USDA Forest Service
U.S. DEPARTMENT OF AGRICULTURE

Pacific Northwest Research Station | Research Paper PNW-RP-618 | August 2021

Simulating the Effort Necessary to Detect Changes in Northern Spotted Owl (*Strix occidentalis caurina*) Populations Using Passive Acoustic Monitoring

Damon B. Lesmeister, Cara L. Appel, Raymond J. Davis, Charles B. Yackulic, and Zachary J. Ruff

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Authors

Damon B. Lesmeister is a research wildlife biologist, U.S. Department of Agriculture, Forest Service, Pacific Northwest Research Station, Forestry Sciences Laboratory, 3200 SW Jefferson Way, Corvallis, OR 97331; **Cara L. Appel** is a graduate research assistant, U.S. Department of Agriculture, Forest Service, Pacific Northwest Research Station, Forestry Science Laboratory and Oregon State University, Department of Fisheries and Wildlife, 3200 SW Jefferson Way, Corvallis, OR 97331; **Raymond J. Davis** is the monitoring lead for older forests and spotted owls, U.S. Department of Agriculture, Forest Service, Pacific Northwest Region, 3200 SW Jefferson Way, Corvallis, OR 97331; **Charles B. Yackulic** is a research statistician, U.S. Department of the Interior, Geological Survey, Southwest Biological Science Center, 2255 N Gemini Drive, Building 4, Flagstaff, AZ 86001; **Zachary J. Ruff** is a research assistant, Oak Ridge Institute for Science and Education and U.S. Department of Agriculture, Forest Service, Pacific Northwest Research Station, Forestry Sciences Laboratory, 3200 SW Jefferson Way, Corvallis, OR 97331.

Cover: Northern spotted owl, by Chris McCafferty.

Abstract

Lesmeister, Damon B.; Appel, Cara L.; Davis, Raymond J.; Yackulic, Charles B.; Ruff, Zachary J. 2021. Simulating the effort necessary to detect changes in northern spotted owl (*Strix occidentalis caurina*) populations using passive acoustic monitoring. Res. Pap. PNW-RP-618. Portland, OR: U.S. Department of Agriculture, Forest Service, Pacific Northwest Research Station. 55 p.

Passive acoustic monitoring is a promising method for monitoring rare and nocturnal species, and for tracking changes in forest wildlife biodiversity. We conducted simulations to compare and evaluate various passive acoustic sampling designs effectiveness for monitoring spotted owl (*Strix occidentalis caurina*) population trends. We found that each design was effective for detecting a decline (or stability) in spotted own populations within 10 years with even a moderate amount of sampling. There are however, important considerations and tradeoffs among the various design options. Often, estimated changes in use of the landscape were biased with a consistently lower magnitude of change compared to simulated changes in the population. Although this method has challenges, passive acoustic monitoring can be used to effectively monitor northern spotted owls in the Pacific Northwest.

Keywords: Passive acoustic monitoring, autonomous recording units, simulation, dynamic occupancy models, northern spotted owl, population monitoring.

Summary

The northern spotted owl (*Strix occidentalis caurina*) is an Endangered Species Act-listed species, and populations have been monitored under the Northwest Forest Plan, which was designed, in part, to restore late-successional forests to encourage spotted owl population recovery. Population monitoring has been conducted using a combination of callback surveys and mark-resight methods, yielding valuable data on demography, biology, and population trends. Despite habitat protections, spotted owl populations have declined steeply rangewide, and only a few individuals remain in some study areas. Estimators from current monitoring methods are becoming unreliable because of low precision in parameter estimates, and callback surveys may be harmful to spotted owls. Passive acoustic monitoring is an alternative for detecting spotted owls over a range of forest conditions. This method can detect and rapidly assess competitor (i.e., barred owl *Strix varia*) threats, is noninvasive to the spotted owl population, and is spatially scalable so that sampling may occur from a larger portion of federal lands throughout the spotted owl range. Managers are considering a transition from mark-resight methods to passive acoustic monitoring to track changes in spotted owl populations. We used computer simulations to assess the effectiveness of six different passive acoustic monitoring designs to detect underlying trends in spotted owl populations. The designs varied based on the number and spatial arrangement of 5-km^2 hexagons chosen from a pool of hexagons that were ≥50 percent forest-capable and had ≥25 percent federally managed lands. Four of the six monitoring designs tested were differentiated by either randomly sampling 2, 5, 10, or 20 percent of hexagons from our pool of available hexagons throughout the spotted owl range. Another design scenario randomly sampled 2 percent of hexagons rangewide, with an additional 20 percent random sampling in historical demography study areas (2+20 percent design). The last monitoring design randomly sampled 2 percent of hexagons rangewide, and for each of these selected hexagons, six adjacent hexagons were also sampled. To simulate spotted owl populations, we defined a set of sites suitable for spotted owl territory centers and simulated territory occupancy of these sites over time with various population trends (declining and stationary). We created annual detection histories for sampled hexagons based on decaying detectability of spotted owls with distance from territory center, and estimated changes in hexagon use with dynamic occupancy models. We found that each design was effective for detecting changes in spotted owl populations within 10 years with even a moderate amount of sampling, but there are important considerations and tradeoffs among the various options. With time and sampling density, precision of estimates improved, but often estimated changes in use were biased toward a consistently lower magnitude of change compared to simulated changes in the population. An

advantage of a consistent and directional bias with increasing precision through time is that there are several avenues to correct magnitude of change estimates. A better understanding of the relationship between vocalization dynamics and distance to territory center is needed to reduce the magnitude of change bias, and the 2+20 percent design provides the best opportunity to fill this knowledge gap. To remain relevant and useful to resource managers, the spotted owl monitoring program must adapt with changing population conditions, but there are also opportunities for it to remain a high-standard monitoring program by leveraging recent analytical and technological advancements, and well-designed sampling methods. Although there will be challenges in the transition, passive acoustic monitoring can be used to effectively monitor northern spotted owls in the Pacific Northwest.

Contents

Introduction

The northern spotted owl (*Strix occidentalis caurina*; hereafter spotted owl) was listed as threatened under the Endangered Species Act in 1990 owing to drastic population declines attributed to loss of habitat from timber harvesting. The listing led to regionwide changes in forest management on federal lands under the Northwest Forest Plan (NWFP). The NWFP is a long-term plan designed to maintain and eventually restore late-successional forests to help stabilize declining populations of spotted owls and other old-forest-dependent species. Monitoring of spotted owls was one of several modules that compose an effectiveness monitoring program—a program established to measure success of achieving goals of the NWFP (Lint et al. 1999). The effectiveness monitoring program was designed to be adaptive—allowing for refinement of specifications and methods as successful monitoring strategies were learned. As results were assessed over time, the scope of the program increased to include biodiversity monitoring (Mulder et al. 1999, Ringold et al. 1999). The spotted owl monitoring plan evaluated three methods for monitoring spotted owl populations: (1) demographic mark-resight studies, (2) random census using vocal lures, and (3) density studies (Lint et al. 1999). The plan called for two phases intended to allow the program to adapt to advancements in population and habitat monitoring methods. Phase I is continued monitoring of historical spotted owl territories on demographic study areas (DSAs) that have been in operation since at least the early 1990s. Demographic monitoring of spotted owls is based on data collected with mark-resight methods to estimate apparent survival and recruitment metrics, which can be used for estimating population growth rate (Forsman et al. 2011). The spatial extent of the DSAs covered 8.1 percent of forested federal lands across the spotted owl range, and the findings were inferred for the broader populations to understand rangewide trends. The planned transition to phase II monitoring will involve a change from demographic studies to a model-driven, habitat-based approach (Lint et al. 1999). Phase I results from the spotted owl monitoring plan highlight that habitat quality and amount (i.e., suitable forest) are not reliable predictors of change in spotted owl demographic performance (Dugger et al. 2005, Franklin et al. 2000, Olson et al. 2004), therefore, phase II monitoring will require population surveys in addition to habitat modeling.

The Northwest Forest Plan called for two phases intended to allow the program to adapt to advancements in population and habitat monitoring methods.

During phase I, spotted owl populations have been monitored by using a combination of callback surveys and mark-resight methods, yielding valuable data on demography, biology, and population trends (Anthony et al. 2006, Dugger et al. 2016, Forsman et al. 2011). However, over the past 20 to 30 years, spotted owl populations have continued to decline and are facing an increasing, and under-anticipated, threat from competition with the invasive barred owl (*Strix varia*)

(Dugger et al. 2016, Lesmeister et al. 2018, Wiens et al. 2014). Early detection and rapid response is the preferred management strategy for preventing the establishment and spread of invasive species but requires that potential threats be identified in time to allow risk-mitigation measures to be taken (Westbrooks and Eplee 2011). Phase I of spotted owl monitoring was designed and has been effective for quantifying changes in spotted owl populations, but it was not designed to be an early warning system to rapidly detect the magnitude of the barred owl threat. The occurrence and density of barred owls are consistently underestimated as estimates are based on convenience sampling taken during spotted owl surveys (Wiens et al. 2011), which has been the primary means to understand the barred owl invasion (Lesmeister et al. 2018; Rossman et al. 2016; Yackulic et al. 2012, 2014; Zipkin et al. 2017). With continued spotted owl population declines and resulting low population densities, mark-recapture methods have become untenable in many areas because of low precision of demographic estimates. Estimators derived from any population monitoring strategy are likely to be a challenge with very small populations, but there may be options that are more practical for monitoring small populations and that can provide other benefits to spotted owls (e.g., noninvasive monitoring) and broader biodiversity monitoring program goals.

Mark-resight methods for phase I monitoring require locating spotted owls by callback surveys that elicit a response by individuals when a recorded spotted owl call is broadcast in their territory. However, there are potentially severe consequences to the widespread use of callback surveys for spotted owls when barred owls are present because barred owls will approach and may react aggressively to the source of a spotted owl broadcast call (Herter and Hicks 2000, Piorecky and Prescott 2004, Wiens et al. 2011). Considering interference competition (Wiens et al. 2014) and aggression observed between the two species (Courtney et al. 2004, Gutiérrez et al. 2007, Leskiw and Gutiérrez 1998, Van Lanen et al. 2011), eliciting spotted owl responses in areas where barred owls occur can increase the negative interactions between the two species. Additionally, spotted owls respond to callback surveys less frequently if barred owls are present (Crozier et al. 2006), requiring more callback survey effort to determine occupancy status on historical survey sites. Although protocols have been implemented to reduce the risk of spotted owl-barred owl interactions, there remain many potential risks associated with callback surveys. With continued spotted owl population declines, agencies have evaluated alternative monitoring methods that do not have many of the potential risks associated with mark-resight methods.

The random census monitoring option considered during the development of the spotted owl monitoring plan is analogous to detection-nondetection surveys conducted in an occupancy modeling framework, but when the monitoring plan was developed, these models had not yet been developed. The random census monitoring option (i.e., detection-nondetection surveys) was recognized as having potential for providing independent estimates of spotted owl population trends, but without reliable field an analytical methods, this option was not implementable at the scale necessary to monitor populations. Further development and research on the random census framework for monitoring was recommended (Lint et al. 1999), and since then, significant advancements have been made in developing analytical methods in occupancy design and modeling (e.g., MacKenzie et al. 2002, 2018; Rossman et al. 2016; Zipkin et al. 2017), thus making it possible to estimate changes in landscape use or occupancy.

Most animals produce and use sound for communication and navigation, including amphibians, birds, fish, and mammals. In producing sound, individuals broadcast information into the environment about themselves, which wildlife researchers can use to understand species distribution, population size, and behavior through passive acoustic monitoring. Often, passive acoustic monitoring is achieved with high-quality sound recorders that are deployed in study areas and scheduled to record at specific times. Species sound data obtained with passive acoustic monitoring can be used in an occupancy modeling framework and is a promising method for monitoring vocally active rare, nocturnal species (Blumstein et al. 2011) and forest wildlife biodiversity (Burivalova et al. 2019). Specific to spotted owls, passive acoustic monitoring is an alternative to callback surveys in the random census survey method considered by Lint et al. (1999), and many methods are available to process and analyze the data. Autonomous recording units (ARUs) are able to record vocalizations passively, without eliciting a response, and are therefore less disruptive to bird behavior (Shonfield and Bayne 2017). Several research groups have tested and refined approaches to autonomous owl surveys and data processing (e.g., Domahidi et al. 2019, Frommolt 2017, Ruff et al. 2020, Shonfield et al. 2018). Passive acoustic monitoring is an effective alternative for detecting spotted owls over a range of forest conditions, as well as for identifying and assessing barred owl threats. This method is noninvasive to the spotted owl population since owls are not handled or banded (removes Animal Care and Use permit requirements for owls and feeder mice), and it is spatially scalable meaning that samples from a larger portion of federal lands throughout the spotted owl range can be collected (Duchac et al. 2020, Lesmeister et al. 2019). Complementary research within the range of the California spotted owl indicates that passive acoustic monitoring can be effective for detecting even small changes in California spotted owl populations (Wood et al. 2019a, 2019b, 2020).

Passive acoustic monitoring is an effective alternative for detecting spotted owls over a range of forest conditions, as well as for identifying and assessing barred owl threats.

In addition to being noninvasive, a passive acoustic monitoring system also allows researchers to draw samples from throughout the entire spotted owl range, with greater temporal extent than mark-resight methods coupled with in-person surveys. ARUs can be deployed for extended-duration sessions, which greatly decreases technician time in the field while greatly increasing the quantity of data collected (Tegeler et al. 2012). Deploying and retrieving ARUs occurs during daylight hours, which is an important consideration when surveying nocturnal species because day work is much safer than night work. The biological training and expertise needed for ARU deployment crews are less than what is needed for callback surveys, point counts, and demographic studies. Recordings provide a permanent record that may be reviewed by experts and stored for future analyses. Automated detection models are now available that employ sophisticated computer-based recognition systems for a range of avian species (Blumstein et al. 2011, Chambert et al. 2018, Kahl et al. 2017, Katz et al. 2016). Ruff et al. (2020) developed a deep convolutional neural network to automate the identification of spotted owl calls in large volumes of acoustic data and demonstrated the ability of these methods to extend to many other species.

Passive acoustic monitoring presents many advantages and opportunities, but the type of data generated from mark-resight methods for spotted owls are not currently available by using only bioacoustics. Therefore, either different estimators must be used to monitor changes in spotted owl populations, or methods will need to be developed to identify individual spotted owls based on vocal characteristics. Individual identification from color leg bands is necessary to estimate vital rates of survival and recruitment that are components of population rate estimates used to measure spotted owl population trends (Forsman et al. 2011). Passive acoustic monitoring does not generate these type of data, so model parameters to estimate change in populations are different. Population monitoring in an occupancy framework is based on multiyear surveys of sample sites drawn from a “population” of sites to estimate rates of site use, colonization, extinction, and measures of change-in-use (MacKenzie et al. 2018).

In 2017, research using passive acoustic monitoring for spotted owl began in three DSAs (Olympic Peninsula in Washington, Oregon Coast Range, and Klamath Mountains in Oregon) (Duchac et al. 2020, Lesmeister et al. 2019). Mark-resight methods were discontinued on the Olympic Peninsula after the 2018 field season, and the switch to only passive acoustic monitoring was made in 2019. Currently, spotted owl populations are being monitored using passive acoustic monitoring in four DSAs (Olympic Peninsula, Cle Elum, Oregon Coast Range, Oregon Klamath). Lesmeister et al. (2019) established a grid of 5-km^2 hexagons throughout the entire spotted owl range. Using a randomly selected subset of those hexagons, field crews deploy ARUs at four stations per hexagon for 6 weeks during the breeding season (March through August). ARUs are scheduled to record about 11 hours per day, with two 4-hour recordings centered on sunrise and sunset and 10-minute intervals each hour throughout the day and night.

Analysis of data collected during the 2017 monitoring season has established the effectiveness of passive acoustic monitoring for estimating detection probabilities and probabilities of use for spotted and barred owls (Duchac et al. 2020). The probability of detecting spotted owls with ARUs when present was found to exceed 95 percent after 3 weeks of sampling, with predictable decreases related to increasing distance to the nearest known spotted owl territory center as well as with increasing levels of background noise, such as wind and rain (Duchac et al. 2020). Using this information, along with locations of known or simulated owl territory centers, it is possible to simulate the effectiveness of several ARU-based sampling designs at detecting changes in spotted owl populations over various periods. Testing different monitoring sampling designs can provide information necessary to move forward with rangewide monitoring of spotted owl populations using passive acoustic monitoring.

Study Objectives

We used computer simulations to assess the ability of different passive acoustic monitoring designs to detect underlying trends in spotted owl populations. The designs varied based on the amount and spatial arrangement of sampling a set of 5-km^2 hexagons from the pool of hexagons that were ≥50 percent forest-capable and had ≥25 percent federally managed lands. We also defined a set of potential sites for owl territory centers and simulated territory occupancy of these sites over time with various population trends (declining and stationary) and with random dispersal among sites. Spotted owl territories may overlap multiple sampling hexagons, so individuals could use and thus be detected in multiple hexagons, even at relatively long distances from the territory center. Therefore, surveys of hexagons would reflect the probability of use rather than true occupancy. Although occupancy and use models are fit to the same type of binary survey data (1 = detection, 0 = nondetection) and parameterized in the same way, the interpretation of parameters differs so it is important to distinguish whether the models denote use or occupancy. Most previous occupancy analyses for northern spotted owls were based on surveys of territories (e.g., Yackulic et al. 2014, 2019), but our simulated sampling was not territory based, so we interpreted the occupancy parameter as use. In probability-of-use models, the detection probability parameter has two components: probability of a spotted owl available for detection (i.e., using a hexagon) and probability of being detected during a survey (MacKenzie et al. 2018). We created detection histories by calculating the distances between individual ARUs and territory centers to predict whether owls would be detected, and estimated changes-in-use

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through dynamic occupancy models (MacKenzie et al. 2018). We ran a range of simulations with all combinations of different levels of sampling density, different rates of spotted owl population decline (4 and 8 percent annual decline) and stationarity (0 percent annual change), and different monitoring durations (5, 10, or 20 years). For sampling density, we included random sampling of 2, 5, 10, and 20 percent from our pool of available hexagons, as well as a scenario with 2 percent rangewide sampling with denser (20 percent) sampling in DSAs (2+20 percent). Our reasoning for including the 2+20 percent design was that if the design met other objectives, it may be a preferred option because additional data would be available from areas where spotted owls have been intensively monitored for several decades. The sixth sampling design we tested was a “random-flower” that included a random sample of 2 percent of the pool of available hexagons with additional sampling at each of the six adjacent hexagons. This design could provide data to support development of distance-based approaches to population monitoring using passive bioacoustics.

The goal of these simulations was to provide managers information on the ability of annual use estimates (based on passive acoustic monitoring) to track underlying population trends under a range of sampling designs, population conditions, and time periods. Previous work has demonstrated that passive acoustic monitoring is effective in detecting spotted owl activity at the scale of individual territories (Duchac et al. 2020). Here our objectives are to extend those results and quantify the general efficacy of passive acoustic monitoring for reliably estimating rangewide or physiographic province-level spotted owl population trends.

Study Area

We evaluated monitoring study designs that could be implemented across the range of the spotted owl on federally managed lands in Washington, Oregon, and California, including those managed by the U.S. Forest Service, Bureau of Land Management, and National Park Service (fig. 1). The study designs we evaluated represented broad-scale, rangewide monitoring efforts at a larger spatial extent than the current spotted owl monitoring program. We also evaluated monitoring study designs at the scale of the physiographic province, but two provinces were not included in the simulation owing to the lack of federal forest lands and spotted owl habitat: Washington Western Lowlands (2) and the Oregon Willamette Valley (6) (fig. 1, table 1). Finally, we considered a monitoring design involving concentrated sampling on existing long-term spotted owl DSAs, where spotted owl are currently monitored annually under phase I of the effectiveness monitoring program for the NWFP (Dugger et al. 2016).

