Ornate Box Turtle (*Terrapene ornata ornata*): A Technical Conservation Assessment

Prepared for the USDA Forest Service,
Rocky Mountain Region,
Species Conservation Project

May 16, 2006

Alan J. Redder[1], C. Kenneth Dodd, Jr., Ph.D.[2], and Douglas Keinath[1]
and Dave Mcdonald[3] with Takeshi Ise[3]

[1] Wyoming Natural Diversity Database, University of Wyoming, P.O. Box 3381, Laramie, WY 82071
[2] U.S. Geological Survey, Florida Integrated Science Center, 7920 N.W. 71st Street, Gainesville, FL 32653
[3] Department of Zoology and Physiology, University of Wyoming, Bioscience Building, Laramie, WY 82071

Peer Review Administered by
Society for Conservation Biology

Redder, A.J., C.K. Dodd, Jr., and D. Keinath. (2006, May 16). Ornate Box Turtle (*Terrapene ornata ornata*): a technical conservation assessment. [Online]. USDA Forest Service, Rocky Mountain Region. Available: http://www.fs.fed.us/r2/projects/scp/assessments/ornateboxturtle.pdf [date of access].

ACKNOWLEDGMENTS

We wish to thank the personnel of the state Natural Heritage Programs and wildlife management agencies in Colorado, Kansas, Nebraska, South Dakota and Wyoming and the many North American natural history museums for providing current and historical distribution and natural history data for ornate box turtle occurrences in USFS Region 2. Discussions with many biologists from these and other states provided essential background for the interpretation of these data and the current status of local box turtle populations. Conversations with Sarah Converse, John Iverson, John Wagner and Bob Hay were particularly helpful. Geoff Hammerson provided his turtle data for Colorado and an excellent ornate box turtle photo. Personnel at many county offices in Colorado and Nebraska helped clarify vague directions and descriptions for localities mentioned in these datasets and in some cases provided information about locations of box turtle road mortality and sites at which local residents no longer saw box turtles. We thank the two anonymous reviewers for their many helpful suggestions and criticisms. We are especially grateful to the Forest Service technical editor, Gary Patton, for his patient guidance and assistance in the improvement of this assessment.

AUTHORS' BIOGRAPHIES

Alan Redder is currently the Data Manager at the Wyoming Natural Diversity Database at the University of Wyoming in Laramie. He received his M.A. in Zoology and Physiology in 1994 and his M.S. in Statistics in 1998, both from the University of Wyoming. His research interests include the biogeography of reptiles and amphibians in western North America, the statistical analysis and presentation of complex biological data, and the philosophy and history of evolutionary theory.

Dr. C. Kenneth Dodd, Jr. is currently southeastern Principal Investigator for the USGS Amphibian Research and Monitoring Initiative. In this capacity, he has conducted research and supervised I&M projects in the Great Smoky Mountains National Park and at five national wildlife refuges (St. Marks, Lower Suwannee, Okefenokee, Harris Neck, Savannah). Dr. Dodd received his Ph.D. at Clemson University in 1974, his M.S. at Arizona State University in 1972, and B.S. at University of Kentucky in 1971. He has written over 180 research and popular articles and published *The Natural History of North American Box Turtles* (University of Oklahoma Press, 2001) and *The Amphibians of Great Smoky Mountains National Park* (University of Tennessee Press, 2004). He currently resides in Gainesville, Florida.

Douglas Keinath has over 10 years experience conducting technical and policy analyses for resource management professionals. His broader scope of research focuses largely on small vertebrate ecology, survey and monitoring at the population and landscape scales. Recent investigations focus on creating accurate predictive distribution maps for a variety of sensitive Wyoming fauna, developing methodological improvements for generating such maps, and guiding development of a proposed distribution modeling tool. Keinath received a B.S. in Interdisciplinary Engineering (*magna cum laude*, 1993) and a B.S. in Natural Resource Management (With Distinction, 1993) from the University of Michigan, Ann Arbor, Michigan. For several years he worked as a private environmental consultant under contract to national and international organizations, including USEPA, USDOE, USAID, and the World Bank. He later obtained a Master's degree in Wildlife Biology from the University of Wyoming (2000), and for the past six years has been the Senior Zoologist for the Wyoming Natural Diversity Database.

