lands at the turn of the century can be compared with those derived from modern inventories (table 11D). Given the differences in classification methods, the forested acreage statistics are remarkably similar.

Table 11D-*Acres* of *forested lands in southern California, as estimated in 1899 and in 1987 and 1988.*

Reserve	Year of estimate	
	1899[1]	1987 and 1988[2]
San Gabriel		
Forested	100,000	145,438
Productive[3]	25,000	26,687
Total acres	650,000	651,874
San Bernardino and San Jacinto		
Forested	441,000	389,892
Productive[3]	122,500	160,631
Total acres	1,474,000	649,900

[1] San Bernardino Reserve (Leiberg 1899a); San Jacinto Reserve (Leiberg 1899b); San Gabriel Reserve (Leiberg 1899c). Leiberg did not know the exact boundaries of the reserves.

[2] Data from the Angeles National Forest correspond to the San Gabriel Reserve (USDA Forest Service 1987); data from the San Bernardino National Forest correspond to the San Bernardino and San Jacinto Reserves (USDA Forest Service 1988).

[3] Productive lands were defined as Class 1 lands (both accessible and capable of producing timber) by Leiberg, and lands capable of producing >20 cubic feet/acre/year for estimates by the USDA Forest Service (1987).

Species Composition in 1897

Leiberg (1899a, p. 356) estimated species composition in the three reserves that he surveyed (figs. 11Y, 11Z, and 11AA). The methods used to obtain these data were not stated in detail, but Leiberg wrote: "These estimates were based on the customary method of scaling standing timber," suggesting that his estimates were based, at least in part, on measured plot data. The survey effort in 1897, however, appears to have been less intense than in 1900 or 1902. Because less time was spent in the area, the extent to which vegetation patterns were derived from inference, instead of direct observation, would increase. Therefore, tree species that are heterogeneously distributed-especially minor species-easily could be either over- or under-represented.

The general pattern in 1900 was one of low-elevation forests dominated by either ponderosa pine or bigcone Douglas-fir, with white fir entering as a major stand component above 6,000 feet. Lodgepole pine was present in quantities only above 8,500 feet.

Nonaboriginal Human Disturbance by 1900

Logging occurred in the San Bernardino Mountains as early as 1865 (Leiberg 1899b), but was limited in extent. By 1897, logging was still limited to an area north of San Bernardino; it did not extend appreciably into the eastern or northern portions of the San Bernardino Reserve. Logged areas mapped in the San Jacinto Reserve were very small, lying primarily in the upper basin of the North Fork of the San Jacinto River and in an area adjacent to the town of Idyllwild, in the Strawberry Creek drainage. The total area logged in the San Jacinto covered "not more than 1 square mile" (Barnard 1900, p. 575). No extensive timber cutting had occurred in the San Gabriel Reserve by the end of last century (Leiberg 1899c).

Little evidence exists of extensive grazing in the forests of southern California at the turn of the century. Leiberg (1899b, p. 360) estimated that no more than "a few hundred head of stock" were regularly pastured in the San Bernardino Reserve, although several thousand head were grazed there in 1897 because of a drought. Leiberg did not state exactly what a "head of stock" was but, judging from his comments on the San Jacinto Reserve, he probably meant cattle. In the San Jacinto, he stated that "An unknown number of cattle and horses-probably 1,500-2,000 head-graze in the reserve" (Leiberg 1899a, p. 354). Grazing was not discussed for the San Gabriel Reserve. There is, however, evidence of extensive grazing by sheep in the San Bernardino and San Jacinto Mountains in the late 1800s. Minnich (1988) reported that sheep grazing occurred over much of the San Bernardino Mountains during the period from 1860 to 1898, to such an extent that many areas were grazed to a bare-earth condition. In particular, as many as 30,000 sheep were grazed in the area around Little Bear Valley and an additional 30,000 were grazed in the Santa Ana River drainage (Minnich 1988, p. 39-40). As with reports of grazing in the Sierra Nevada, the extent of destruction that resulted from sheep grazing may have been exaggerated because of the biases of early observers.

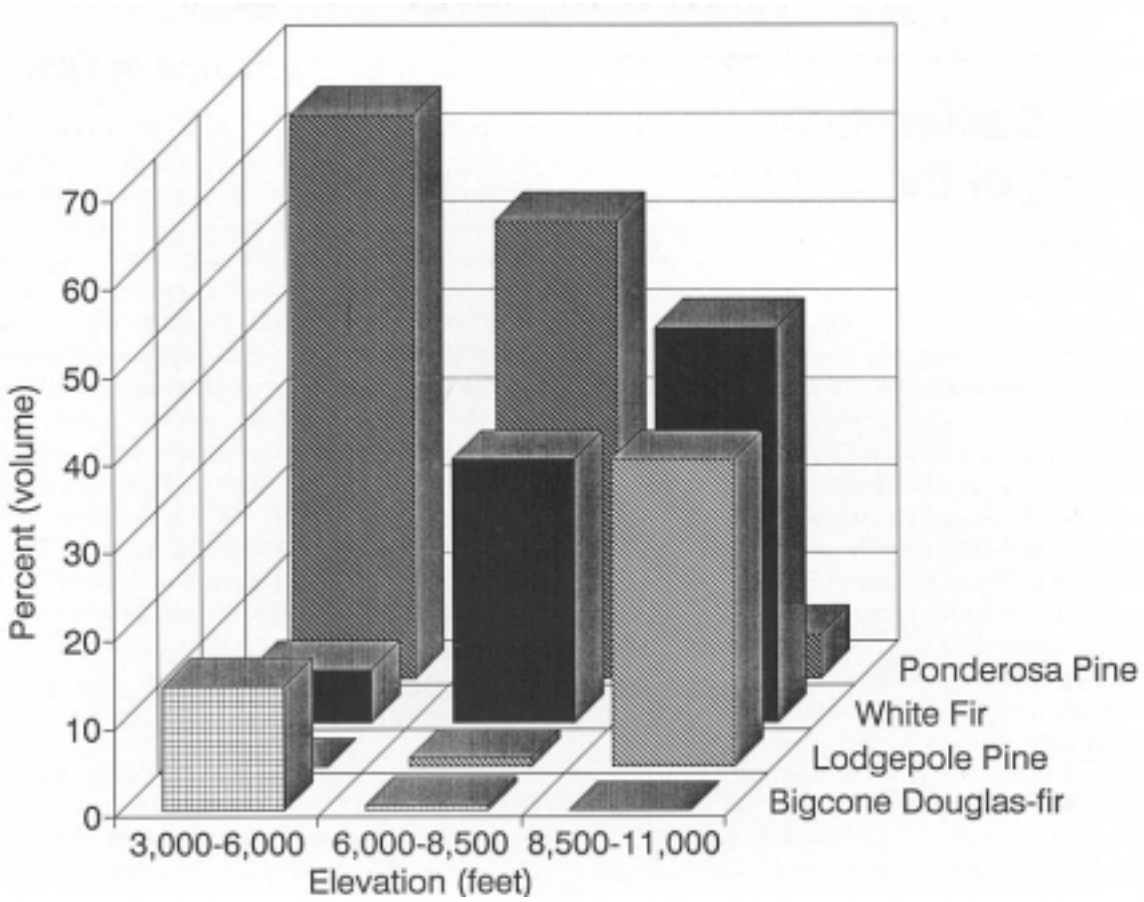

Figure 11Y-Species composition in the San Bernardino Forest Reserve in 1897 (Leiberg 1899b). Hardwood species, with the exception of oaks, were not used when Leiberg calculated percent contribution, by species.

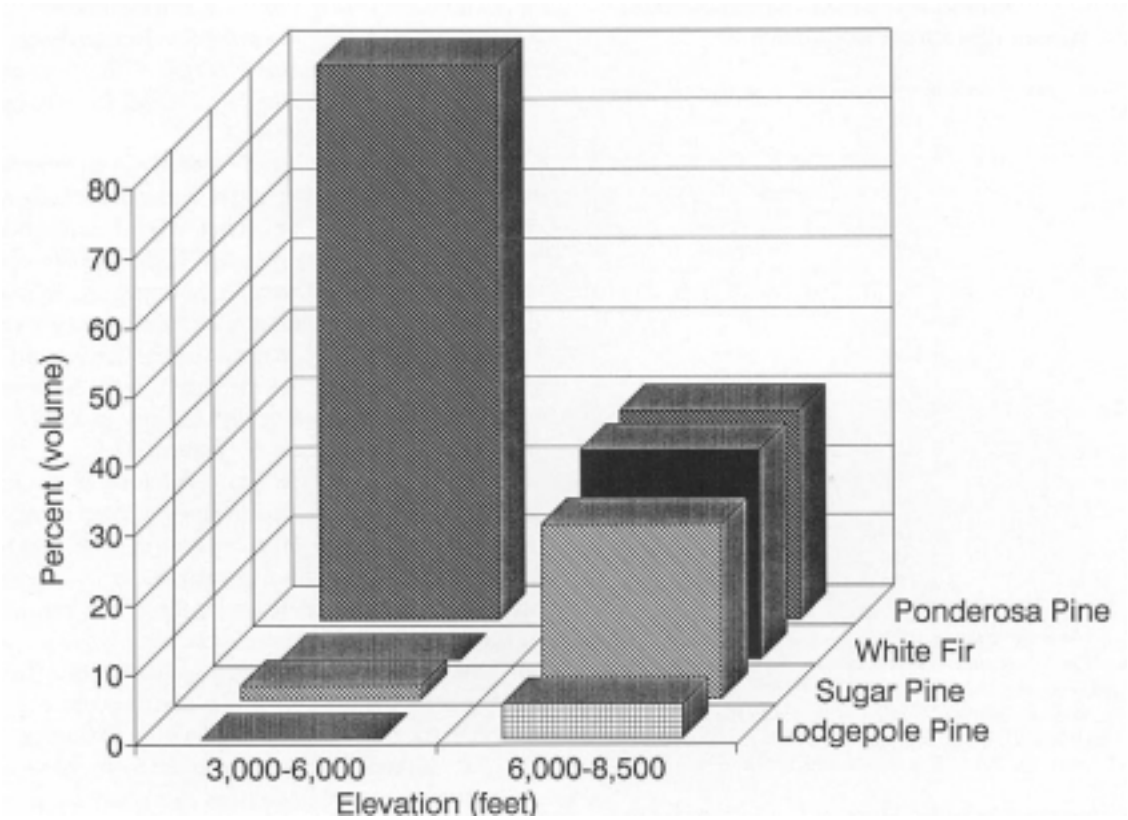

Figure 11Z--Species composition in the San Jacinto Forest Reserve in 1897 (Leiberg 1899a). Hardwood species, with the exception of oaks, were not used when Leiberg calculated percent contribution, by species.

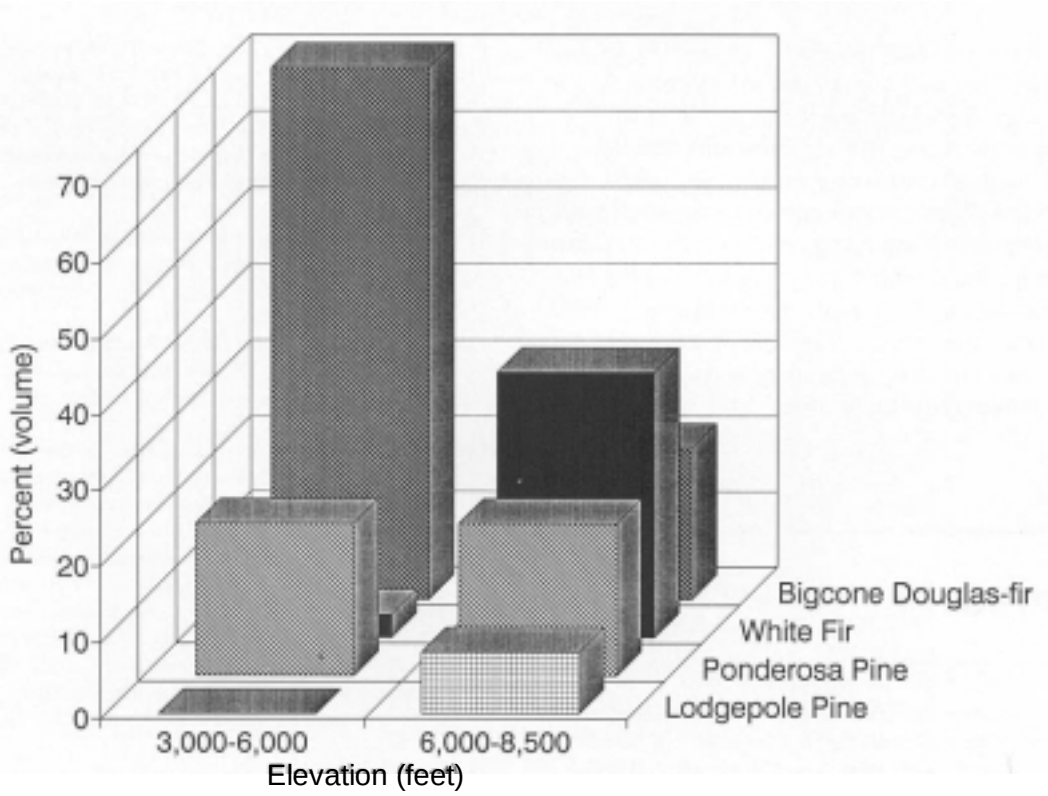

Figure 11AA--Species composition in the San Gabriel Forest Reserve in 1897 (Leiberg 1899c). Hardwood species, with the exception of oaks, were not used when Leiberg calculated percent contribution, by species.

The San Gabriel Mountains are extremely steep, so they were not logged or grazed extensively. They were (and still are) very susceptible to burning, however. In particular Leiberg (1897c, p. 369) noted the destruction of bigcone Douglas-fir stands by fire:

> *Among the non-commercial species of trees the bigcone fir has suffered the most. Large tracts once covered by it have been totally laid waste and much of what remains is partially burned or scarred... It is not improbable that a considerable portion of the areas now grown up in brush were in the past covered with a forest of bigcone fir. The very numerous small groves and individual trees of the species rising from the sea of chaparral would lead one to infer that they represent remnants of a more extensive forest. It is also noteworthy that the worst-burnt areas in the three reserves examined are to be found in the San Gabriel Reserve in the region of the most extensive mining operations.*

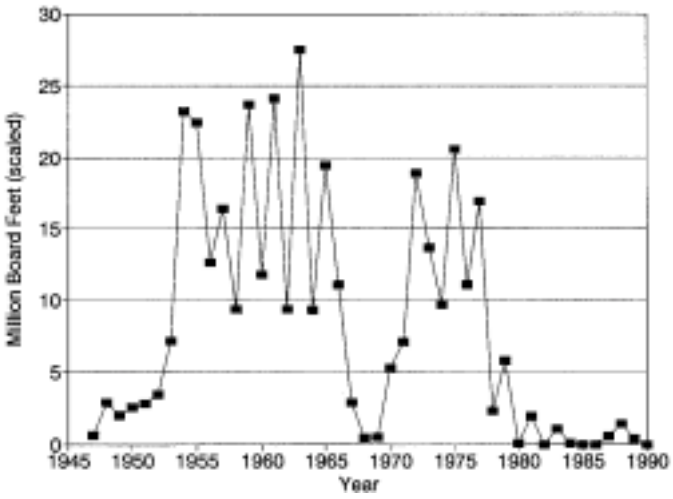

Figure 11AB-Logging intensity in San Bernardino and Los Angeles Counties, 1947-1990 (California Department of Forestry and Fire Protection 1947-78, California State Board of Equalization 1979-90).

Cutting History in Southern California

We have reconstructed the history of the removal of timber volume from San Bernardino and Los Angeles counties. Volume removed from 1947 to 1990 was based on data from the California Department of Forestry and Fire Protection (1947-78) and the California State Board of Equalization (1979-90). The San Bernardino NF had a very active timber program after World War II, cutting 27.4 MMBF in 1963 alone (fig. 11AB). Altogether, 362.3 MMBF of timber have been removed from these counties since 1947.

Discussion

Changes induced by nonaboriginal man in the southern California forests appear to have been slight by the turn of the century. Some logging and grazing had occurred by then. Leiberg described fires as being widespread but, with the exception of bigcone Douglas-fir stands in the San Gabriel Mountains, he apparently did not believe that forest structure or the balance

between brush and conifer forests was being changed by the fire patterns. Leiberg had no way to ascertain the extent to which burning patterns at that time were unnatural.

In the period after World War II, forest structures would have been significantly altered where timber was logged. Because logging would have been concentrated on sites with higher productivity, it undoubtedly impacted spotted owl habitat, though we cannot determine the extent of that impact. In general, the proportion of the area supporting conifer forests appears to have been reasonably static over the last 90 years. No evidence supports the idea of either spreading or shrinking acreage of chaparral in southern California over that period.

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Chapter 12

Fire and Fuels Management in Relation to Owl Habitat in Forests of the Sierra Nevada and Southern California

C. Phillip Weatherspoon, Susan J. Husari, and Jan W. van Wagtendonk

Over the millennia, fire has influenced the structure and function of most forested ecosystems and, consequently, most spotted owl habitat in California. Fire is a force that we must understand and attempt to deal with--as a shaper of ecosystems, as a tool, and as a potential destroyer of habitat-if we are to manage intelligently for the California spotted owl. In this chapter we discuss some fire management considerations related to protecting and possibly enhancing owl habitat. We concentrate on Sierran mixed-conifer forests--the most important and extensive habitat type statewide for the spotted owl, and on live oak/bigcone Douglas-fir forests--one of the most important habitat types in southern California (table 1B). We include brief discussions of three additional types-Sierran red fir and southern California mixed-conifer and riparian/hardwood.

Sierran Mixed-Conifer

Sierran mixed-conifer forests contain an estimated 62 percent of all California spotted owl sites in California (table 1B). They are characterized by mixtures of white fir, ponderosa pine, sugar pine, incense-cedar, black oak, Douglas-fir, and giant sequoia. The forest type occurs throughout middle elevations of the Sierra Nevada (Tappeiner 1980; table 1B).

An appreciation of the concept of fire regimes is helpful in understanding the role of fire in mixed-conifer forests. A fire regime is an expression of the frequency, severity, and extent of fires occurring in an area (Agee 1990). It is a function of the frequency with which fuels are dry and continuous enough to carry fire at a time when ignition sources are available, and thus is strongly related to climate. In general, the longer the fire-free interval, the more severe the fire that follows, because more fuels have accumulated in the interim.

Prior to European settlement in the mid-1800s, Sierran mixed-conifer forests were characterized by a short-interval, low- to moderate-severity fire regime. As a result of human activities since the mid-1800s (Chapter 11), including a policy of fire suppression initiated soon after the beginning of the twentieth century, this fire regime has been changed to one of less frequent but substantially more severe fires.

Presettlement Fire Regimes

Several studies have shown that mixed-conifer forests burned rather frequently during the centuries preceding European settlement. Lightning and, in many areas, Native Americans provided the ignition sources. The most comprehensive body of work on fire history in the Sierra Nevada has been done in the giant sequoia groves (Swetnam et al. 1991, Swetnam pers. comm.). These studies documented fire occurrence for 1,500 years and indicated a mean fire interval of 5 to 10 years since 1300 AD for the five groves studied. Maximum fire intervals recorded were 20 years. Other studies (Kotok 1933, Wagener 1961, Kilgore and Taylor 1979, Warner 1980, Skinner 1991) suggested that the mixed-conifer type had a mean fire interval in the range of 5 to 30 years. Mean fire intervals varied in response to site and environmental factors that affected ignition source, fuel accumulation, fuel moisture, and burning conditions. Thus, more mesic sites (for example, moist canyon bottoms, northerly slopes, and higher elevations) and sites protected from winds burned less often than relatively xeric and/or exposed sites (Kilgore and Taylor 1979, Teensma 1987). (The relatively mesic sites may tend to be more closely associated with nesting and roosting habitat used by the spotted owl.) Furthermore, climatic fluctuations on a time scale of centuries (fig. 11X) were reflected in more frequent fires during drier periods (Swetnam et al. 1991).