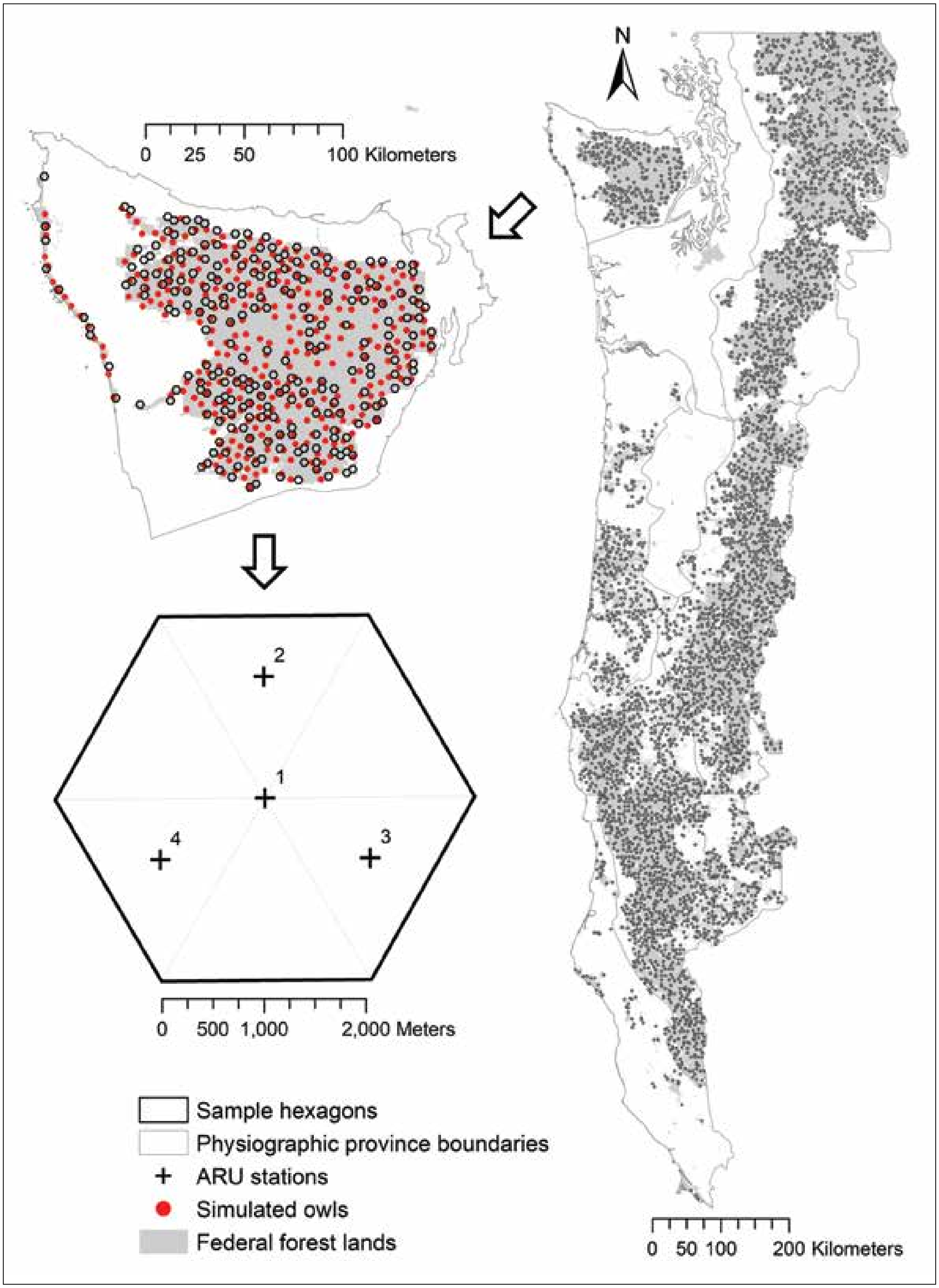


Figure 1—Hexagon sampling design and physiographic province boundaries within the range of the northern spotted owl (main figure). Here 20 percent of hexagons (n = 4,257) were randomly selected from the pool of available hexagons that were ≥25 percent federally managed and ≥50 percent forest-capable lands (gray shading). The top inset of the Olympic Peninsula physiographic province shows the spatial arrangement of randomly selected hexagons and simulated northern spotted owl territory centers. The bottom inset shows placement of four autonomous recording unit (ARU) stations within each hexagon.

Table 1—The number of available sample hexagons (#HEX) in each physiographic province with federally managed forest land and the number of northern spotted owl territory centers in the starting population of 1993 (#OWLS) used for evaluating passive acoustic monitoring of northern spotted owls

			Sampling density (%)[b]					
Physiographic province[a]	**#HEX**	**#OWLS**	**2**	**5**	**10**	**20**	**2+20**	**Random flower**
1. Washington Olympic Peninsula	1,204	344	24	60	120	241	151	146
3. Washington Western Cascades	2,750	771	55	138	275	550	56	322
4. Washington Eastern Cascades	2,433	369	49	122	243	487	107	283
5. Oregon Coast Range	1,691	804	34	85	169	338	190	202
7. Oregon Western Cascades	4,111	1,486	82	206	411	822	206	505
8. Oregon Eastern Cascades	1,285	305	26	64	129	257	73	154
9. Oregon Klamath	2,194	1,432	44	110	219	439	90	251
10. California Coast Range	406	404	8	20	41	81	9	33
11. California Klamath	4,089	2,328	82	204	409	818	110	511
12. California Cascades	1,121	305	22	56	112	224	22	124
Total	21,284	8,548	426	1,064	2,128	4,257	1,014	2,531

[a] The physiographic province numbers correspond to province boundaries shown on figure 1.

[b] The number of sampled hexagons in each of our simulated monitoring designs (2, 5, 10, 20, 2+20 percent, random flower) by physiographic province.

Methods

Monitoring Study Designs

Within federally managed forest lands across the range of the spotted owl, Lesmeister et al. (2019) generated a grid of 5-km^2 hexagons that reflect ecologically relevant space use by spotted owls during the breeding season. Spotted owl territories decrease in size from north to south latitudes (Forsman et al. 2011), so hexagons of 5 km^2 are smaller than most spotted owl home ranges, but larger than a territory core area centered around a primary breeding activity center or nest tree (Glenn et al. 2004, Schilling et al. 2013). We randomly selected a subset of these hexagons that contained ≥50 percent forest-capable lands and ≥25 percent federally managed forest at sampling densities of 20, 10, 5, and 2 percent of the total hexagons in each physiographic province (figs. 2 and 3, table 1). We defined forest-capable as areas with elevations below 2000 m and soil types suitable for supporting forest growth in the Pacific Northwest. Within each hexagon, an array of four points to represent ARU stations were systematically arranged, such that one station was located at the center of the hexagon, and three stations were arranged in an equilateral triangle around it (fig. 1). Stations were separated by ≥800 m.

We considered rangewide monitoring designs with a randomly selected subset of hexagons at four levels of sampling density (2, 5, 10, and 20 percent). We also considered a “random-flower” design at the rangewide level, for which we started

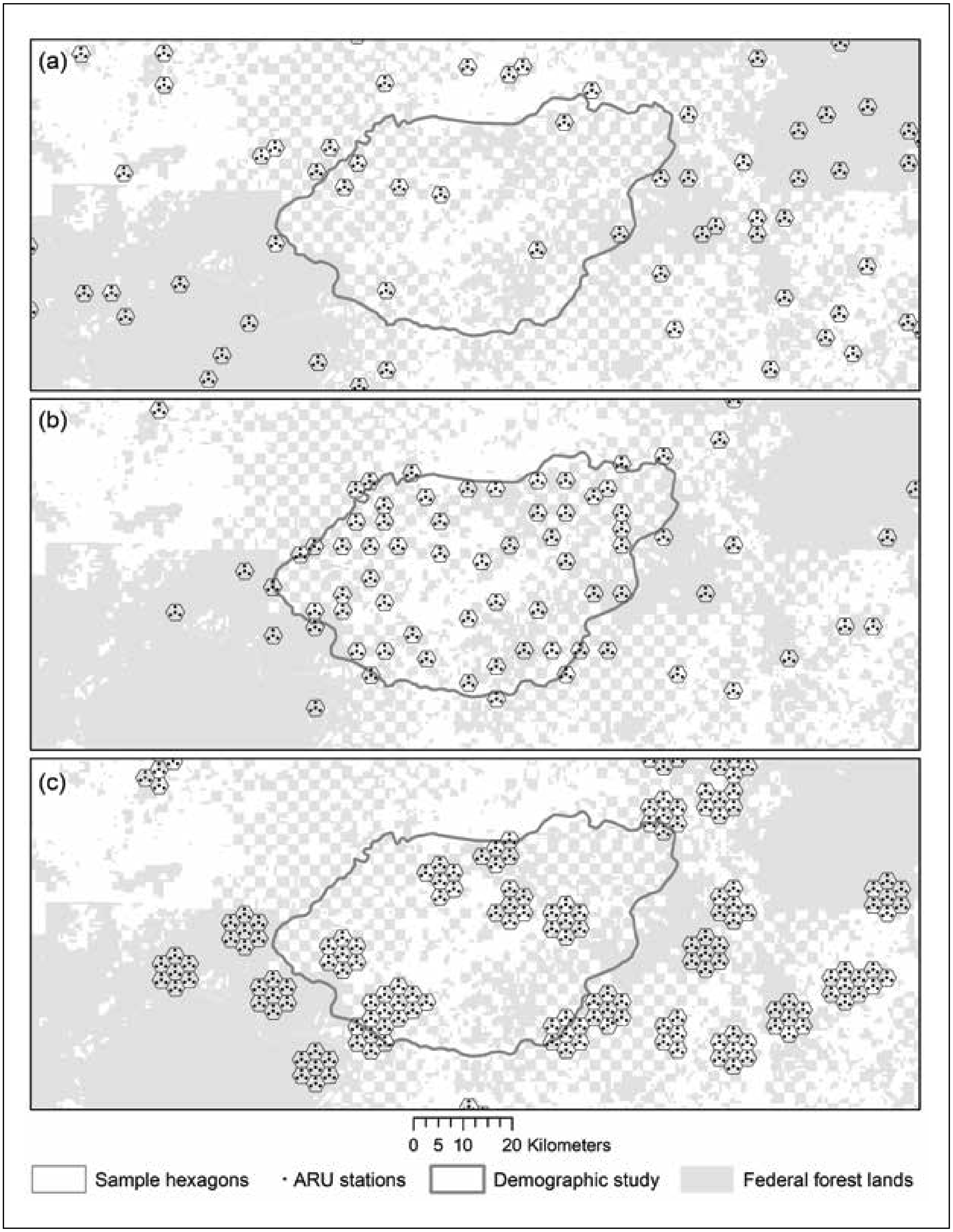


Figure 2—Examples of hexagon spatial placement and autonomous recording unit (ARU) stations in each hexagon with three different sampling designs for simulated passive acoustic monitoring of northern spotted owls: (a) 5 percent random sampling rangewide, (b) 2+20 percent, which was 2 percent random sampling rangewide and 20 percent random sampling within the Klamath demographic study area; and (c) random-flower design, which was a 2 percent random sampling rangewide plus six additional hexagons directly adjacent. Hexagons were randomly selected from the pool of available hexagons that were ≥25 percent federally managed and ≥50 percent forest-capable lands.

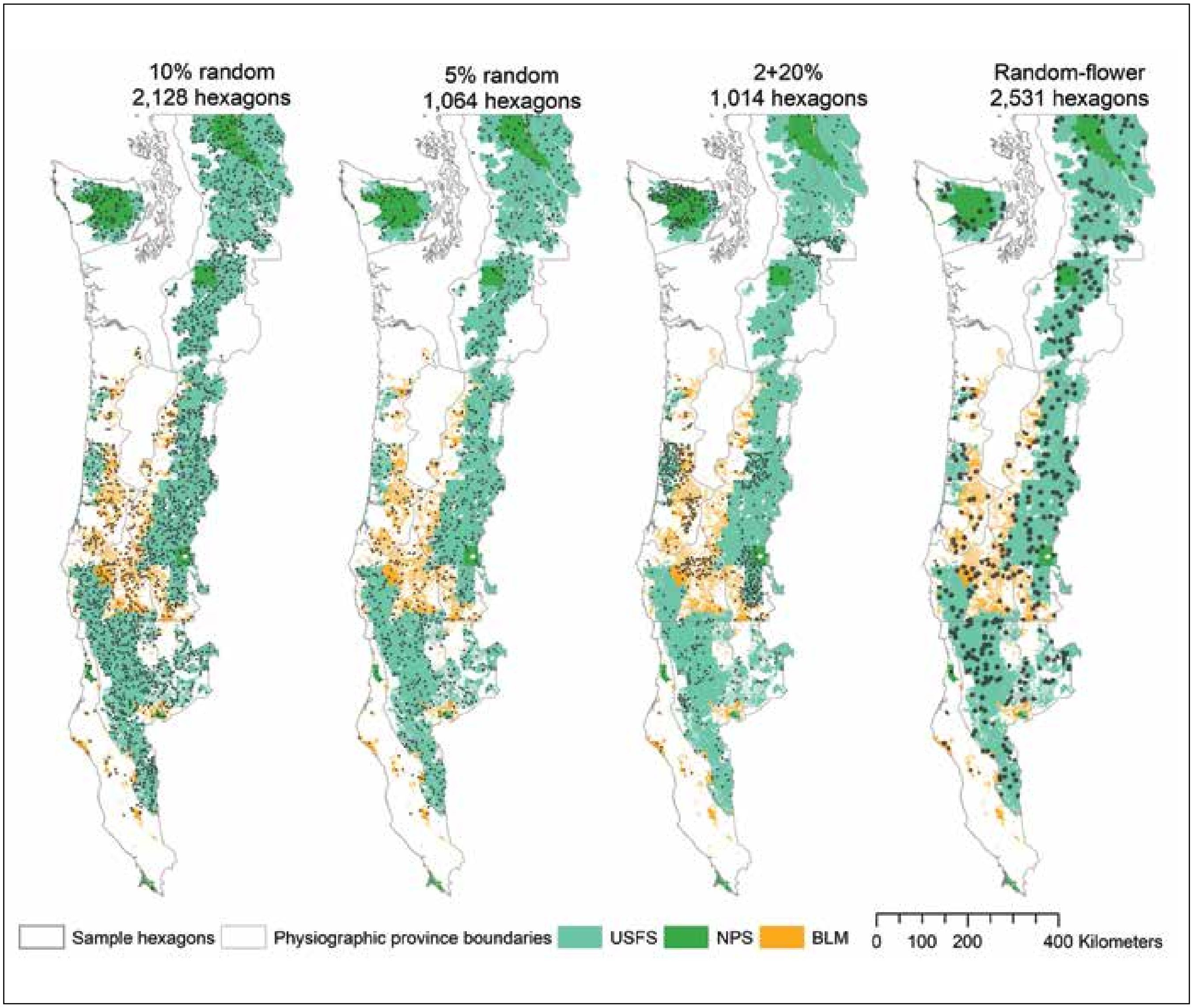


Figure 3—Four sampling designs for passive acoustic monitoring of northern spotted owls, representing various densities of random sampling and spatial arrangement (5 percent, 10 percent, 2+20 percent, and random-flower design). Within each hexagon are four autonomous recording unit stations. Hexagons comprised ≥50 percent forest-capable and ≥25 percent federally managed land: USFS = U.S. Forest Service, NPS = National Park Service, and BLM = Bureau of Land Management. Note that sampling density design scenarios, 2 percent and 20 percent rangewide were also simulated however they were just not included in the figure above.

with the hexagons selected for 2 percent random sampling (n = 426) and also included up to 6 adjacent hexagons for each, excluding those not within federally managed forest (n = 2,531 total hexagons) (figs. 2 and 3). Finally, we included a 2+20 percent design which was 20 percent random sampling within established spotted owl DSAs and 2 percent random sampling outside of these areas (n = 1,014 hexagons) (figs. 2 and 3). All of the designs we considered were a random selection of hexagons because we reasoned these could be effective for monitoring spotted owl populations, but also improve the applicability of these designs for a multitude of other vocalizing wildlife species.

Table 2—Summary of scenarios considered for evaluating passive acoustic monitoring of northern spotted owls

Spatial scale	Sampling design	Number of scenarios
Rangewide	2%, 5%, 10%, and 20% random	72
Rangewide	2+20% random	18
Rangewide	2% random flower	18
Province (ORWC)	2%, 5%, 10%, and 20% random	72
Province (ORWC)	2+20% random	18
Province (ORWC)	2% random flower	18
Province (ORCOA)	2%, 5%, 10%, and 20% random	72
Province (ORCOA)	2+20% random	18
Province (ORCOA)	2% random flower	18
Province (CACOA)	2%, 5%, 10%, and 20% random	72
Province (CACOA)	2+20% random	18
Province (CACOA)	2% random flower	18
Total		432

Note: For each sampling design we included scenarios for spatial scale of rangewide and physiographic province (Oregon West Cascades = ORWC; Oregon Coast Range = ORCOA; California Coast Range = CACOA), monitoring durations of 5, 10, and 20 years; rates of population change (λ) of 0.92, 0.96, and 1.00; and distance thresholds for detectability of 2 km and 4 km. See "Methods" section for descriptions of sampling designs.

In addition to rangewide monitoring designs, we also considered scenarios at the three physiographic provinces that represented the maximum, median, and minimum number of available hexagons for sampling (table 2). The Oregon West Cascades (ORWC) had the highest (n = 2,750), Oregon Coast Range (ORCOA) was the median (n = 1,691), and California Coast Range (CACOA) had the fewest (n = 406) hexagons (fig. 4, table 1). We considered four densities of random sampling (2, 5, 10, and 20 percent) as well as province-level versions of the random-flower and 2+20 percent designs for the province-specific scenarios (table 2).

Spotted Owl Territory Centers

We generated a 1993 starting population of spotted owl territories, each with a center point, occupied by pairs across the entire area covered by the simulation. To derive the 1993 population estimate, we used methods to estimate habitat carrying capacity adjusted by occupancy rate estimates described by Glenn et al. (2017) and forest conditions. We generated locations of spotted owl territory centers based on the amount and spatial arrangement of forests suitable for territory occupancy. Determining territory characteristics, such as spacing, was based on information from the past three decades of spotted owl population monitoring. To estimate the number of territories occupied in 2020, we used 27 annual intervals (starting in 1993) and DSA-specific rates of annual population decline (λ) as estimated from the most recent meta-analysis of spotted owl population dynamics (Dugger et al. 2016).

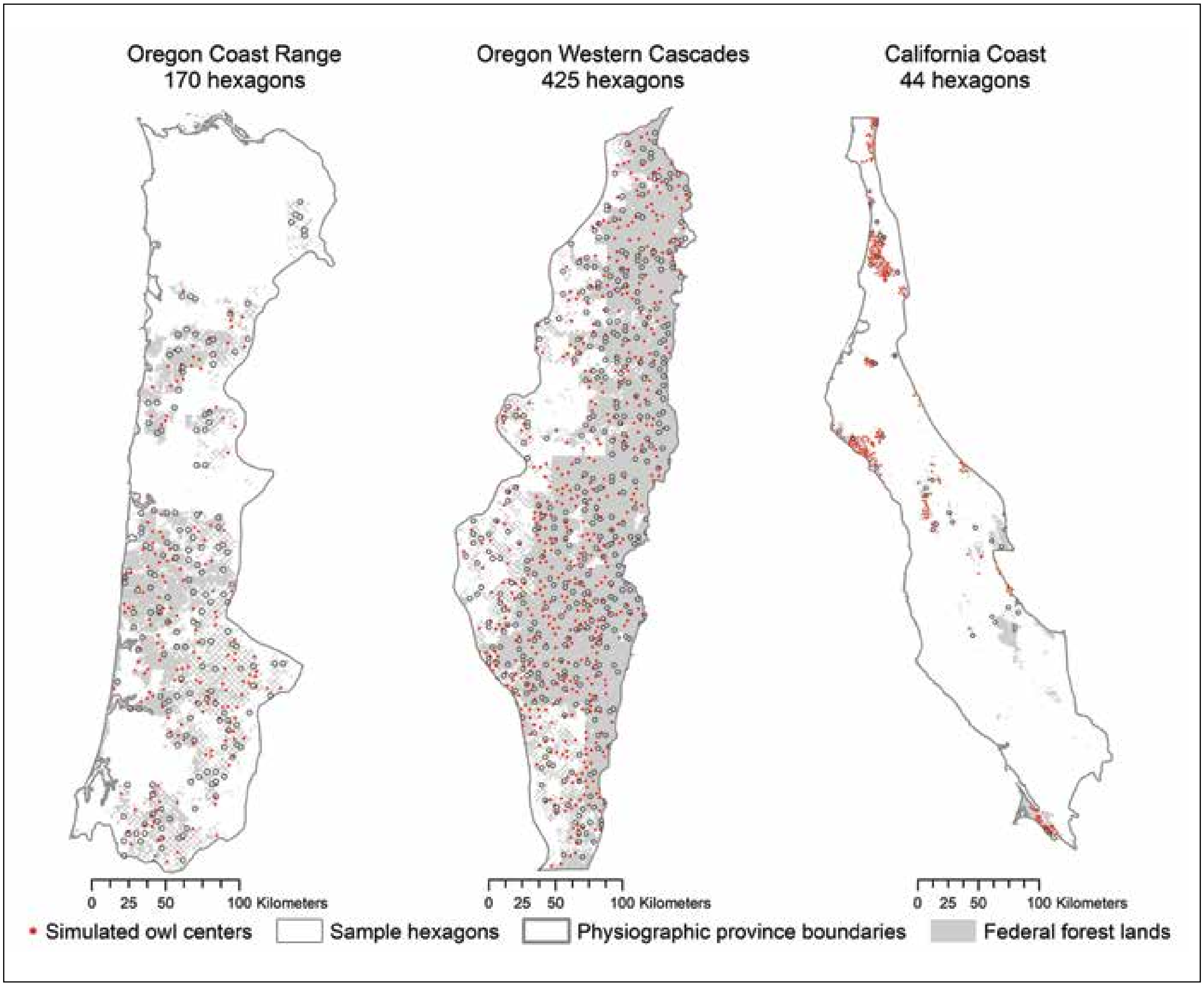


Figure 4—Random 10 percent sampling design and simulated northern spotted owl territory centers on federally managed lands in three physiographic provinces that represent the largest (Oregon Western Cascades), medium (Oregon Coast Range), and least (California Coast) amount of federal lands available for sampling.