COVER PHOTO CREDIT

The adult female ornate box turtle. Photograph by G. Hammerson, used with permission.

SUMMARY OF KEY COMPONENTS FOR CONSERVATION OF THE ORNATE BOX TURTLE

Ornate box turtles (*Terrapene ornata ornata*) remain relatively common* throughout much of their North American range, but population declines have been documented in some localities. However, recent distribution and abundance data are inadequate for rigorous inference about population status and trends in most states within Region 2 of the USDA Forest Service. Ornate box turtles are protected in Colorado, Iowa, Indiana, Nebraska, Kansas, and Wisconsin, and international export has been prohibited. A conservation program that has attempted to headstart hatchlings and to translocate adults into endangered Wisconsin populations is currently in progress.

The primary conservation threats to the ornate box turtle include: 1) the destruction, degradation, and fragmentation of its grassland habitats; 2) declines in population sizes due to collection by individuals and for domestic and international pet trade; and 3) road mortality and other anthropocentric effects. The intrinsic vulnerability of this species, due to low reproductive output and high egg and hatchling mortality rates, and typical chelonian life history traits, such as long lifespan and delayed sexual maturity, exacerbate the effects of these external threats. If populations have been sufficiently reduced in size due to the loss of mature reproductive females, recovery may be difficult or impossible. The combination of long lifespan with home range and nest site fidelity also allows for the possibility of inbreeding depression and genetic drift, especially in isolated populations. Strong home range and nest site fidelity also probably limit gene flow between populations. Another potential threat to this species is the interaction of climate change with temperature-dependent sex determination, which could result in successive single-sex cohorts of hatchlings, with detrimental long-term effects on population size and persistence due to reduced mating opportunities because of the absence of mates. Events like recent drought episodes in some areas may also reduce recruitment because of high embryonic mortality resulting from desiccated nest sites.

Surveys for extant populations of ornate box turtles in Region 2 states and subsequent monitoring efforts should be undertaken to determine their population locations, status, structure, and the extent and condition of their associated habitat. Because of the long lifespan and delayed sexual maturity of this taxon and thus, the long-delayed response to management actions, immediate and long-term demographic work is needed to understand if, and to what extent, ornate box turtle populations on the Great Plains risk the same long-term, and perhaps permanent, declines now evident in other turtle populations in North America.

Regardless of the current status of Region 2 ornate box turtle populations, immediate measures should be taken to minimize human impacts on populations by prohibiting the collection, harvest, or destruction of adult, especially female, ornate box turtles. Judging from the results of both matrix population modeling and long-term studies of other declining terrestrial and freshwater turtle populations, this would be the single most important step that could be taken, in addition to the preservation of large areas of native prairie habitat, that would reduce the chances of catastrophic declines in this species.

---

[*] Dodd and Franz (1993) define a "common" species as "a species that can reasonably be expected to be observed or collected in its natural habitat, assuming that appropriate sampling techniques are used in appropriate habitats at appropriate times of year".

TABLE OF CONTENTS

EDITOR: Gary Patton, USDA Forest Service, Rocky Mountain Region

LIST OF TABLES AND FIGURES

Tables:

Figures:

INTRODUCTION

Goal

The goal of this assessment is to summarize the scientific literature on the ornate box turtle (*Terrapene ornata ornata*) to assist USDA Forest Service (USFS) biologists and managers, as well as other federal, state, and local resource managers, in their conservation and management efforts on USFS units of the Rocky Mountain Region (Region 2) and surrounding jurisdictions throughout the range of this species.

Scope

This assessment examines the biology, ecology, conservation, and management of the ornate box turtle throughout its range, with particular emphasis on its characteristics in USFS Region 2. Occurrence data were obtained from state Natural Heritage Programs in South Dakota, Nebraska, Kansas, Colorado, and Wyoming and from museums containing ornate box turtle specimens. Scientific literature summarized in this report includes peer reviewed publications, reports from management agencies, symposia and conference proceedings, discussions with knowledgeable herpetologists and managers, and descriptions of conservation plans, efforts and techniques relevant to box turtles and other terrestrial turtles and tortoises.