Frequent fires in the mixed-conifer type maintained surface fuels at fairly low levels, and kept understories relatively free of trees and other vegetation that could form fuel ladders to carry surface fires into the main canopy. This effect of frequent fires, together with widespread, heavy grazing by sheep after the mid-1800s (Chapter I1), probably accounts for the common reports by early observers that forests of the Sierra Nevada were open and parklike (Sudworth 1900, Biswell 1989). Because fuel accumulation was limited, most fires were of low to moderate severity (Sudworth 1900, Kilgore 1973, Biswell 1989). High-severity crown fires usually could not be sustained over large areas (Show and Kotok 1924, Kilgore 1973, Kilgore and Taylor 1979). On the other hand, crown fires that affected small areas .(ranging in size from a single tree, to groups of trees, to perhaps several acres) probably were relatively common and an important influence on stand structure. These patches of high fire severity, interspersed within a "matrix" of low-severity fires (Stephenson et al. 1991), occurred in areas with heavy fuel accumulations, sometimes reinforced by steep slopes or extreme weather conditions. This complex fire regime, along with other agents of disturbance (for example, group kills of trees by bark beetles), produced a variable, irregular patchwork of even-aged

groups, most from less than an acre to several acres in size (Show and Kotok 1924; Rundel et al. 1977; Bonnicksen and Stone 1981, 1982; Biswell 1989). Consequently, a relatively fine-grained pattern of variability, modified by topography, existed at a landscape scale.

Openings created by fires and other disturbances provided conditions favorable for regeneration and growth of shade-intolerant and relatively fire-resistant trees and other plants. These species include ponderosa pine, giant sequoia, and California black oak, which is only moderately resistant to top-kill by fire but sprouts vigorously. They were able to regenerate successfully in the presence of frequent fires because of the fuel dynamics of openings in which they became established: A typical scenario may have begun with the death of a small group of trees-by bark beetles, locally-intense fire, or other causes. The resulting concentration of fuel was reduced by one or more fires. Mineral soil was exposed, and competing vegetation (including reserves of dormant seeds stored in duff and soil) was reduced. Given a good cone crop and favorable soil moisture and other conditions, seedlings became established. Subsequent fires in the vicinity burned only lightly, if at all, through the opening because of the local lack of an overstory to provide sufficient litter to carry the fire. By the time the new regeneration produced enough litter to carry a fire of appreciable intensity through the opening, some of the young trees were large enough to survive the fire (Kilgore 1973, Biswell 1989). Fire-resistant species would have comprised a disproportionate number of the survivors.

The more shade-tolerant and fire-sensitive species (white fir and incense-cedar) regenerated beneath overstory trees as well as in openings. Periodic fires, however, kept their numbers relatively low, especially in the understory. The more mesic sites generally experienced longer fire intervals and thus permitted more individuals of fire-sensitive species to survive and grow (Kilgore and Taylor 1979).

Twentieth Century Fire Regimes

Twentieth century fire regimes bear little resemblance to those of presettlement times, largely because of human activities since the mid-1800s. One marked difference has been in the annual acreage burned. For example, using a conservative mean fire interval of 20 years for the 586,000-acre Eldorado National Forest (NF), we would expect a mean of 29,000 acres to burn annually. In fact, 13,944 acres burned during the entire period from 1970 through 1990-an average of only 664 acres per year. On the 1,168,500-acre Plumas NF, 85,000 acres burned in the same 21-year period-an average of 4,048 acres per year, although about 58,000 acres would be expected to burn there each year with a mean fire interval of 20 years.

We must get beyond the number of ignitions and acres burned, however, to evaluate relations of wildfires to spotted owl habitat. A study of lightning fires by vegetation type in Yosemite National Park (NP) showed that over 50 percent of the 2,000 fires ignited between 1930 and 1983 occurred in the mixed-conifer zone (van Wagtendonk 1986). Forest Service statistics do not categorize fires according to vegetation types. Most NFs, however, do have maps that can provide useful information about the spatial and temporal distribution of fires during the twentieth century. Figures 12A and 12B, for example, show the distribution of all lightning fires and all large fires (100+ acres) on the Lassen NF since 1900. Lightning-caused ignitions were scattered over the entire forest. Fires that escaped initial attack and grew large, however, were not evenly distributed. Large fires were grouped in Sierran foothill areas and on the east side of the crest. Similar patterns occurred farther south in the Sierra Nevada. In the 1920s and 1930s, many fires occurred in Sierran foothills and at lower elevations in the mixed-conifer belt-the same general areas where early timber operations (Chapter 11) and widespread burning for range improvement were concentrated. Fires east of the Sierran crest accounted for much of the balance of the large fires this century. Over 50 percent of the nearly 85,000 acres of forested land burned on the Plumas NF since 1970, for example, have burned east of the crest. Within these two broad zones that dominate forest fire statistics in the Sierra Nevada, owls use significant portions of the lower-elevation forests on the western slopes, at least down through the ponderosa pine/hardwood type to the upper digger pine/blue oak type, but they are rare in the eastside forests. In these two zones, fires more often move rapidly beyond the initiating stage and defy initial attack because of flashy fuels, drier conditions, and exposure to high winds.

By comparison, success of initial attack on wildfires evidently is greater in areas of owl habitat within the Sierran mixed-conifer type. Countryman's (1955) description of fuel conditions within old-growth stands applies in large measure to fuel conditions within many mixed-conifer stands used by the California spotted owl. These stands are less flammable under most conditions, because the dense canopies maintain higher relative humidities within the stands and reduce heating and drying of surface fuels by solar radiation and wind. The reduction of wind velocity within closed stands discussed by Countryman is supported by wind reduction factors identified by Rothermel (1983) for stands with closed canopies. Windspeed at mid-flame height for fires burning in surface fuels is approximately one-tenth of the windspeed 20 feet above the stand canopy.

As fuels accumulate, however, fires that do escape initial attack -usually those burning under severe conditions-are increasingly likely to become large and damaging. Success in excluding fire from large areas that were once regulated by frequent, low- to moderate-severity fires has simply shifted the fire regime to one of long-interval, high-severity, stand-replacing fires (van Wagtendonk 1974, Kilgore 1973, Parsons and DeBenedetti 1979, Agee and Edmonds 1992). Forests where owls are found more often than expected (Chapter 5) satisfy the structural requirements outlined by Rothermel (1991) for the propagation and spread of crown fires-heavy accumulations of dead-and-downed fuels, conifer reproduction and other ladder fuels, and continuous forests of conifer trees. Crown fires occur when these features are combined with dry fuels, low humidities, high temperatures, steep slopes, strong winds, and unstable atmosphere.

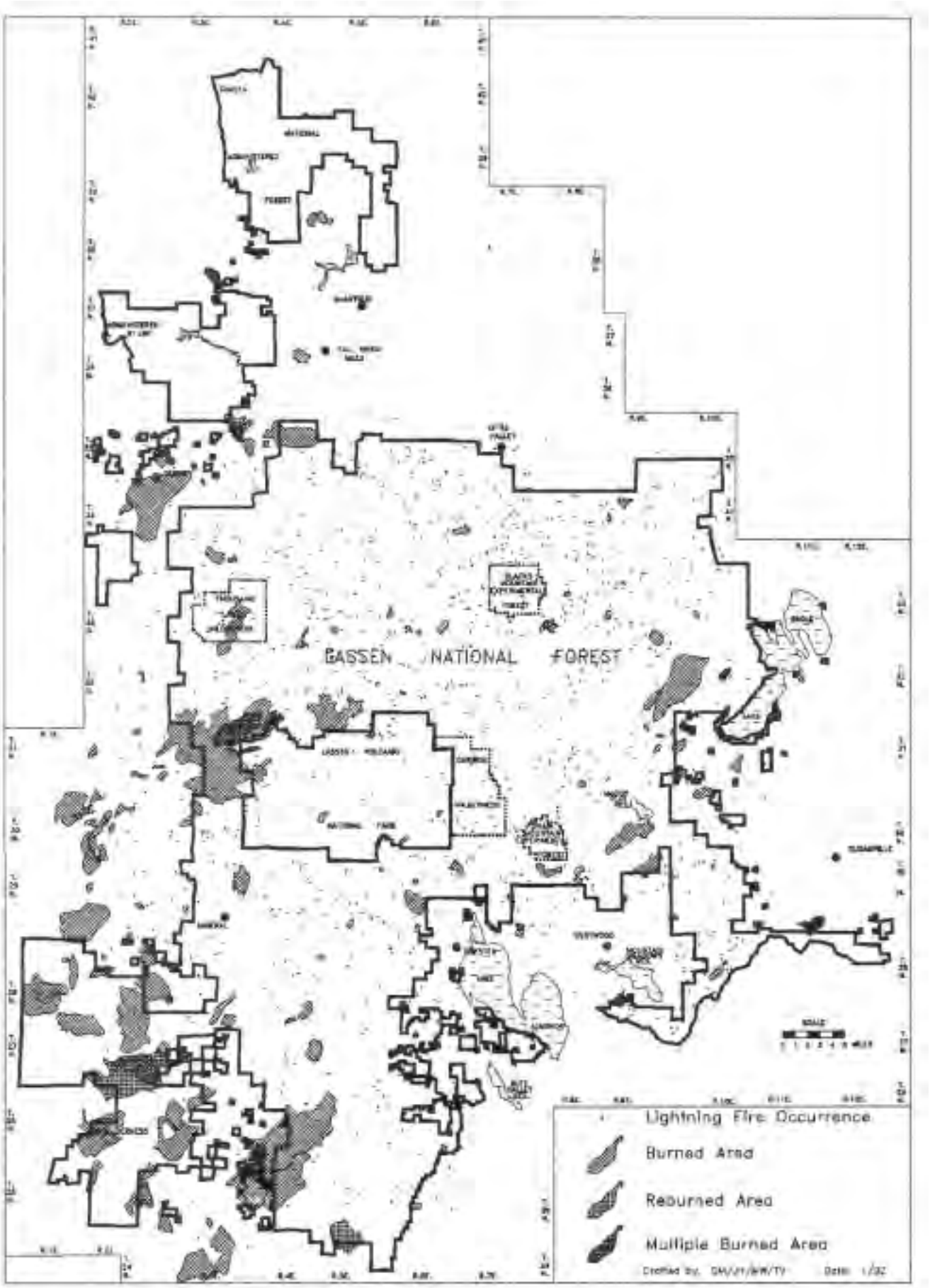

Figure 12A--Fire history of the Lassen National Forest from 1900 through 1939.

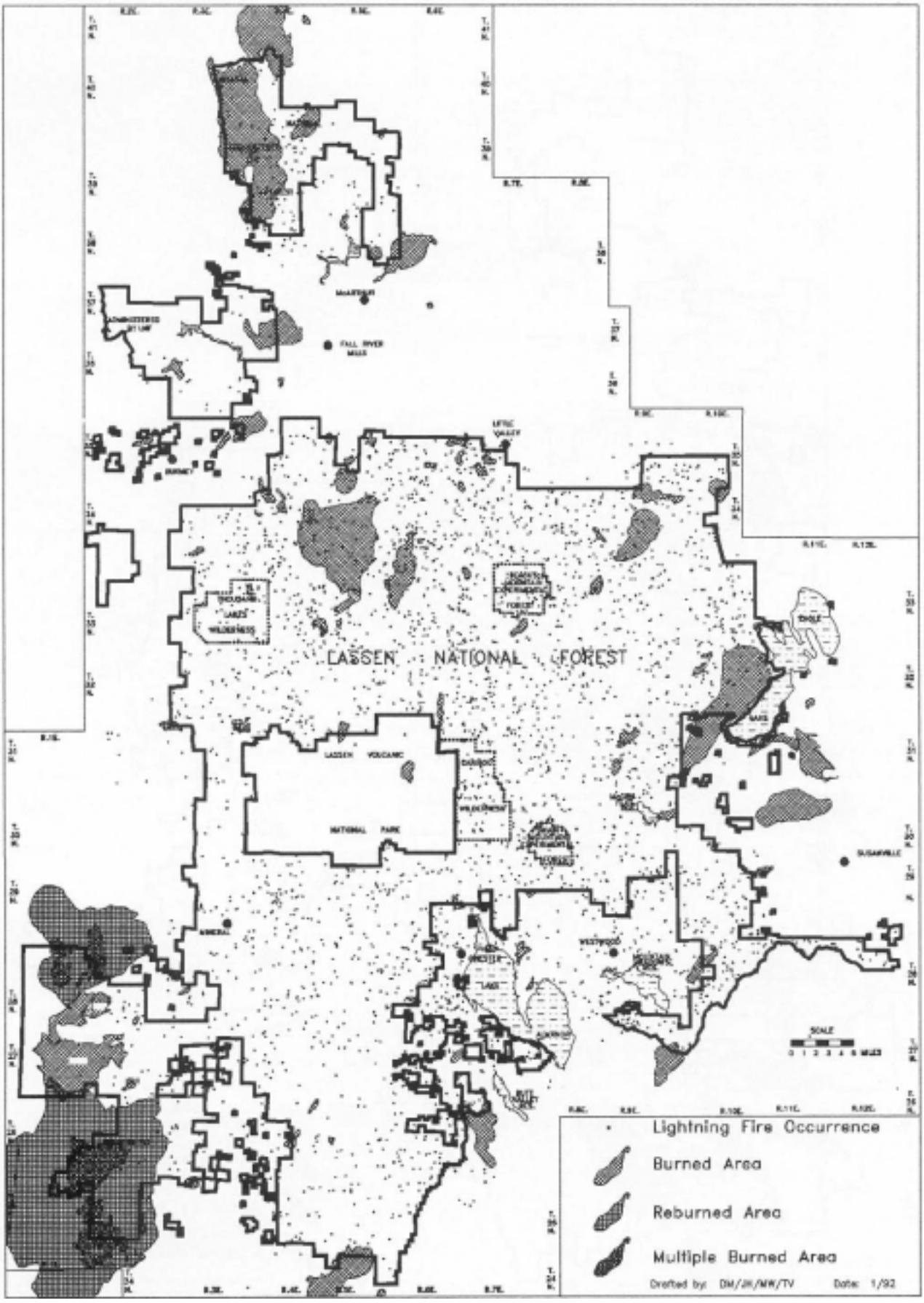

Figure 12B--Fire history of the Lassen National Forest from 1940 through 1990.

Two recent examples of severe, stand-replacing wildfires in owl habitat in the mixed-conifer type were the Stanislaus Complex (1987) on the Stanislaus NF and the Stormy Fire (1990) on the Sequoia NF. Both of these fires burned areas with known owl sites. Numerous other large fires have burned in the general elevational band where owl habitat is found. Although these areas had not been surveyed for owls prior to burning, we assert that they were also home to owls prior to fire. Based on such fires, we suggest three scenarios for severe wildfires in Sierran or southern California mixed-conifer types:

Scenario l: A fire initiates low on the slope, typically in brushfields, and spreads into the mixed-conifer zone. The fire does not drop to the forest floor because heavy fuel accumulations and fuel ladders, combined with steep slopes, promote either spread through crowns or widespread torching of trees. This is the expected model for areas of mixed-conifer forest lying directly upslope from large brushfields and for imbedded habitat in brushfields in southern California forests. Such fires bum for one to several burning periods (see glossary). Fire behavior is controlled by topography and fuels. Generally the fire is contained within one or several drainages. Control lines are constructed at the break in slope. Regular occurrence of this type of fire results in gradual loss of habitat.

Scenario 2: Many lightning fires are ignited simultaneously and fire-fighting resources are quickly exhausted. All resources are devoted to initial attack or to protection of structures and communities threatened by fires that escape initial attack. Fires become large and burn under changing weather and fuel conditions, until enough resources can be gathered and organized to effect control. In such cases fires burning in uniform fuels become so large that suppression remains unsuccessful until weather conditions moderate, spread ceases, and firelines can be constructed around the entire perimeter. Groups of lightning fires in 1977 and 1987 were examples of this scenario. Weatherspoon and Skinner (1992) found that the effects of such unconstrained fires depended on the fuel conditions they burned through, and corresponded well with prior management actions, including fuel treatments.

Scenario 3: A human-caused fire starts under severe fire weather conditions. Fire spread continues through the duration of the wind event. Examples of synoptic weather patterns associated with such events are detailed by Schroeder et al. (1964). Examples are east winds in the northern Sierra Nevada and Santa Ana conditions in southern California.

A study of lightning fires and spotted owl territories in Yosemite NP showed that owls can and do exist with extensive fires of varying intensities where forest structure has been affected relatively little by human activities. Fifty-six owl sites were confirmed in the Park during surveys in 1988 and 1989 (Gould pers. comm.), and an additional 45 locations were identified as probable owl sites in unsurveyed areas of the Park where the habitat appears to be suitable for the owls (Steger pers. comm.). Among the 56 confirmed sites, six had been burned by prescribed natural fires during the 8 years prior to the surveys when owls were located there (fig. 12C). Over 800 acres of habitat within a 1,200-foot radius of confirmed owl sites had been burned, and an additional 1,300 acres had been burned within a 2,000-foot radius. Crown fires were extensive in one case, although the nest site itself was under-burned. The remaining fires were primarily low to moderate in intensity, with only occasional torched areas.

Effects of Fire Suppression

The structure and composition of Sierran mixed-conifer forests have been affected profoundly by fire suppression policies begun in the early 1900s. This and other forest types with short-interval fire regimes have been changed more by suppression than types with longer fire intervals because more cycles of fire and associated fire effects have been excluded in the short-interval regimes.

As frequent fires of low to moderate severity ceased to be a dominant ecological force, shade-tolerant and fire-sensitive tree species (especially white fir) increased dramatically in abundance, particularly in small to medium size classes. Previously much less common except in the cool and moist extremes of the type, multiple-canopied stands consisting largely of these shade-tolerant species are now common (Parsons and DeBenedetti 1979, Bonnicksen and Stone 1982, van Wagtendonk 1985). Regeneration of pines, black oak, and other shade-intolerant species has declined, except in areas opened by wildfires or management activities. "Selective" cutting has reinforced the changes in stand structure and composition brought about by fire exclusion (color photo 5-10). The patchwork of small, even-aged aggregations that characterized the mixed-conifer type before 1900 has become less distinct (Bonnicksen and Stone 1982). Consequently, stands have become more complex when viewed vertically, but less complex and more homogeneous in terms of areal arrangement.

With fire suppression, fuels on the forest floor (including coarse woody debris) have accumulated far beyond their normal levels (Parsons and DeBenedetti 1979). The increased prevalence of white fir in the understory has created hazardous fuel ladders, linking surface fuels to upper canopy layers (color photos 5-5, 5-10, 5-12 to 5-14). Increases not only in quantity, but also in horizontal and vertical continuity, of fuels have substantially increased the probability of large-scale, catastrophic fires (Kilgore and Sando 1975, van Wagtendonk 1985).

Unnaturally dense stands mean more competition for available water, and therefore greater moisture stress. During periods of drought, notably the current one (fig. 4H), extensive mortality is the result-some directly from drought stress, much from stress-induced bark beetle outbreaks. These stands may be more prone to damage from defoliating insects and various root and stem diseases as well. The dead and dying trees also add greatly to the already high fuel loads, thereby increasing intensity and rate of spread in the event of a wildfire. More snags and large woody fuels are likely to increase fire spotting and suppression difficulty, and greater heating damage to soils may result from consumption of more large materials. Moreover, opening of the canopy as a result of tree mortality permits more solar radiation and wind to reach the ground, resulting in warmer and drier fuels (Countryman 1955), which ignite more easily and support more intense, faster-spreading fires.