We used the λ estimates from DSAs for the corresponding physiographic province (table 3). The 1993 population estimates and the λ estimates were point estimates, most with wide confidence intervals, so our estimated 2020 populations were simply the most plausible starting point for simulations. For example, we estimated that there were 344 spotted owl pairs in 1993 in the Washington Olympic Peninsula province (WAOLY), which, following a 3.9 percent annual decline between 1993 and 2020, resulted in an estimated 117 occupied territories in 2020. Each iteration of the simulation randomly drew a different set of occupied territories; however, the number of occupied territories was constant across simulations.

Table 3—Summary of northern spotted owl demographic results from Dugger et al. (2016) by physiographic province and demographic study area (DSA)

Physiographic province	DSA[a]	ψ1995 *Percent*	λ	%Δ *Percent*
Washington Olympic Peninsula	OLY	81	0.961	-59
Washington Western Cascades	RAI	100	0.953	-61
Washington Eastern Cascades	CLE	56	0.916	-77
Oregon Coast Range	COA	75	0.949	-64
Oregon Western Cascades	HJA	88	0.965	-47
Oregon Eastern Cascades	CAS	69	0.963	-44
Oregon Klamath	KLA	71	0.972	-34
California Coast Range	GDR	92	0.988	-31
California Klamath	NWC	79	0.970	-55
California Cascades	CAS	69	0.963	-44

Note: We used the annual rates of population change (λ) in our simulations to generate a starting population of occupied territories in 2020 by sampling randomly from available territories in 1993. Also presented are the occupancy rate estimates for 1995 (ψ1995) and total amount of population decline (%Δ) simulated.

[a] Definition of DSAs: OLY = Olympic Peninsula, RAI = Rainier, CLE = Cle Elum, COA = Oregon Coast Range, HJA = H. J. Andrews, CAS = Oregon South Cascades, KLA = Oregon Klamath, GDR = Green Diamond Resources, NWC = Northwest California.

Simulating Population Change

Starting with the spotted owl territories considered to be occupied in 2020, we then projected populations forward in time from 2020 (“year 0”) by applying three different rates of population change (λ): 1.0 (no change), 0.96 (4 percent annual decline), and 0.92 (8 percent annual decline). These λ values represent what we considered a plausible range of trends in spotted owl populations, and territories were randomly removed (i.e., considered to be unoccupied) annually for a specified period of time depending on the duration of the simulation (5, 10, or 20 years into the future) (fig. 5, table 2).

Because adult spotted owls may conduct breeding dispersal movements among territories between years (Forsman et al. 2002, Jenkins et al. 2019), we incorporated a *Pstay* parameter into our simulations, representing the probability that if an owl pair “survived” from one year to the next, the pair would remain in the same location instead of dispersing. To simulate this, we allowed a proportion of the remaining occupied spotted owl territories (1 – *Pstay*) to move locations each year to another available territory within the physiographic province, by removing them and adding an equivalent number of other random territories back into the simulation. We used a value of *Pstay* = 0.8 for all scenarios herein, representing an annual breeding dispersal rate of 20 percent. Jenkins et al. (2019) reported median breeding dispersal distances of 3.26 km for females and 3.10 km for males; therefore, we only permitted dispersing birds to move to unoccupied

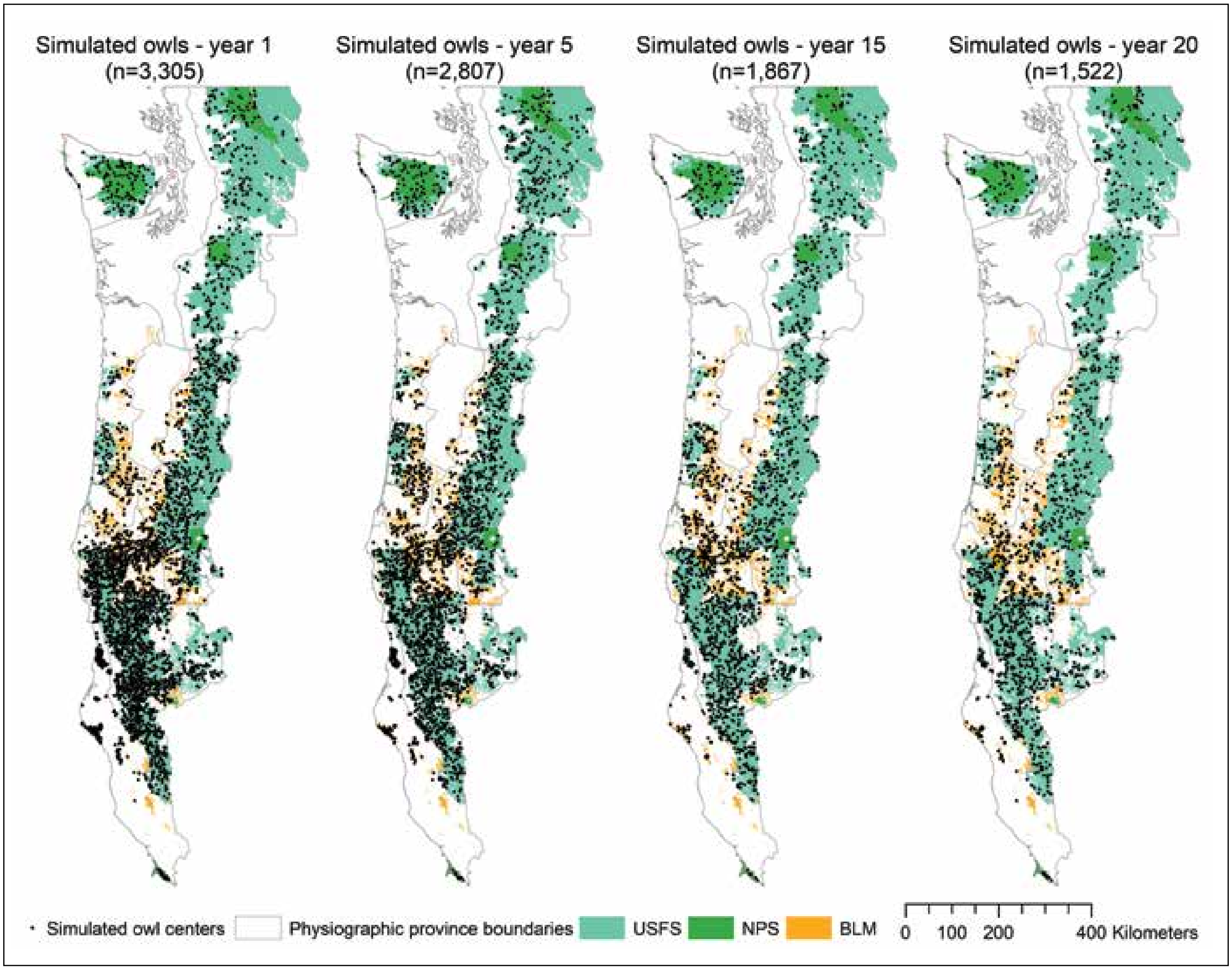


Figure 5—Example of one iteration of a simulated decline in northern spotted owl territory centers over 20 years of simulated passive acoustic monitoring with annual rate of population change (λ) = 0.96. Each simulation iteration begins with a different random draw of northern spotted owl territory centers in year 0 from a pool of available territories. USFS = U.S. Forest Service, NPS = National Park Service, BLM = Bureau of Land Management.

territories within the same physiographic province. This was intended to ensure that populations declined evenly across the subspecies' range relative to initial levels of territory occupancy. Without this constraint, and because the simulation did not have province-specific population change rates, we found that owls in the simulation tended to immigrate from provinces with high densities of occupied territories to provinces with lower densities, which equalized the proportion of occupied territories across all physiographic provinces within the first few years of the simulation. We suggest that this was the simulation reflecting the underlying model and occupied territories heading toward a spatial equilibrium. The observed rate of territorial occupancy is not equal across physiographic provinces (table 3), so this effect would have been an artifact of the simulation.

Simulating Detection Histories

For each scenario, we used the corresponding locations of the ARU stations for each hexagon and the simulated spotted owl territory centers to generate detection histories. Our simulated monitoring ran for 6 weeks per season to match current field protocols (Lesmeister et al. 2019). We incorporated parameter estimates for detection probability (*p*) and probability of use (ψ) from occupancy models (MacKenzie et al. 2018) conducted using spotted owl acoustic monitoring data from 2017 to predict whether each ARU station would detect spotted owls from one or more of the occupied territory centers in a given year of the simulation (fig. 6). Duchac et al. (2020) reported on the logit scale that ψ (intercept = 0.1 ± 0.2, slope = -0.4 ± 0.3) and *p* (intercept = -0.9 ± 0.1, slope = -1.0 ± 0.1) decrease with distance (mean = 1525 m, standard deviation (SD) = 1271 m) to the nearest known spotted owl territory center.

Because detection probability is known to be a function of the distance between an ARU and the spotted owl territory centers (Duchac et al. 2020), we calculated the pairwise Euclidean distances between each ARU station and each spotted owl territory center used in our simulations. For a given subset of hexagons and "occupied" spotted owl territories, we extracted the minimum distance value for each ARU station (i.e., the distance to the nearest "occupied" spotted owl territory

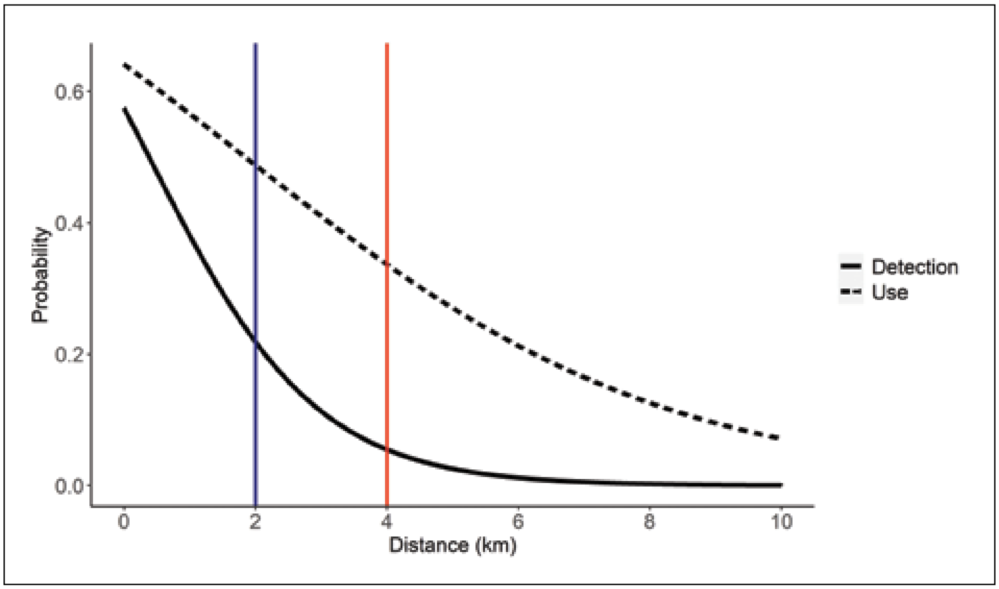


Figure 6—Detection function by distance from territory centers for determining whether northern spotted owls were detected (solid black line) and used (dashed black line) the area directly surrounding autonomous recording units in monitoring simulations. The functions follow an inverse logit form, incorporating slope and intercept parameters for detection probability and probability of use from previous occupancy models. We used distance thresholds of 2 km (blue vertical line) and 4 km (red vertical line) on use and the detection function to test the effect on bias and precision if northern spotted owls are detected at distances far from territory centers.

center) and standardized these values using the mean and SD of actual distances from the 2017 data. We then used these distances and the parameter estimates to calculate the probability of use and probability of detection of spotted owl for each ARU station, using an inverse logit function:

$$p_{detection} = \frac{e^{p(int)+p(slope)*zdist}}{1+e^{p(int)+p(slope)*zdist}}$$

$$p_{use} = \frac{e^{\psi(int)+\psi(slope)*zdist}}{1+e^{\psi(int)+\psi(slope)*zdist}}$$

where $p(int)$, $p(slope)$, $\psi(int)$, and $\psi(slope)$ are the intercept and slope parameter estimates for detection probability and probability of use (Duchac et al. 2020) and *zdist* is the standardized distance (z-score) between each ARU station and the closest "occupied" spotted owl territory center.

To reduce the possibility that simulated ARU stations would detect owls at distances far from their territory centers, we imposed a distance threshold *Dmax*, such that if the distance between a given ARU station and its closest occupied spotted owl territory center was greater than *Dmax*, that station would have no spotted owl detections during that season. We used values of *Dmax* = 2 km and *Dmax* = 4 km for our simulations (table 2). We simulated spotted owl detection histories for each ARU within a hexagon and then combined those detection histories into hexagon-level detection histories. Each annual detection history consisted of six sampling occasions, one for each survey week. If any ARU station within a hexagon detected a spotted owl within a sampling occasion (weeks 1 through 6), we assigned a "1" to the hexagon detection history for that sampling occasion or a "0" if no ARU detected a spotted owl during the sampling occasion.

We conducted 100 iterations of the simulation for each scenario, starting at the step in which potential owl territories were removed from 1993 to 2020, so that each iteration had a different random draw of owls in "year 0" (2020). In contrast, the hexagons selected for monitoring remained constant across iterations. For example, we used the same randomly selected set of 426 hexagons for each rangewide scenario at the 2% random sampling level, but each of the 100 iterations began with a random draw of spotted owl territory centers for 2020. In total, we simulated 432 scenarios, and, owing to computation limitations, we limited our simulations to 100 iterations for each scenario which we recognize is a relatively small number of simulations and there may have been a reasonable amount of Monte Carlo uncertainty in our results. Perhaps small differences between simulations are expected within the bounds of random variation, but we were confident the number of iterations were suitable for quantifying differences among most scenarios.

Estimating Change-in-Use With Dynamic Occupancy Models

Using the simulated weekly hexagon-level encounter histories, we ran multiseason occupancy models using the *RPresence* package (MacKenzie and Hines 2020) in Program R (R Core Team 2019). Because spotted owl territories may overlap multiple sampling hexagons, owls could use multiple hexagons even if their territory centers only occupy a single hexagon. Conceptually, detection histories from ARUs therefore reflect the probability a hexagon is used by a pair. In comparison, past spotted owl occupancy work focused on nest sites and territory sites for determining the probability a territory was occupied, assuming that individuals were not detected on more than one territory each year. Although the models used to fit use and occupancy data are the same, the interpretation of parameters is different. We used the first parameterization of multiseason occupancy models to estimate probability of use (ψ) and probability of detection (p) for spotted owl while allowing colonization (γ: defined here as the probability that a hexagon not used in time t-1 is used in time t) and extinction (ε: defined here as the probability that a hexagon used in time t-1 is not used in time t) to change annually according to a linear trend (MacKenzie et al. 2003, 2018). An underlying assumption in these simulations is that spotted owls maintain a constant movement rate and territory size throughout the duration of each scenario. In reality, dynamics of space use within wildlife populations are rarely constant, which could affect the ability to detect population change. To evaluate the ability of each monitoring design to detect changes in spotted owl use over time, we compared ψ at the beginning and the end of the simulation for each iteration, as:

$$\lambda(\mathrm{est})_{\mathrm{i}} = \frac{\psi_{\mathrm{i,nyears}}}{\psi_{\mathrm{i,1}}}$$

where $\psi_{\mathrm{i,nyears}}$ is the derived estimate of probability of use in the final year of the simulation (i.e., after nyears − 1 time intervals) from simulation iteration i (i = 1–100) and $\psi_{\mathrm{n,1}}$ is the derived estimate of probability of use in the first time interval from iteration i. We used the delta method (Williams et al. 2002) to estimate variance and standard errors for the differences in estimated use ($\lambda(\mathrm{est})_{\mathrm{i}}$) for each iteration. We also used this approach to calculate the variance of *log*($\lambda(\mathrm{est})_{\mathrm{i}}$) to estimate confidence intervals at the 50% and 95% confidence levels, as follows:

$$\lambda(\mathrm{est})_{\mathrm{i}} \times \mathrm{e}^{\pm(\frac{z_a}{2})\times \mathrm{SE}(\log\,\lambda(\mathrm{est})_{\mathrm{i}})}$$

where SE(log $\lambda(\mathrm{est})_{\mathrm{i}}$) was estimated using the delta method, and $^{z_a}/2$ = 1.96 corresponded with a 95% confidence level and $^{z_a}/2$ = 1.67 corresponded with a 50% confidence level.

We were interested in the direction and magnitude of the estimated changes in spotted owl hexagon use (ψ) and how well those changes corresponded to changes in the underlying spotted owl population at the end of the simulation.

For each scenario, we calculated the mean λ(est) among all 100 iterations of the simulation. We then subtracted these estimates from 1 to get the percentage of decline (instead of proportional change) and plotted them against the "true" simulated declines:

$$1 - \lambda(\text{sim})^{\text{nyears}\ -1}$$

where λ(sim) = 0.92, 0.96, or 1.0, and nyears = 5, 10, or 20 (the duration of the simulation).

In assessing the performance of each scenario, we were interested in the direction and magnitude of the estimated changes in spotted owl ψ and how well those changes corresponded to changes in the underlying spotted owl population at the end of the simulation. Additionally, we considered both the bias of estimated changes in use among scenarios—compared to the simulated change in occupied spotted owl territories—as well as the precision of estimated changes in use among the 100 simulation iterations within each scenario. We calculated absolute bias as the difference between the mean estimated change-in-use among all 100 iterations ($\lambda(\text{est})_i$) and the "true" simulated decline ($\lambda(\text{sim})^{\text{nyears}-1}$). We assessed precision by examining boxplots and evaluated coverage of estimates of change-in-use for each scenario by calculating the proportion of iterations for which the 95 and 50 percent confidence intervals overlapped the "true" simulated decline, as well as the proportion that did not overlap 1 (i.e., predicting whether or not a decline occurred).

Results

We considered 432 scenarios for monitoring spotted owls using passive acoustics that covered a range of six spatial sampling designs, three monitoring durations, three levels of spotted owl rates of population change, and two distance thresholds for detectability away from territory centers (table 2). Mean estimates from the 100 iterations consistently demonstrated the ability to detect the change in the population, but precision and bias varied by sampling density, monitoring duration, and distance threshold.

Sampling Duration

We assessed monitoring scenarios lasting 5, 10, and 20 years into the future, with occupancy models run at the end of the sampling period (i.e., after 4, 9, and 19 annual intervals). Based on the use estimates, simulated scenarios were generally robust in their ability to correctly detect declines or stationary levels in spotted owl populations (fig. 7, app. 1, figs A1.1 through A1.3). However, the detection of a population decline was less precise (i.e., varied more) at low sampling densities and with short monitoring durations. The precision of estimates of proportional change-in-use consistently improved with increased sampling density and duration in all three spotted owl rates of population change (0.92, 0.96, 1.0) (fig. 8), but bias tended to increase with the duration of the scenarios.

At the rangewide scale with random sampling, mean estimates (of the 100 iterations/scenario) of decline in spotted owl use differed from the simulated population decline (absolute bias) by between –2.5 and 4.5 percent among scenarios with a 2-km threshold and between –1.8 and 14.9 percent with a 4-km threshold. The range in values represented the differences in bias among the 54 scenarios considered with each distance threshold, accounting for six levels of sampling density, three monitoring durations, and three population growth rates. For example, the mean estimated change in spotted owl use for simulations at 2 percent random sampling and simulated λ = 0.92 after 10 years was 49.4 percent, compared to the simulated change in the number of spotted owl territory centers of 47.2 percent (an absolute bias of 2.2 percent; app. 1, fig. A1.1). For rangewide scenarios with random sampling after 5 years, absolute bias ranged from –2.5 to –0.4 percent with a 2-km threshold and from –1.8 to 6.2 percent with a 4-km threshold (18 scenarios each). After 10 years, absolute bias ranged from –0.3 to 2.8 percent and from –0.3 to 12.7 percent for 2-km and 4-km thresholds, respectively. After 20 years, absolute bias ranged from –0.1 to 4.5 percent and from 0.5 to 14.9 percent. Bias generally increased with increased sampling duration at simulated λ = 0.96 (i.e., estimates were most biased after 20 years), while for scenarios with simulated λ = 0.92, estimates were most biased after 10 years. For scenarios with simulated λ = 1.0 (no change in number of spotted owl territory centers), bias of estimates changed very little over time (app. 1, figs. A1.1 through A1.3).