Uncertainty

Considerable uncertainty is inevitable when attempting to understand a widely distributed species with few data on many aspects of its biology. Many of the most useful studies of ornate box turtles were conducted decades ago in diverse locations and have not been replicated. Current (within the last decade) distribution and abundance data are uncommon despite this species' occurrence across much of the Great Plains and midwestern United States. Much uncertainty results from the inherent limitations of short-term studies on a long-lived species, especially concerning demography and life history parameters. To determine the essential links in the life history of this species and to explore the consequences of changes in vital statistics on future population viability, we developed and present a matrix population model. When appropriate, we have drawn on information about other terrestrial turtle and tortoise species to fill gaps in our knowledge, but inferences from species with somewhat similar traits living in different habitats must be interpreted cautiously.

Peer Review and Publication on the World Wide Web

This manuscript has been peer reviewed prior to its publication on the World Wide Web. Peer review was managed by the Society for Conservation Biology, which employed two experts on this or closely related taxa. Publication of this assessment on the USFS Region 2 website allows rapid dissemination of information to USFS personnel, other agencies, and the public, as well as facilitating future revisions.

MANAGEMENT STATUS AND NATURAL HISTORY

Management Status

The ornate box turtle is not a listed or candidate species under the provisions of the Endangered Species Act of 1973, as amended: nor is it present on any Species of Concern list maintained by the USFS or the U.S. Bureau of Land Management. However, the USFS Region 2 has identified it as a species of possible localized concern, recommending that individual USFS plains units in Region 2 evaluate its status locally and the possible need to accord it special attention on those units (Patton personal communication 2005). It is also listed as an Appendix II species by the Convention on International Trade in Endangered Species of Wild Fauna and Flora (CITES) because of the potentially detrimental impacts on populations resulting from commercial collection and exportation, including tens of thousands of box turtles during the early 1990's.

Colorado, Kansas, and Nebraska prohibit the commercial collection of this species, but all three states allow some non-commercial collection by individuals of small numbers (less than 5) (Levell 1997, Fritz personal communication 2003, Swarth and Hagood 2005, Jackson personal communication 2006, Brunson personal communication 2006). The ornate box turtle has been the official state reptile in Kansas since 1986 (Collins 1993). Elsewhere within its range the ornate box turtle is protected by state law in Iowa (as threatened; Christiansen and Bailey 1988), Indiana (as protected; Swarth and Hagood 2005), and Wisconsin (as endangered; Levell 1997). Texas is currently considering the restriction of box turtle collection (Smith 2004).

NatureServe (2006) and the Natural Heritage Programs (NHP) in the states of USFS Region 2 assess the conservation status of the ornate box turtle as S5 (secure) in Nebraska, Kansas, and Colorado; S2 (imperiled) in South Dakota; and S1 (critically imperiled) in Wyoming. The S1 rank in Wyoming is a result of a single historical record at the western edge of the taxon's range and the subsequent absence of well-documented observations in eastern Wyoming. The S5 ranks in Nebraska, Kansas, and Colorado may be in need of revision since few records of box turtle occurrence in those states currently available to the authors were recent. Despite the NHP rankings in South Dakota and Wyoming, neither of these states provides legal protection to this species.

Existing Regulatory Mechanisms, Management Plans, and Conservation Strategies

Currently only one management or conservation plan directed specifically at the ornate box turtle exists, but a second program may be in the planning stage (Hay personal communication 2003). The Wisconsin Department of Natural Resources has been attempting to restore isolated and declining populations in southwestern Wisconsin. This plan was implemented in 1992 and is scheduled to continue until at least 2012. The plan has used a combination of headstarting of eggs and juveniles from local populations and relocating adults from populations in Texas, Kansas, and northeastern Nebraska (Hatch 1996, Cristoffel 1999). Use of roadside barriers and signs has also been implemented to reduce road mortality (Cristoffel and Hay 1995). Results are presently inconclusive.

Colorado, Kansas, and Nebraska prohibit the commercial collection of this species and moving animals across state lines in violation of state law constitutes a violation of the federal Lacey Act. Still, considerable domestic trade occurs (Wagner personal communication 2003), and given the high prices paid for these turtles to commercial collectors, international trade continues as well, despite CITES restrictions (Wagner personal communication 2003) imposed by its Appendix II listing.