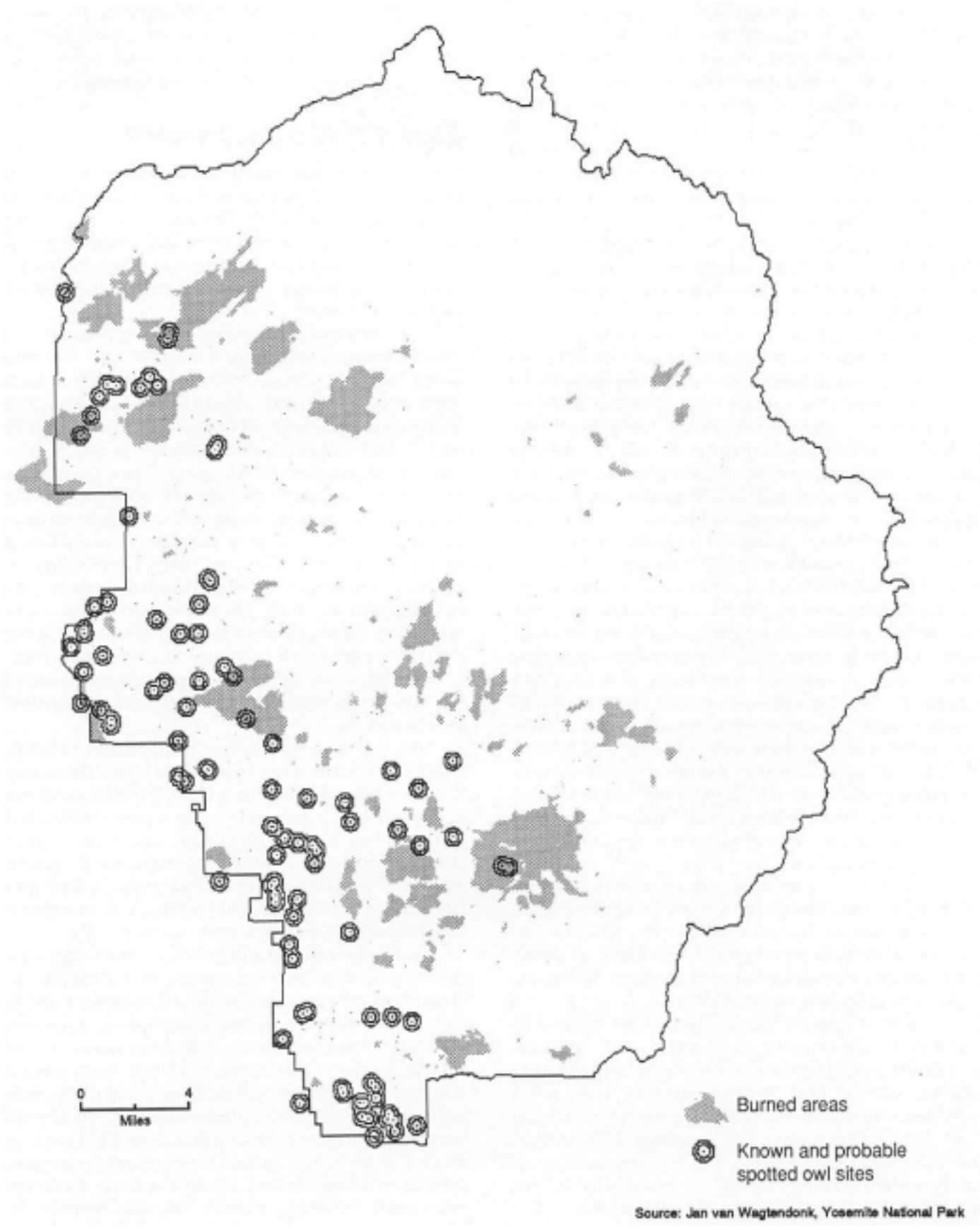

Figure 12C--Known and probable spotted owl sites and lightning fires in Yosemite National Park from 1930 through 1989 (based on data from Gould pers. comm., Steger pers. comm., and J. W. van Wagtendonk pers. observ.).

Implications for Spotted Owl Management

Several changes at least partly attributable to fire suppression (for example, increased stand density, greater development of middle and lower canopy layers, more snags, more coarse woody debris) have been associated with biologists' perceptions of suitable owl habitat. Other such changes may be detrimental to habitat quality. Excessively dense understories may impede foraging and, to the extent that diversity of tree species-to include pines and oaks-is important, continued exclusion of fire may be degrading habitat quality. Much uncertainty still clouds our understanding of which stand attributes are critical for owls and which are only incidental. Nevertheless, it is possible that fire exclusion in Sierran mixed-conifer forests has led to a net improvement in spotted owl habitat there.

If owl habitat has improved as a result of fire suppression, such improvement may well be illusory and short-lived. Fire is inevitable in these forests, and the probability of catastrophic fire-certainly one of the greatest threats to owl habitat-increases as surface fuels and ladder fuels continue to accumulate (Kilgore and Sando 1975, van Wagtendonk 1985). Overly dense stands are subject to extensive mortality from drought and insects, including loss of the most desirable large, old trees.

Another possibility is that owls were highly successful in presettlement stand structures resulting from the unimpeded functioning of natural processes, including fire. For Sierran mixed-conifer forests, such a landscape probably consisted of a complex array of mostly small, even-aged aggregations and/or stands representing a wide range of age- and size-classes. Compared with current stand structures, stands would have been less dense, and groups of different-sized trees would have been separated more horizontally into even-aged aggregations with less vertical diversity within groups.

In either case, a management policy characterized as "hands-off plus fire exclusion" (allow forest succession to proceed uninterrupted by periodic natural disturbances) would likely lead to degraded and depauperate, rather than healthy and biologically diverse, ecosystems. A more prudent and conservative policy for the spotted owl, as well as for other species and ecosystem components, would be to use our understanding of natural ecosystem processes (including fire) to guide management (see management options later in this chapter and in Chapter 13).

Fuels

Nesting and roosting areas in Sierran mixed-conifer forests exhibit structural characteristics (Chapter 5) that affect fire behavior. These stands have large trees, closed canopies, and multiple layers. Vertical and horizontal structures are continuous, encouraging the movement of fire into tree crowns. Such movement is discouraged if lower canopy layers are removed, interrupting the upward spread of fire.

The limited quantitative data on surface fuels at spotted owl sites (see tables in Chapter 5) suggest that loadings of large-diameter (greater than 11 inches) woody fuels are variable, but generally moderately heavy when compared to the range of loadings of natural fuels described by Blonski and Schramel (1981) for mixed-conifer forests in the Sierra Nevada. The guidelines in Chapter 1 for retention of at least 10-15 tons/acre of large downed wood represent the low end of the range of values observed in owl habitat-a loading probably acceptable from a fuels standpoint in most situations. Residues less than 11 inches in diameter probably are less essential to owls. Removal of smaller fuels, especially those less than 3 inches in diameter, results in reduced fire intensities, lower rates of spread, and lower resistance to control.

Fire and Fuels Management Options

Chapter 1 includes general guidelines for fuels management as part of its recommendations for interim management of "Other Forested Public Lands" in the Sierra Nevada. An alternative approach for interim management of *"Selected Timber Strata"* presented in Chapter 13 also includes guidelines for fuels management. In addition, Chapter 13 offers suggestions for fuels management as part of a set of potential long-term strategies to manage for owl habitat in Sierran mixed-conifer forests. Management activities described in Chapters 1 and 13 involve various kinds of cuttings. Because of the additional fuels created by these cuttings, and the warmer and drier microclimate at the forest floor resulting from stand openings, adequate treatment of slash fuels is essential. Otherwise, wildfire hazard is likely to be greater than before the activity (Countryman 1955, Weatherspoon and Skinner 1992). Several options are normally available to treat fuels, and revenues from harvested timber often will fund part or all of the planned fuels management.

In this section, we discuss a general approach for using prescribed burning to manage fuels (in addition to any other benefits that might accrue) in areas of nesting and roosting habitat where commercial harvesting of timber or other wood products will not be done. Such areas might include *"Protected Activity Centers"* (Chapter 1) and any other areas of owl habitat from which logging has been excluded administratively or legally. They might also include *"Selected Timber Strata"* in locations where harvesting is not economical for various reasons, given the constraints outlined in Chapter 1. Effects of prescribed burns should be carefully monitored as part of adaptive management experiments designed to improve our understanding of owl habitat and our ability to manage for it (Chapters 2 and 13).

Considering the significant and increasing risk of stand-destroying wildfire, as discussed earlier, we recommend that prescribed burning in these areas be given a high priority. Without substantial increases in funding for prescribed burning, the likelihood of losing large acreages of owl habitat to severe wildfires will increase over time. Additional prescribed burning would produce more smoke at a time when regulation of air quality is becoming increasingly restrictive. Consequently, the benefits of underburning-for owl habitat, for other ecosystem values, and for reducing smoke from wildfires-and associated

tradeoffs in air quality will need to be clearly defined and articulated. This should be coupled with increased utilization of woody material and greater use of nonburning methods of fuels management in timber harvest areas, to the extent that they make sense ecologically and managerially. The prescribed burning recommended here should be coordinated, on a broad scale, with fuels management activities described in Chapters 1 and 13 to ensure the most effective and efficient use of dollars and other resources for protecting owl habitat. In many areas, succession and fuel accumulation have progressed to the point that prescribed burning is impractical as a first treatment. Outside *"Protected Activity Centers,"* such areas may require some combination of understory thinning and mechanical treatment of fuels, or removal prior to burning, to ensure that fire intensities remain within an acceptable range. We suggest the following priorities for prescribed burning within nonharvested areas of owl habitat in the Sierran mixed-conifer type.

First Priority

All hazard-reduction objectives of prescribed burning involve reducing amounts and continuity of fuels. Our recommended first priority is to isolate (that is, disrupt fuel continuity around) known nest and roost sites within *"Protected Activity Centers,"* using a band of prescribed bums. We recognize that this strategy poses some small risk to existing birds, but these risks can be at least partially mitigated. To the extent possible, burns should be concentrated, at least initially, on south-facing slopes (aspects from southeast through west) and ridges surrounding or adjoining nest/roost sites. Compared with more northerly slopes, these aspects have drier, more flammable fuels likely to support severe wildfires under a wider range of burning conditions (given effects of fire suppression). On the other hand, southerly slopes offer several advantages for prescribed burning: (1) They dry out earlier in the year, sometimes allowing spring burns to be done with minimal construction of firelines (thus lower cost) at times when fire will not spread onto adjacent northerly slopes. (2) Stands on south-facing slopes tend to be more open, with less dense understory to provide troublesome fuel ladders. (3) They tend to have a higher proportion of ponderosa pine, which not only resists fire damage rather well but also provides litter that can carry fire at the cool, moist end of a prescription-frequently desirable conditions for a first burn.

After many decades of fuel accumulation, initial prescribed burns can result in excessive consumption of duff and coarse woody debris. This is undesirable for at least two reasons: First, duff and coarse woody debris are important substrates for hypogeous fungi-prime food for flying squirrels (Chapters 4 and 10); and second, long-duration heating from extended smoldering of duff can damage tree roots and root crowns, sometimes causing delayed mortality even in large, old trees (Thomas and Agee 1986, Swezy and Agee 1991, Sackett pers. comm.). Conducting initial prescribed burns in the spring, when the moisture content of duff and large fuels is high, will help to minimize the problem of excessive duff consumption. The more flammable surface fuels-litter and small woody debris-can still be largely consumed. An additional advantage of low consumption of duff and large woody fuels is a reduction of atmospheric emissions. As adaptive management experiments continue over time, efforts should be made to align prescribed burns more closely with natural fire regimes in terms of the frequency and season of burns. In the meantime, however, effects of initial spring prescribed burns should be carefully monitored to assure that species diversity is retained and that birds and other wildlife are not disturbed during the breeding season.

In stands with many small understory trees and low crowns, burning should be initiated carefully, using small test burns at first. Flame lengths and their effect on torching of small trees should be closely monitored, and firing patterns should be adjusted as necessary to keep flame lengths within prescribed limits (Martin and Dell 1978, Kilgore and Curtis 1987, Weatherspoon et al. 1989). An initial prescribed burn will usually create some interruption of vertical fuel ladders (after scorched needles drop to the ground). Many small trees will be killed, however, and often more dead fuels will be created than consumed. Such understory burns, therefore, carry an implied commitment that the stand will be reburned at least once, generally within 10 years or so, to clean up fuels created by the first prescribed burn and to reduce vertical fuel ladders further.

Second Priority

After nest and roost sites have received some protection, a more general program of prescribed burning should be initiated. The objective is to break up fuel continuity on a larger scale and to begin to restore fire as a natural process in the ecosystem. Southerly slopes and ridgetops would be favored for burning, as suggested above. Followup burns would be implemented as needed to effect and maintain a meaningful interruption of fuel continuity and reduction in wildfire hazard. Burns should be well-distributed, creating a mosaic of broad "fuelbreaks" covering one-third or more of the total area. Such a program would be expected to limit substantially the size and severity of subsequent wildfires. Special emphasis should be given to prescribed burning that reinforces natural and constructed barriers to fire, such as rocky outcrops, bare ridges, roads, and constructed fuelbreaks. These provide relatively defensible areas from which firefighters can safely implement fire suppression strategies.

As indicated earlier, the approach discussed in this chapter assumes no commercial harvesting (including biomass harvesting of small trees). Outside *"Protected Activity Centers"* or similarly restrictive areas, however, initial prescribed burns in some stands with dense understories and dangerous fuel ladders may be facilitated by felling many of the small trees before burning. To limit intensity and consumption, and thus damage to the residual stand, the prescribed burn could then be done before the newly felled trees have fully dried.

Third Priority

For long-term protection, prescribed burning should be applied throughout owl habitat in the mixed-conifer zone with a frequency distribution similar to presettlement fire intervals. Northerly aspects and other areas not previously included in the prescribed burning program should be incorporated. Limitations

on such a program and factors to consider include: (1) availability of resources; (2) need for improved information from research and monitoring activities concerning habitat attributes, fire history, and fire effects; (3) need for prescribed fire to maintain and improve owl habitat in the absence of other silvicultural tools; (4) need for fire to provide other ecosystem values; and (5) smoke management and air quality implications of a widespread prescribed burning program (including information about estimated background levels of smoke during presettlement fire regimes, and tradeoffs between increased smoke from prescribed fires versus reduced smoke from wildfires). If the second priority program is carried out successfully-coupled with appropriate fuels management in adjoining harvested areas (Chapters 1 and 13)---occurrence of large, catastrophic wildfires within owl habitat will be of less concern. The focus of prescribed fire for this third stage will then shift generally from hazard reduction to reestablishment of an important ecosystem process. Long-term sustainability of owl habitat on a landscape scale should result.

Red Fir

Fire Regimes

The relatively few studies of natural fire regimes in the red fir type have indicated mean fire intervals ranging between about 40 and 100 years (Kilgore 1981, Pitcher 1987, Taylor and Halpern 1991). Higher-elevation areas tend to have less frequent fires because biomass (fuel) accumulates more slowly and weather conditions that will support a fire occur less often. Despite longer fire intervals than in the mixed-conifer type, fire has been the dominant disturbance factor associated with episodes of regeneration in much of the red fir type. A range of severities and frequencies of fire has led to a complex pattern of various patch sizes and tree ages (Pitcher 1987, Taylor and Halpern 1991). Compared with lower-elevation forest types, fire suppression has had less effect on the red fir type. Suppression activities began later in red fir forests, and fewer fires would have burned there even without suppression. In addition, because red fir forests are largely monospecific and red fir is relatively shade tolerant, the successional trend toward more shade-tolerant species in the absence of fire (a concern in the mixed-conifer type) is not a factor in the red fir type.

Despite many lightning-caused ignitions in the red fir type (Maupin pers. comm.), such fires seldom have gotten large on lands where a suppression strategy is used, because initial attack is almost always successful. The behavior of natural fire has been extensively documented in Yosemite and Sequoia/Kings Canyon NPs, where much of the red fir type is included in the prescribed natural fire zone. To date, no evidence suggests that the prescribed natural fire programs in the NPs have had an adverse impact on the owls found there. Lightning fires in the red fir type usually burn with relatively low intensity and spread slowly over long periods, with occasional episodes of rapid spread during periods of severe fire weather. Crown fire is unusual in this type except under rare high-wind events, partly because sparse understory vegetation (Rundel el al. 1977) provides limited fuel ladders. Some examples of crown fire, however, were observed during the 1987 fire season. Torching also has been observed when human-caused fires burned into the red fir forest under extreme conditions.

Sixteen percent of the fires recorded in Yosemite NP between 1930 and 1983 occurred in the red fir zone, even though it comprises only 8 percent of the park. The majority of those fires were single trees, although larger fires occurred when red fir was mixed with chaparral (van Wagtendonk 1986).

Fuels

Color photo 5-1 provides an excellent illustration of typical fuel conditions in red fir. Fuel bed characteristics are quite different from those in the other habitat types. The short needles form a dense litter layer, which is further compacted by a heavy snow pack. This litter burns slowly, with relatively low intensities. Fuel ladders are nearly always interrupted. Dead-and-downed fuel loadings may be heavy in older stands, but fuel moistures remain high during most years in these high-elevation stands.

Fire Management Options

Fire may be allowed to play its natural role in much of the red fir type. Large sections of red fir forest found in wilderness areas should be evaluated for inclusion in wilderness fire-management programs that emphasize the role of fire as a natural process.

Southern California Mixed-Conifer

Fire Regimes

The natural role of fire in the southern California mixed-conifer community is similar to that described for the Sierran mixed-conifer community. Studies of fire history in the Los Padres NF (Talley and Griffin 1980) and the San Bernardino Mountains (McBride and Laven 1976, McBride and Jacobs 1980) suggest slightly longer mean fire intervals in these forests than those found in the Sierra Nevada. This may be explained by the lower incidence of lightning storms there, as well as smaller contiguous areas of mixed-conifer vegetation. In the southern California mixed-conifer type, as in the Sierra Nevada, the early

fire regime was typified by frequent low- to moderate-severity fires, which burned over long periods under a variety of fuel and weather conditions (Minnich 1988).

Fire suppression has been effective in reducing the number of large fires in the mixed-conifer type in the mountains of southern California. An analysis of fire records by McBride and Laven (1976) indicated that fire suppression has been effective in sharply reducing the number of acres burned on the San Bernardino NF, for example, from an annual acreage of 5,890 acres during the 1940s to 3,774 acres during the 1960s.

Talley and Griffin (1980) found evidence that twentieth century fire regimes result in infrequent fires of an intensity causing widespread mortality in pine stands that survived the frequent low- to moderate-severity fires of the past. Coniferous forests, which once burned more frequently than the chaparral stands below them, now burn at a frequency similar to that in the chaparral.

Examination of fire records indicates that most large wildfires in mixed-conifer forests in southern California fall under Scenarios 1 and 3, described for the Sierran mixed-conifer type.

Fire Management Options

Current practices of protecting all pairs of owls in this type should be continued. The fire management options described for Sierran mixed-conifer forests apply in southern California as well. It is essential, however, that fuels also be managed in the chaparral communities surrounding the conifers, to avoid catastrophic wildfires that spread from below into the mixed-conifer zone.

Live Oak/Bigcone Douglas-Fir Forests

The live oak/bigcone Douglas-fir community provides habitat for an estimated 41 percent of owl sites in southern California (tables 1B and 3I). Within the lower portions of its elevational range, this community occurs near streams in moist, shaded canyons and draws, where aspects are mostly north and east. As elevation increases, it occurs on other aspects and is less restricted to canyons (McDonald and Littrell 1976). Typically, bigcone Douglas-fir comprises a scattered overstory of single trees or small groups of trees, and tree-sized canyon live oaks form a relatively continuous midstory canopy. Shrubs and herbaceous plants are largely absent in the understory except beneath openings and along the margins of stands (McDonald 1990). Stands of live oak/bigcone Douglas-fir usually intergrade with chaparral along their margins.

Fire Regimes and Fire Effects

McDonald and Littrell (1976, p. 319) described "the overall pattern of the bigcone Douglas-fir-canyon live oak community [as] that of a stable, self-perpetuating, somewhat exclusive community, with tendencies toward the climax or even postclimax successional stage." The community evidently is not well-adapted to frequent fires. Bigcone Douglas-fir is unusual among conifers in its ability to sprout from a fire-scorched crown (color photo 5-39), but it is weakened from repeated fires that deplete energy reserves (McDonald 1990). It does not survive "torching" of the crown (consumption of foliage by flames). Seeds contained in cones in torched crowns almost certainly would not survive to provide regeneration. Indeed, natural regeneration of the species is very slow following severe fires (Minnich 1980). Young bigcone Douglas-firs are moderately shade-tolerant, and establishment of natural regeneration is often most successful in the partial shade provided by the canyon live oak canopy (McDonald 1990). Young trees grow slowly in the understory, however, and are easily destroyed by surface fires.

Oaks in general are not noted for their resistance to fire damage. Even among oaks, however, canyon live oak is unusually sensitive to damage and top-kill by fire (Minnich 1980, Plumb 1980). Its thin, dry, flaky bark ignites easily, often carrying fire several feet up a bole and commonly burning completely through the bark to expose the underlying wood. Frequently, heat kills enough cambium to girdle the bole, even with low-intensity surface fires (Plumb 1980). The relatively closed, compact canopy architecture also tends to trap heat from a fire beneath the canopy, thereby increasing crown scorch. On the other hand, canyon live oak sprouts vigorously from the root crown following top-kill by fire, and frequently after sublethal damage as well.