To evaluate the probability that our estimates of spotted owl use would track the actual changes in spotted owl populations (i.e., the similarity between estimated declines in use and the simulated population decline), we also calculated coverage, i.e., the proportion of individual iteration estimates whose confidence intervals overlapped the “true” simulated decline in spotted owl territory centers (app. 2, table A2.1). For many scenarios, the proportion of confidence intervals overlapping the “true” decline was highest for 5-year simulations and lower for 10- and 20-year simulations. For the scenarios with declining population (λ = 0.96 and 0.92), all but one scenario had 100 percent of confidence intervals not overlapping 1.0 at the 10-year monitoring duration, indicating certainty in detecting a decline in the population within 10 years. For the remaining scenario, with λ = 0.96 and 2 percent random sampling, 86 percent of the iterations had 95 percent confidence intervals not overlapping 1.0 at 10 years, and 100 percent did not overlap at 20 years (table 4). With simulated λ = 0.92, all scenarios accurately estimated that there was a population decline after 10 years, and for most scenarios, the 95 percent confidence interval did not overlap 1.0 after 5 years (app. 2, table A2.1). At the 5-year duration

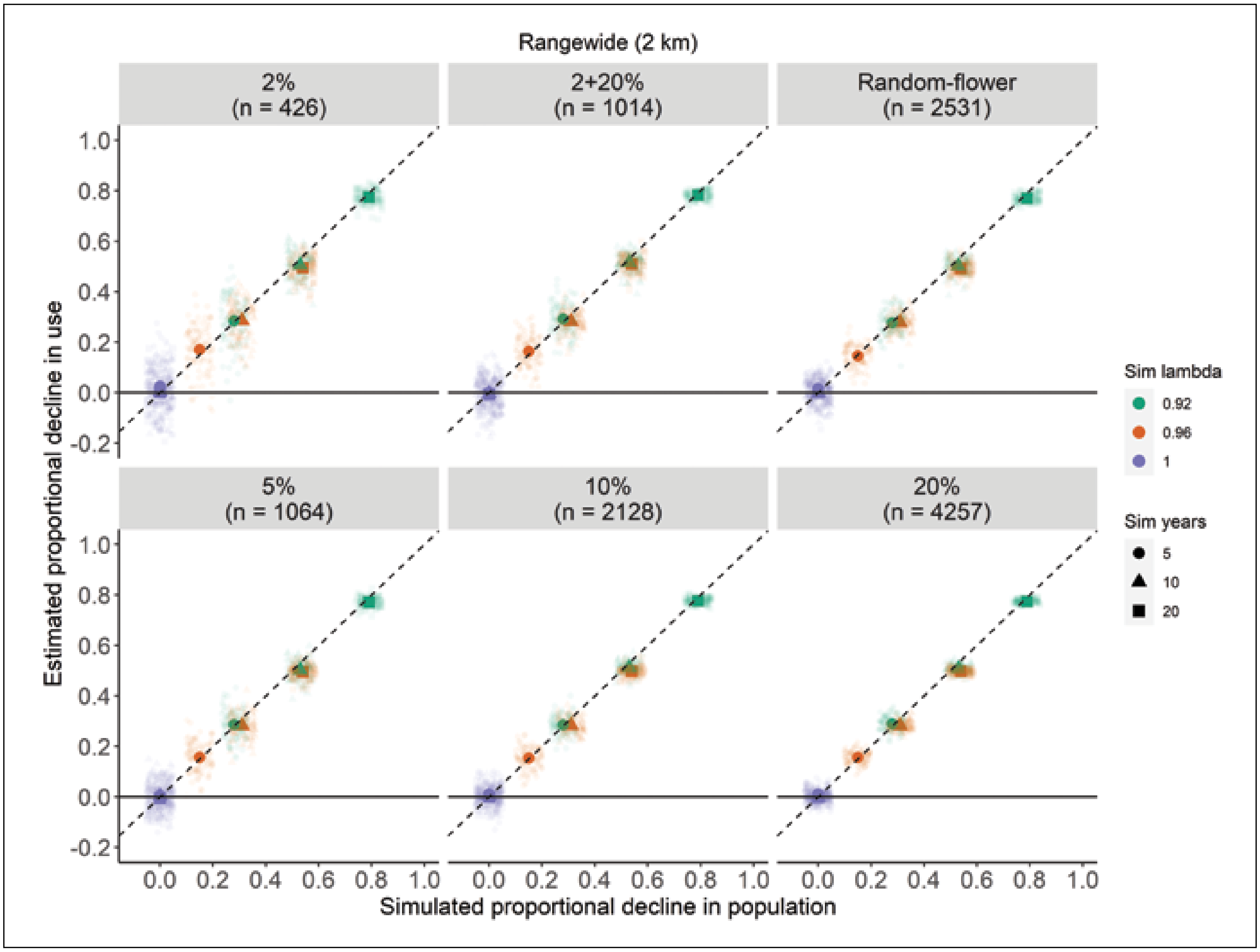
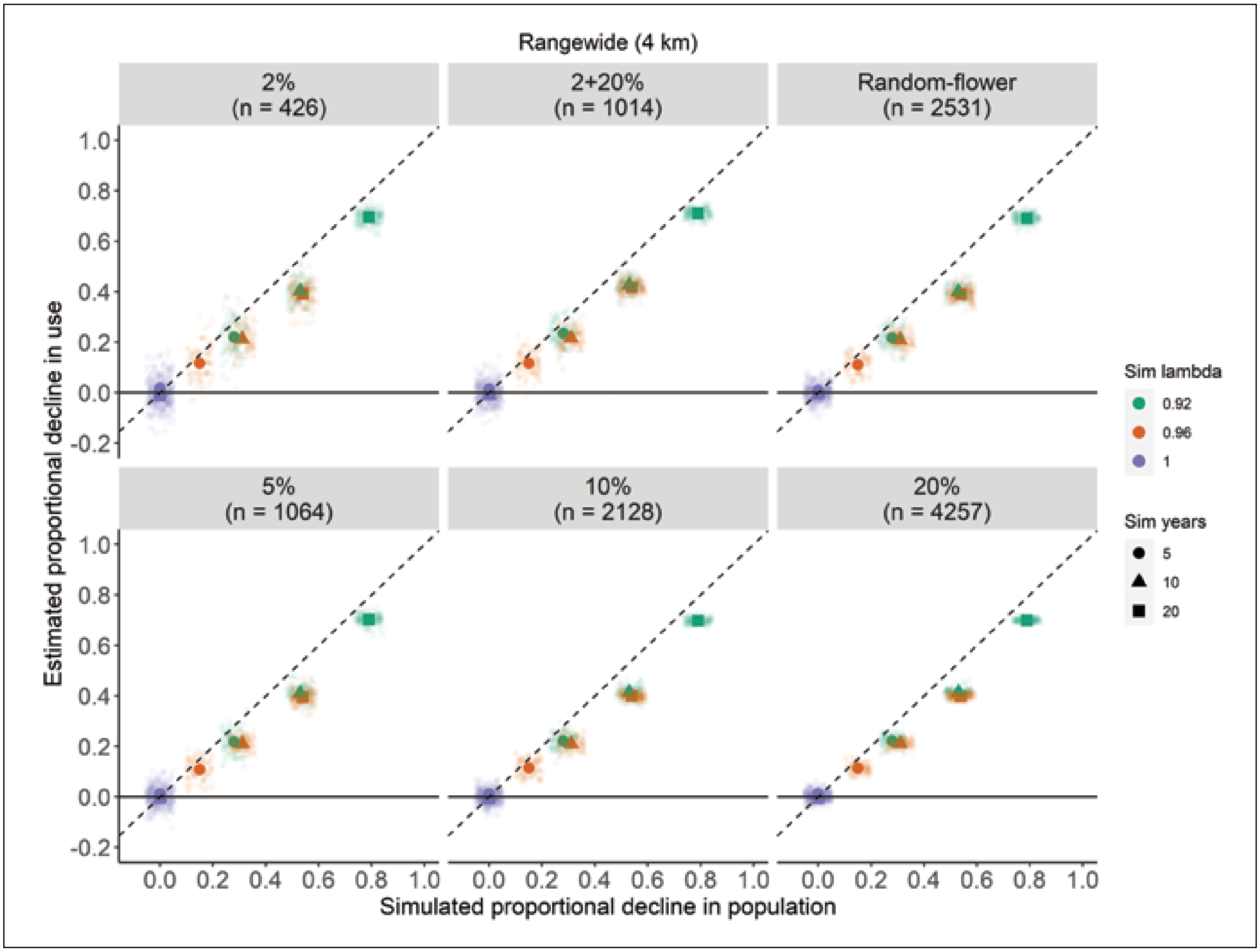


Figure 7—Estimated proportional decline-in-use by northern spotted owls compared to the simulated proportional decline in the number of spotted owl territory centers over 54 different scenarios of simulated monitoring using passive bioacoustics. Sampling designs are described in-text and are shown here with the corresponding number of hexagons monitored under each design. Point estimates represent the means of $\lambda(\text{est})_i$, or the proportional change in estimated spotted owl use in the final year of the simulation compared to the beginning for all 100 iterations per scenario. Individual $\lambda(\text{est})_i$ values are shown in transparency and we spread points horizontally to facilitate interpretation of vertical spread that represented variation in estimates of use. Both axes here are 1 – change, representing a decline. Shown here are scenarios at three different rates of population change: "Sim lambda" = 0.92 (green), 0.96 (orange), and 1.0 (purple), as well as three different monitoring durations: "Sim years" = 5 (circles), 10 (triangles), and 20 (squares). The dashed line represents a 1:1 relationship between the simulated decline in the number of spotted owl territory centers and the estimated decline in spotted owl use. Scenarios shown here include distance thresholds of 2 km (a) and 4 km (b) between an autonomous recording unit station and simulated spotted owl territory center for determining a detection.

(with simulated $\lambda = 0.92$), the 2 percent random sampling design had 74 and 77 percent (difference between distance thresholds) of iteration estimates without confidence intervals overlapping 1.0 (app. 2, table A2.1).

Sampling Density and Design

For monitoring scenarios with randomly placed hexagons at the rangewide scale, there was little difference in the bias of estimated decline in spotted owl use among scenarios at the 2, 5, 10, and 20 percent density of random sampling. However,



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precision among simulation iterations increased with higher levels of sampling density (figs. 7 and 8, app. 1, fig. A1.1).

The 2+20 percent (app. 1, fig. A1.2) and random-flower (app. 1, fig. A1.3) designs performed comparably to random monitoring designs with a similar number of hexagons being monitored—i.e., results from the 2+20 percent design were similar to those from the 5 percent random design (n = 1,014 and 1,064 hexagons, respectively), and results from the random-flower design were similar to those from the 10 percent random design (*n* = 2,605 and 2,128 hexagons, respectively) (figs. 7 and 8). Estimates of decline in spotted owl use from the 2+20 percent scenarios at the rangewide level were more precise than those from the 2 percent random scenarios and slightly less biased across sampling durations and simulated rates of population change. Absolute bias for these scenarios ranged from –1.4 to 3.0 percent for scenarios with a 2-km threshold and from –1.4 to 12.2 percent with a 4-km threshold. Estimates from the rangewide random-flower sampling

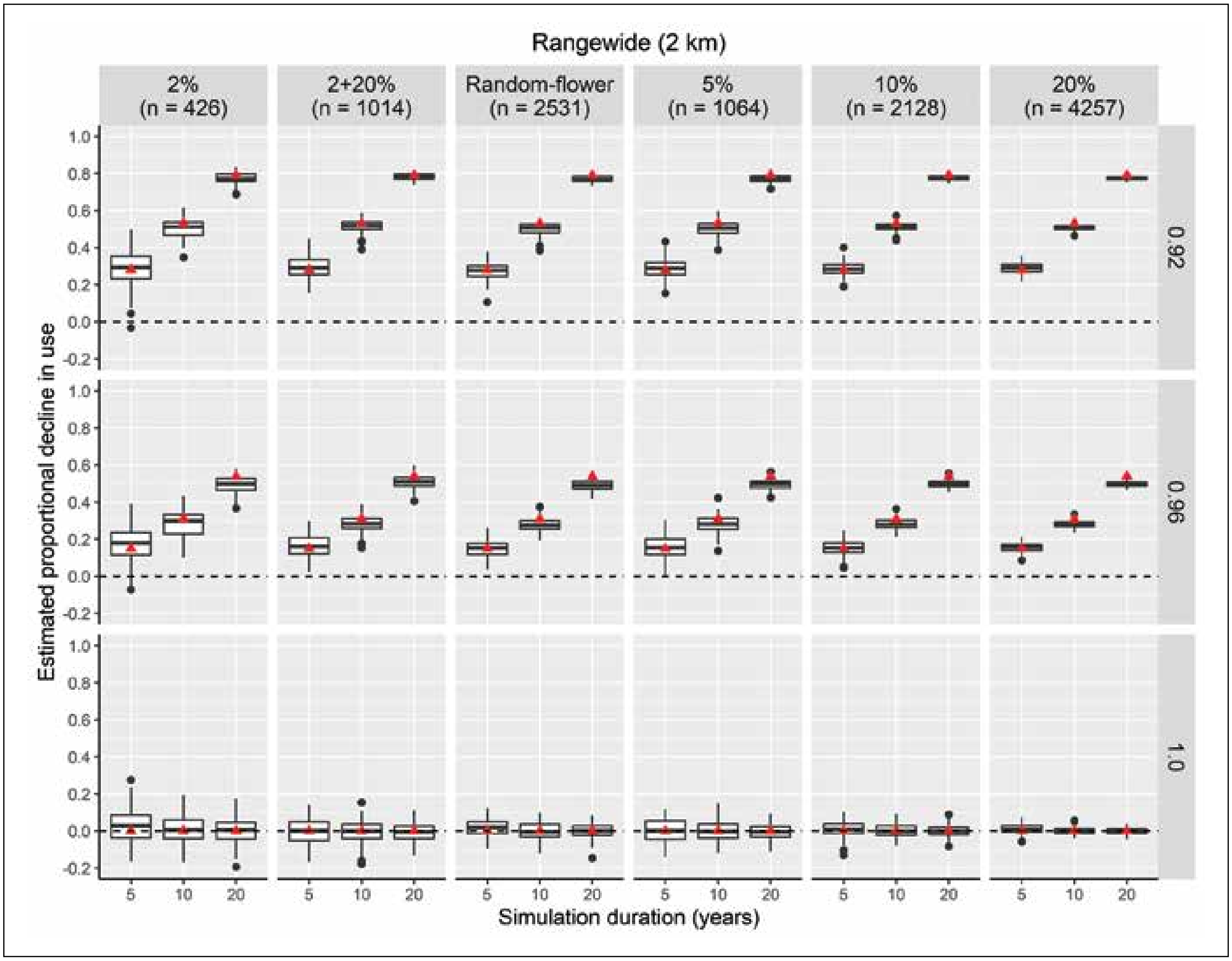
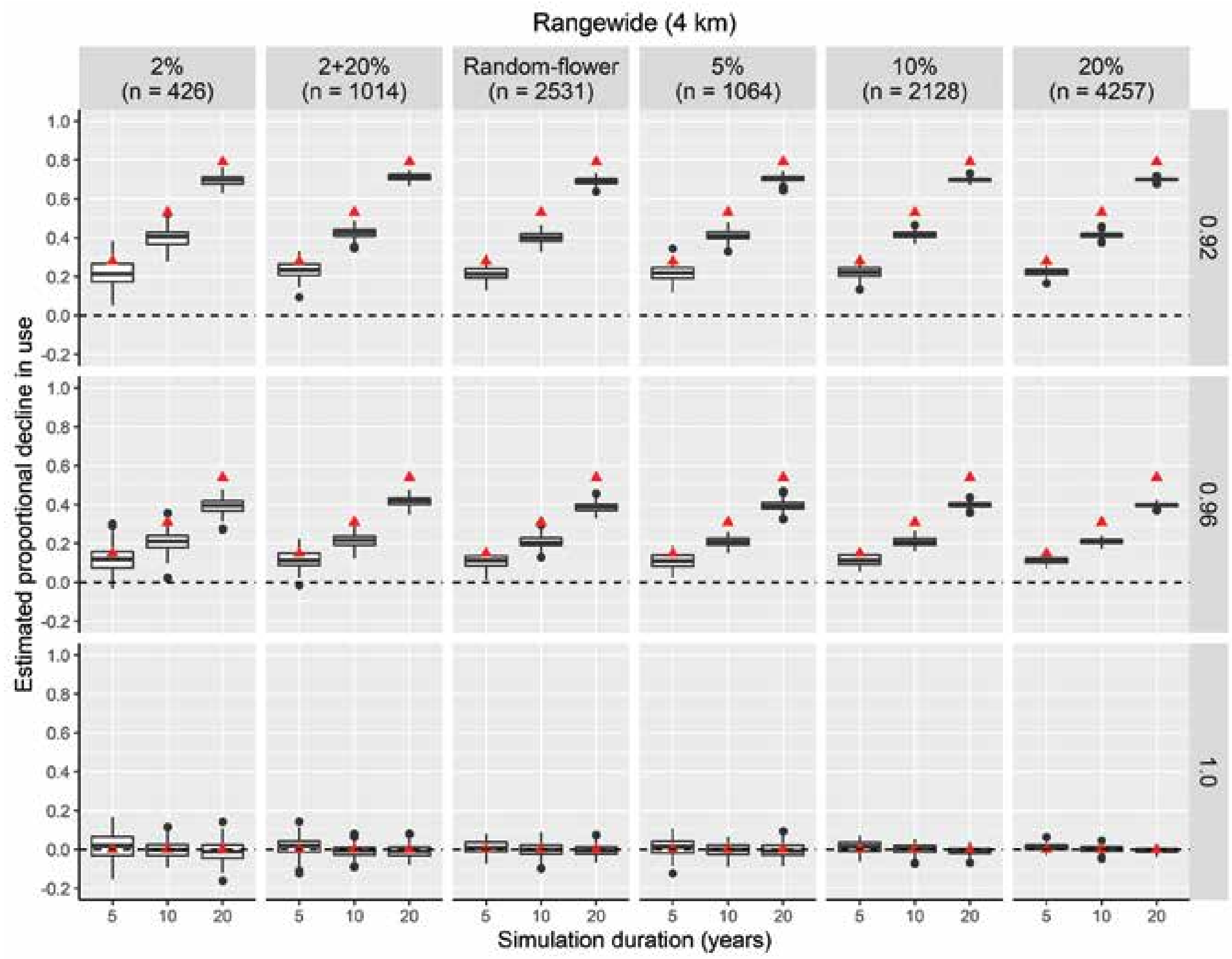


Figure 8—Boxplots of estimated proportional decline in use by northern spotted owls over a range of passive acoustic monitoring scenarios at 5-, 10-, and 20-year durations with annual simulated rates of population change (λ) of 0.92, 0.96, and 1.0 (rows). Sampling designs (columns) are described in-text and are shown here with the corresponding number of hexagons monitored under each design. Boxes represent the median and quartiles of $\lambda(\text{est})_i$ values, or the proportional change in estimated spotted owl use at the final year of the simulation compared to the beginning (subtracted from 1 to represent a decline). Red triangles are the "actual" simulated decline in the number of occupied spotted owl territory centers over each sampling duration. Scenarios shown here include distance thresholds of 2 km (a) and 4 km (b) between an autonomous recording unit station and simulated spotted owl territory center for determining a detection.

design were also more precise than those from the 2 percent random scenarios but not necessarily less biased. Absolute bias for these scenarios ranged from –1.6 to 4.7 percent for scenarios with a 2-km threshold and from –0.9 to 15.0 percent with a 4-km threshold. The increase in precision was consistent with improvements seen at higher rates of sampling density regardless of sampling design.

Distance Thresholds

We ran simulations for all scenarios with two different distance thresholds for how far ARUs were located away from spotted owl territory centers (*Dmax* = 2 km and 4 km). Estimates of decline in spotted owl use were consistently less biased at the



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2-km threshold than the 4-km threshold across scenarios (app. 1, figs. A1.1 through A1.3), with a greater proportion of iterations producing estimated declines with confidence interval overlapping the "true" simulated decline (app. 2, table A2.1). For example, with simulated λ = 0.96, a 2 percent sampling level, 20- year duration, and 2-km threshold, the simulations correctly detected that there was a decline (i.e., confidence intervals did not overlap one) in spotted owl use in 100 percent of iterations at both 50 and 95 percent confidence levels (table 4). Detecting a change in the population occurred with full confidence for most other designs with a 10-year duration (app. 2, table A2.1). The amount of overlap with the "true" simulated decline at both the 95 and 50 percent confidence levels consistently decreased with more years of the simulation, indicating a bias with time and sampling density for estimating the magnitude of change in the population (app. 2, table A2.1). Scenarios with the 2-km threshold consistently outperformed those with the 4-km threshold in detecting change in the population as well as the correct magnitude of change (figs. 7 and 8, app. 1, figs A1.1 through A1.4). The relationship between monitoring duration and bias was consistent between both distance threshold levels, where bias was highest after 20 years for simulated λ = 0.96 and highest after 10 years for λ = 0.92 (app. 1, fig. A1.1). Precision among estimated change in spotted owl use did not appear to differ considerably between scenarios with 2- and 4-km thresholds.