Biology and Ecology

Description and systematics

The ornate box turtle is a small terrestrial turtle with an adult carapace length between 95 and 154 mm (**Figure 1**). Males are usually smaller than females. The carapace varies in color from black to dark gray to reddish brown, with yellow lines radiating from the center of every pleural scute. Central scutes have yellow dashes and form a discontinuous mid-dorsal line. The carapace has an oval outline and a domed and dorsally flattened shape resembling a box, with little or no mid-dorsal keel. The plastron is hinged between the hyoplastral and hypoplastral bones (at the joint between the pectoral and abdominal scutes) (see Figures 1-2 and 1-3 in Dodd 2001, "Carapace" and "Plastron" diagrams in Stebbins 2003), and it can be completely closed against the carapace, allowing box turtles to completely withdraw their head and feet. All plastral scutes have yellow streaks. The skin is brown with yellow spots. There are four toes (rarely three) on each hind foot.

Figure 1. Adult female ornate box turtle. (Photograph G. Hammerson, by permission.)

Males have an enlarged, recurved inner claw on the hind feet that is used during copulation. Reproductive-age males have a concave plastron (females are flat or convex, although male concavity is sometimes not very pronounced), a red iris (females are yellow, although eye color often is similar between sexes), a more posterior cloacal opening compared to females, a longer and thicker tail, and red coloration on the legs and sometimes on the jaw.

Young have the vertebral stripe more pronounced than the yellow scute streaks. The plastron is solid brown with yellow peripherally. The carapace after hatching is nearly flat and circular. The egg tooth is retained for up to 30 days after hatching (Legler 1960). Rings on the scute margins appear to be added with each growing season, allowing for reasonable age estimation up to the age of about 14; afterward, the rings become too close together to distinguish (St. Clair 1998).

Various sources exist for more detailed physical descriptions, general accounts, information on skull structure, photographs, and range maps of the ornate box turtle: Ernst and Barbour (1972), Ward (1978), Vogt (1981), Stebbins (1985), Collins (1993), Ernst et al. (1994), Hammerson (1999), Dodd (2001), and Stebbins (2003). Dodd (2001, 2006) summarized the literature for this species and provided a comprehensive review of its biology.

The classification of ornate box turtles (Crother 2000, NatureServe 2006): *Terrapene ornata ornata*, Agassiz 1857, Smith and Ramsey 1952: Kingdom Animalia, Phylum Craniata, Class Chelonia, Order Testudines, Family Emydidae, Genus *Terrapene* (derived from the obsolete English *terrapine*, of Algonquin origin akin to the Delaware *torope* turtle [Webster's 3rd International Dictionary]).

Agassiz originally described *Terrapene ornata* as *Cistudo ornata* in 1857 from "the Upper Missouri . . . and from Iowa" (Ward 1978). Smith and Ramsey (1952) collected the lectotype specimen (MCZ 1536) for *T. o. ornata* in northeastern Texas and restricted the type locality to Burlington, Des Moines County, Iowa. They distinguished *T. o. ornata* from the subspecies *T. o. luteola* (desert box turtle) primarily by the number of yellow streaks on the second pleural scute (5 to 9 for *T. o. ornata*; 10 to 16 for *T. o. luteola*) and by the tendency for the ground color of older *T. o. luteola* to become uniformly straw-colored while *T. o. ornata* individuals normally retain the ground color/yellow streak color contrast with age. See Ernst and McBreen (1991) and Dodd (2001) for reviews of the species. There are no other turtles within Region 2 that are likely to be confused with the ornate box turtle.

Distribution and abundance

The ornate box turtle ranges from southern Wisconsin and northern Indiana through the central Great Plains from southern South Dakota and southeastern Wyoming through eastern Colorado and New Mexico to the Gulf Coast in Texas (**Figure 2**; Ward 1978, Stebbins 1985, Ernst et al. 1994, Dodd 2001, Stebbins 2003). The eastern edge of its range extends from western and central Louisiana throughout Arkansas, Missouri, and Illinois. The northern extent of this species' distribution is approximately the 44th parallel across the Great Plains, except for southern Minnesota (Breckenridge 1944, MHS 1985, Oldfield and Moriarty 1994), and most of Iowa (Christiansen 1988). The northern edge (and also probably the western edge) of its distribution is influenced by a combination of its spring emergence behavior, availability of friable soils for hibernation, and freeze-tolerance (Costanzo et al. 1995, Curtin 1997). The western edge of its range is in southeastern Wyoming (Baxter and Stone 1985) and the eastern plains of Colorado. At this western limit, the lack of properly sandy soils and increasing altitude are probably the limiting factors on distribution.