The unusual susceptibility of canyon live oak to top-kill by fire suggests that stands with many large, old trees (seemingly high-quality owl habitat-Chapter 5) probably have not experienced fires of any significance for many decades (Minnich 1988). The species grows more quickly to tree size in more mesic habitats, where fire intervals also are generally longer. Canyon live oaks that escape burning long enough to attain tree stature, in turn, tend to bestow a fire-retardant quality on the stands in which they grow (Minnich 1980). Possible reasons include: (1) chaparral shrubs or other understory plants that might provide a flammable fuel ladder into tree crowns are virtually absent; and (2) litter tends to be meager beneath canyon live oak and it is not particularly flammable, perhaps in part because of dry ravel on steep slopes that promotes mixing of litter and soil. Minnich (1977, p. 447) described fires spreading from chaparral into live oak/bigcone Douglas-fir stands that "usually incinerated the outermost fringe of stands. With further progress into the grove, the pattern of total combustion graded into a hot surface fire which only scorches the oaks as the distance between the tree canopy and ground fuels increases." Where wind and other burning conditions sustain a crown fire through the stand, however, restoration of prefire stand conditions will likely take a long time. Without intervention, canyon live oak sprouts will come up in a sea of seedling chaparral

shrubs. For many decades, the new community will be more likely to reburn than the old one-until the oaks again attain tree stature and shade out the shrubs. Meanwhile, bigcone Douglas-fir probably will be very slow to return, particularly if no surviving seed trees are nearby.

Fire and Fuels Management Options

We do not recommend prescribed burning within live oak/bigcone Douglas-fir stands (see Plumb 1980). From the standpoint of wildfire hazard, these stands are relatively nonflammable, as described earlier. They probably will not support a stand-destroying crown fire except under extreme conditions in which prescribed burning or other surface fuel reduction will have made little difference in fire behavior. Under less extreme conditions, the stand probably will support a moderately intense surface fire, which would top-kill many or most of the live oaks and allow many of the bigcone Douglas-firs to crown sprout. Restoration of suitable owl habitat would take place sooner than after a crown fire. If prescribed burning were done, it would be difficult and expensive in many stands because of the steep, broken terrain. Moreover, given the discontinuous, low-flammability fuels occurring in many stands, moderately severe burning conditions probably would be required to carry fire and reduce fuels significantly, and those conditions might produce levels of damage to canyon live oaks approaching those that prescribed burning was intended to prevent. To the extent that the canopy is opened by top-kill of oaks during prescribed burning, chaparral shrubs probably would invade the stand, making it more likely to burn severely in the future.

If the decision is to use prescribed burning, it should be concentrated on gentler slopes where access is easier, fuels are more continuous, and probable damage from wildfires is greater. Minnich (1980) observed 37 percent survival of bigcone Douglas-fir following wildfires on slopes less than 20 degrees, but more than 90 percent survival on slopes greater than 40 degrees.

A better fuels management strategy to protect live oak/bigcone Douglas-fir stands may be to concentrate prescribed burning in chaparral near these stands. Highest priority should be given to the more flammable chaparral types and to more decadent chaparral with higher dead-to-live fuel ratios, which would support more intense wildfires and thus be more likely to carry a crown fire into adjacent trees. Similarly, higher priority should be given to chaparral near live oak/bigcone Douglas-fir stands with more continuous surface fuels and those on gentle to moderate slopes (as opposed to very steep, broken slopes and canyons). Movement of fire into live oak/bigcone Douglas-fir should be minimal if prescribed burns are planned for relatively moderate burning conditions (which should be suitable for burning decadent chaparral or relatively flammable chaparral species) and in such a way that slope and wind direction favor movement of the fire away from the live oak/bigcone Douglas-fir stand. Prescribed burning of decadent chaparral should improve owl foraging habitat because of increased production of woodrats (more succulent and nutritious foliage in the new growth) and improved access to woodrats (see Chapter 10).

In the event of a severe wildfire in live oak/bigcone Douglas-fir, active measures should be taken to restore owl habitat. Because prospects are poor for natural regeneration of bigcone Douglas-fir, nursery-grown seedlings should be planted as soon as possible. Competing shrubs and other vegetation should be controlled adequately to ensure survival and rapid early growth of the bigcone Douglas-fir seedlings. Some thinning of sprouting clumps of canyon live oaks might speed their return to tree size.

Southern California Riparian/ Hardwood

Accumulations of dead-and-downed woody fuels are generally low in this type. Fire behavior depends on understory composition, which can be variable (color photos 5-29 to 5-32, 5-45 to 5-47). Areas with a grass understory burn rapidly with low to moderate intensities. Effects are generally benign. Stands with a shrub understory show great variability in fire behavior and effects, depending on species composition and abundance of shrubs. These stands should be examined on a case-by-case basis, because they are of great importance, relatively limited in acreage, and vary in their vulnerability to wildfire. Management should focus on maintaining a closed canopy of trees. In some stands, prescribed burning or other fuels treatment may be needed to prevent overstory mortality from wildfire. Fire also may be necessary in some situations to regenerate overstory trees, such as oaks.

Considerations for Fire Suppression in Spotted Owl Habitat

The wildland fire agencies have demonstrated the efficacy of initial attack in excluding wildland fire from some types of spotted owl habitat (Sierran mixed-conifer, red fir, and southern California mixed-conifer). Such suppression efforts are essential to prevent large, severe wildfires, while concurrently making efforts to condition stands to reduce wildfire hazard. Continued success depends on maintaining sufficient initial attack resources to protect the habitat. Wiitala (1991) proposed a way to quantify the risk of experiencing unacceptable fire events in areas that are highly valued, but for which we have no method of assigning a monetary value for input into the loss portion of cost-plus-loss

equations. A similar analysis should be developed for California owl habitat, to justify the initial attack organization needed for its protection.

A consideration in suppression of wildfire in high-value areas is the trade-off between efficient suppression that minimizes the fire size and the damage that can result from aggressive suppression action. The concept of appropriate suppression response has been articulated by Mohr (1989) and Mohr and Moody (1991), emphasizing techniques that effectively and efficiently suppress fires while minimizing direct impacts.

Selecting suppression strategies at initial attack, extended attack, and project fire level also requires weighing the advantages of backing off to the exterior of high-value areas to minimize suppression impacts, against the amount of damage that the fire is expected to cause within the selected perimeter. The fire manager has considerable latitude in selecting a strategy, ranging from aggressive control to confinement. Selection of suppression alternatives should be based on projected or observed fire behavior to predict fire effects. This analysis will be fire-specific because of variation in such factors as fuel loading, fuel moisture, weather, and topography. Interaction among wildlife biologists or resource advisors, fire behavior analysts, and operations personnel is essential to develop a balanced display of the suppression costs and resource damage of alternatives. Successful implementation requires preplanning by fire managers in consultation with biologists.

Fire suppression must be done in a manner that reflects a high regard for public and firefighter safety. The following additional factors should be considered when managing wildfires that start in or threaten spotted owl habitat:

1. The degree of involvement of canopy layers, based on the intensity of surface fire and the amount of torching predicted in each canopy layer.

2. The expected amount of consumption in litter and duff layers.

3. The relative patchiness of the burn, and the percent of various fire intensities projected within the fire perimeter.

4. The expected amount of downed-log volume to be consumed, especially logs greater than 9 inches in diameter. This evaluation should include both rotten and sound logs.

5. Location of the fire relative to known nest sites.

6. Timing of the event relative to the owl's breeding season.

7. The quantity and quality of habitat in the area of the fire. If the fire is burning in an area where suitable owl habitat is rare, greater effort would be taken to minimize habitat destruction by the fire.

8. Expected impact on the owl's prey base.

Conclusions

Fire has been a dominant force in shaping the forested ecosystems that provide habitat for the California spotted owl. The various habitat types used by the owl differ in terms of (1) the influence of historical fire regimes on their structure, composition, and function; (2) the extent to which the habitat types have been altered by human activities since European settlement; and (3) the risk of substantial habitat loss by severe wildfires. In this chapter we have summarized fire management considerations relating to protection and possible enhancement of owl habitat, with emphasis on the Sierran mixed-conifer and the live oak/bigcone Douglas-fir forest types.

The Sierran mixed-conifer type is the State's most important and extensive habitat type for the California spotted owl. Human activities since the mid-1800s-especially sheep grazing, fire suppression, and "selective" cutting-have profoundly affected the structure and composition of these forests. Changes include a marked increase in the density of shade-tolerant understory trees. The vertical fuel ladders thereby created, along with substantial increases in surface fuels, have greatly increased the potential for stand-replacing crown fires. Severe wildfire in Sierran mixed-conifer forests may represent the greatest threat to current owl habitat.

The wildland fire agencies must maintain an effective suppression organization to minimize the damage from such fires. Problems resulting from many decades of over-zealous suppression cannot be resolved overnight by allowing wildfires to run their course in highly hazardous fuel complexes. Concurrently, however, managers must pursue aggressive, environmentally sound fuels management programs to reduce wildfire hazard in and around owl habitat. As described in this chapter, prescribed fire has an important role to play in reducing hazard and enhancing a variety of ecosystem values associated with the natural functioning of fire. In addition, fuels management methods (including but not limited to prescribed fire) should be considered integral components of silvicultural approaches to managing owl habitat, such as those discussed in Chapters 1 and 13.

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Chapter 13

Projected Trends in Owl Habitat

Kevin S. McKelvey and C. Phillip Weatherspoon

Here we attempt to synthesize many of the analyses presented in other chapters in this document, and to look ahead to the future. As such, this chapter is necessarily more speculative and conclusions expressed here should not be viewed as hard and prescriptive. We hope, however, to highlight areas of concern for future owl habitat, and for the health of the forest ecosystem more generally. Finally, we propose alternate forest management methods that we believe have merit. We do not consider the management methods described here to be an exclusive set to be prescribed forestwide. Rather we view them as potential experiments which, if effective, will alleviate many of the shortcomings that we perceive in current management systems as they relate to owl habitat. This report covers a wide range of forest types and topographic regions. We will focus almost exclusively on the Sierran mixed-conifer forest type, as it contains an estimated 82 percent of the spotted owl sites in the Sierra Nevada and 62 percent of all known California spotted owl sites.

The Forest, Past and Present

Vegetation Dynamics

Forests of the Sierra Nevada have been impacted by nonaboriginal man over the last 150 years. The first major perturbation, on lands that now are managed by the Forest Service (FS), was the grazing of millions of sheep (Chapter 11). This grazing pressure and the fire patterns associated with its promulgation impacted regeneration and the grass/forb community. This pattern probably amplified a structure already maintained by frequent fires-one of open stands dominated by large, old trees (Chapter 12). It also resulted in excellent seed beds for tree regeneration by creating bare-soil conditions over much of the forest (figs. 13A and 13B as examples; Chapter 11).

With removal of sheep and fire, stands experienced ingrowth of conifers, dominated by shade-tolerant species such as white fir. Stands became dense, and a combination of logging and natural attrition of the old forest led to a decline in the number of large, old trees. Past logging activities that concentrated on removal of the large, valuable trees broke up the patchy mosaic of the natural forest, and this too encouraged development of dense regeneration patterns with very little horizontal heterogeneity (figs. 11P-11S; Chapter 12). These developments, particularly in Sierran mixed-conifer and ponderosa pine/hardwood forests, reduced large-diameter trees in many areas to a small, remnant population. This condition can be seen by comparing owl nest locations, which generally are in larger, denser stands in today's forest (color photos 5-9 to 5-16 as examples), to forest conditions about 1900 (figs. 13A to 13D as examples).

These changes have not occurred to the same degree in the red fir as they have in mixed-conifer and ponderosa pine types at lower-elevations. The red fir type differs from the mixed-conifer in several particulars, including in its natural disturbance regime. Fires are less frequent, occurring at intervals of 40+ years (Taylor and Halpern 1991) rather than the 5- to 30-year return periods observed in mixed-conifer stands (Chapter 12). The forest consists of blocks of various sizes, often with a high degree of horizontal heterogeneity (color photos 5-1 to 5-6). In many areas fire was the dominant disturbance factor responsible for this mosaic (Pitcher 1987). In addition, windthrow created small gaps, and red fir regeneration often established more or less continuously between disturbance events (Taylor and Halpern 1991). This led to a complex horizontal pattern with the juxtaposition of blocks of various ages and sizes. Removal of fire from the red fir type has had less impact than in the Sierran mixed-conifer type because of the longer mean fire interval. Many red fir stands would not have burned in the twentieth century even if the natural fire patterns were intact. Red fir also occurs in mostly pure stands at higher elevations. On these sites, red fir appears to be a self-perpetuating, climax species (Barbour and Woodward 1985, Taylor and Halpern 1991), and the successional trend toward more shade-tolerant species that characterizes the mixed-conifer zone is not a factor.

Red fir was also not extensively logged until recent years. Most logging of red fir in the Swain Mountain area, for instance, occurred after 1960 (Chapter 7). Partial cutting has not broken up the large-diameter groups and, in many places, the forest has never been logged (color photos 5-1 to 5-6 as examples). The pattern in red fir is more that observed in the Pacific Northwest-recent, often even-aged harvest intermingled with blocks in reasonably pristine condition. In logged areas, regeneration records maintained by the FS R5 show that survival of planted seedlings is low (Fiske pers. comm.; fig. 13E).

Fire Patterns

Fire patterns in the Sierran mixed-conifer zone have changed radically in the twentieth century. The annual acreage burned may have declined by two orders of magnitude when compared with historic levels (Chapter 12). This, in turn, has led to historically unprecedented buildups in fuels and to stand structures that are prone to crown fires (Chapter 12). Because of these conditions, fires that escape initial suppression efforts-usually those occurring during extreme weather conditions-tend to become large, stand-replacing events.

Figure 13A--Sugar and ponderosa pine in Foresthill block showing size of timber and open character of forest. Note extensive, branchless tree trunks and the absence of underbrush on the forest floor.

Date: ----------7 July 1911
Source: ----------Tahoe National Forest Historical Photo
Photographer: ----------USDA Forest Service

Figure 13B--A woman and her dog following an old road through a stand of old-growth Jeffrey pines.

Date: ----------About 1920
Source: ----------Lassen National Forest Historical Photo
Photographer: ----------USDA Forest Service

Figure 13C--Pure stand of cedar along Mill Creek above Morgan Springs.

Date: ----------About 1920
Source: ----------Eldorado National Forest Historical Photo
Photographer: ----------USDA Forest Service

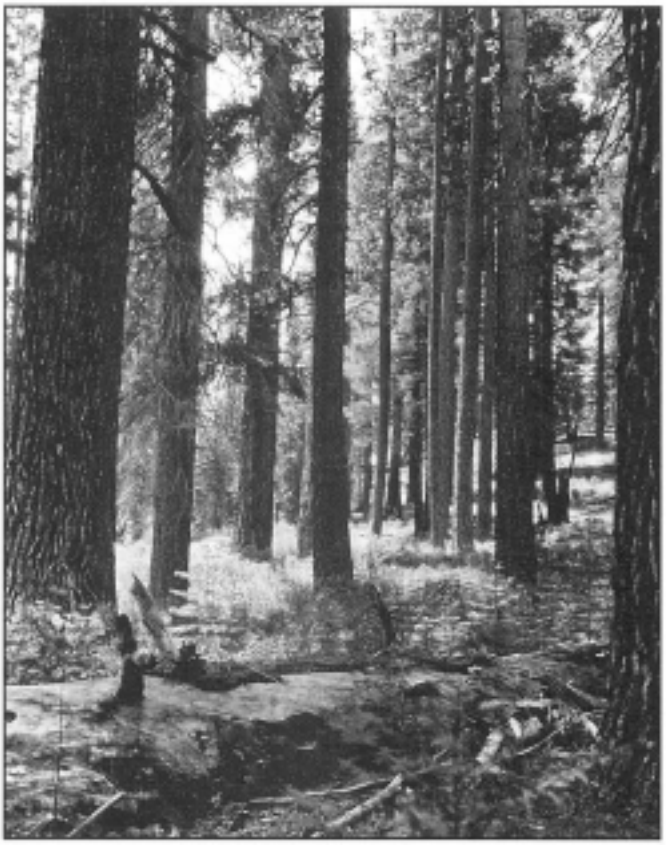

Figure 13D--Near Strawberry, a virgin forest including sugar pine, ponderosa pine, fir, and incense-cedar. Observe the downed, rotting tree and open character of the forest floor.

Date: ----------About 1920
Source: ----------Stanislaus National Forest Historical Photo
Photographer: ----------USDA Forest Service

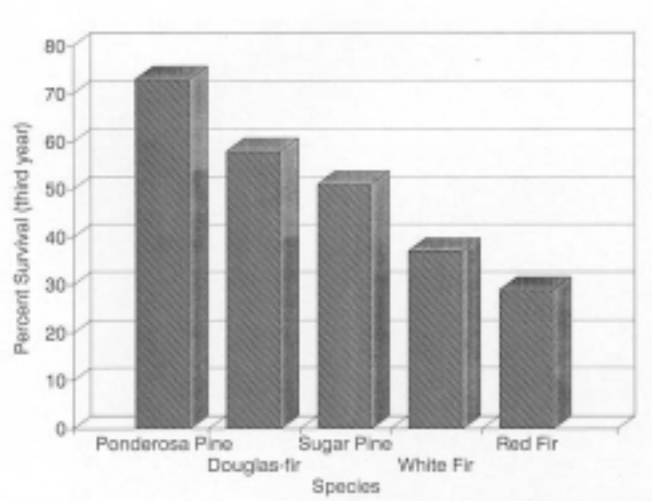

Figure 13E-Regeneration survival in plantations, by species, based on 3-year postcut inventories. Survival rates were averaged over the years 1986-1991 (Fiske pers. comm.).

Owl Habitat in Current Forests

Spotted owls in the Sierra Nevada have used all of the dense (>40 percent canopy closure) mixed-conifer stands at or greater than expected levels for nesting (Chapter 5). The only stands used significantly greater than expected, however, were dense stands with large-diameter trees [>24 inches in diameter at breast height (d.b.h.)] in the overstory. Within these stands, snag densities were higher than in the general forest matrix, and the average nest tree exceeded 40 inches in d.b.h. Most of the nest trees appeared to be old-growth remnants of stands present at the turn of the century (Chapter 5). These stands tend to be very heavily stocked with trees in smaller diameter classes (color photos 5-9 to 5-16, for example).

We have few data concerning nest stand selection in the red fir type. The nests that we observed on our field trips were in uncut blocks of timber (color photos 5-1 to 5-6, for example).

Future Trends

Human Population Trends

The human population in both the Sierra Nevada and southern California is growing rapidly (fig. 13F). Of particular concern is population growth in the foothill regions of the mid-Sierra Nevada. In these areas (Nevada, Placer, El Dorado, Amador, Calavaras, and Tuolumne Counties), human populations have increased by 50 percent over the last 10 years and are expected to continue to grow at that rate through the year 2000. From 1980 to 1990, they were among the top 10 California counties in growth. By the year 2000, the combined population of these counties is estimated to exceed 670 thousand (Rountree 1992). A large proportion of this population will be living in widely dispersed housing "in the pines." Impacts from this type of development on spotted owl habitat are unknown. We do know, however, that spotted owls currently occur in these foothill areas and that this type of housing pattern makes management and monitoring very difficult. Any resulting negative impacts on the owls will be difficult to detect and even more difficult to control.

While much of the population growth in southern California is in the basins, towns in the San Bernardino Mountains, such as Big Bear Lake, are expected to grow 50 percent by 2010 (Ruth

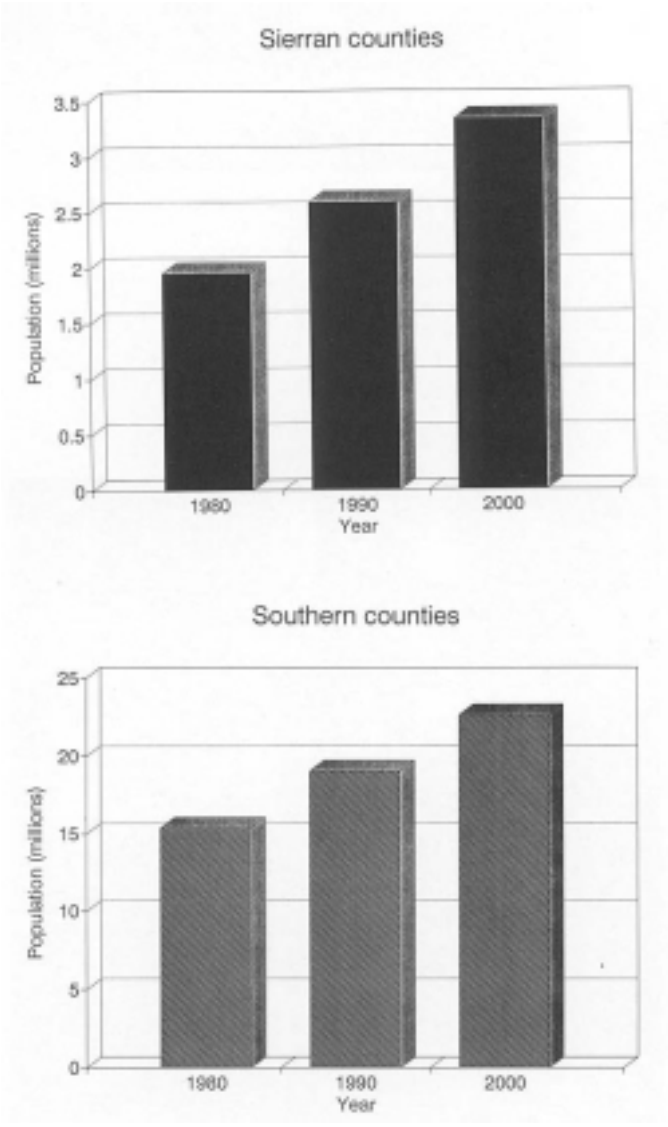

Figure 13F-Human population trends in the Sierra Nevada and southern California. Only counties containing spotted owls were included in this analysis (data from Rountree 1992).

pers. comm.). Impacts of increased population on the spotted owl in southern California will most likely be more direct than they are in the mid-Sierra Nevada. Because many owls in southern California depend on narrow riparian/hardwood forests, pressure on them will increase as waters are diverted to a variety of human needs.