Table 4—Coverage of estimates of change-in-use by northern spotted owls form simulation scenarios with a population growth rate of λ = 0.96, multiple sampling designs (random: 2%, 5%, 10%, 20%; 2+20%; random-flower) and monitoring durations (5, 10, 20 years), and a distance threshold of 2 km

		Overlap sim λ		Do not overlap 1	
Sampling design	Years	95% CI	50% CI	95% CI	50% CI
2%	5	99	53	27	83
	10	96	53	86	100
	20	92	39	100	100
Random-flower	5	95	48	88	100
	10	82	28	100	100
	20	42	10	100	100
2+20%	5	99	56	55	97
	10	96	56	100	100
	20	90	38	100	100
5%	5	97	54	59	96
	10	95	50	100	100
	20	79	18	100	100
10%	5	98	59	89	100
	10	94	39	100	100
	20	63	6	100	100
20%	5	100	64	100	100
	10	89	28	100	100
	20	24	1	100	100

Note: Presented are the number of iterations (out of 100) for which confidence intervals (CI; at the 95 or 50 percent level) overlapped the "true" simulated decline in spotted owl territories ("Sim λ") assuming a simulated population growth of 0.96 and distance threshold of 2 km. Also presented are the number of iterations with CIs that did not overlap or exceed 1.0, indicating the number of iterations that detected a change in the spotted owl population.

Province-Level Analyses

We ran three sets of province-level scenarios, simulating spotted owl population change, generating detection histories and fitting occupancy models similar to rangewide simulations. As with the rangewide scenarios, precision among estimates of the change in spotted owl use for different physiographic provinces increased with longer monitoring duration scenarios and higher sampling density (figs. 9 through 11). Estimates of the change in spotted owl use were most precise and least biased for the ORWC province which had the largest sample size of any individual province, ranging from 82 to 822 hexagons at 2 and 20 percent sampling density, respectively (table 1, fig. 9, app. 1, figs. A1.4 and A1.5). For most scenarios with sampling of at least 200 hexagons, mean estimates from the 100 iterations demonstrated the ability to detect change in the population and the magnitude of change. Province scenario results also indicated that change in the population could be effectively detected at the ORCOA, but with less precision than at the ORWC (figs. 9 and 10, app. 1, figs. A1.4 through A1.7). With sample size (n) of hexagons ranging from 8 to 81, the estimates for CACOA were the least precise and most biased, and had low confidence in the ability to detect change in the population (fig. 11, app 1, fig. A1.8). In fact, sample sizes were so low for the CACOA province at low levels of sampling density that models often did not converge, so we were unable to calculate probability of use (ψ) or confidence interval coverage estimates for some scenarios.

At the 2-km threshold level with random sampling, absolute bias in estimates ranged from –4.6 to 3.8 percent for the ORWC province (among 36 scenarios), from –6.7 to 17.9 percent for the ORCOA province, and from –20.9 to 30.1 percent for the CACOA province. At the 4-km threshold level, absolute bias ranged from –0.6 to 9.7 percent for the ORWC province, from –0.3 to 9.1 percent for the ORCOA province, and from –19.4 to 40.9 percent for the CACOA province. The tendency of simulations with a 4-km threshold to underestimate the magnitude of decline was true for the ORWC and CACOA provinces but was not as strong for the ORCOA province, where there was not a discernable difference between the 2- and 4-km thresholds in bias and precision (figs. 9 through 11). Additionally, bias was generally higher after 10 or 20 year durations for the ORWC and CACOA provinces, as with the rangewide scenarios (figs. 8 through 11).

We also considered scenarios with the 2+20 percent and random-flower designs at the province level. For the ORWC province, estimates of the change in spotted owl use were less biased with the 2+20 percent design compared to random sampling at both 2- and 4-km thresholds (fig. 9). Estimates at the province scale with the random-flower design were considerably less biased at a 2-km threshold but not with a 4-km threshold. Estimates of change in spotted owl use for the ORCOA province were considerably less biased with both the 2+20 percent and random-flower designs (compared to random sampling) at a 2-km threshold but not at a 4-km threshold (fig. 10, app. 1, fig. A1.7). For the CACOA province, change in estimates of use were not measurably less biased with either the 2+20 percent or random-flower designs, all of which had relatively very few hexagons being monitored (fig. 11, app. 1, fig. A1.8).

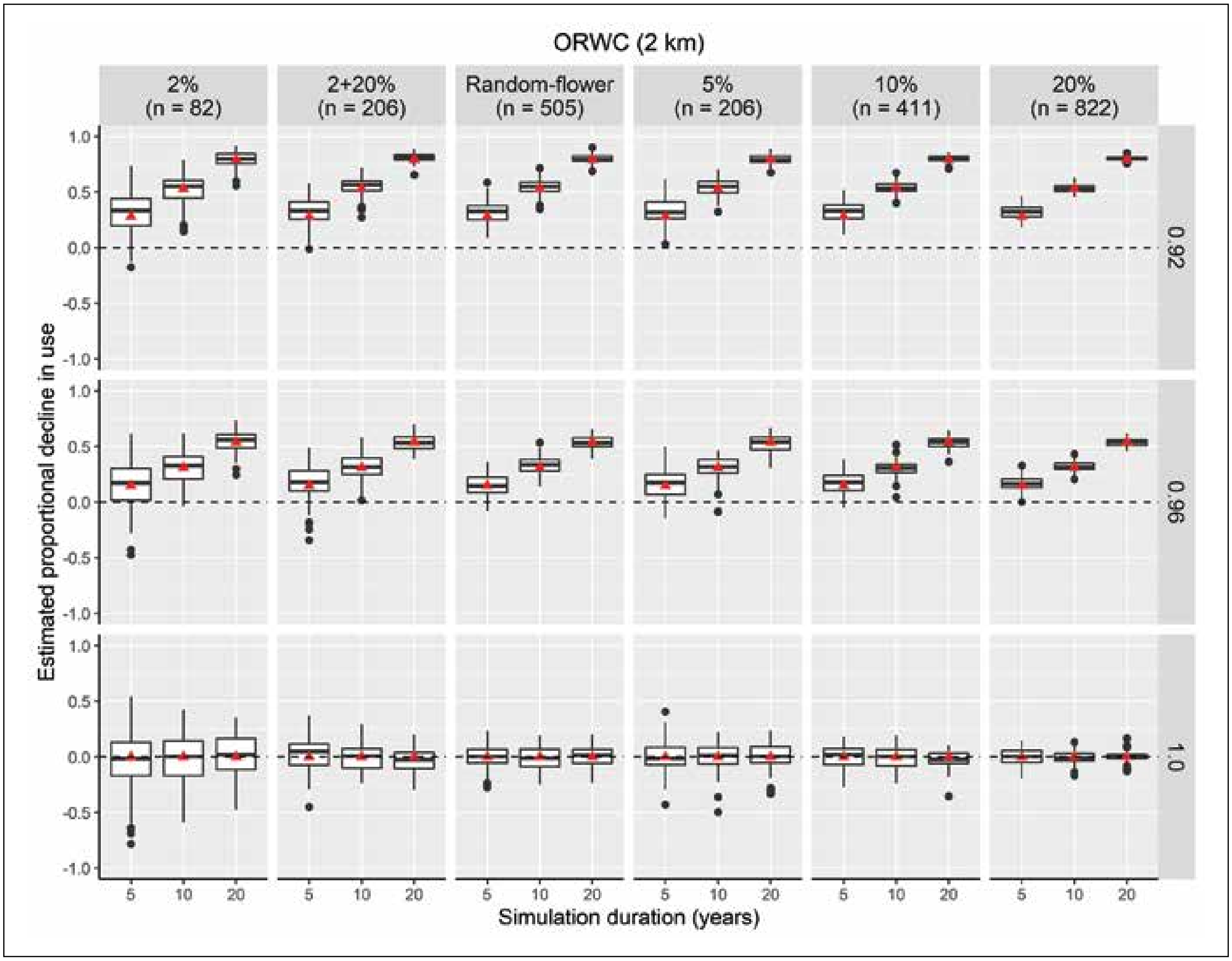
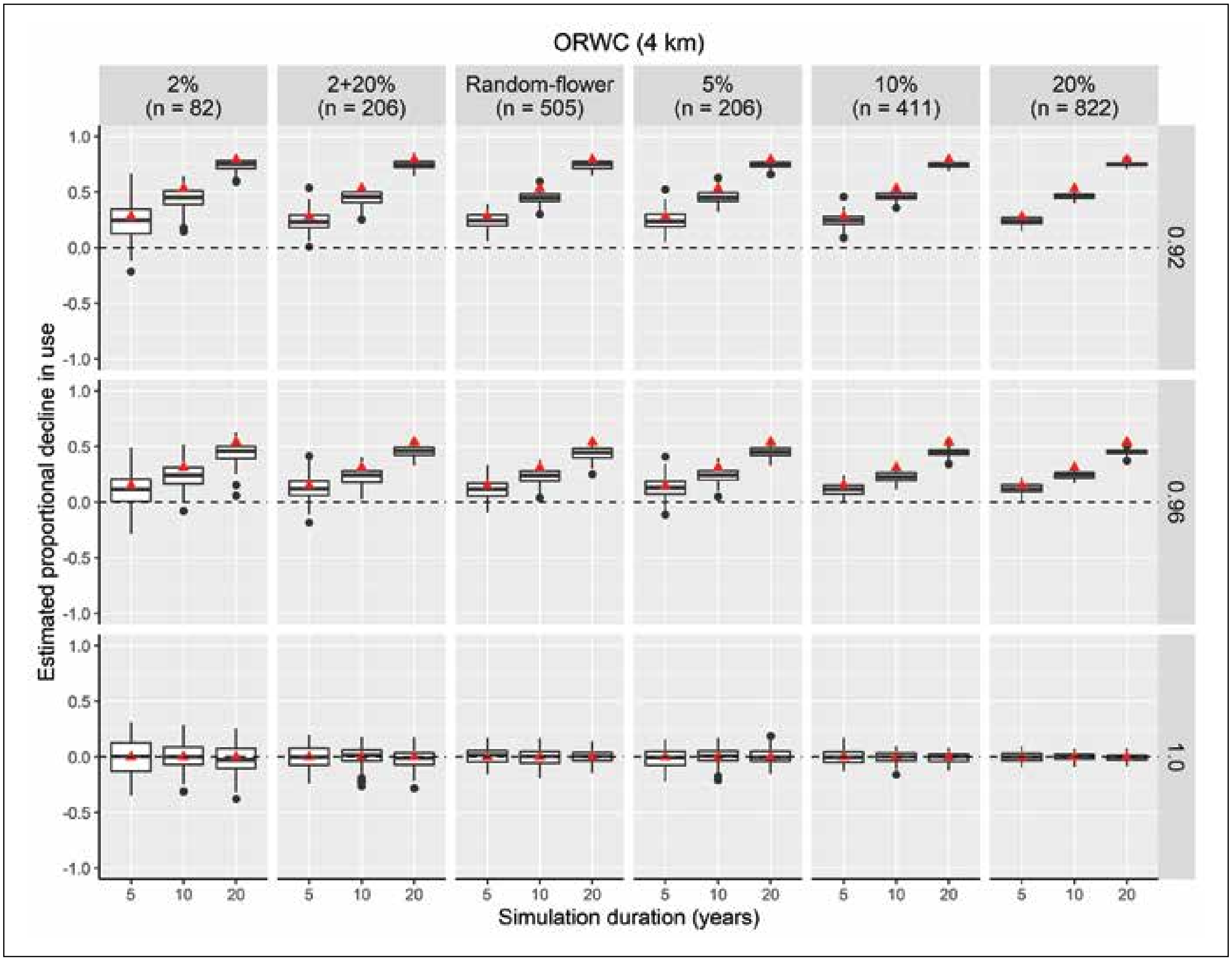


Figure 9—Boxplots of estimated proportional decline-in-use by northern spotted owls over a range of passive acoustic monitoring scenarios within the Oregon West Cascades (ORWC) physiographic province. Scenarios shown here include distance thresholds of (a) 2 km and (b) 4 km.

Discussion

We illustrated the ability of passive acoustic monitoring under a range of sampling designs to detect changes in spotted owl hexagon use over time that reflect changes in territory occupancy for the underlying population. Although different than those generated from mark-resight estimators, recent advances in wildlife survey techniques and statistical methods give us the ability to estimate population change and distribution from detection-nondetection data. Collectively, these advancements have increased the feasibility to noninvasively monitor vocal species of wildlife communities at large spatial scales (Noon et al. 2012, Shonfield and Bayne 2017, Tempel and Gutiérrez 2013, Woodet al. 2019). Networks of passive survey devices can monitor biodiversity at all spatial scales, answer pressing ecological



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questions, and inform management and policy in ways that were not possible just a few years ago (Steenweg et al. 2017). Passive acoustic monitoring provides many potential advantages over mark-resight surveys for evaluating trends in spotted owl populations, which includes supporting: crew safety, noninvasive owl handling practices, high-quality data collection for multiple species, increased spatial and temporal monitoring, and reduced costs. However, some population vital rates such as apparent survival and recruitment may be lost if only passive bioacoustics data are available for quantifying population change. In a passive approach, sites are monitored, and colonization and extinction rates of those sites are estimated to understand changes in the underlying wildlife population. In our simulations, we found that in scenarios with a declining population, the estimates for change in hexagon use were lower in magnitude than the simulated change in the underlying population. This bias was especially prominent in scenarios of

Networks of passive survey devices can monitor biodiversity at all spatial scales, answer pressing ecological questions, and inform management and policy in ways that were not possible a few years ago.

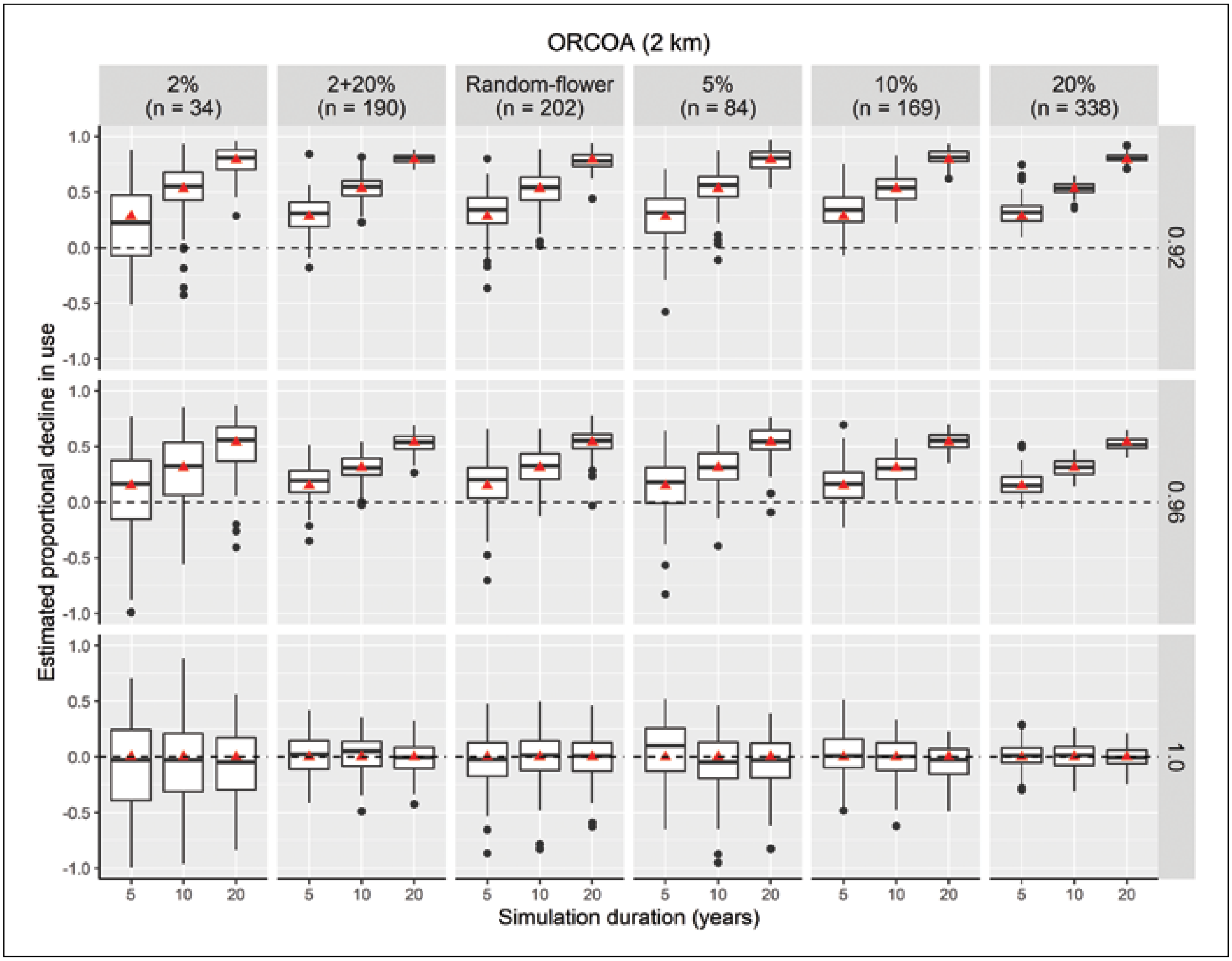

Figure 10—Boxplots of estimated proportional decline-in-use by northern spotted owls over a range of monitoring scenarios within the Oregon Coast Range (ORCOA) physiographic province. Scenarios shown here include distance thresholds of (a) 2 km and (b) 4 km.

4 km-distance threshold compared to those scenarios with no detections farther than 2 km from territory centers. This finding highlights the need to understand spotted owl calling behavior at various distances from territory centers, especially detection probabilities of pairs beyond 2 km of a territory center during the breeding season.

We simulated passive acoustic monitoring scenarios and estimated change-in-use by spotted owls using an occupancy framework to approximate change in landscape use, and then assessed how well those changes in use matched changes in the underlying territory occupancy in simulated populations. We found that our simulated passive acoustic monitoring designs were able to detect declines (and stationary status) in the occupancy rate of territorial spotted owl pairs, even at relatively low sampling densities and with monitoring durations as short as 5 years. However, these findings assumed a constant decline, while estimates from

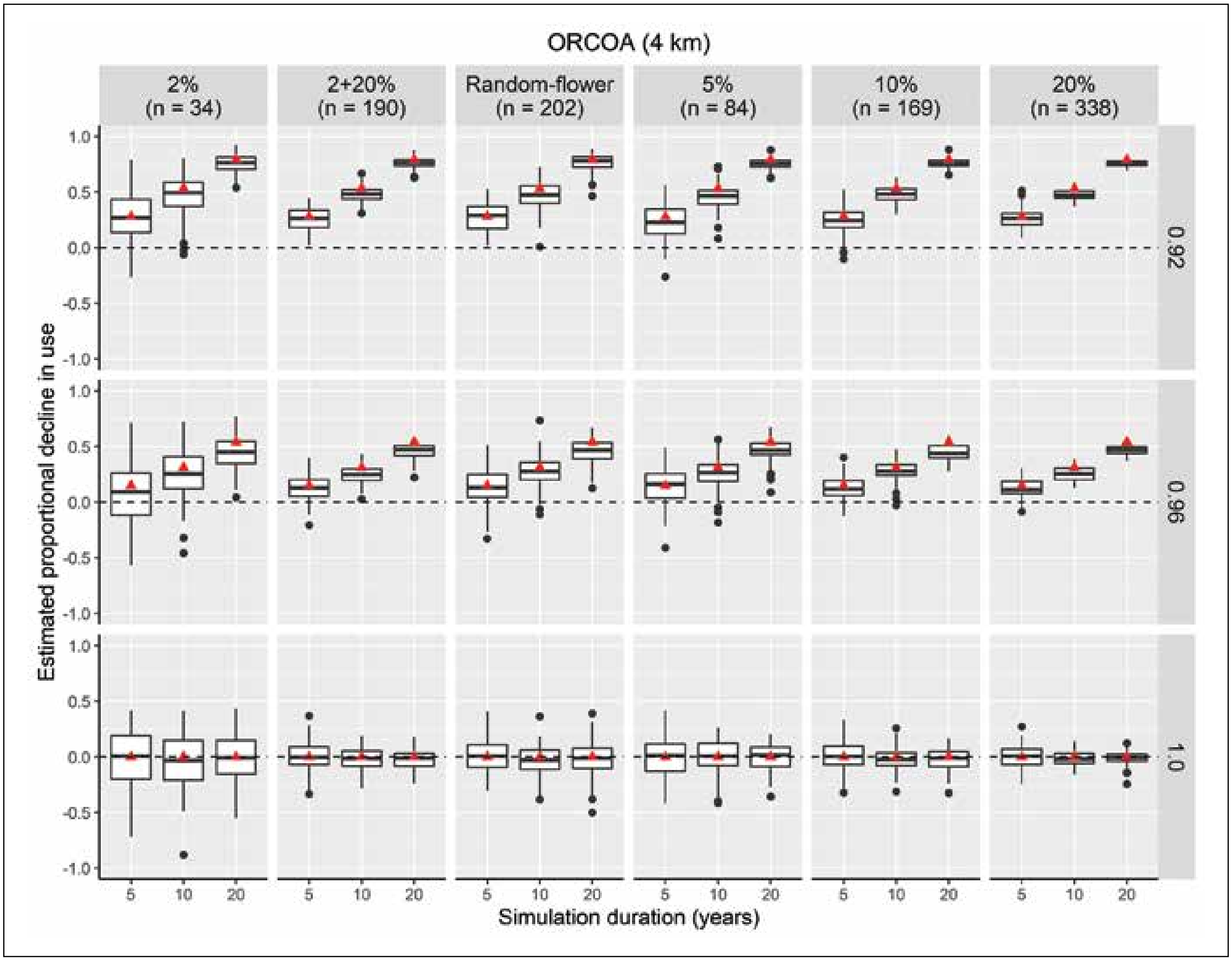

Figure 10—continued.

field-collected data will be based on data with more variability, so reliable change-in-use estimates may take longer than 5 years. Our simulations also revealed several key considerations that will affect interpretation of estimates of spotted owl hexagon use within this framework.