Probably the earliest observation of box turtles in the Nebraska Sandhills was in 1795 by Mackay who described "some little varicolored turtles, of which there are vast numbers." (cited by Diller [1955]). The ornate box turtle may have been sighted as far up the Missouri River drainage as the Yellowstone River by F.V. Hayden in 1871 (Cahn 1937, Black and Black 1971), but there are no specimens or subsequent sightings from that far west. Agassiz's 1857 location description, "the Upper Missouri . . ." (Ward 1978), suggests that this species may have existed farther north in the Missouri River basin than the current southern South Dakota localities. Hammerson (1999) stated that scattered occurrences in Colorado west of the high plains were almost certainly the result of escaped or introduced animals. Sightings in the deserts of central and western Wyoming were of released animals (Dunder personal communication 2003) as were two sightings along the Missouri River near Pierre, South Dakota (Backlund personal communication 2005).

The desert box turtle inhabits the grasslands of eastern New Mexico into southeastern Arizona and northern Mexico (Degenhardt 1996), and an intergradation zone (gray area on **Figure 2**) with the ornate box turtle exists in eastern New Mexico and

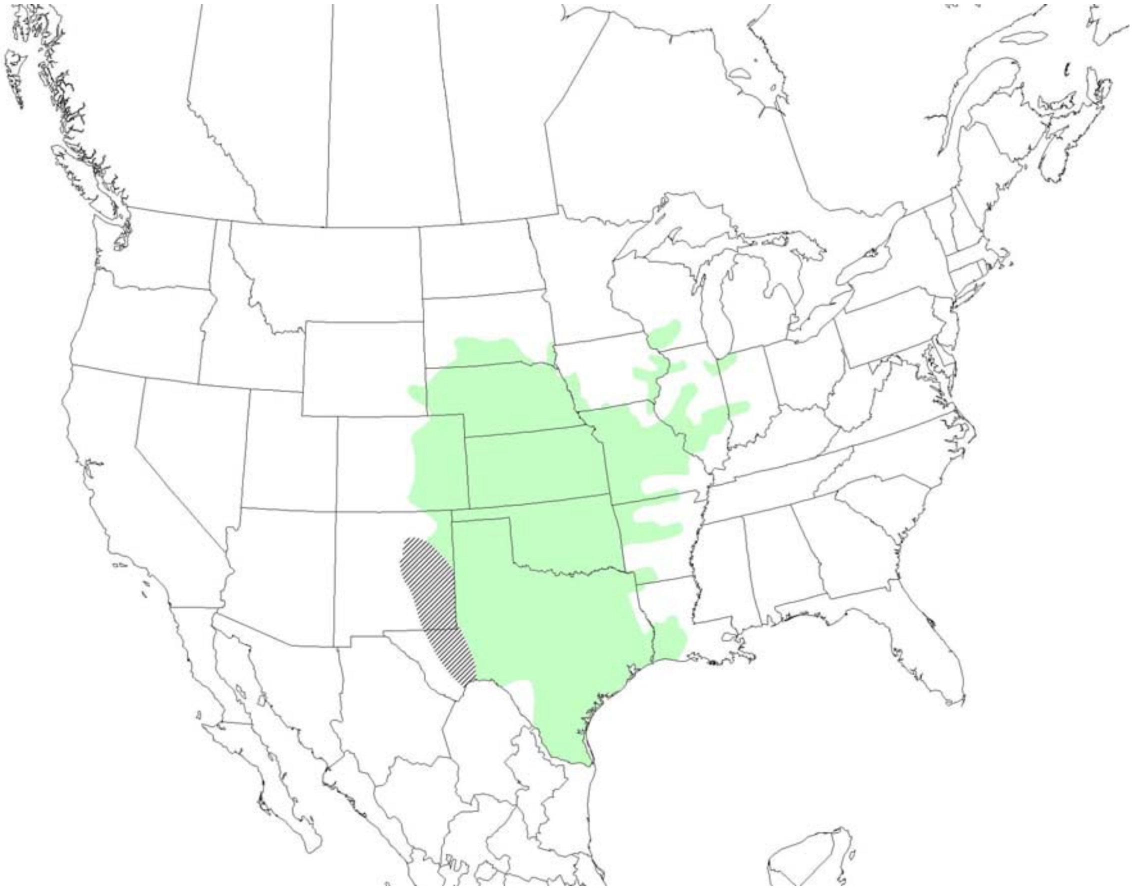

Figure 2. North American distribution of the ornate box turtle (adapted from Hammerson 1999, Map 8.3: Dodd 2001, Map 5; Stebbins 2003, Map 65). Green areas represent the current range of the ornate box turtle. The gray area represents an intergradation zone between this species and the desert box turtle (Ward 1978, Stebbins 1985, 2003).

western Texas (Ward 1978, Stebbins 1985, 2003). The holotype of the desert box turtle was collected in Culbertson County, Texas in 1950.

Population trend

Because few quantitative estimates of abundance appear in the literature, little solid information is available on the population trends of the ornate box turtle. Thus, most trend estimates rely on anecdotal accounts from local residents and researchers. Declines are known and suspected at locations in the eastern part of its range. Ernst and Barbour (1972) suggested a general decline as a result of insecticide accumulation, but they presented no data. Vogt (1981) mentioned that circa 1970 box turtles were common in isolated populations in Wisconsin, with the implication that this was no longer true by 1980. Doroff and Keith (1990) mentioned a decline over the 10 year period of their research from 1977 to 1987 in Wisconsin. Ward's review (1978) suggested that the status of some populations in Iowa may be uncertain. LeClere (2006) states that "[m]any areas [in Iowa] that once had good box turtle populations are now gone due to habitat destruction" but does not provide specific locations of extirpation.