Fire Trends

As the human population increases, human-caused wildfires can also be expected to increase. The presence of so many houses within the forest will shift the emphasis of fire suppression even further from one of saving forests to one of saving property. Fuels will also continue to accumulate. Especially as a direct result of our current drought, recent bark beetle infestations will contribute a major pulse of new fuels over the next few decades. The likely result is a gradual increase in the number and acreage of large, stand-replacing wildfires.

Cutting Trends: Land Management Plans

According to Land Management Plans (LMPs) collectively for National Forests (NFs) of the Sierra Nevada, 65 percent of the forested acres are classified as suitable and available for timber production (USDA, FS 1986-1991b). If we exclude from the forested base the acres that are physically unsuitable because they cannot produce timber in commercial quantities, cannot be successfully regenerated, or have unstable soils, 74 percent of the lands that can potentially produce timber will be harvested in some manner (table 13A). On many acres, harvest will be light.

Table 13A-*Categorization of forested acreage from the Land Management Plans.*

National Forest	Thousands of acres			
	Forested	Physically unsuitable[1]	Suitable and available[2]	Suitable and unavailable[3]
Lassen	825.1	0	596.3	228.8
Plumas	1,102.4	145.7	898.9	57.8
Tahoe	681.6	31.7	528.5	121.4
Eldorado	458.0	63.2	307.6	87.2
Stanislaus	784.6	308.3	328.5	147.8
Sierra	562.9	26.8	328.9	207.2
Sequoia	679.0	40.0	345.0	294.0
All Forests	**5,093.6**	**615.7**	**3,333.7**	**1,144.2**

[1] Includes acreage not capable of producing commercial timber, in which irreversible damage would be caused if timber were harvested, and that cannot be regenerated in 5 years after harvest.

[2] Includes lands capable of producing commercial timber that have not been withdrawn from timber management, lands that can be regenerated within 5 years after logging, and lands that can be managed for timber production without irreversible damage. Suitability here refers to areas that could physically sustain timber yields over time, not necessarily spotted owl suitability.

[3] Includes lands that are physically suitable but that have been withdrawn from timber management for dedication to other uses (for example, Wilderness Areas, Spotted Owl Habitat Areas, and so on).

Seventy-two percent of the timber volume removed from these lands will be taken through even-aged systems, the most common even-aged system being the clearcut (table 13B). Of the 528,474 acres of suitable timber land on the Tahoe NF, for instance, 68 percent will be managed for even-aged silviculture (24 percent long rotation, 44 percent short rotation) (USDA, FS 1990). On the Plumas NF, 52,000 acres are scheduled for even-aged cutting per decade and 8,000 acres for selection cutting methods (USDA, FS 1988b; table 13C).

Even-Aged Logging and Owl Habitat

Clearcuts, seed-tree, and shelterwood cutting methods all have the same goal: produce even-aged stands. In this regard, seed-tree and shelterwood systems can generally be thought of as two-stage (sometimes three-stage) clearcuts. In nearly all of these cutting systems, all of the original stand will be removed before the new stand is scheduled to be cut.

Table 13B-*Harvest volumes from the forest Land Management Plans.*

National Forest	Millions of board feet			
	Clearcut	Seed tree/ shelterwood[1]	Other[2]	ASQ[3]
Lassen4	40.6	23.5	31.9	96.0
Plumas	144.2	31.3	90.0	265.5
Tahoe	64.7	48.2	29.4	142.3
Eldorado	58.4	55.4	23.4	137.2
Stanislaus[4]	3.9	67.6	16.5	88.0
Sierra'	25.5	32.5	30.0	88.0
Sequoia'	64.8	3.1	29.1	97.0
All Forests	**402.1**	**261.6**	**250.3**	**914.0**

[1] Includes removal sales as well.

[2] Includes all other sale types that enter into the calculation of ASQ.

[3] Annual sale quantity.

[4] These data are given in cubic feet in the LMPs.

Table 13C--*Number of acres scheduled for logging, annually, during the first decade of draft and final Land Management Plans for Sierran National Forests, by prescription.*

National Forest	Acres per year			
	Clearcut	Seed tree/ shelterwood[1]	Selection[2]	Intermediate[3]
Lassen	1,600	1,000	1,400	10,200
Plumas	4,000	1,200	800	16,286
Tahoe	2,046	1,657	162	3,500
Eldorado	2,084	1,836	948	2,700
Stanislaus	510	2,386	8,7284	1,500
Sierra	1,550	1,170	2,970	4,000
Sequoia	1,734	128	742	6,727
All Forests	**13,524**	**9,377**	**15,750**	**44,913**

[1] Includes acres of overstory removal.

[2] Both group- and individual-tree selection.

[3] Includes stand improvement, thinning, salvage, etc.

[4] This figure represents the acres to be examined rather than the acres to be treated.

In terms of owl biology, the primary impact of traditional, even-aged logging practices lies in the creation of simple stand structures and, perhaps more importantly, the removal of all large, old trees from vast areas of the forest. Even if silvicultural prescriptions are modified so that snags and live culls are left at the first cutting, no provision is made for a predictable recruitment of replacement trees for these relics when they fall. This, in turn, will lead to a loss of large-diameter, downed woody materials. Log slash can create much small-diameter woody debris, but it cannot replace the large logs. In an even-aged system, these old-growth features can be recreated only by an extreme extension of the rotation interval. Even if the rotation were extended to 150 years, for instance, no trees would match the average age of the forest at the turn of the century (Chapter 11). Decadent features in stands are functions of age, not just d.b.h. (fig. 13G), and any animals that depend on decadent features (cavities, broken-tops, snags), or the large woody debris that they create, will simply drop out of these forests (see Chapters 4, 5, and 10 for examples specific to the spotted owl and its prey species). The rate of conversion to even-aged systems in the western Sierra Nevada is estimated by the LMPs to be 229,000 acres per decade.

Even on lands set for selection logging (about 80,000 acres per decade), we have no guarantee that harvest prescriptions will leave many of the large, old trees. Ideally, stands managed for individual-tree selection are harvested in a manner that brings the diameter distribution in the stand into conformity with an idealized distribution characterized by a declining exponential function (in forestry referred to as an inverse "J"). The number of large trees within the stand is dictated by the slope of this function (fig. 13H) and the specified intercept representing the number of trees in the smallest diameter class (or, alternatively, the designated diameter of the largest tree). In selection systems, timber is removed from all diameter classes, as required to maintain this diameter distribution. Little evidence exists, however, that historic patterns of partial cutting have followed classic single-tree selection theory. "Selective" harvest in the Sierra Nevada has, in the past, primarily targeted the large trees. This system, sometimes called "pick and pluck,"

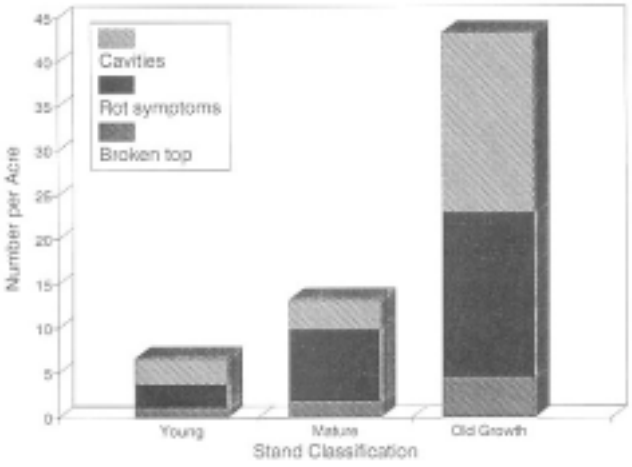

Figure 13G-Increasing decadence as a function of stand age, based on data from Bingham and Sawyer (1992).

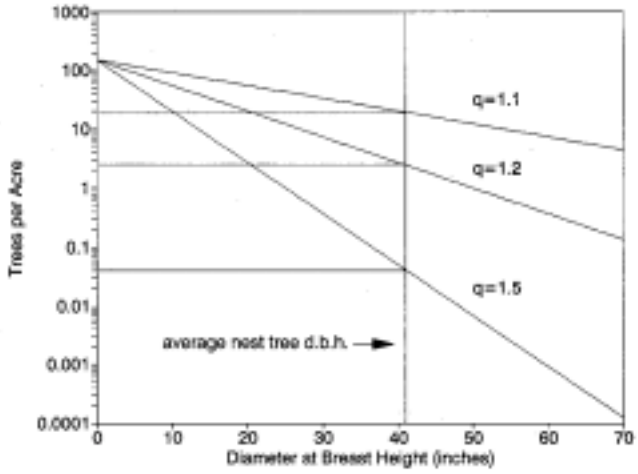

Figure 13H-Theoretical, uneven-aged distributions. Uneven-aged management allows for retention of very large trees. "Q" values of 1.2--similar to those measured in owl nest stands---will leave two to three trees per acre 40 inches in diameter at breast height on a site.

will not produce the simple structures that characterize even-aged methods, but its effect on the presence of large, old trees is similar. If the large trees are removed and no stocking control is performed on the smaller stems, replacement trees in these diameter classes will be produced very slowly, if at all, and they will consist primarily of the more shade-tolerant species. Even with classical single-tree selection, a gradual loss of shade-intolerant species would be likely.

A large proportion of the future forest, as projected by the LMPs, will very probably be split between areas of even-aged plantations and areas of dense, and increasingly small-diameter stands.

A Different Paradigm

Two important questions that the FS needs to answer are: (1) What kind of forest structures does it want to create and perpetuate? (2) Are the life history requirements of spotted owls and other species associated with late-seral forest conditions met by those forest structures? Fundamental to these questions is the paradigm that guides NF timber management. Insights to this paradigm can be gained by studying the LMPs produced by the Sierran NFs. The LMPs are as much statements of goals, priorities, and paradigms as they are implementation strategies. The scheduling appendix for timber removal on Stanislaus NF, for example, states these goals clearly:

> *A regulated forest should be regarded as an objective that may never be fully attained... However, the concept of regulation as an objective, is the tool used to control present harvest levels and plan future harvests to assure sustained yield within reasonable limits.*
>
> *A forest consisting of wild and unmanaged stands with highly variable stocking levels and age-class distribution is made to approach regulation through harvest and scheduling regeneration over a period of time called the conversion period. During the conversion period an attempt is made to meet three criteria:*
>
> 1. *Obtain the maximum yield of timber possible.*
> 2. *Provide for essentially a non fluctuating yield over the conversion period.*

3. *Provide a balance of age-classes and stocking levels capable of producing the forest's full potential timber growth at the end of the conversion period* (USDA, FS 1991b, appendix D, D-3).

This description closely follows the ideal of the "fully regulated forest" as it is presented in forest management text books (for example, Davis and Johnson 1987, chapter 14). By this definition, the regulated forest differs in fundamental ways from a wild forest, and the current status of the forest is seen as being in a conversion period in which wild stands are brought into regulated conditions through harvest and regeneration. Really only one general template is used to define a fully regulated forest-the diameter distribution, forest wide, should fit an "inverse J" distribution form, with optimized spacing (Husch et al. 1982). This pattern can be achieved through a series of large blocks (even-aged clearcutting), blocks smaller than 2 acres (group selection), or on an individual tree basis (individual-tree selection). All three models are generic, derived from European forestry in the late 1800s (Davis and Johnson 1987) and used for timber production in Europe, New Zealand--and in the Sierra Nevada. The purpose of the classic, fully regulated forest, in any of its permutations, is to allow for an even flow of wood products, not necessarily to mimic natural stand conditions and processes:

> *The essential requirements of a fully regulated forest are that age and size classes be represented in such proportion and be consistently growing at such rates that an approximately equal annual or periodic yield of products of desired sizes and quality may be obtained in perpetuity. A progression of size and age classes must exist such that an approximately equal volume and size of harvestable trees are regularly available for cutting* (Davis and Johnson 1987, p. 540).

Most other LMPs share a single emphasis concerning their paradigm for timber management. No certainty exists that ecosystem processes, whether they are the population dynamics of a single species or the successional trends of a multi-species complex, will be maintained in a fully regulated forest. The concept of forest regulation has traditionally not been defined in these terms, and the long-term ecological consequences of the paradigm are unknown.

Recent discussion has concerned a significant shift in the basic forestry paradigm, from one that stresses the production of commodities (or amenities) to one in which the maintenance of ecosystem processes is the primary goal (National Research Council 1990). This new paradigm "...involves a shift in management focus from sustaining yields of competing resource outputs to sustaining ecosystems" (Kessler et al. 1992, p. 221). Toward this objective, the goal of management activities is to maintain, protect, and, where necessary, to create natural forest structures. Logging is practiced only to the extent and in a manner that it does not impair ecological processes or environmental assets. This system does not guarantee an even flow of wood products from the forests. The efficacy of silvicultural practices is evaluated by biological rather than market-based criteria.

Under this paradigm, logging would be explicitly designed to achieve or maintain ecological goals. These goals might, for instance, include remedial actions such as the generation, within a topographically defined unit such as a drainage basin, of a pattern of stand structures that mimic historical stand conditions. Because those structures were very different from the stands that presently exist, much manipulation of vegetation will need to occur before the goal is achieved-and active management will subsequently be needed to maintain it. A great deal of sophisticated silviculture will be required. What represents a major paradigm shift is that the silviculture will not be constrained by the equal volume/equal entry area requirements that are definitional to the concept of the fully regulated forest. This is not to say that forest regulation and a sustainable yield of forest products are necessarily incompatible with ecosystem functioning. Rather, it is a question of priorities: The new paradigm "...would involve a view of forest lands-including soils, plants, animals, minerals, climate, water, topography, and all of the ecological processes that link them together-as living systems that have *importance beyond traditional commodity and amenity uses"* (authors' emphasis) (Kessler et al. 1992, p. 222).

Under this paradigm, the answer to the first question (the type of forests we want) is that we wish to create forests in which natural processes are fully functional and stable. The answer to the second question (how spotted owls fit into this structure) is the subject of the remainder of this chapter.

Current Stand Structures at Spotted Owl Nests

Nest stands have definable properties-high canopy closure, a considerable snag component, and the presence of large, old trees that are used by the owls for nest sites. To generate and maintain these stand structures we need to be more specific. Data on the silvicultural characteristics of owl nest stands is, however, surprisingly sparse.

To evaluate the diameter distributions of owl nest stands, we obtained diameter distributions for areas immediately adjacent to 24 nest trees in the mixed-conifer zone of Lassen NF and 11 nest trees in the Sierra NF. These data were based on plots

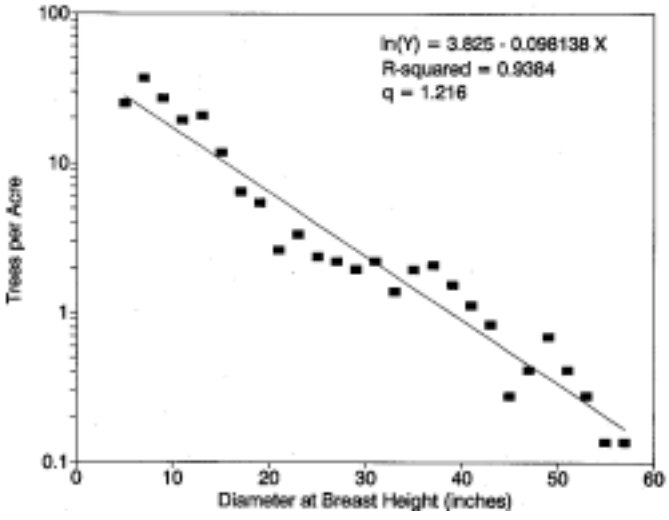

Figure 13l-Log-linear display of the mean number of trees/diameter class, based on 24 nest sites in the Lassen National Forest.

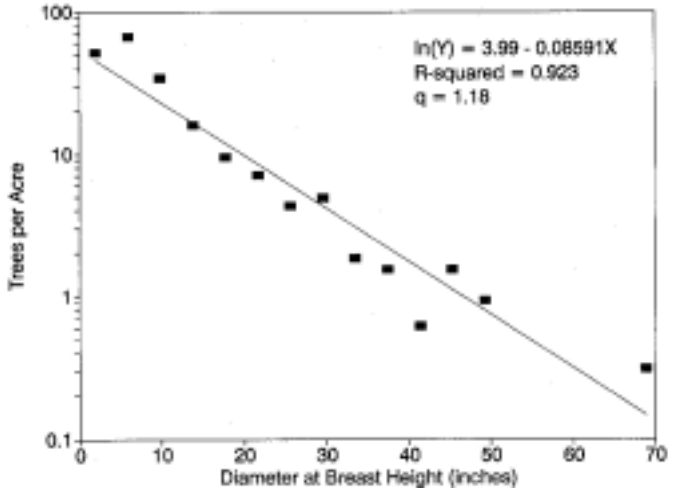

Figure 13J-Log-linear display of the mean number of trees/diameter class, based on 11 nest sites in the Sierra National Forest.

centered on the nest tree and forming a cross with the nest tree at the center. All trees 15.7 inches in d.b.h. were sampled within an area of 0.296 acre. Smaller trees were sampled within four subplots 32.8 feet square. To avoid any possible bias by the inclusion of a large, central tree, the nest tree itself was excluded from density calculations. When the natural log (In) of the mean tree density (stems/acre) for the combined plots in these two areas was regressed on d.b.h., the resulting pattern was linear (figs. 13I and 13J), suggesting a classic "inverse J" form-the idealized distribution for uneven-aged management-with a "q" value between 1.18 and 1.21 [here q is based on 2-inch d.b.h. groups (Daniel et al. 1979)]. This pattern, by itself, is not sufficient to suggest that uneven-aged management is warranted. Stands with differing structures will tend to conform to the inverse J when they are combined. Viewed individually, nest stands in Lassen NF formed three logical groups (figs. 13K and 13L). Eight of the stands lacked the larger diameter classes and conformed closely to the log-linear model. Thirteen of the stands

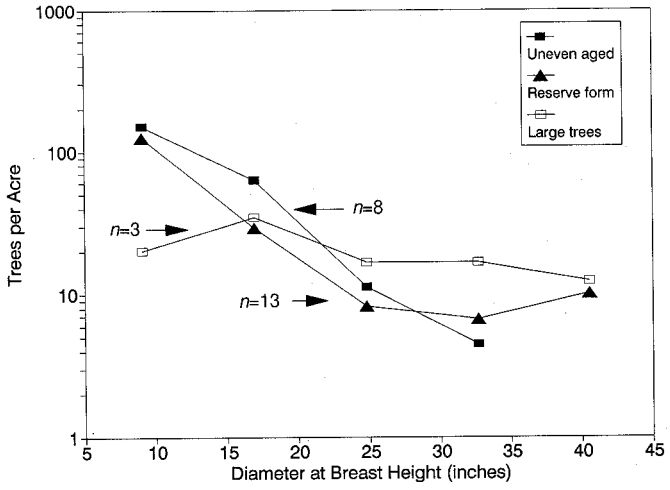

Figure 13K-Nest sites on the Lassen National Forest divided into logical groupings based on stand structure. Data presented are the mean values for each group. The groups consisted of 8, 13, and 3 sites, respectively.