We found relatively consistent trends between bias and precision of estimates that should be considered when interpreting monitoring results. Monitoring designs with higher density of sampling consistently had higher precision. Bias did not appear to be affected much by sampling density (i.e., survey sample size), suggesting that 2 percent random sampling is sufficient to detect declines in use by spotted owls over long periods, but with low precision. Bias often increased with increasing monitoring duration and distance threshold, resulting in the magnitude of decline in estimated use being less than the change in the population at 10 and 20 years. We found that in population decline scenarios,

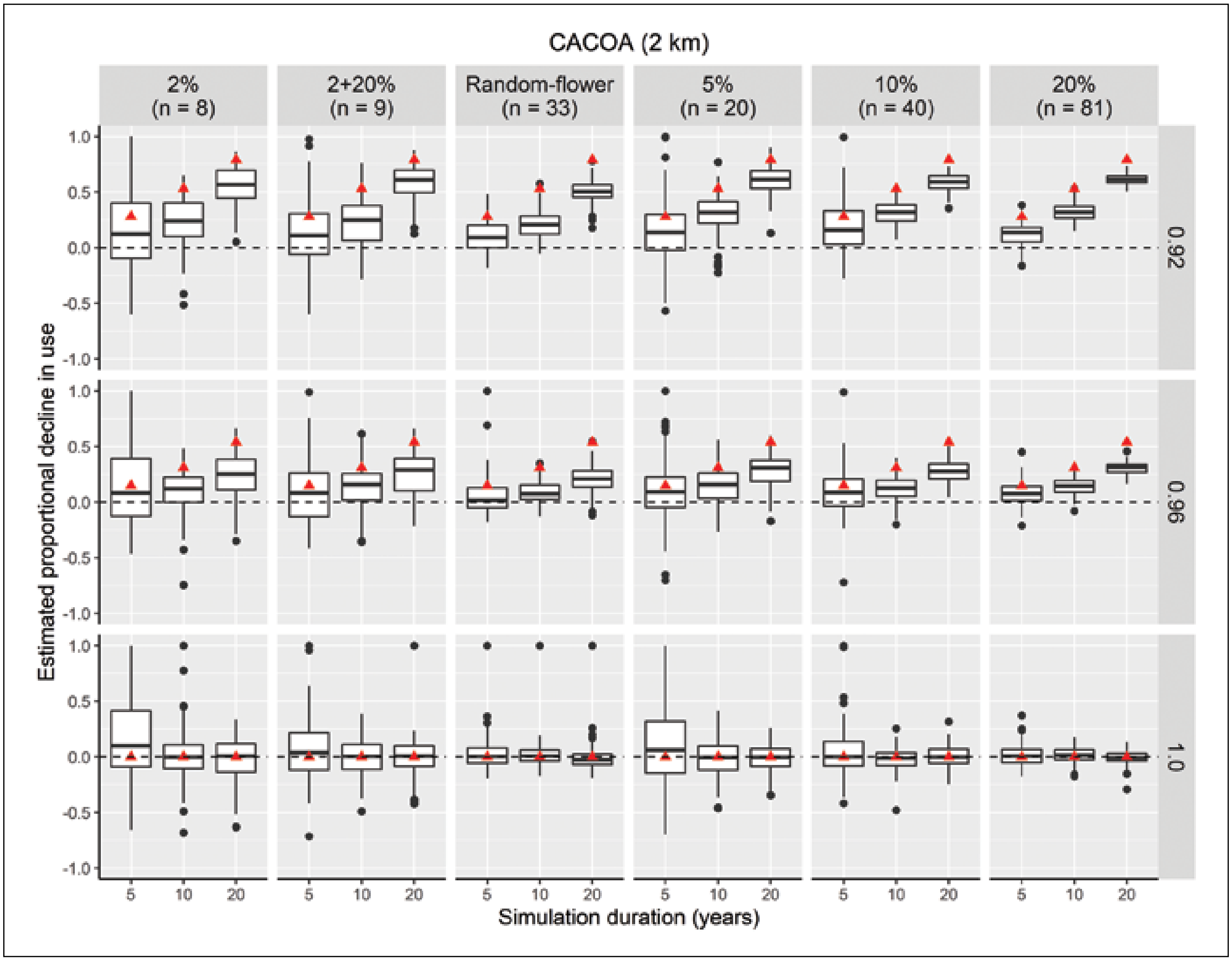

Figure 11—Boxplots of estimated proportional decline-in-use by northern spotted owls over a range of monitoring scenarios within the California Coast Range (CACOA) physiographic province. Scenarios shown here include distance thresholds of (a) 2 km and (b) 4 km.

the number of used hexagons did not change in direct proportion with the decline in the number of occupied territories, but we observed little bias in scenarios of stationary populations. There may have been several underlying drivers for this bias that resulted in a dampened magnitude of change-in-use estimates compared to the proportional change in the population. One possibility may be spatial autocorrelation that was especially pronounced in high-density sampling designs with the 4-km threshold. Early in the simulation, a large proportion of sampled hexagons were overlapped by multiple occupied territories. Therefore in declining population scenarios, a smaller proportion of used hexagons transitioned to unused hexagons in comparison to the proportion of occupied territories transitioning to unoccupied territories. With declining populations, many hexagons became unused, and the remaining hexagons, on average, had fewer overlapping territories. These findings reemphasize the importance in making the distinction between occupancy

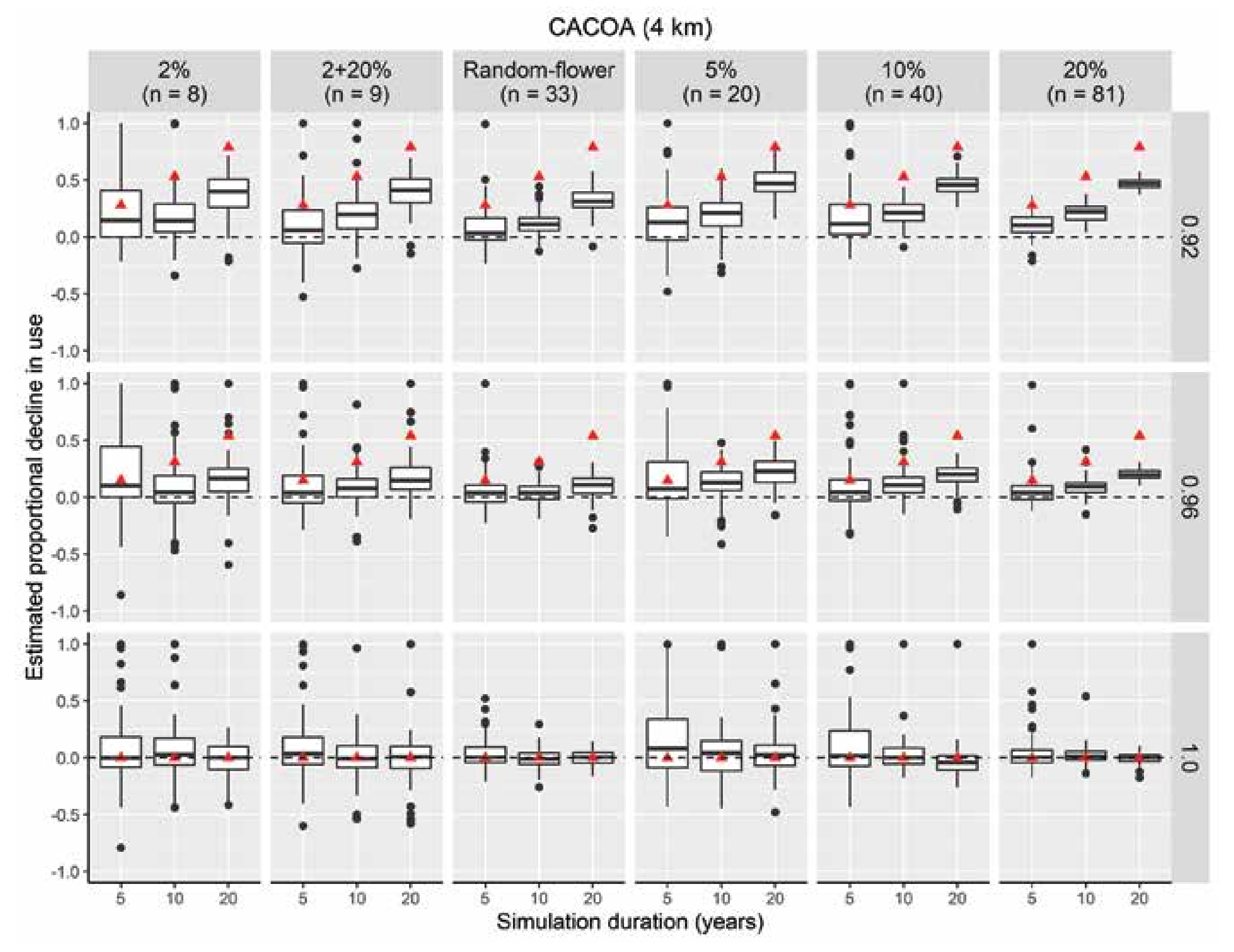

Figure 11—continued.

and use when interpreting parameters estimated from monitoring data, and that a proportional change in hexagon use does not perfectly equate to a proportional change in the number of spotted owls. Additional study of this issue is needed, and we suggest there are several options that may reduce the consistent bias and bring the magnitude of change-in-use in line with population change. To reduce bias and to identify appropriate statistical corrections, the monitoring program will need to develop criteria that will reliably predict whether an ARU station is within or beyond 2 km of a territory center.

Precision among simulation iterations for each scenario increased with increasing monitoring duration and sampling density. We believe that it will be important for the monitoring program to consider differences in precision among sampling designs because there will be only one observation of spotted owl use each year, not 100, as in our simulations. The variation among sampling designs allowed us to evaluate what range of population metrics are possible. For example, although mean use estimates accurately predicted declines in all scenarios with simulated λ < 1, some individual iterations in low-density sampling were ambiguous regarding whether use by spotted owls was increasing or decreasing. Although the magnitude of declines was generally underestimated at 10- and 20-year durations, precision in these estimates was high; i.e., the degree of underestimation was consistent across iterations. This suggests that with higher levels of sampling and by applying a statistical correction, we can expect the estimated magnitude of change-in-use to more accurately reflect the change in the underlying population.

We have limited evidence that spotted owls behave territorially as far as 4 km from their established territory center within a breeding season, but adults do, on average, move over 3 km between breeding seasons when they disperse (Jenkins et al. 2019). With increasing harassment by barred owls, spotted owls are dispersing now at higher rates (about 25 percent of breeding spotted owls) than documented in the past (Jenkins et al., in press). In some instances, California spotted owls move long distances within a breeding season (Berigan et al. 2018). Therefore, with increasing adult dispersal rates and distance (between season), we felt it imperative to understand how estimates derived from monitoring may be affected by long-distance movements within a breeding season. We found that this can have important implications for a monitoring program because bias in estimates increased with wider ranging movements and detections farther from the territory center (i.e., 4-km threshold scenarios). The mechanism behind this appeared to be that hexagons often had multiple overlapping territory detection zones, resulting in lower magnitude of change in estimated use than the true change in the population. When we restricted detections to within 2 km of an occupied territory center, bias decreased and the change-in-use more closely approximated the magnitude of population change.

Decreasing the distance threshold for detectability from 4 to 2 km improved bias of the estimated population change, which highlighted the need to understanding how bioacoustic data from spotted owls differ within and beyond 2 km of a territory center. A key aspect in a monitoring program will be to not simply treat all documented spotted owl sounds as detections, and certainly not only a few spotted owl detections within a season. The probability of detecting spotted owl at distances greater than 2 km from their territory centers depends on several factors, including how detections are defined from ARU recordings and calling behavior of spotted owls at distances far from their territory centers. Determining pair status will also be an important way to reduce bias and more accurately estimate magnitude of change in the population.

For California spotted owl populations on three study areas, Conner et al. (2016) compared estimates of realized population change from mark-resight data (Pradel models) to those from site detection-nondetection data (occupancy models) and found that Pradel model reported greater magnitudes of change. For that study, they summarized data from the field surveys differently for occupancy and Pradel models. For the Pradel model, Conner et al. (2016) created encounter histories for all known resident banded owls which were those owls on a territory and a member of a pair. They created encounter histories for each territory in the occupancy model considered a detection as any owl (single or a member of a pair) that was detected at least once during a survey. The less restrictive criteria for what was defined as a detection for occupancy models may have contributed to the potential bias of dampened magnitude of change. These findings highlight the need to determine if a site is used by a territorial pair vs. a resident or transient single owl and develop standardized detection criteria. One such criteria could be that a site is not considered to have a "detection" unless vocalizations from both sexes are observed within a survey period which has typically been 1 week. Multistate occupancy models could also be fit with "0" being no owl detected, "1" if a single owl is detected, and "2" if a pair is detected. Further, because spotted owls call much less frequently farther from their territory centers, a threshold for number of calls could be imposed to prevent single recordings of a spotted owl call from being considered detections. For example, Duchac et al. (n.d.)[1] conducted a bioacoustics survey for owls in a postfire landscape and removed the lowest 1 percent of detections for each species' overall range of detections at any given station to minimize the effects of detections of nonterritorial owls. In this postfire landscape, they detected spotted owl on a few occasions at a few sites but made little inference from those detections. Those few spotted owl detections were not likely from a territorial individual but rather a transient owl spending little time in the study area. An alternative could have been to weight the data based on the number of calls rather than exclude data below some predetermined threshold.

Other methods could be developed to further improve interpretation of bioacoustic data for spotted owl. For example, Wood et al. (2020) developed three methods for extracting additional ecological details beyond simple "detection" of California spotted owl hoots, and were able to distinguish calls by sex using vocal variation in pitch. Dale et al. (n.d) were able to complete a similar process and identify vocal variations for northern spotted owls.[2] As was observed by Duchac

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[1] Duchac, L.S.; Lesmeister, D.B.; Dugger, K.M.; Davis, R.J. [N.d.]. Differential landscape use by forest owls two years after a mixed-severity wildfire. Manuscript in preparation. On file with: D. Lesmeister, USDA Forest Service, Pacific Northwest Research Station, Corvallis Forestry Sciences Laboratory, Corvallis, OR 97331.

[2] Dale, S.S.; Jenkins, J.M.A.; Ruff, Z.J. [et al.]. [N.d.]. Vocal variation in pitch distinguishes female and male northern spotted owls. Manuscript in preparation. On file with: D. Lesmeister, USDA Forest Service, Pacific Northwest Research Station, Corvallis Forestry Sciences Laboratory, Corvallis, OR 97331.

If, in the future, individual spotted owls can be reliably identified using bioacoustics, it raises the possibility of noninvasive demographic studies.

et al. (2020) for spotted owls, call rates (vocalizations/time) at occupied sites help to characterize pair status and interactions with interspecific competitors. More research is warranted on individual identification, but Wood et al. (2020) developed an approach to differentiate individual California spotted owls based on vocal characteristics. Some initial work with northern spotted owls suggests promise for identifying individuals within a breeding season (e.g., Horan et al. 2020), but substantially more research will be needed to determine effectiveness of identification based on vocalizations for this subspecies. Vocal individuality is known for some spotted owls, and individual identification based on vocalizations has been demonstrated for many other owls including *Strix* species (Choi et al. 2019, Delport et al. 2002, Freeman 2000, Galeotti and Pavan 1991, Grava et al. 2008, Rognan et al. 2009, Tripp and Otter 2006). Ongoing work should improve our understanding of spotted owl call rates and call types produced within certain distances of territory centers, allowing the monitoring program to set thresholds and interpret bioacoustics data in an informed manner. If, in the future, individual spotted owls can be reliably identified using bioacoustics, it raises the possibility of noninvasive demographic studies.

At the province scale, we observed considerable variability in bias and precision among provinces that appeared to be driven by spatial extent and arrangement of federally managed lands. In addition to the extent of federal lands, there are key ecological differences among provinces, especially in prey type, spotted owl home range sizes, forest structure, and disturbance regimes (Lesmeister et al. 2018). We found that mean estimates of change-in-use successfully tracked the underlying population in the Oregon West Cascades and Coast Range, especially at the 2-km threshold, and precision improved with increased time and sampling density. The California Coast Range was the exception as only a small portion of the province is under federal management—resulting is a small pool of hexagons available for sampling. The number of sampled hexagons ranged from 8 to 81, and they were densely arranged in a few locations. We observed that the precision of estimated use increased with time, but estimates were highly biased for most scenarios. These simulations demonstrated that the scenarios tested here could be appropriate for tracking province-specific population change in many of the provinces (e.g., Oregon West Cascades and Coast Range) but are not likely appropriate for reliably tracking population changes in some provinces like the California Coast Range. Province-level population monitoring may be desired given ecological differences, so for some provinces, a range of other scenarios are needed to determine the most appropriate sampling design. For example, a monitoring design that includes sampling on state and private lands may be required for a province like the California Coast Range.

At the rangewide level, the sampling designs of 2+20 percent and the random-flower performed equally well as the straight random sampling designs with a similar number of hexagons. For example, the 2+20 percent design (1,014 hexagons) performed similarly as the sampling design of 5 percent random (1,064 hexagons), and the random-flower design (2,531 hexagons) performed most similarly to the 10 percent random design (2,128 hexagons). The advantage of random-flower and 2+20 sampling designs are that they afford the opportunity to learn and better interpret findings from random-only designs, particularly if there is some overlap with traditional mark-resight data in some areas. For example, concentrated or clustered deployments, as in the random-flower design, could allow for the development of distance-based approaches to further refine the detectability and calling behavior at various distances from a territory center. Spatial mark-resight methods would be possible if individuals can be identified by vocal characteristics, but these methods may limit some of the applicability of the program to other non-spotted owl species that may be of interest to managers. Focusing additional sampling within DSAs (e.g., 2+20 percent) with a range of different designs would also provide the opportunity to gather additional data in areas where spotted owls have been intensively monitored for over three decades. This would be particularly important if mark-resight and callback surveys are continued in DSAs for several seasons as bioacoustic sampling occurs. Such an overlap in studies would provide valuable insight into the relationship between spotted owl use and territory occupancy as well as the relationship between spotted owl calling behavior and distance to territory center.

Each design we tested could be effective for detecting a decline in spotted owl populations within 10 years with even a moderate amount of sampling, but there are important considerations and tradeoffs among the various options.

Conclusions

Our objective with these simulations was to explore the ability of passive acoustic monitoring to detect changes in landscape use by spotted owls over time. A key finding was that each design we tested could be effective for detecting a decline in spotted owl populations within 10 years with even a moderate amount of sampling, but there are important considerations and tradeoffs among the various options. Often, estimated changes-in-use were biased with a consistently lower magnitude of change compared to actual simulated changes in the population. An advantage of a consistent and directional bias with increasing precision through time is that there are several avenues to correct magnitude of change estimates to reduce the bias. For example, with study area overlap in demographic studies and bioacoustics surveys, we could better understand the relationship between vocalization dynamics and distance to territory center, which can help refine the distance threshold in detection probability and identifying appropriate statistical corrections for estimates of change-in-use. Monitoring studies and surveys would also afford the opportunity to define criteria for what will be considered a detection from bioacoustics data. In practice, we expect that bioacoustics surveys will often not have independent data on territory center locations, so future monitoring efforts will benefit from combined efforts of demography and bioacoustics surveys in the near term. An effective adaptive monitoring program will include the ability to further refine interpretation of bioacoustic data, especially improving the distance probability function identified here as a key piece of knowledge to greatly improve the population parameter estimates derived from passive acoustic monitoring. Our results suggest a monitoring program similar to the 2+20 percent sampling design, with a relatively short overlap (2 years) with current demographic studies, will provide the best opportunity to adapt to changing conditions and fill important knowledge gaps early in the monitoring effort. The distance function for detection probability may also be informed by project-level surveys if they include traditional methods (similar to demography studies) and bioacoustic sampling that covers the extent of the project area. In the future, project surveys could be used to validate models from monitoring data, and in some cases, perhaps project data could be fully integrated into monitoring datasets.