The situation is somewhat more optimistic in most western states. Although there have been reports of declines in some populations in northeastern Nebraska (Iverson personal communication 2005), Kansas (U.S. Fish and Wildlife Service 1996), and Colorado (Hammerson 1999), most reports from those states indicate that populations continue to be at least common and sometimes abundant or increasing. See the Conservation Status section for a detailed discussion of those areas.

Activity and movement patterns

Ornate box turtle emergence from hibernation occurs over a range of dates in late spring in most northern locations, depending on local spring weather, the severity of the preceding winter, and depth of hibernation. See **Table 1** for a summary of activity data. Fitch (1956) observed emergence in Kansas only after air temperatures reach ca. 26 ºC. Legler (1960) rarely observed emergence until body temperatures exceed 15 ºC. Ornate box turtles near St. Louis, Missouri emerged after subsurface temperatures at a depth of 10 to 20 cm reached 7 ºC and were maintained for five consecutive days (Grobman 1990). The earliest emergence observed by Grobman occurred on 12 April. Death resulted from earlier emergence if turtles did not return to the hibernaculum.

After emergence, turtles remain near their hibernacula until warm spring rains stimulate dispersal. The earliest spring activity reported in Kansas was 1 April (Clarke 1958), 26 April in Wisconsin (Vogt 1981), and early May in western Nebraska (Costanzo et al. 1995). Seasonal activity occurs from mid-May to mid-September in Indiana (Minton 1972), and from March to November near Austin, Texas, with peak activity in May and June (Blair 1976). Peak seasonal activity occurs from May to July in Wisconsin, with a sharp drop after August (Vogt 1981). The latest recorded activity in the fall was 24 October in Kansas (Clarke 1958) and late October in southern Illinois (Cahn 1933).

The cue for burrowing in preparation for hibernation appears to be low air temperature. The depth at which hibernation occurs changes with soil temperature. By spring, turtles have moved to within only a few centimeters of the soil surface (Legler 1960, Ernst and Barbour 1972, Grobman 1990). During hibernation, body temperatures can be maintained at 1 to 3 ºC above soil temperature, possibly because of air retained in the soil above the hibernating turtle (Peters 1959). The lowest recorded temperature that ornate box turtles have been known to survive was 2.7 ºC in Kansas (Legler 1960), but Costanzo et al. (1995) found that in a more rigorous environment in western Nebraska they were freeze-tolerant and could survive temperatures as low as -2.6 ºC, at least for a few hours. Despite freeze-tolerance, hatchlings often burrow deeper for hibernation into the nesting sites in which they hatched.