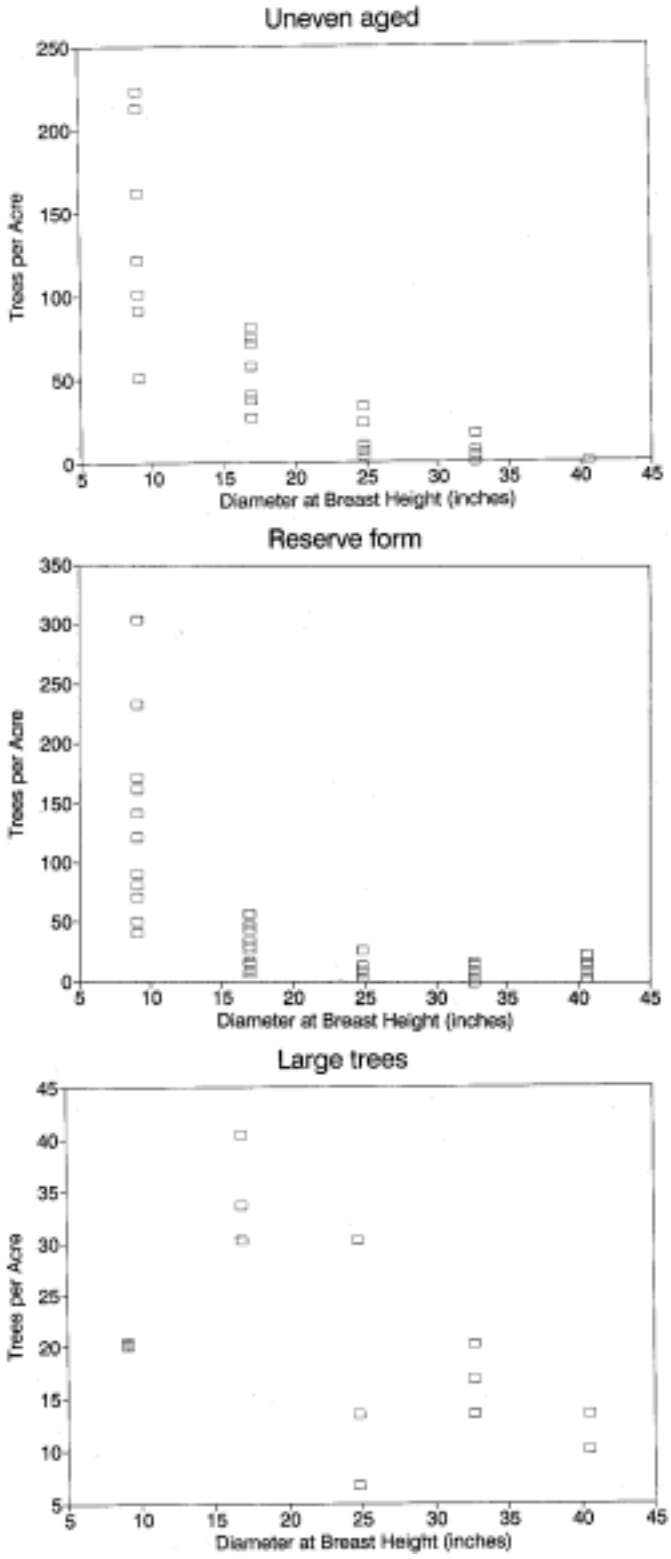

Figure 13L-Diameter distributions for the three types of nest stands measured in the Lassen National Forest. Both the "reserve form" and the "large trees" groups had more large-diameter stems than an idealized, uneven-aged stand structure would specify.

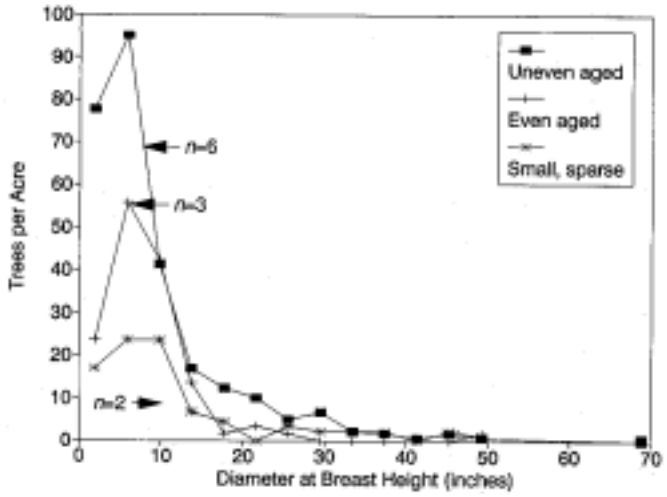

Figure 13M-Nest stand structures in the Sierra National Forest. None of these stands had a large proportion of large-diameter stems, and several were dominated by small-diameter trees,

generally conformed to the uneven-aged structure in the smaller diameter classes, but not in the large diameter classes. Three stands had most of their trees in the larger diameter classes. Nest stands on the Sierra NF also grouped logically into three classes (fig. 13M). Six of them generally fit an uneven-aged distribution form, but the others did not. Stands at two of the sites were made up primarily of stems <12 inches in d.b.h..

Most of these stand structures could be produced through a variety of management methods. Partial removal of the over story in the past and subsequent ingrowth probably led to the formation of many of these stands. We have no reason to believe that uneven-aged management, if properly applied, could not be used to maintain these structures-but the system should be sensitive to maintaining the large trees, and perhaps modified to generate "reserve form" stands. Reserve form stands are charac terized by an inverse "J" distribution in the smaller diameter classes and a normal distribution in the larger diameter classes. In all stands lacking frequent large stems, at least one large tree was present the nest tree, which was not included in the calculations.

The simple premise that forest structures similar to owl habitat can probably be created and maintained through silviculture does not answer a fundamental question. In the long run, are these the types of stands we wish to maintain? We have many reasons to doubt whether these stand types represent either a necessary or ideal template as an owl nest site. Perhaps the most important reason is that dense stands characterized by single tree-sized openings would have been unusual in mixed-conifer forests before the turn of this century. Dense stands would have existed, particularly in riparian areas and at higher elevations (figs. 13C and 13D), but they would not have been widely distributed across the landscape. A second reason is that these stands are unstable-the stand structure is likely to be altered quickly and unpredictably due to the probability of stand-replacing fires or insect and disease outbreaks. We do not know whether owls inhabited the more open stands that dominated much of the landscape in the past (figs. 13A and 13B). Because such stands are rare today, we are unable to infer anything from current owl locations. We do, however, need to begin to explore potential, alternate stand structures. These structures should be chosen to better mimic natural stands, to maintain tree species diversity, and to be more resilient to wildfires.

Some Potential Management Systems for Mixed-Conifer Ecosystems

General Considerations

A fundamental assumption underlies management of owl habitat, as well as much of forest management in general: Ecosystems are inherently dynamic; they do not stand still. Changes take place both rapidly (through a variety of natural and man-made disturbances) and slowly (through climatic change and natural successional processes), and occur at many spatial and temporal scales. Changes have occurred in the past, and they will occur in the future even if we "do nothing." Given this assumption, management recommendations should consider provision of adequate amounts and distribution of suitable owl habitat both in the short-term and in the long-term. For the short-term, Chapter 1 details management recommendations to be applied during an interim period of at least 5 years. These recommendations are intended to provide some degree of protection to existing owl habitat and to maintain future options for whatever long-term management strategy may be adopted at the end of the interim period. Below, we offer an example of one way in which the short-term (interim period) recommendations in Chapter 1 could be implemented in stand types shown to be selected for nesting by the spotted owl. These short-term practices and resulting stand conditions are not designed to be sustainable over long periods, however. The remainder of this section, therefore, offers potential silvicultural strategies that might be useful for producing and maintaining owl habitat over the long-term.

An Example of a Short-Term Approach

Recommendations in Chapter 1 set limits for cutting large trees-and managing other stand components. By definition, management practices cannot exceed these limits-for example, cut more large trees than specified-and still conform to the recommendations. In some situations, however, management objectives may be better achieved by not taking the recommendations to their limits. Following is one example of such an approach to interim management of *"Selected Timber Strata"* (P4G, M4G, M4N, M5G, M5N, M6-codes for timber strata defined in table 1C). (Compare item #1 under "Other Forested Public Lands" in Chapter 1.) Objectives that this example could help to meet include: (1) provide for a shorter recovery period for nesting/

roosting habitat; (2) keep some stocking in middle and lower canopy layers, both to retain existing multiple-canopy character of the stand and to ensure quicker replacement of large trees; (3) provide for some thinning in middle and lower canopy layers to promote growth of trees in these layers into desirable larger size classes; and (4) provide some quantification of fuels management treatments, including reduction of vertical fuel ladders (Chapter 12). Managers should recognize that this example (like any other that places additional constraints) is more restrictive than the basic interim-period recommendations in Chapter 1. Thus, in exchange for the potential benefits indicated above, timber volumes (and associated revenues) will generally be lower, and costs of treating submerchantable stems and other fuels will generally be higher. (Basal area limits and other quantitative data in this example are only approximations. They are not based rigorously on Chapter 5 or any other real data pertaining to owl habitat. If an approach similar to this is to be used, it should be based on the best and most nearly site-specific data available.)

A. Enter a stand for harvesting only once before a long-term strategy for managing the California spotted owl has been implemented on public lands.

B. For stands with a Dunning and Reineke (1933) site index (SI) of ≥60, enter the stand for harvesting only if total basal area of live trees ≥5 inches d.b.h. is greater than 200 square feet per acre. Harvesting will not reduce total basal area to less than 200 square feet per acre or canopy closure to <40 percent. For stands with SI <60, the corresponding basal area limit is 160 square feet per acre. To the extent possible, a mix of tree species should be retained.

C. Remove no live tree ≥30 inches in d.b.h.

D. For stands with SI ≥60, limit cutting in the 21- to 30-inch d.b.h. class so that the combined basal area of live trees in d.b.h classes 21-30 inches and 30+ inches is no less than 120 square feet per acre. A wildlife biologist should be involved in training tree markers to identify potential nest and roost trees in the 21- to 30-inch d.b.h. class so that those trees (including live culls) will be retained as part of the residual basal area. In stands currently having less than 120 square feet per acre basal area in those two size classes, no cutting of trees 21-30 inches d.b.h. will take place. For stands with SI <60, the corresponding basal area limit is 100 square feet per acre.

E. For stands with SI ≥60, limit cutting in the 11- to 20-inch d.b.h. class so as to retain a basal area of at least 60 square feet per acre in that diameter class. In stands currently with basal area <60 square feet per acre in that d.b.h. class, no cutting of trees 11-20 inches d.b.h. will take place. If the stand is entered for harvesting, and if current basal area in the 11- to 20-inch d.b.h. class is >80 square feet per acre, this diameter class will be thinned to a basal area of 60 to 80 square feet per acre. For stands with SI <60, the corresponding range of basal areas would be 40 to 60 square feet per acre.

F. Limit cutting in the 5- to 10-inch d.b.h. class so as to retain a basal area of at least 20 square feet per acre in that diameter class. In stands currently having <20 square feet per acre basal area in that d.b.h. class, no cutting of trees 5-10 inches in d.b.h. will take place. If the stand is entered for harvesting, and if current basal area in the 5- to 10-inch d.b.h. class is >30 square feet per acre, this diameter class will be thinned to a basal area of 20 to 30 square feet per acre. Trees cut in the 5- to 10-inch d.b.h. class will be removed from the stand. Utilization of these trees is encouraged.

G. If the stand is entered for harvesting, and if canopy cover in trees 0-4 inches in d.b.h. is, greater than 20 percent, trees will be felled, crushed, masticated, or otherwise rearranged to reduce canopy cover in that size class to no more than 20 percent. The surface fuel bed resulting from these trees, as well as slash from logging of larger trees, should be treated mechanically or with prescribed fire to reduce wildfire hazard to an acceptable level. The emphasis should be on reducing vertical and horizontal continuity of fuels and associated risk of crown fires, especially in the vicinity of large trees. Fuel treatments and logging activities should be designed to minimize disturbance of duff and coarse woody debris. In most cases this will preclude machine piling of slash. Where prescribed burning is used, it should be done when lower duff and large woody debris have high moisture contents to minimize consumption of these materials.

H. Follow guidelines in Chapter 1 for retention of snags and downed wood.

Some Potential Long-Term Strategies

A full discussion of management activities that may be appropriate to manage for owl habitat over the long-term is beyond the scope of this chapter. Instead, our purpose is to provide a sampling of ideas and considerations to stimulate thinking. Innovative managers and resource specialists may be able to use some of these ideas as a starting point in developing suitable management regimes to fit their local conditions and needs. On public lands, initial (interim period) implementation of the long-term strategies described here would be compatible with recommendations (Chapter 1) for *"Other Timber Strata"* used for nesting by owls but not significantly selected in relation to availability. We encourage managers of private lands to explore these approaches as well. Treatments should be viewed as ongoing management experiments (adaptive management, Chapter 2). Effects of treatments on stand structure and key ecosystem components should be carefully monitored, and owl habitat models should be tested. These experiments would incorporate information from monitoring and research activities into feedback loops that would serve to improve both our management practices and our knowledge of what constitutes suitable owl habitat.

Although the scenarios discussed below describe generalized target stand structures and associated management practices primarily at the stand level, great flexibility exists for distributing variations and combinations of these structures across the landscape and through time. In these scenarios, silviculture would be viewed as the art and science of shaping stands and landscapes to meet management objectives-spotted owl habitat in this case. Timber volume would be an output of, rather than a driving force for, the silviculture undertaken to meet management objectives. Protection of current or future habitat would

continue to be a primary concern. Accordingly, appropriate fuels management would be integrated with silvicultural activities.

We focus here on good-quality nesting and roosting habitat for the spotted owl as the "target" conditions for management activities. Foraging habitat appears to be more variable and less restrictive (Chapter 5), and its requirements should be met more easily and with a wider range of management practices. In contrast, successful management to produce, maintain, improve, and protect nesting and roosting habitat may require significant changes from conventional management practices. Some institutional barriers may need to be overcome. It will be more complex and expensive but should provide new and stimulating professional challenges for a variety of specialists to exercise creative thinking and pursue interdisciplinary objectives and activities.

We make several simplifying assumptions about attributes of suitable nesting/roosting habitat (Chapter 5) to help define target stand structures and associated management practices: (1) high canopy closure; (2) stand basal area and canopy closure distributed among two or more size classes of trees; (3) diversity of tree species within the stand; (4) "adequate" numbers of large live trees; (5) "adequate" numbers of large snags; and (6) "adequate" quantities of duff and large woody debris.

Accepting these six assumptions places limits on the range of stand structures that can be targeted by management. Both classical, even-aged silviculture and the classical, single-tree-selection form of uneven-aged silviculture have difficulties in meeting one or more of these assumptions, for reasons discussed below. We believe that two other kinds of stand structures-mosaics of small, even-aged groups or aggregations, and two- or three-storied stands-hold greater promise for producing and maintaining suitable owl habitat over the long-term. We recommend that these two structures, together with their associated silvicultural and fuels management practices, receive emphasis in long-term, adaptive management experiments concerned with owl habitat. Both can be considered intermediate between even- and uneven-aged (single-tree selection) management. But they can be thought of as representing two ends of a continuum,, with many intermediate structures differing in density and spatial arrangement of age/size-classes to help meet various specific objectives and to increase diversity across the landscape. Even- and uneven-aged (single-tree selection) methods should be included in these experiments, but at a reduced level.

Even-Aged Silviculture

The requirement for two or more size-classes of trees (assumption #2 above) probably could be met with even-aged silviculture, but it would involve significant modifications from conventional practice. The natural segregation of crown classes could be emphasized by "thinning from the middle"-that is, thinning in codominant and intermediate trees, thereby promoting the separation of dominant from suppressed crown classes and increasing growth in the dominants. Suppressed trees probably would not survive long enough to be of much value for owl habitat unless stand density were reduced below usual target stocking levels, or the lower canopy level consisted largely of shade-tolerant species. The latter scenario probably would be more practical and sustainable in mixed-species stands.

Assuming that such an approach eventually would meet needs for a two- or more-storied stand, the rotation age necessary to meet tree size and decadence requirements (assumptions #4 and #5) probably would be much longer than called for in currently practiced even-aged management. As compared with alternative silvicultural methods, the rime from plantation establishment to achievement of conditions suitable for owl nesting and roosting is likely to be much longer. This long time period would necessitate development and/or retention of suitable replacement habitat in the interim.

Whatever may be the disadvantages of even-aged silviculture with respect to owl habitat, even-aged plantations in the Sierra Nevada will continue at some level for the foreseeable future, if for no other reason than because severe wildfires will continue to occur. Even-aged plantations, therefore, should be included in owl-related management experiments.

Uneven-Aged Silviculture Using Single-Tree Selection

To meet the need for tree species diversity (assumption #3 above), stand openings must be large enough to permit regeneration of shade-intolerant species such as ponderosa pine. This requirement generally is not met with the single-tree selection form of uneven-aged silviculture, at least where openings are mostly the size of individual large trees rather than groups of trees. Furthermore, retention of the smallest size-classes of trees well distributed through a stand-a necessity for sustaining this stand structure through time-creates dangerous fuel ladders and makes prescribed burning or other fuels management treatments essentially impracticable. As described earlier, many owl nesting stands had roughly an inverse J-shaped diameter distribution characteristic of uneven-aged stands. Composition of the smaller size classes, however, was strongly weighted toward shade-tolerant species, especially white fir. This resulted from many decades of fire suppression, augmented by partial cutting and preferential harvest of pines. In the absence of stand openings by cutting or by natural agents of disturbance such as fire and. insects, these stands will become increasingly dominated by shade-tolerant conifers. Single-tree selection should be included at a reduced level in management experiments to evaluate changes in structural attributes, owl use, managerial difficulty, and costs of implementation. Combining single-tree selection with group selection (discussed below) may work to maintain some vertical structure while permitting regeneration of shade-intolerant species.

Mosaic of Small, Even-Aged Groups

One kind of structure that may have promise for production and long-term maintenance of owl habitat is a multi-aged mosaic of small, even-aged groups or aggregations. Groups would generally range in size from about 2 acres down to a quarter-acre, or possibly less. Probably this type of structure best approximates presettlement stand structures (Chapter 12), thus warranting serious consideration. Openings would be sufficiently large to permit regeneration of shade-intolerant as well as shade-tolerant

species. Multiple size classes in general would be separated horizontally rather than vertically, but in sufficient proximity to satisfy this attribute of suitable owl habitat. The horizontal separation of size classes also would confer some degree of resistance to crown fires (Chapter 12).

Group selection cuttings, or modifications thereof, would be used to create and maintain this structure over time. Keeping track of a large number of small openings and groups for management purposes, long considered a major obstacle to the use of group selection, should be significantly easier with the advent of geographic information systems and satellite-based global positioning systems. Treatments certainly would be more complex and more expensive than with even-aged management, however, especially on steeper slopes.

Viewed from the standpoint of area regulation-approximately equal areas maintained in each of several age-classes-a given "stand" of, say, 20-100 acres under steady-state conditions might contain three to six or more different age-classes. Each age-class would comprise many small, variable-sized aggregations and occupy a total area roughly equal to the area of the entire stand divided by the number of age-classes. "Rotation age"-the age at which the oldest aggregations would be regenerated-could be as long as needed to meet and maintain targets for large and/or decadent trees and snags. Periodic entries preceding regeneration cutting for a given age-class could be used to adjust stand structure to meet desired habitat attributes. These intermediate treatments might include thinning to speed development of large trees or to alter species composition, creating snags by girdling or other means, or wounding selected trees to induce decay. In practice, these intermediate treatments would take place within the various age-classes (aggregations) in the stand when the oldest age-class is being regenerated. As an example, if six age-classes and a 240-year "rotation" were selected, entries could be made every 40 years to regenerate one-sixth of the stand and conduct appropriate intermediate cuttings in the remainder of the stand. Or 20-year entries could be made, but regeneration cuttings would be made only every other entry. Successive age-classes would be separated by about 40 years.

In groups to be regenerated, all trees could be removed or, especially in larger groups, scattered live trees and/or snags could be retained. To facilitate fuels treatment and reduce damage to the surrounding stand, cut trees should be felled as much as possible into the newly created opening. Site preparation/fuels treatment methods used on clearcuts should be usable in these small openings, although they are likely to be much more expensive. One promising possibility may be jackpot burning of slash concentrations in the opening at a time of year when fire would not spread into the adjacent stand, thereby minimizing the need for firelines. Shortly thereafter, the rest of the stand could be underburned during somewhat drier conditions. Alternatively, the rest of the stand could be underburned at the same time as the openings. Local trials would help define a workable regime. In any case, we recommend that fuels be treated after each entry into the stand to reduce chances of severe wildfire. Various fuels-treatment methods may be appropriate for a given area. Prescribed underburning, however, has the advantage that it would begin to restore the natural role of fire and associated processes in the ecosystem (Chapter 12). In the scenario described earlier, with successive age-classes separated by 40 years, the youngest (40-year-old) trees probably would be large enough to tolerate an underburn without excessive mortality, assuming early vegetation management to permit relatively rapid early growth.