To remain relevant and useful to resource managers, the spotted owl monitoring program must adapt with changing population conditions, but there are also opportunities to remain as a high-standard monitoring program by leveraging recent analytical and technological advancements, and well-designed sampling methods.

Insights from our findings, as well as information from ongoing monitoring efforts, will continue to increase our understanding of how changing dynamics of spotted owl populations can be observed with passive bioacoustics data. The NWFP fundamentally altered how land management decisions are made for 10 million hectares of federal land and established policies for multiagency efforts to conserve biodiversity associated with old-growth forests (Spies et al. 2019). Phase I of spotted owl monitoring under the NWFP effectiveness monitoring program has been held as a shining example for monitoring a single species (Nichols et al. 2019). However, declining spotted owl populations throughout their range have increased the logistical effort required for data collection, and detecting trends in vital rates are more difficult with the decreased precision in estimates. To remain relevant and useful to resource managers, the spotted owl monitoring program must adapt with changing population conditions, but there are also opportunities to remain as a high-standard monitoring program by leveraging recent analytical and technological advancements, and well-designed sampling methods. The use of passive acoustic monitoring for spotted owls could be an important component in the transition to phase II NWFP effectiveness monitoring. The fundamental change in the approach to spotted owl monitoring will certainly have challenges. A network of ARUs throughout the NWFP area will require significant collaboration among agencies, which has been firmly established under phase I of the effectiveness monitoring program, but will also require standardized data collection protocols, metadata, and security measures to protect records about sensitive species such as spotted owl. Although there will be challenges, passive acoustic monitoring can improve how individual species (including spotted owls) and entire wildlife communities of the Pacific Northwest are monitored, while also being safer for field crews. With the transition to phase II, federal agencies will benefit from passive acoustic monitoring since this approach can sample species of ecological and managerial concern at multiple scales and further supports program efforts to effectively assess terrestrial biodiversity over time.

Acknowledgments

Funding and support for this research was provided by the U.S. Department of the Interior Bureau of Land Management, and U.S. Department of Agriculture Forest Service Pacific Northwest Region and Research Station. We appreciate the brainstorming sessions with Paul Anderson, Bruce Hollen, and George McFadden that were critical in early stages of broad- scale passive acoustic monitoring in the Pacific Northwest. We thank Becky Gravenmier for her unwavering support of our work and assistance in communicating its importance. We are indebted to the science transition team (Alan Franklin, Erin Bayne, Katie Dugger, Bill Kendall, Taal Levi, Daryl MacKenzie) for spending considerable time to provide comments and feedback on scenarios and earlier report drafts that greatly improved the final version. Bridgette Tuerler and Scott Vanderkooi provided comments that helped improve the manuscript. We thank Leila Duchac for her tireless efforts that have led to the foundation of what we can learn about spotted owls using passive acoustic monitoring. The findings and conclusions in this report are those of the authors and should not be construed to represent any official U.S. Department of Agriculture or U.S. Government determination or policy.

English Equivalents

When you know:	Multiply by:	To find:
Meters (m)	3.28	Feet
Hectares (ha)	2.47	Acres
Kilometers (km)	.621	Miles
Square kilometers (km^2)	.386	Square miles

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Appendix 1

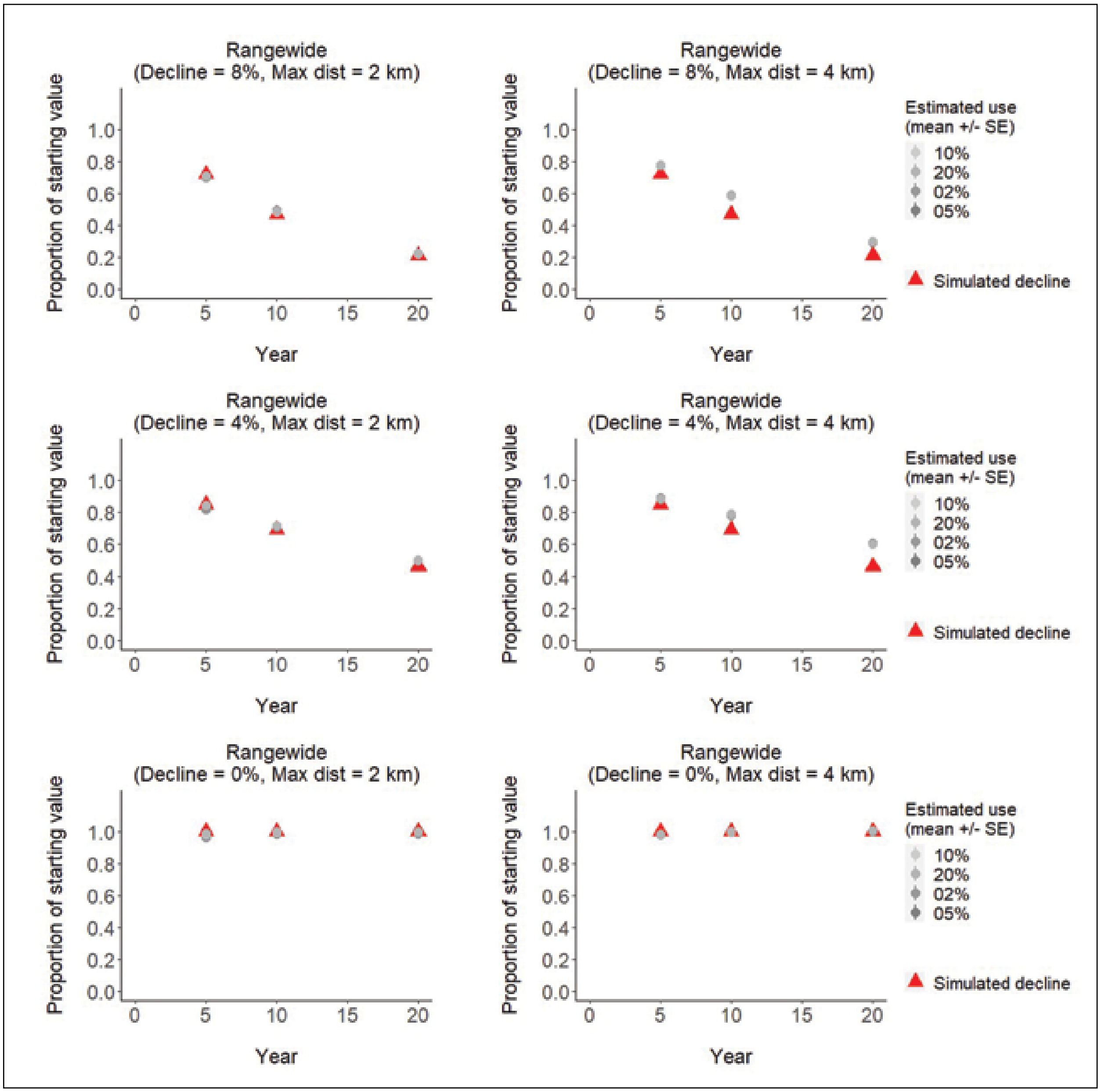

Figure A1.1—Comparison of the estimated change-in-use by northern spotted owls among simulation scenarios at the rangewide level with random sampling. Shown are summary estimates with 95 percent confidence intervals (gray dots) for different densities of random sampling (light gray to dark gray), along with the simulated decline in occupied spotted owl territories (red triangles). Scenarios represent three different rates of simulated decline (rows) and two different distance thresholds (columns).

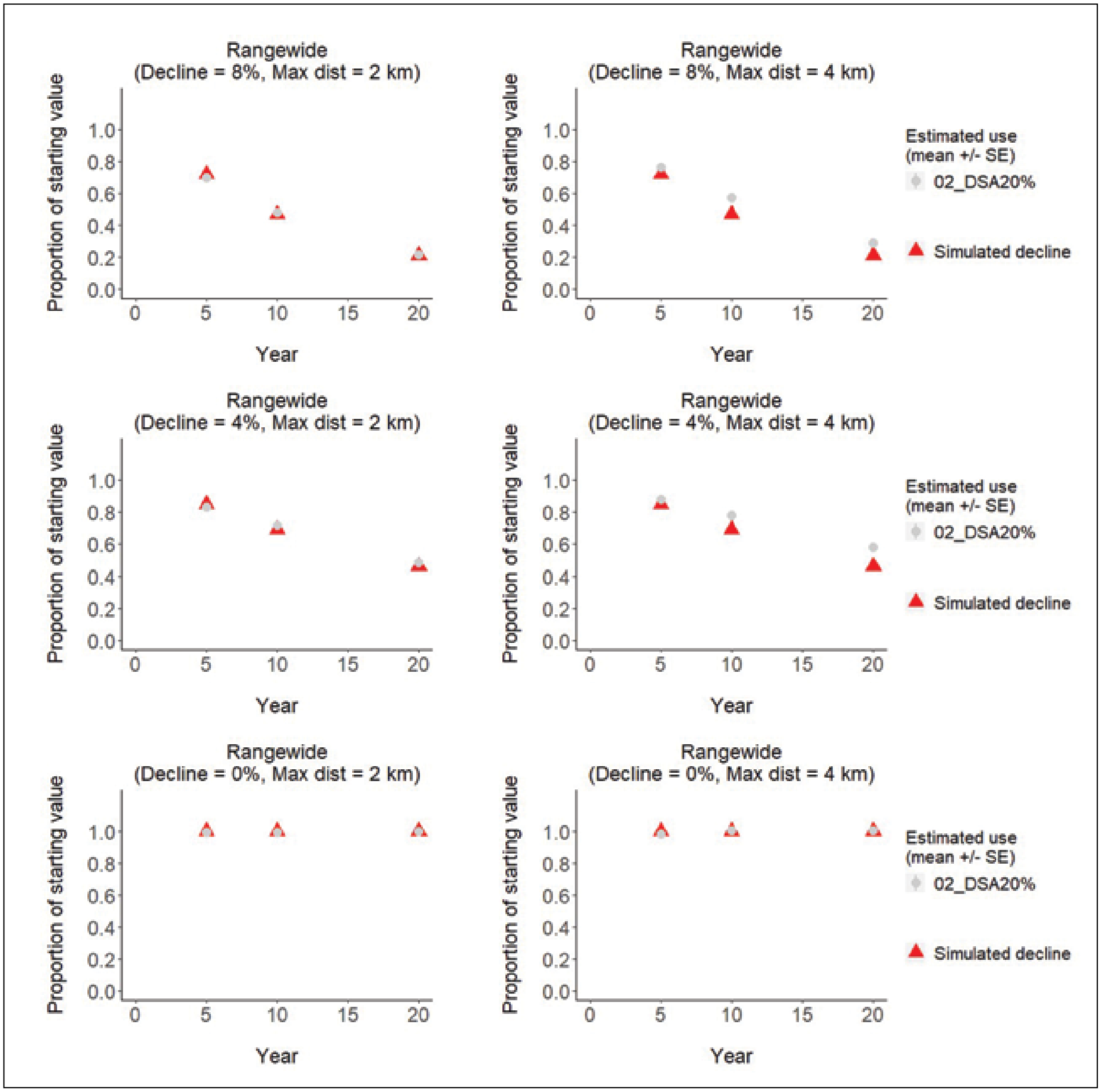

Figure A1.2—Comparison of the estimated change-in-use by northern spotted owls among simulation scenarios at the rangewide level with 2+20 percent sampling design. Shown are summary estimates with 95 percent confidence intervals (gray dots), along with the simulated decline in occupied spotted owl territories (red triangles). Scenarios represent three different rates of simulated decline (rows) and two different distance thresholds (columns). DSA = demographic study area.

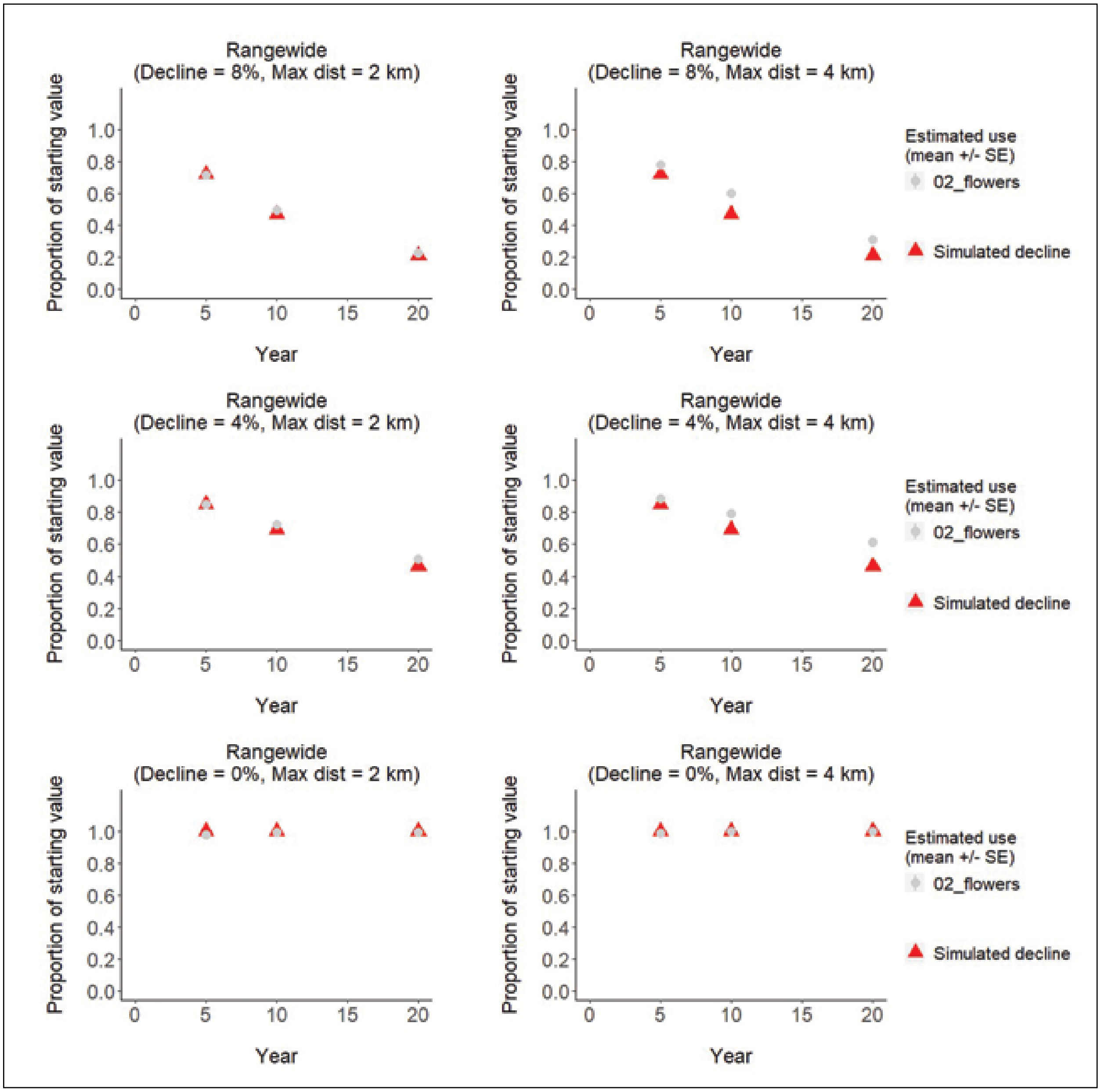

Figure A1.3—Comparison of the estimated change-in-use by northern spotted owls among simulation scenarios at the rangewide level with the random-flower sampling design. Shown are summary estimates with 95 percent confidence intervals (gray dots), along with the simulated decline in occupied spotted owl territories (red triangles). Scenarios represent three different rates of simulated decline (rows) and two different distance thresholds (columns).

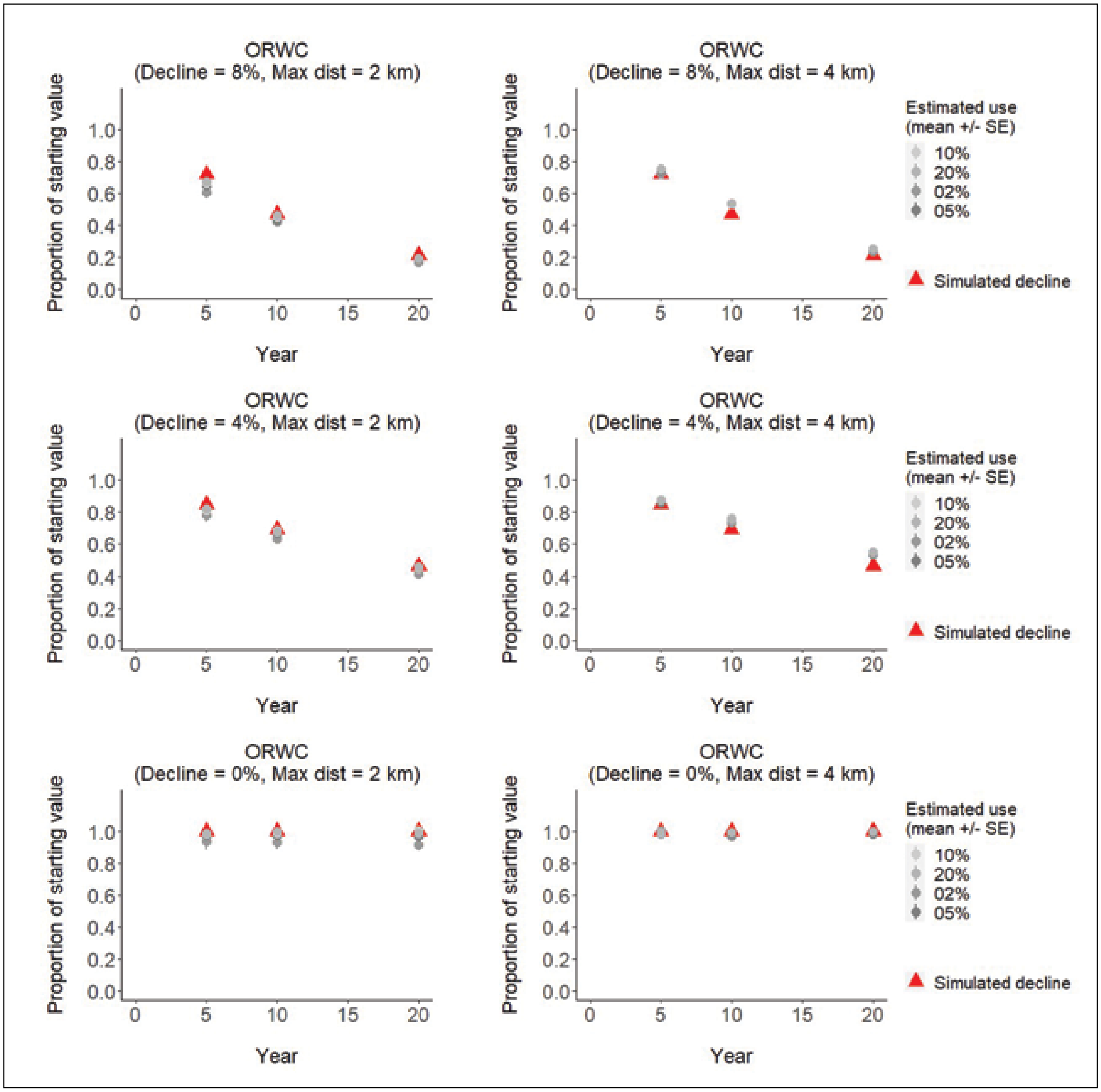

Figure A1.4—Comparison of the estimated change-in-use by northern spotted owls among simulation scenarios within the Oregon West Cascades (ORWC) province. Shown are summary estimates with 95 percent confidence interval (gray dots) for different densities of random sampling (light gray to dark gray), along with the simulated decline in occupied spotted owl territories (red triangles). Scenarios represent three different rates of simulated decline (rows) and two different distance thresholds (columns).