Ornate box turtles tend to maintain body temperatures in an approximately 20 ºC range for active movement but can tolerate a wider range

Table 1. Summary of seasonal activity data for the ornate box turtle at various locations across its range in North America.

Location	Emergence Date	Emergence Temperatures (ºC)	Peak Activity Dates	Peak Activity Temperatures (ºC)	Submergence Dates	Citation
Kansas		Air >26				Fitch 1956
Kansas		Body >15		<30		Legler 1960
St. Louis, MO	April 12	Soil > 7 for five days				Grobman 1990
Kansas	April 1			24 – 32	October 24	Clarke 1958
Wisconsin	April 26				September	Vogt 1981
western Nebraska	early May					Costanzo et al. 1995
Indiana	mid May				mid-September	Minton 1972
Texas	March		May-June		November	Blair 1976
Illinois					late October	Cahn 1933
Texas			July	21 – 34		Rose 1978
Texas				13.0 – 35.9		Brattstrom 1965
Wisconsin				12 – 34		Ellner and Karasov 1993
Colorado	Late April				October	Hammerson
western Nebraska	May				October	Converse et al 2002

when less active. Daily activity tends to be minimal at temperature extremes; hot mid-day temperatures are avoided by taking cover under vegetation or in burrows, whereas the warmth of midday is preferred in spring and fall; cold nights are spent in burrows (Ernst and Barbour 1972, Vogt 1981). Converse et al. (2002) presented detailed hourly activity data showing that most activity occurs between 0600 and 1200, with peak activity occurring between 0800 and 1000 and a minor activity burst between 1600 and 1800. As with many desert reptiles, sudden increases in activity are sometimes seen after heavy rains (Rodeck 1949, Vogt 1981, Nenneman personal communication 2006, Redder personal observation). Norris and Zweifel (1950) reported a strong correlation between activity and rainfall in New Mexico.

Ornate box turtles kept in an outdoor enclosure in west Texas from May through September maintained body temperatures in a fairly narrow range (21 to 34 ºC), with the highest temperatures in July (Rose 1978). Clarke (1958) observed activity in Kansas at temperatures between 13 and 39 ºC, with peak activity between 24 and 32 ºC (median temperature = 26 ºC). Legler (1960) found the optimum body temperature for activity in Kansas to be 30 ºC, above which shelter was sought. Brattstrom (1965) observed activity between 13.0 and 35.9 ºC (mean = 28 ºC). Prolonged exposure to temperatures above ca. 40 ºC is lethal.

Ellner and Karasov (1993) compared daily activity and body temperatures of ornate box turtles in Wisconsin and Kansas. In the Wisconsin population, ornate box turtles had a wide range of body temperatures associated with movement (12 to 34 ºC, middle 50 percent of movement activity between 22 and 28 ºC). The mean range of body temperature for basking and burrowing were approximately 4 ºC lower than for Kansas turtles, indicating that the Wisconsin populations had thermal set points for activity significantly lower than Kansan turtles. This suggests that northern turtles can significantly increase the amount of daily time for activity available to them when compared with southern populations (9.6 h vs. 7.6 h). The increase in daily activity probably allows them to compensate for the shorter activity season in Wisconsin (5 months vs. 6.5 months). There is no evidence that Wisconsin females lay a second clutch of eggs, whereas about one-third of Kansan female box turtles do so.

In a multi-year radio-telemetry study of activity in the Sandhills of western Nebraska, Converse et al. (2002) found that the activity season is dominated by inactivity; turtles were classified as inactive in 80 percent of known locations. Significantly, juveniles were inactive at 90 percent of known locations, which may account for the low numbers of juveniles seen in non-telemetric studies.