Openings could be regenerated either naturally or artificially, and with or without vegetation management. Even with planting and vegetation management, growth of tree seedlings would be slower in an opening typical of group selection than in a larger opening because of competition for site resources from large trees surrounding the opening. Without planting and some control of nonconifer vegetation, however, development of conifers could be delayed for several decades. Fuels treatment would be complicated as well.

Development of a mosaic of small groups could be initiated in a wide range of stand conditions-for example, an older plantation, a variable-aged young-mature stand, or an old stand becoming excessively unbalanced in terms of size-class distribution or species composition.

Two- or Three-Storied Stands

Another kind of structure that might be suitable for production and maintenance of owl habitat is a two- or three-storied stand. It differs from the even-aged aggregation structure in that each age/size-class would be more or less uniformly distributed throughout the stand (although many variations in spatial arrangement would be possible). In a two-storied stand, the upper canopy would be sufficiently open to permit regeneration of shade-intolerant species in the understory. If a third canopy layer were to be managed, both of the upper two canopy layers would need to be thinned enough to allow regeneration and growth of multiple species. Typically, this kind of structure would be initiated with a shelterwood cutting. After regeneration is established, the overstory would be retained indefinitely-a practice referred to as irregular shelterwood-instead of being removed as occurs with even-aged management. Understocked stands, traditionally a high priority for clearcutting, could instead be underplanted, leaving most of the overstory in place. An overstory infected with dwarf mistletoe could be underplanted with species other than the one(s) infected.

If desired, this kind of structure could be initiated relatively early in the life of a plantation by having a heavy commercial thinning double as a shelterwood-type regeneration cutting. The cut would be followed by site preparation/fuels treatment and underplanting with the desired mix of species. Throughout the "rotation" of such a stand, thinnings could be applied as needed to maintain desired size classes and species. These should be followed by prescribed burning or other fuels treatments. Snags could be created as needed. Once created, the stand would never be devoid of large trees: each regeneration cutting would be accompanied by retention of some trees in one or two overstory layers. Thus a relatively short period of time would elapse between a regeneration cutting and restoration of a desired stand structure.

Fuels treatments, including use of prescribed burning, should not be particularly difficult for a two-storied stand. Initial site preparation/fuels treatment before establishment of the understory would be the same as for a shelterwood cut. Subsequent treatments would be comparable to those for an even-aged plantation. Separation of canopy layers normally would be sufficient to keep wildfires out of overstory crowns. A three-storied stand could be somewhat more problematical, in terms of maintaining adequate stocking of shade-intolerant species, protecting the small understory during fuels treatments, and keeping wildfires out of the overstory. In all these respects, a three-storied stand would begin to approach conditions in a single-tree selection stand.

Conclusions

We believe that the dynamic trends in forest structure and fuels profiles that are occurring on NFs in the Sierra Nevada are cause for concern. The most troubling aspects are the loss of old, large-diameter trees and associated woody debris, a shift toward more shade-tolerant species, the buildup of fuels associated with mortality in the small diameter classes, and the continued presence of abundant ladder fuels that enable crown fires to occur. We do not believe the management directions elucidated in the current LMPs alleviate these trends; in fact, single-tree selection systems are likely to accelerate them. Even-aged systems can reduce fuel loadings and encourage the growth of shade-intolerant species, but they do so at the expense of the remnant large trees. We believe that other options exist that could deal directly with these concerns. Management plans should focus on addressing undesirable trends, designing potential solutions, and proceeding experimentally to implement those plans on the landscape.

Owl habitat can be described in terms that are compatible with silvicultural methods. In this chapter we have presented preliminary examples of how this process might proceed. The FS can easily gather basic stand-level statistics from known owl nest stands throughout the range of the California spotted owl. To date, most of the data collected are either very coarse (for example, at the timber strata level) or based on ocular estimation and, therefore, are not as reliable as we would like.

Looking to longer-term solutions, we need to begin changing the forest structure back to a form more akin to historical patterns: to generate fire-resistant structures with small-scale horizontal heterogeneity and a significant large-tree component. The silvicultural systems suggested here provide for the maintenance of large trees and complex stand structures, while significantly decreasing the risk of catastrophic wildfire. Through management experiments, we need to ascertain which, if any, of these stand structures may also be suitable for spotted owls.

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1988c Sequoia National Forest; 225 p.
1990 Tahoe National Forest; 817 p.
1991a Lassen National Forest; 334 p. Draft
1991b Stanislaus National Forest; 458 p.

Appendices

Appendices

Marlene B. Verner, Compiler

Appendix A-Technical Assessment Team and Chronology of Activities

Technical Assessment Team

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Robert Taylor, Director of Wildlife Ecology, California Forestry Association, Sacramento, California.

Chronology of Activities

4-6 June 1991--Sacramento

The Core Group met to set up a tentative calendar; schedule field trips; identify and schedule needed workshops; assess the information needed from each National Forest, such as maps and other spotted owl data; discuss other needs, such as a reference library and computer hardware and software.

11 June--Sacramento

Arranged for office furnishings and equipment..

12 June-Berkeley
Meeting to discuss editorial needs and related matters.
18 June-Sacramento
Review of timber sales in planning stage or under contract.

24-29 June-First field trip
On-the-ground inspection of California spotted owl habitat and research study areas in the Sierra Nevada, including nesting, roosting and foraging sites. The first two days were spent on the Eldorado National Forest (NF) and Fruit Growers Supply Company's lands; the third day was on the Tahoe NF, taking us to one of our highest elevation nests at 7,000 feet; the fourth day was spent in visiting Sierra Pacific Industries' lands on the Tahoe NF; the fifth day was on the Plumas NF; and the sixth day was spent on the Lassen NF.

8-13 July-Second field trip
This week was a continuation of visits to California spotted owl habitat and research study areas. The first day was spent on the Stanislaus NF and Fiberboard Industries' lands; the second day was on the Sierra NF; Sequoia National Park was visited on the third day; the fourth day was spent on Sequoia NF; the fifth and sixth days were spent on the Los Padres NF visiting the southern part and northern part, respectively.

22-26 July-Sacramento
The Team invited Forest Biologists and Conservation Biologists to attend up-coming meetings.
26 July
Meeting with fire specialists. Informal discussion of fire history and current fuel conditions in the Sierra Nevada and southern chaparrel areas.
26 July
Meeting to discuss information needs on timber resources.

29-30 July-Sacramento
29 July
Met with Sierran Forest Biologists (from the Lassen, Plumas, Tahoe, Eldorado, and Lake Tahoe Basin Management Unit) to apprise them of the September 27-28 Biology Workshop to be held in Sacramento. Additional invitations went to the Sierra, Sequoia, Angeles, San Bernardino, Cleveland, and Los Padres NFs.

5-9 August-Sacramento
Technical Assessment Team still contacting people with regard to the upcoming Biology Workshop.
5 August
Session with biologists from Tahoe NF.
6 August
Meeting with Northern Spotted Owl Recovery Team biologist's subcommittee to review Dr. McKelvey's spatially explicit population simulation model. Recommended structural changes and methods of parameterization.
8 August
Mapping session with biologists from the Tahoe NF.
9 August
Planning session with cartographers.

19-22 August-Third field trip
The first day was spent on the Angeles NF; the San Bernardino NF was visited on the second day; the third day was divided between Mount San Jacinto and Palomar Mountain; and the fourth day was spent on the Cleveland NF in the Laguna Mountains.
26-30 August-Sacramento
26 August
Meeting with cartographers to discuss options for producing maps.
27-28 August
Biology Workshop with 55 participants from all the NFs in Region 5 to discuss the California spotted owl's current status, habitat use and distribution, and future trends of the owl in each National Forest.
30 August
Meeting with Steve Self, Sierra Pacific Industries, Redding, California. Presentation and discussion of Sierra Pacific Industries' owl plan--approach, habitat descriptions, implementation, guidelines, and so on.

8-13 September-Sacramento
Formulating working library and gathering data.
10 September
Meeting with Jonathan Bart, Northern Spotted Owl Recovery Team Leader, Portland, Oregon. Reviewed recommendations on parameter values for Kevin McKelvey's simulation model.
10-11 September
Conservation Biology Workshop with 36 participants from numerous State and Federal agencies, universities, and private industries throughout the U.S.; discussed a variety of issues and concepts from conservation biology as they might relate to planning for the California spotted owl.

23-27 September-Sacramento .
25 September
Meeting with History Group to discuss objectives of their contribution to the CASPO report.

1 October-Sacramento
Meeting with timber staffs from all Sierran NFs to discuss the kinds of timber inventory information that could be provided, and how soon. Resolved details on instructions to National Forests on maps needed and tabular information to accompany some maps.

7-11 October-Sacramento
7 October
Meeting to discuss fuels management.
8 October .
Information exchange with representatives of environmental organizations.
11 October
Bureau of Land Management presented their potential owl habitat information.

12-13 October-Fourth field trip
Team visited Roseburg Resources Company's lands to gain additional firsthand information on owl habitat on industry lands.

14-18 October-Sacramento
17 October
Silviculture Workshop; all-day session with 24 agency, academic, and industry silviculturists participating, along with members from the Core Group.

28 October-1 November-Sacramento
30 October
Fifth field trip. Visited Michigan-California Timber Company's lands and compared current forests with old, historic photos of forests and land management from the past 80-100 years.

4-8 November-Sacramento
Compiling information for library, mapping, and general data.
18-22 November-Sacramento
19 November
Meeting with Fuels Management Specialists to have a full review of all habitat photos taken on the field trips. Discussed their use in depicting spotted owl habitat. Also discussed dead-and-downed woody material and forest stands with regard to fire hazards.
20 November
Reviewed progress of the History Group. Viewed and picked possible habitat photos for use in Chapter 5.
21 November
Met to review cumulative effects analysis used by Region 5 to determine impacts of green timber sales on California spotted owl habitat.
2-6 December-Sacramento
2 December
Meeting to discuss ways in which the Technical Assessment Team and the Policy-Implementation Team can interact most efficiently.
5 December
Presentation on the influence of fire on forest structure and composition by John Maupin, Fire Management Officer, Plumas NF, Quincy, California.

6-10 January 1992-Sacramento
Team working session.

20-24 January-Sacramento
Team working session. 24
January
Coordination meeting with Policy-Implementation Team.

3-14 February-Sacramento
4 February
Discussion of possible approaches to risk assessment.
11 February
Presentation on forest conditions to be expected, over the long-term, if. the California Forestry Reform Act of 1992, or something like it, is enacted by the State Legislature.
13 February
Briefing for co-chairs of Steering Committee on current status of the Team's discovery process.

24-28 February-Sacramento
Team working session.

2-6 March-Sacramento
Team working session.

9 March-Fresno
Nine of 13 report chapters sent from Fresno to peer reviewers picked by presidents of scientific societies:

American Ornithologists' Union
Dr. Richard N. Conner, Research Wildlife Biologist, Southern Forest Research Station, USDA Forest Service, Nacogdoches, Texas.

The Wildlife Society
Dr. David Graber, Research Biologist, Sequoia/Kings Canyon National Parks, Three Rivers, California.

The Society for Conservation Biology
Dr. Stanley A. Temple, Professor, Department of Wildlife Ecology, University of Wisconsin, Madison, Wisconsin.

Ecological Society of America
Dr. Ted Case, Professor, Department of Biological Sciences, University of California, La Jolla, California.

Society of American Foresters
Dr. Arthur Cooper, Head, Department of Forestry, North Carolina State University, Raleigh, North Carolina.

10 March-Arcata
Two additional chapters sent to reviewers.

16-18 March-Sacramento
Team working session.

23-31 March-Sacramento
Team working on last two chapters of the CASPO report. Vacated Sacramento offices 31 March.

1 April-7 May-Fresno and Arcata
Team finishing report with regard to review suggestions and final revisions.

8 May-Sacramento
Final report presented to the Steering Committee.

Appendix B-Glossary

Activity center-an area within which an owl or pair of owls finds suitable nesting sites and several suitable roost sites, and in which a substantial amount of their foraging occurs. An activity center can generally be identified by the location of a nest or a primary roost. Other identifiers are recent locations of owls, especially of pairs or reproductive pairs.

Adaptive kernel technique-a method of estimating home-range size in which, first, a bivariate probability distribution is estimated using the observed locations, and then the area of the contour that contains 95 percent of the observed locations is calculated.

Adaptive management-process of implementing policy decisions as scientifically driven management experiments that test predictions and assumptions in management plans.

Algorithm-mathematical rule for solving a problem.

Allee effect-a depression in the encounter rate between males and females resulting from low population densities; the probability of finding a mate drops below that required to maintain the reproductive rates necessary to support the population.

Allowable sale quantity-(ASQ) the maximum quantity of timber that may be sold by a given National Forest from land capable, available, and suitable for timber production for a time period; usually expressed on an average annual basis.

Basal area-the area of the cross-section of a tree stem near its base, generally at breast height and inclusive of bark.

Biological diversity-the variety of life's forms-that is plants, birds, insects, and so on.

Biomass-the total quantity (at any given time) of living organisms of one or more species per unit of space, or of all the species in a biotic community.

Biomass sale-sale of wood fiber such as logging residue (slash), small diameter live trees and cull logs (other than saw logs), for the purpose of energy co-generation or chip production.

Birth-pulse population-a population assumed to produce all of its offspring at an identical, and instantaneous, point during the annual cycle.

Blowdown-trees felled by high winds.

Bonferroni confidence interval-an individual confidence interval constructed about each estimated proportion within a multinomial contingency table. The width of each confidence interval is adjusted downward to account for the estimation of simultaneous intervals.

Bottleneck-see "population bottleneck."

Burning period-the anticipated period of greatest fire activity during a 24-hour period, typically from 1000 until 1800.

Cambium-a layer of formative cells between the wood and bark in woody plants: the cells increase by division and differentiate to form new wood and bark.

Canopy closure-the degree to which the crowns of trees are nearing general contact with one another.

Carrying capacity-the maximum number of animals that can be sustained over the long-term on a specified land area.

Center of activity-owl's nest site or primary roost area.

Checkerboard ownership-a land ownership pattern in which every other section (square mile) is in Federal ownership as a result of Federal land grants to early western railroad companies.

Cohort-individuals all resulting from the same birth-pulse, and thus all of the same age.

Colonization-the act or process of establishing a new colony or population.

Commercial forest land-forest land tentatively suitable for the production of crops of timber and that has not been withdrawn for other reasons.

Confidence interval-a region lying above and below a parameter estimate (for example, the mean) in which the true parameter value is believed to occur with some specified probability.

Connectivity-a measure of the extent to which intervening habitat truly connects habitats for juvenile spotted owls dispersing between them.

Core area-a defined area that includes the center of activity of a pair, including the nest site if known.

Corridor-defined tract of land, usually linear, through which a species must travel to reach habitat suitable for reproduction and other life-sustaining needs.

Cull-a tree that is not healthy (diseased, broken top, stunted, and so on) and is rejected as not being up to standard for regular timber harvest.

D.b.h.-diameter of a tree at breast height, typicallly measured in inches.

Demographic rescue-see "rescue."

Demographic stochasticity-random fluctuations in birth and death rates.

Density-dependent-process, such as fecundity, whose value depends on the density of animals in the population.

Dispersal-the movement, usually one way, and on any time scale, of plants (seeds) or animals from their point of origin to another location where they subsequently produce offspring.

Dispersal capability-ability of members of a species to move from their area of birth to another suitable location and subsequently to breed.

Dispersal distance-the straight-line distance traveled by an individual from its birth place until it stops dispersing (assumed to be a breeding site) or dies.

Dominant canopy closure (cover)-canopy closure of only the dominant trees in a stand, expressed as a percentage.

Dry ravel-a form of surface erosion in which dry, unconsolidated material moves down slope under the influence of gravity.

Duff-decaying vegetable matter that forms a layer on the forest floor.

Eastside pine forest-general name for a habitat type occurring generally east of the Sierran crest. It is dominated by ponderosa and/or Jeffrey pine.

Ecological integrity-the condition in which all key components of an ecological system are intact and functioning normally.

Ecotone-contact zone between two plant communities, where elements of each intermingle.

Edge effects-differences in microclimate, flora, fauna, stand structure, habitat values, stand integrity (including resistance to being blown down by high winds) that occurs in or as a result of a transition zone where two plant communities or successional stages come together.

Emigration-permanent movement of individuals of a species from a population.

Environmental stochasticity-random variation in environmental attributes such as temperature, precipitation, and fire frequency.

Epigeous fungi-above-ground fruiting bodies of fungi, in the form of mushrooms; these make up part of the diet of spotted owl prey.

Even-aged forest-a forest stand composed of trees with less than a 20-year difference in age between the oldest and youngest.

Extinction rate-the number of elements (individuals, populations, species) lost per unit of time.

Extinction time-predicted period of time for a population to become extinct.

Fecundity-the number of young per breeding-age female. In model formulations, fecundity usually refers to the number of female young per breeding-age female, calculated by assuming a 1:1 sex ratio.

Fire regime-a description of the frequency, severity, and extent of fires that occur in an area.

Floaters-nonbreeding adults and subadults that move and live within a breeding population, often replacing breeding adults that die; nonterritorial individuals.

Foothill riparian/hardwood forest-general name for a habitat type occurring at low elevations in the Sierran foothills. It includes stands of hardwoods immediately adjacent to streams, as well as dense stands of hardwood forests on the adjoining slopes. Tree species along streams include cottonwood, California sycamore, interior live oak, California buckeye, Oregon ash, and occasionally white alder. Tree species on the adjoining slopes include blue oak, interior live oak, and digger pine.

Forest landscape-land presently forested or formerly forested and not currently developed for nonforest use.

Fragmentation-process of reducing the size and continuity of patches of habitat; specifically in this document, fragmentation is used in reference to forests.

Fuel ladder-dead or living fuels that connect surface fuels to tree or brush foliage and promote spread of fire from ground to vegetation crowns.

Fuel loading-the amount of combustible material present per unit area, usually expressed in tons per acre.

Fuels-combustible materials.

Gene flow-movement of genetic material between populations.

Genetic stochasticity-random changes in gene frequencies from such factors as inbreeding.

Genetic variability-the number of different genes possessed by an individual or population.

Habitat capability-capacity of a habitat to support an estimated number of pairs of a species.

Habitat Conservation Area-(as proposed by the ISC), a contiguous block of habitat to be managed and conserved for breeding pairs, connectivity, and distribution of owls; application may vary throughout the range according to local conditions.

Habitat fragmentation-see "fragmentation."

Habitat mosaic-the mix of habitat conditions across a landscape.

Home range-the area to which the activities of an animal are confined during a defined period of time.

Home range of a pair-the sum of the home ranges of each member of a pair, minus the area of home-range overlap.

Home-range overlap-percentages of the home ranges of two individuals that are shared between them.

Hypogeous fungi-below-ground fruiting bodies of fungi, known as true and false truffles; these are an important part of the flying squirrel's diet.

Initial attack-first action taken to suppress a wildfire, via ground or air.

Interbirth interval-the interval between birth pulses.

Internal recruitment-addition of new breeding individuals to a local population that were born within that same population.

Lambda-the finite rate of population change (population size in year 2 divided by the population size in year 1).

Land Management Plan-a plan written for the management of a National Forest unit, as directed by regulations of the National Forest Management Act of 1976, in which the integrated management of all major resources has been determined through an interdisciplinary team process.

Lands not suited for timber production-lands incapable of producing 20 cubic feet of wood fiber per acre per year, or lands withdrawn from commercial forest harvest for other reasons (see reserved lands).

Lands suited for timber production-commercial forest land identified as appropriate for timber production.

Large sawtimber-forest stands that are characterized by trees that are ≥21 inches in d.b.h.

Late seral stage forest-near-final stage in development of a forest from grasses and forbs, through shrubs, small trees, and finally to large, old trees.

Leave strips-generally narrow bands of forest trees that are left along streams and rivers to buffer aquatic habitats from upslope forest management activities.

Lefkovich matrix-a two-dimensional array of numbers whose entries represent stage-specific estimates of demographic (birth and death) rates. The matrix is used to project population stage structures through time.