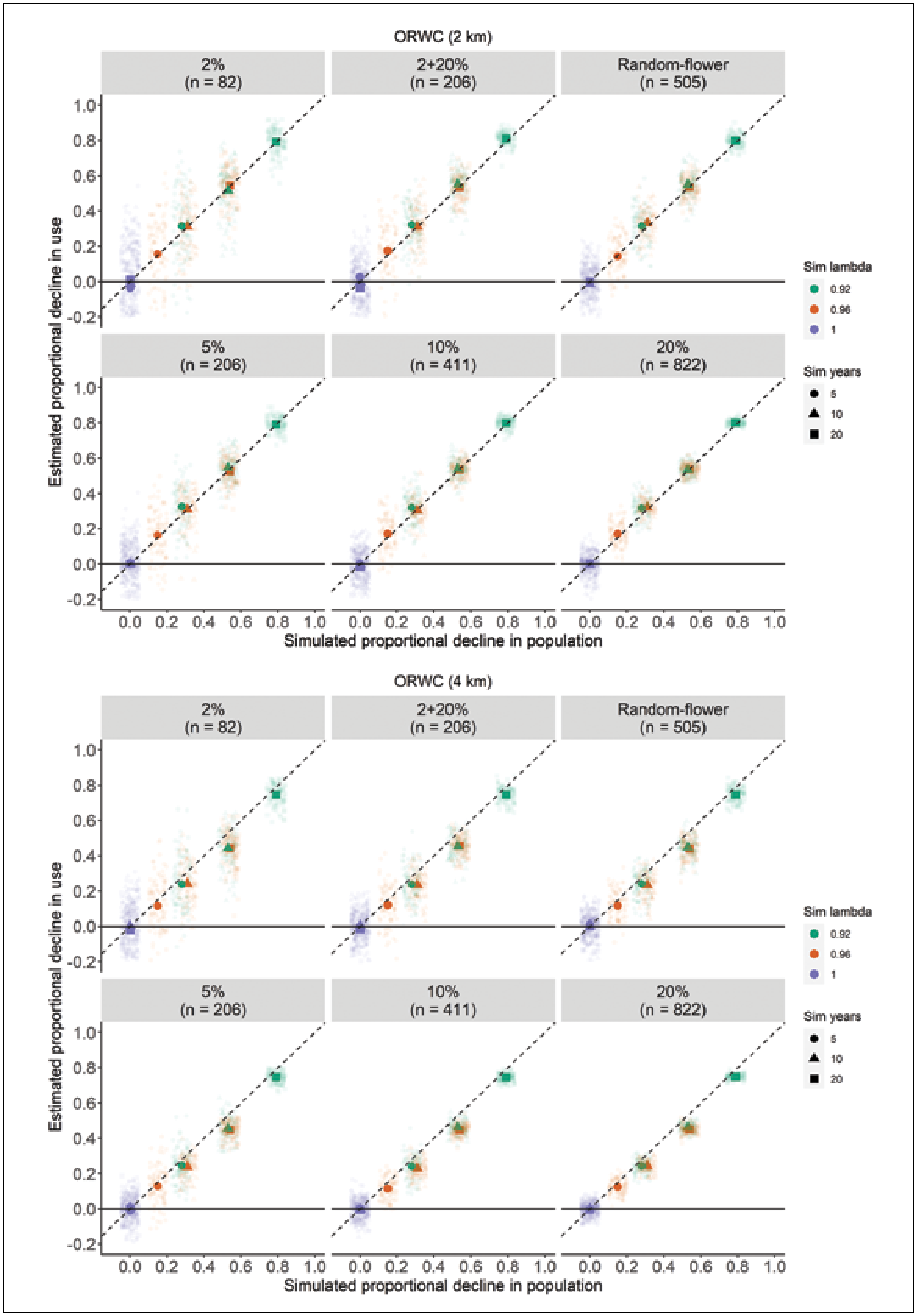

Figure A1.5—Estimated proportional decline-in-use by northern spotted owls compared to the simulated proportional decline in occupied spotted owl teraritories within the Oregon West Cascades (ORWC) province. We spread estimated use points horizontally to facilitate interpretation of vertical spread that represented variation in estimates of hexagon use. Scenarios shown here include distance thresholds of (a) 2 km and (b) 4 km.

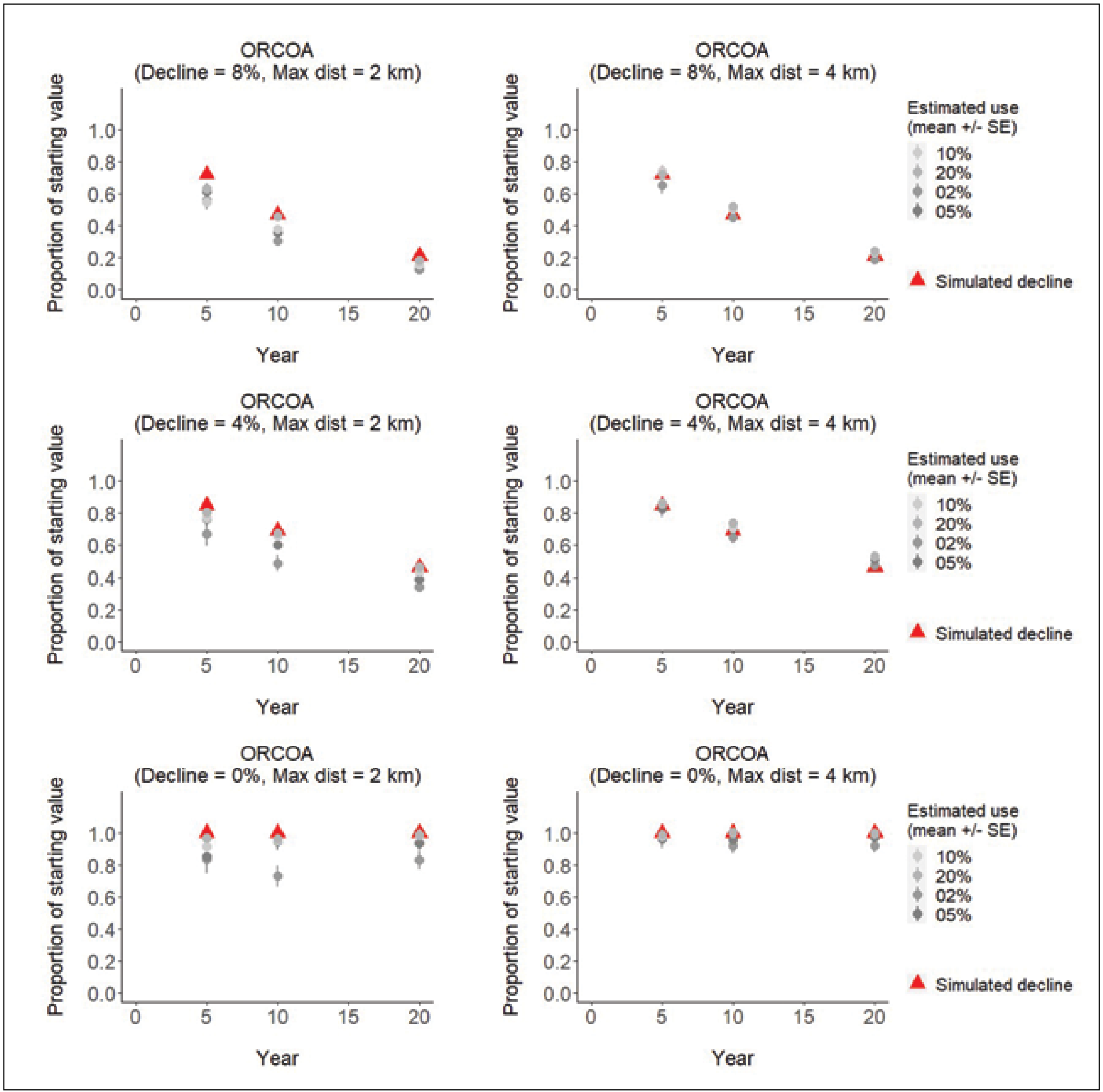

Figure A1.6—Comparison of the estimated change-in-use by northern spotted owls among simulation scenarios within the Oregon Coast Range (ORCOA) province. Shown are summary estimates with 95 confidence interval (gray dots) for different densities of random sampling (light gray to dark gray), along with the simulated decline in occupied spotted owl territories (red triangles). Scenarios represent three different rates of simulated decline (rows) and two different distance thresholds (columns). SE = standard error.

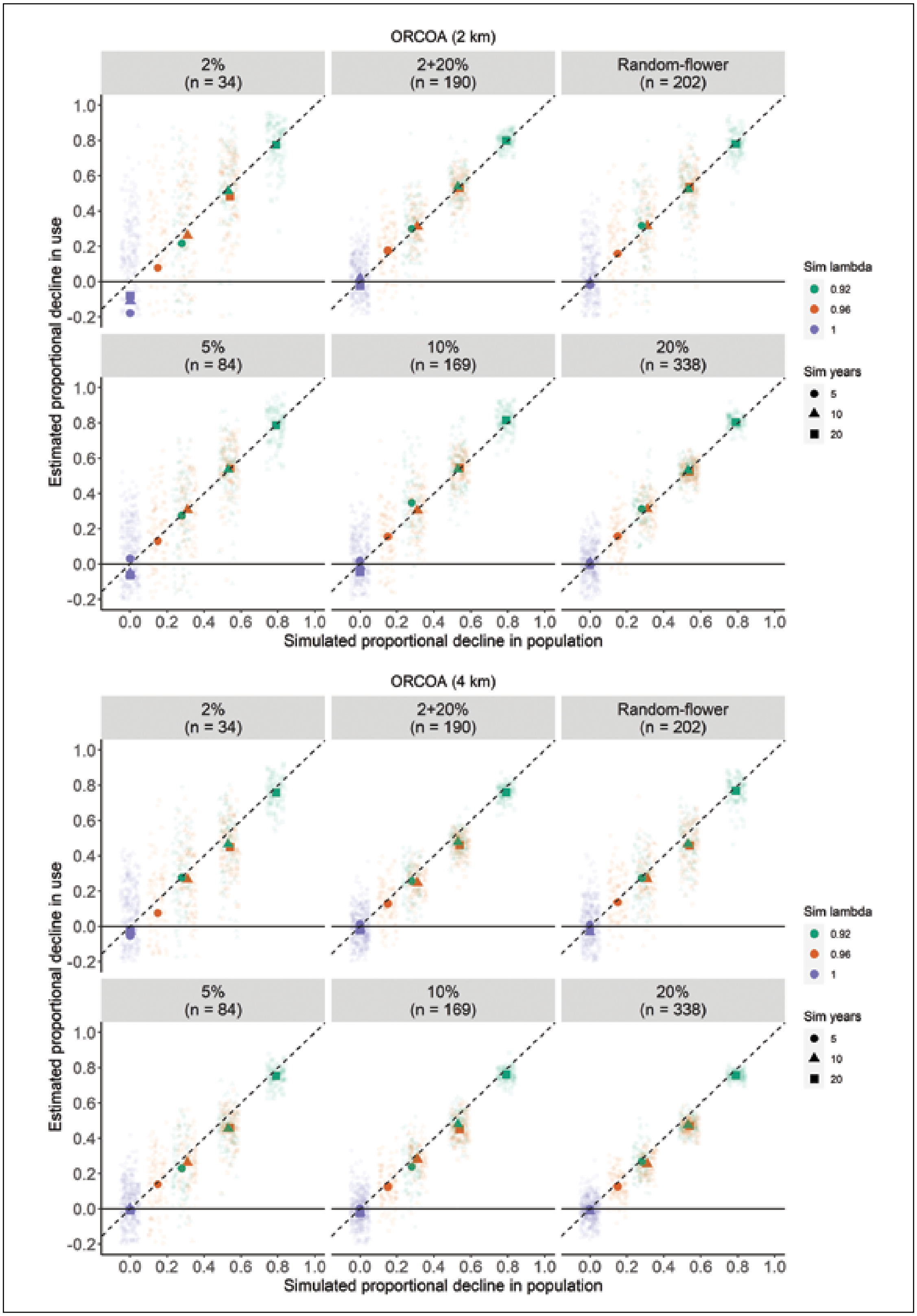

Figure A1.7—Estimated proportional decline in use by northern spotted owls compared to the simulated proportional decline in occupied spotted owl territories within the Oregon Coast Range (ORCOA) province. We spread estimated use points horizontally to facilitate interpretation of vertical spread that represented variation in estimates of hexagon use. Scenarios shown here include distance thresholds of (a) 2 km and (b) 4 km.

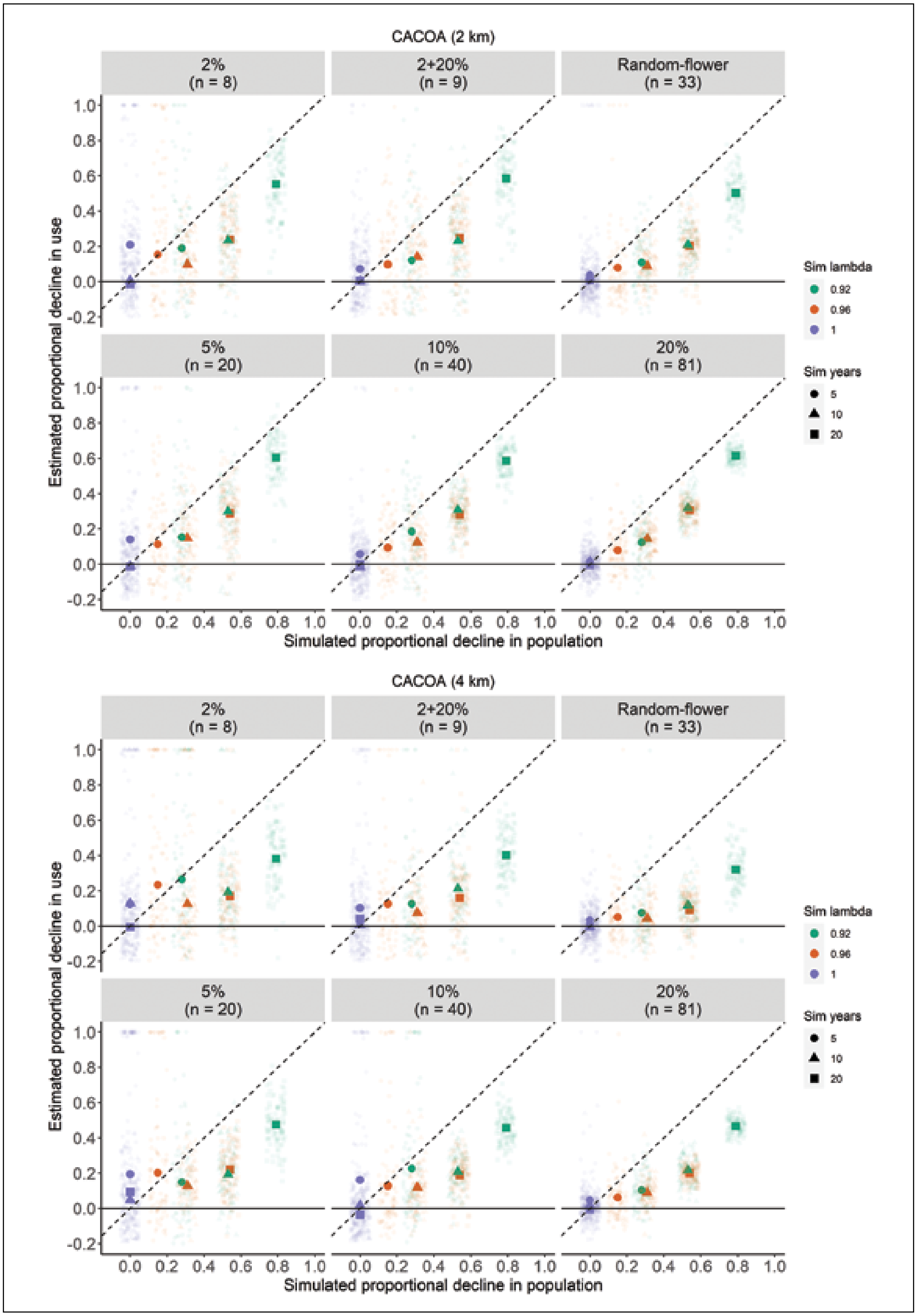

Figure A1.8—Estimated proportional decline-in-use by northern spotted owls compared to the simulated proportional decline in occupied spotted owl territories within the California Coast Range (CACOA) province. We spread estimated use points horizontally to facilitate interpretation of vertical spread that represented variation in estimates of hexagon use. Scenarios shown here include distance thresholds of (a) 2 km and (b) 4 km.

Appendix 2

Table A2.1—For each scenario of all combinations of simulated northern spotted owl population growth (sim λ; 0.92, 0.96, 1.00), sampling design (random: 2, 5, 10, 20; 2+20 percent in demographic study areas; 2 percent random flower), monitoring duration (5, 10, 20 years), and distance threshold (2 km, 4 km) are the number of iterations (n = 100) for which confidence intervals (CI; at the 95 percent or 50 percent level) overlapped the "true" simulated decline in territories ("Sim λ"). Also presented is the number of iterations with CIs that did not overlap or exceed 1.0 (suggesting unambiguous decrease in hexagon use).

Sim λ	Sampling design	Duration (years)	Distance threshold (km)	Overlap sim λ (95% CI)	Overlap sim λ (50% CI)	Do not overlap 1 (95% CI)	Do not overlap 1 (50% CI)
0.92	2%	5	2	96	51	74	97
			4	91	41	77	99
		10	2	98	59	100	100
			4	20	4	100	100
		20	2	96	45	100	100
			4	1	0	100	100
0.92	Flower	5	2	93	46	100	100
			4	42	16	100	100
		10	2	81	37	100	100
			4	0	0	100	100
		20	2	56	21	100	100
			4	0	0	100	100
0.92	2+20%	5	2	98	55	99	100
			4	90	28	99	100
		10	2	94	62	100	100
			4	5	0	100	100
		20	2	97	53	100	100
			4	0	0	100	100
0.92	5%	5	2	98	63	99	100
			4	79	22	100	100
		10	2	94	47	100	100
			4	4	0	100	100
		20	2	90	37	100	100
			4	0	0	100	100
0.92	10%	5	2	99	61	100	100
			4	59	12	100	100
		10	2	95	51	100	100
			4	0	0	100	100
		20	2	88	35	100	100
			4	0	0	100	100
0.92	20%	5	2	98	51	100	100
			4	31	0	100	100
		10	2	88	30	100	100
			4	0	0	100	100
		20	2	70	18	100	100
			4	0	0	100	100

Table A2.1—For each scenario of all combinations of simulated northern spotted owl population growth (sim λ; 0.92, 0.96, 1.00), sampling design (random: 2, 5, 10, 20; 2+20 percent in demographic study areas; 2 percent random flower), monitoring duration (5, 10, 20 years), and distance threshold (2 km, 4 km) are the number of iterations (n = 100) for which confidence intervals (CI; at the 95 percent or 50 percent level) overlapped the "true" simulated decline in territories ("Sim λ"). Also presented is the number of iterations with CIs that did not overlap or exceed 1.0 (suggesting unambiguous decrease in hexagon use). (continued)

Sim λ	Sampling design	Duration (years)	Distance threshold (km)	Overlap sim λ (95% CI)	Overlap sim λ (50% CI)	Do not overlap 1 (95% CI)	Do not overlap 1 (50% CI)
0.96	2%	5	2	99	53	27	83
			4	97	53	16	84
		10	2	96	53	86	100
			4	66	12	94	99
		20	2	92	39	100	100
			4	2	0	100	100
0.96	Flower	5	2	95	48	88	100
			4	72	28	85	99
		10	2	82	28	100	100
			4	4	1	100	100
		20	2	42	10	100	100
			4	0	0	100	100
0.96	2+20%	5	2	99	56	55	97
			4	95	44	55	97
		10	2	96	56	100	100
			4	28	2	100	100
		20	2	90	38	100	100
			4	0	0	100	100
0.96	5%	5	2	97	54	59	96
			4	88	42	51	94
		10	2	95	50	100	100
			4	16	0	100	100
		20	2	79	18	100	100
			4	0	0	100	100
0.96	10%	5	2	98	59	89	100
			4	82	39	85	100
		10	2	94	39	100	100
			4	4	0	100	100
		20	2	63	6	100	100
			4	0	0	100	100
0.96	20%	5	2	100	64	100	100
			4	73	14	100	100
		10	2	89	28	100	100
			4	0	0	100	100
		20	2	24	1	100	100
			4	0	0	100	100

Sim λ	Sampling design	Duration (years)	Distance threshold (km)	Overlap sim λ (95% CI)	Overlap sim λ (50% CI)	Do not overlap 1 (95% CI)	Do not overlap 1 (50% CI)
1.00	2%	5	2	99	59	1	41
			4	100	53	0	47
		10	2	98	59	2	41
			4	100	70	0	30
		20	2	98	65	2	35
			4	98	54	2	66
1.00	Flower	5	2	97	46	3	54
			4	95	47	5	53
		10	2	89	40	11	60
			4	90	39	10	61
		20	2	90	45	10	55
			4	89	43	11	57
1.00	2+20%	5	2	99	53	1	47
			4	94	54	6	46
		10	2	96	63	4	37
			4	100	64	0	36
		20	2	97	52	3	48
			4	98	54	2	46
1.00	5%	5	2	100	54	0	46
			4	98	58	2	42
		10	2	97	57	3	43
			4	100	60	0	40
		20	2	100	67	0	33
			4	96	52	4	48
1.00	10%	5	2	99	56	1	44
			4	100	48	0	52
		10	2	99	59	1	41
			4	98	59	2	41
		20	2	99	65	1	35
			4	99	63	1	37
1.00	20%	5	2	99	59	1	41
			4	99	56	1	44
		10	2	100	68	0	32
			4	98	61	2	39
		20	2	100	75	0	25
			4	100	57	0	43

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Pacific Northwest Research Station
1220 SW 3rd Avenue, Suite 1400
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Portland, OR 97208-3890