Legacy-remnant trees of original forest stands, both alive and dead.

Leslie matrix-a two-dimensional array of numbers whose entries represent the age-specific estimates of demographic (birth and death) rates. The matrix is used to project population age structures through time.

Life table-mathematical table illustrating the age-specific birth and death rates of a population.

Linear model-a combination of random variables, none of which has exponents that differ from 1.0.

Linear regression model-an equation that explains some amount of the variation in a dependent variable with a linear combination of one or more independent variables.

Live oak/bigcone Douglas-fir forest-general name for a habitat type that occurs in a narrow band, mostly at mid-elevations, in mountains of all four NFs in southern California. Dominant tree species are canyon live oak, coast live oak, and bigcone Douglas-fir.

Locus-the point (for example, along an axis of a graph) at which the shape of a mathematical function changes dramatically.

Long term-here, 50 to 100 years and sometimes beyond.

M2G, M3G, M3N, M3P, M4G, M4N, M4P, M5G, M5N, M6-see timber strata.

Managed forest-forest land that is harvested on a scheduled basis and contributes to an allowable sale quantity.

Medium sawtimber-forest stands that are characterized by trees that are 11-20.9 inches in d.b.h.

Metapopulation-a population comprised of a set of isolated subpopulations that are "linked" by the dispersal of individuals, allowing for recolonization of unoccupied habitat patches after local extinction events.

Mesic-moderately moist, in referring to habitats.

Microenvironment-the sum total of all the external conditions in a small or restricted area that may influence organisms.

Microhabitats-a restricted set of distinctive environmental conditions that constitute a small habitat, such as the area under a log.

Minimum convex polygon technique-a method of estimating home-range size in which the smallest possible convex polygon is drawn around the outermost locations where an animal was observed; the area within the polygon is then calculated.

Mixed-conifer forest-general name for similar habitat types in the Sierra Nevada and southern California. It is the predominant timber-producing forest of the Sierra Nevada, consisting of various mixtures of white fir, ponderosa pine (at lower elevations), incense-cedar, sugar pine, black oak, and red fir (at higher elevations). Douglas-fir is an important component from Yosemite NP northward, and giant sequoia occurs in widely scattered localities. In southern California, this type is best developed at relatively high elevations in the San Gabriel and San Bernardino Mountains, and on Mount San Jacinto. Species composition is similar to that of Sierran mixed-conifer, although Coulter pine occurs, bigcone Douglas-fir occasionally occurs at lower elevations; but red fir, Douglas-fir, and giant sequoia are missing.

Mixed-evergreen forest-a forest community that is dominated by two or more species of broad-leaved hardwoods whose foliage persists for several years; important western species include madrone, tanoak, chinquapin, canyon live oak, and California-laurel.

Model-an idealized representation of reality developed to describe, analyze, or understand the behavior of some aspect of it; a mathematical representation of the relationships under study.

Monitoring-a process of collecting information to evaluate whether or not objectives of a management plan are being realized.

Monitoring program-see "monitoring"; the program used to monitor a population and its habitat.

Natal cluster-a group of adjacent animal territories, in one of which an individual was born.

Network-a particular spatial arrangement of entities (blocks or patches of owl habitat in this case) that are interconnected in some fashion (by dispersal of owls in this case).

Null hypothesis-a supposition of no difference between test comparisons (situation A no different from situation B).

Old growth-forest stand with moderate to high canopy closure; a multilayered, multispecies canopy dominated by large overstory trees; a high incidence of large trees with large, broken tops, and other indications of decadence; numerous large snags; and heavy accumulations of logs and other woody debris on the ground.

Owl site-an area of unspecified dimensions where a single owl or a pair of owls has been located, usually repeatedly. In demographic and radio-tracking study areas, where efforts to locate all owls are more intense than elsewhere, most owl sites with single owls have eventually been found to have a pair. All owl sites have been mapped and given unique spatial references, so they can be tallied. Designation of an owl site makes no assumption about home-range or territory boundaries of the owls, although usually a center of activity can be identified by the location of a nest or a primary roosting area. The terms "owl site" and "site" are general and often used generically to refer to home ranges, territories, or to sites designated by agencies for special owl management.

Owl use area-an irregularly shaped polygon that contains a known or predicted activity center and encompasses the amount of nesting and foraging habitats typically found within home ranges during the breeding season.

Pair site-an area of variable dimensions on the landscape assumed to be large enough to have an amount of habitat capable of supporting one pair of spotted owls; see "owl site."

Paradigm-an underlying model or representation that characterizes a process.

Physiographic province-a geographic region in which climate and geology have given rise to a distinct array of land forms and habitats.

Ponderosa pine/hardwood forest-(montane hardwood) general name for a habitat type that blends with the upper portion of the foothill riparian/hardwood forest. In the southern Sierra Nevada, ponderosa pine at its lowest elevation generally occurs with interior live oak, canyon live oak, and black oak, with incense-cedar and white fir coming into stands at slightly higher elevations. In the northern Sierra Nevada, tanoak and Pacific madrone commonly contribute to the hardwood component of this type.

Population-a collection of individuals that share a common gene pool through interbreeding.

Population bottleneck-the phenomenon experienced by a small population that is susceptible to the deleterious effects of demographic and genetic stochasticity; also a zone of constriction in the distribution of a population.

Population density-number of individuals of a species per unit area.

Population persistence-general term for the capacity of a population to maintain sufficient numbers and distribution over time.

Population viability-probability that a population will persist for a specified period of time across its range, despite normal fluctuations in population and environmental conditions.

Potential habitat-(1) habitat that has been altered (for example, logged or burned) and is not presently suitable for owls but is believed to have the potential to regenerate into suitable habitat; (2) unsurveyed habitat that ap-. pears to be suitable based on comparisons with habitat elsewhere that has known owl sites.

Power analysis-a statistical method for estimating the probability of making a type-II error (failure to detect a difference or a trend that actually occurs, such as a decline in a population of spotted owls).

R3G, R3N, R3P, R4G, R4N-see timber strata.

Red fir forest-general name for a habitat type that blends with the higher portions of Sierran mixed-conifer forest. It is dominated by red fir, with increasing amounts of white fir at lower elevations until it becomes mixed-conifer forest. At upper elevations it often includes some lodgepole pine and occasionally quaking aspen.

Redwood/California-laurel forest-general name for a habitat type that is restricted to the central coast range, where coast redwood, California-laurel, tanoak, Pacific madrone, red and white alder, coast live oak, Santa Lucia fir, and bigleaf maple form various mixtures.

Regulated forest-theoretical managed forest from which the same acreage of trees can be removed annually, in perpetuity.

Rescue (rescue effect)-periodic immigration of new individuals sufficient to maintain a population that might otherwise decline toward extinction.

Reserved land-Federal lands unavailable for timber yield or management due to being a National Park or classified as a Wilderness Area in a National Forest.

Reserves-tracts of forest temporarily or permanently set aside from logging.

Restricted harvest-land either withdrawn from logging or where timber production is limited to less than clearcutting.

Riparian/hardwood forest-general name for a habitat type that varies considerably in different parts of southern California. In deep canyons in the Los Padres NF, for example, it occurs in narrow strips adjacent to permanent or near-permanent streams. Common tree species include coast live oak (near coast), canyon live oak (interior locations), California sycamore, white alder, California-laurel, and cottonwood. In shallower canyons in the Cleveland NF, these forests may consist almost exclusively of coast live oak.

Rotation-the planned number of years between the regeneration of an even-aged stand and its final cutting at a specified stage.

Saw kerf-the cut or channel made by a saw.

Scansorial-adapted for climbing.

Search capability-the ability of a dispersing juvenile or adult owl to locate suitable habitat.

Search efficiency-proportion of dispersing juveniles or adults that locate minimally suitable habitat before they die.

Search time-number of days required for an average dispersing individual to locate suitable or better habitat.

Seed-tree cut-an even-aged regeneration cutting in which only a few seed trees per acre (fewer than for a shelterwood cut) are retained until after new tree seedlings are established.

Senescence-state of being old; characterized by having attributes associated with old age.

Sensitivity coefficient-term that measures relative degree of change in outcome of a mathematical expression or equation after a specified change in an individual component.

Shelterwood cut-an even-aged regeneration cutting in which new tree seedlings are established under the partial shelter of seed trees.

Short term-here, 1 to 5O years.

Sink-population whose average reproductive rate is less than its average rate of mortality; area that attracts immigrants not expected to contribute significantly to future populations (see "source").

Site-an area considered from the standpoint of its use for some specified purpose (for example, habitat studies, owl locations-see "owl site," and logging operation).

Small sawtimber-forest stands that are characterized by trees that are <11 inches in d.b.h.

Snag-standing dead tree.

Source-an actively breeding population that has an average birth rate that exceeds its average death rate; produces an excess number of juveniles that may disperse to other areas.

Standards and guidelines-directions generated and followed in management plans.

Stochastic-random, uncertain; involving a random variable.

Stochastic fecundity-random fluctuation in a population's rate of producing offspring.

Subpopulation-a well-defined set of interacting individuals that comprise a proportion of a larger, interbreeding population.

Suitable habitat-here, an area of forest vegetation with the age-class, species of trees, structure, sufficient area, and adequate food source to meet some or all of the life needs of a California spotted owl.

Sustained yield or production-the amount of timber that a forest can produce continuously from a given intensity of management; implies continuous production; a primary goal is to achieve a balance between incremental growth and cutting.

Synoptic weather pattern-large-scale weather pattern.

Territory-the area that an animal defends, usually during the breeding season, against intruders of its own species.

Threshold phenomenon-a pattern or trend, as in population growth rate, that exhibits relatively long periods of slow change followed by precipitous increase or decrease in response to a slight change in an environmental gradient.

Timber strata-M = mixed conifer, R = red fir, P = ponderosa pine; 2 = trees <l2 inches in d.b.h., 3 = trees 12-23.9 inches in d.b.h., 4 = trees ≥24 inches in d.b.h.; G = good canopy cover (70+ percent), N = normal canopy cover (40-69 percent), P = poor canopy cover (0-39 percent). Hence, an M4G stand is mixed-conifer with trees ≥24 inches in d.b.h., and canopy cover ≥70 percent; an R2P stand is red fir with trees <l2 inches in d.b.h., and 0-39 percent canopy cover.

Torpid-having lost temporarily all or part of the power of sensation or motion, as a hybernating animal.

Total canopy closure (cover)-canopy cover by all vegetation 7 feet or higher above the ground, expressed as a percentage.

Truffles-the below-ground fruiting bodies of hypogeous fungi, which are a major food source for flying squirrels and other small mammals.

Turnover-a term in population analysis that indicates the rate or number of identifiable adults that die and are replaced during a specified period.

Type conversion-conversion of an area from one habitat type to another, such as oak woodland to annual grassland.

Type-I error-statistical term for the error made when a null hypothesis that is true is rejected; for example, concluding that a difference exists between two populations that are identical.

Type-II error-statistical term for the error that is made when a null hypothesis that is false is not rejected; that is, concluding that no difference exists in a comparison between two populations when a difference does exist.

Variance-a statistical tern that indicates a measure of variability within a finite population of a sample; the total of the squared deviations of each observation from the arithmetical mean divided by one less than the total number of observations.

Viability-ability of a population to maintain sufficient size so that it persists over time, in spite of normal fluctuations in numbers; usually expressed as a probability of maintaining a specific population for a specified period.

Vital rates-collective term for the age-specific birth and death rates of a population.

Windthrow-a tree or group of trees uprooted by the wind.

Xeric-dry, in referring to habitats.

Appendix C-Species List

Common Name	Scientific name
Lower Plants	
Algae	Division Chlorophyta (various species)
Fungi, epigeous	Divisions Ascomycota and Basidiomycota. Common genera in the Sierra Nevada include *Boletus, Amanita, Cortinarius,* and *Armillaria*
Fungi, hypogeous	Divisions Ascomycota and Basidiomycota. Common genera in the Sierra Nevada include *Rhizopogon, Gautieria, Geopora, Melanogaster,* and *Hymenogaster*
Lichens	Division Ascomycota (various species)
Chartreuse	*Letharia vulpina*
Hair	*Bryoria fremontii*
Staghorn	*Usnea ceratina*
Moss	Division Bryophyta, Class Muscopsida, (various species)
Grasses/Forbs	
Bitterroot, meadow	*Lewisia nevadensis*
Brodiaea, golden	*Brodiaea lutea*
Buckwheat, California	*Eriogonum fasciculatum*
Chinese nests	*Collinsia concolor*
Grass	*Gramineae* spp.
Lupine, broad-leaf	*Lupinus latifolius*
Trefoil (bird's foot)	*Lotus* spp.
Shrubs	
Blackberry, California	*Rubus ursinus*
Buckbrush	*Ceanothus cuneatus*
Buckeye, California	*Aesculus californica*
Ceanothus	*Ceanothus* spp.
Chamise	*Adenostoma fasciculatum*
Cherry, hollyleaf	*Prunus ilicifolia*
Chinquapin, golden	*Castanopsis sempervirens*
Chokecherry	*Prunus virginiana*
Coffeeberry, California	*Rhamnus californica*
Currants	*Ribes* spp.
Deerbrush	*Ceanothus integerrimus*
Elderberry	*Sambucus* spp.
Gooseberry, rock	*Ribes quercetorum*
Hazel, California (Hazelnut)	*Corylus cornuta* var. *californica*
Jim brush	*Ceanothus sorediatus*
Juniper, mountain	*Juniperus communis* var. *saxatilis*

Common Name	Scientific name
Shrubs	
Manzanita	*Arctostaphlyos* spp.
Mountain mahogany, curlleaf	*Cercocarpus ledifolius*
Poison oak	*Rhus diversiloba*
Rose, California wild	*Rosa californica*
Sage, coastal	*Artemisia californica*
Sage, White	*Salvia apiana*
Sagebrush, big	*Artemisia tridentata*
Sagebrush, California	*Artemisia californica*
Serviceberry, western	*Amelanchier alnifolia*
Sumac, lemonade	*Rhus integrifolia*
Toyon	*Heteromeles arbutifolia*
Whitethom, mountain	*Ceanothus cordulatus*
Willows	*Salix* spp.
Yerba-Santa	*Eriodictyon* spp.
Yucca	*Yucca whipplei*
Other	
Mistletoes, dwarf	*Arceuthobium* spp.
Trees	
Alder, red	*Alnus rubra*
Alder, white	*Alnus rhombifolia*
Ash, Oregon	*Fraxinus latifolia*
Aspen, quaking	*Populus tremuloides*
Boxelder, California	*Acer negundo*
Buckeye, California	*Aesculus californica*
California-laurel (bay)	*Umbellularia californica*
Cedar, incense -	*Libocedrus decurrens*
Chinquapin, giant	*Castanopsis chrysophylla*
Cottonwood	*Populus* spp.
Dogwood, Pacific	*Cornus nuttallii*
Douglas-fir	*Pseudotsuga menziesii*
Douglas-fir, bigcone	*Pseudotsuga macrocarpa*
Fir, red (Shasta)	*Abies magnifica*
Fir, Santa Lucia	*Abies bracteata*
Fir, white	*Abies concolor*
Hazelnut, California (hazel)	*Corylus cornuta* var. *californica*
Hemlock, mountain (black)	*Tsuga mertensiana*
Incense-cedar	*Libocedrus decurrens*
Juniper, California	*Juniperus californica*
Juniper, western	*Juniperus occidentalis, J. australis*
Laurel, California- (bay)	*Umbellularia californica*
Madrone, Pacific	*Arbutus menziesii*

Common Name	Scientific name

Trees

Maple, bigleaf	*Acer macrophyllum*
Oak, black	*Quercus kelloggii*
Oak, blue	*Quercus douglasii*
Oak, California scrub	*Quercus dumosa*
Oak, canyon live	*Quercus chrysolepis*
Oak, coast live	*Quercus agrifolia*
Oak, interior live	*Quercus wislizenii*
Oak, shrub live	*Quercus turbinella*
Oak, valley	*Quercus lobata*
Pine, Coulter	*Pinus coulteri*
Pine, digger	*Pinus sabiniana*
Pine, foxtail	*Pinus balfouriana*
Pine, Jeffrey	*Pinus jeffreyi*
Pine, lodgepole	*Pinus contorta*
Pine, pinyon	*Pinus monophylla*
Pine, ponderosa (yellow)	*Pinus ponderosa*
Pine, sugar	*Pinus lambertiana*
Pine, western white	*Pinus monticola*
Redwood (coast)	*Sequoia sempervirens*
Sequoia, giant	*Sequoiadendron giganteum*
Sycamore, California	*Platanus racemosa*
Tanoak	*Lithocarpusdensijlorus*
Willows	*Salix* spp.

Invertebrates

Beetle, bark	*Dendroctonus* spp., *Ips* spp., *Scolytus* spp.
Beetle, fir engraver	*Scolytis ventralis*
Beetle, June	*Ploeocoma hoppingi*
Cricket	*Gryllus* spp.
Fly, hippoboscid	*lcosta americana, Ornithomya anchineuria*
Worn, flat	*Cestoda*
Worm, round	*Nematoda*
Worm, spiny-headed	*Acanthocephala*

Birds

Goshawk	*Accipitergentilis*
Hawk, Cooper's	*Accipiter cooperi*
Hawk, red-tailed	*Buteo jamaicensis*
Hawk, sharp-shinned	*Accipiter striatus*
Mallard	*Anas platyrynchos*
Owl, barn (common)	*Tyto alba*
Owl, barred	*Strix varia*
Owl, boreal (Tengmalm's)	*Aegolius funereus*

Common Name	Scientific name

Birds

Owl, California spotted	*Strix occidentalis occidentalis*
Owl, eagle	*Bubo bubo*
Owl, great gray	*Strix nebulosa*
Owl, great horned	*Bubo virginianus*
Owl, long-eared	*Asio otus*
Owl, Mexican spotted	*Strix occidentalis lucida*
Owl, northern hawk	*Surnia ulula*
Owl, northern spotted	*Strix occidentalis caurina*
Owl, pygmy (Eurasian)	*Glaucidium passerinum*
Owl, short-eared	*Asio flammeus*
Owl, snowy	*Nyctea scandiaca*
Owl, tawny	*Strix aluco*
Owl, ural	*Strix uralensis*
Partridge, gray	*Perdix perdix*
Raven	*Corvus corax*
Sparrowhawk (Eurasian)	*Accipiter nisus*
Woodpecker, acorn	*Melanerpes formicivorus*
Woodpecker, red-cockaded	*Picoides borealis*

Mammals

Bats	*Chimptera*
Chipmunk	*Eutamias* spp.
Gopher, Great Basin pocket	*Thomomys talpoides*
Gopher, mountain pocket	*Thomomys monticola*
Gopher, southwestern pocket	*Thomomys bottae*
Mole	*Scapanus* spp.
Mouse, brush	*Peromyscus boylii*
Mouse, cactus	*Peromyscus eremicus*
Mouse, California	*Peromyscus californicus*
Mouse, California pocket	*Perognathus californicus*
Mouse, deer	*Peromyscus maniculatus*
Mouse, house	*Mus musculus*
Mouse, pinyon	*Peromyscus truei*
Mouse, western harvest	*Reithrodontomys megalotis*
Mouse, western jumping	*Zapus princeps*
Mouse, white-footed	*Peromyscus* spp.
Pika	*Ochotona princeps*
Rabbit	*Sylvilagus* spp.
Rabbit, brush	*Sylvilagus bachmani*
Rabbit, cottontail	*Sylvilagus audubonii*
Shrew	*Sorex* spp.
Squirrel, ground	*Spermophilus* spp.
California	*Spermophilus beecheyi*
Golden-mantled	*Spermophilus lateralis*

Common Name	Scientific name
Mammals	
Squirrel, northern flying	*Glaucomys sabrinus*
Squirrel, southern flying	*Glaucomys volans*
Squirrel, tree	*Sciurus* spp.
Vole	*Microtus* spp.
Vole, California	*Microtus californicus*
Vole, long-tailed	*Microtus longicaudus*
Woodrat	*Neotoma s*pp.
Woodrat, bushy-tailed	*Neotoma cinerea*
Woodrat, desert	*Neotoma lepida*
Woodrat, dusky-footed	*Neotoma fuscipes*

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The Forest Service, U.S. Department of Agriculture, is responsible for Federal leadership in forestry. It carries out this role through four main activities:

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- improve living conditions in rural areas
- Research on all aspects of forestry, rangeland management, and forest resources utilization.

The Pacific Southwest Research Station

- Represents the research branch of the Forest Service in California, Hawaii, American Samoa and the western Pacific.