Habitat

General requirements

The ornate box turtle is primarily a terrestrial turtle that prefers the open grasslands of the Great Plains although it utilizes other adjacent habitat types on occasion. Kuchler (1964) listed seven potential vegetation types (all grasslands) in the areas within Region 2 that have been inhabited by this turtle. Clarke (1958) found them in all habitats at his Kansas site except aquatic settings (i.e., riparian areas, oak-walnut hillside forests, buckbrush-sumac shrubland, prairie). They were most common in the prairies and wooded hillsides. In Kansas, Caldwell and Collins (1981) specified rolling grasslands, with greatest densities “near some kind of break in a grassy area, such as a fence, rocky hillside, ravine, or stream bed.” Also in Kansas, Fitch (1958) reported habitat preferences as “grazed pastureland”, “woodland”, “open fields with undisturbed prairie vegetation”, in order of preference; none were found in “rank weed habitat of recently fallowed fields”. A study of lowland and stream habitat in Colorado found the ornate box turtle only in “Prairie”, “Open Park”, and “Open Cottonwood” categories (Graul and Bissell 1979). Sand dunes and sandy river flood plains also are used in Colorado (Rodeck 1949, Hammerson 1999, Wagner personal communication 2004, Patton personal communication 2005). Timken (1969) suggested that the presence of this species in the southwestern counties of South Dakota was due primarily to a combination of the warm climate and the sandy substrate resulting from the Dust Bowl years that have now become grasslands. However, Platt et al. (2005) noted that specimens from Shannon, Jackson and Todd counties were collected north of the sandhill region.

Ornate box turtles require three types of microhabitat: 1) feeding areas consisting primarily of grassland/prairie habitat, but with some access to free water and occasional use of other habitat types; 2) nesting sites, which are often the same burrows females use for overwintering; 3) resting/thermoregulatory sites (called “forms”) in which partial or total burial in soft soil or litter is used to avoid extreme temperatures and to maintain water balance (Dodd 2001, Converse and Savidge 2003).

Unlike most pond turtle species (family Emydidae), ornate box turtles do not heavily utilize standing or flowing water habitats and do not depend on free water (Degenhardt et al. 1996). However, they occasionally frequent small ponds and streams (Clarke 1950, Blair 1976, Converse 1999, Iverson personal communication 2005). Iverson stressed the importance of small ponds in the western Nebraska Sandhills both for rehydration in the spring after emergence from hibernation and for thermoregulation during hot periods in summer. Despite the substantial percentage of available wetland habitat (24 percent), Doroff and Keith (1990) found that their radiotracked animals avoided water in Wisconsin; prairie habitat was used disproportionately more when compared to availability. In western Nebraska, Costanzo et al. (1995) found ornate box turtles in "rolling mid-grass prairie punctuated by shallow lakes and ephemeral ponds lying in swales among sandhills and occasional clear, spring-fed streams". Converse and Savidge (2003) found that while box turtles in western Nebraska generally prefer upland sites, their selection of particular microhabitats depended on activity level. Open sites were preferred during activity, while shrubby and litter-covered sites were preferred when inactive. Yucca plants were particularly important for thermoregulation. Trail (1995) also mentioned the importance of shrubs for cover and thermoregulation. **Figure 3** illustrates typical sandhills habitat in western Nebraska.

Ornate box turtles typically avoid areas dominated by rock or pebble substrates (Norris and Zweifel 1950) and cultivated areas (Vogt 1981, Doroff and Keith 1990), but Clarke (1958) found them occasionally moving through cultivated fields and Metcalf and Metcalf (1970) regularly saw them in vegetable gardens. Taggart (2006) reported that some ornate box turtles are occasionally seen in croplands and other developed sites.

Autumn activity is common in wooded areas along fence lines and streams (Legler 1960). Metcalf and Metcalf (1970) mentioned the preference for a particular blackberry thicket for hibernation. Many ornate box turtles dig their own burrows and hibernate alone, often after fall precipitation has softened the ground (Ernst and Barbour 1972); others show no hesitation to use burrows excavated by other turtles (Metcalf and Metcalf 1970). Some individuals return to the same burrows for hibernation in successive years (Doroff and Keith 1990, Hay personal communication 2004). Hibernation burrows may be as close as 0.5 m from one another. Mammal burrows (e.g., *Dipodomys*, *Geomys*) are sometimes used for shelter (Rodeck 1949, Vaughn

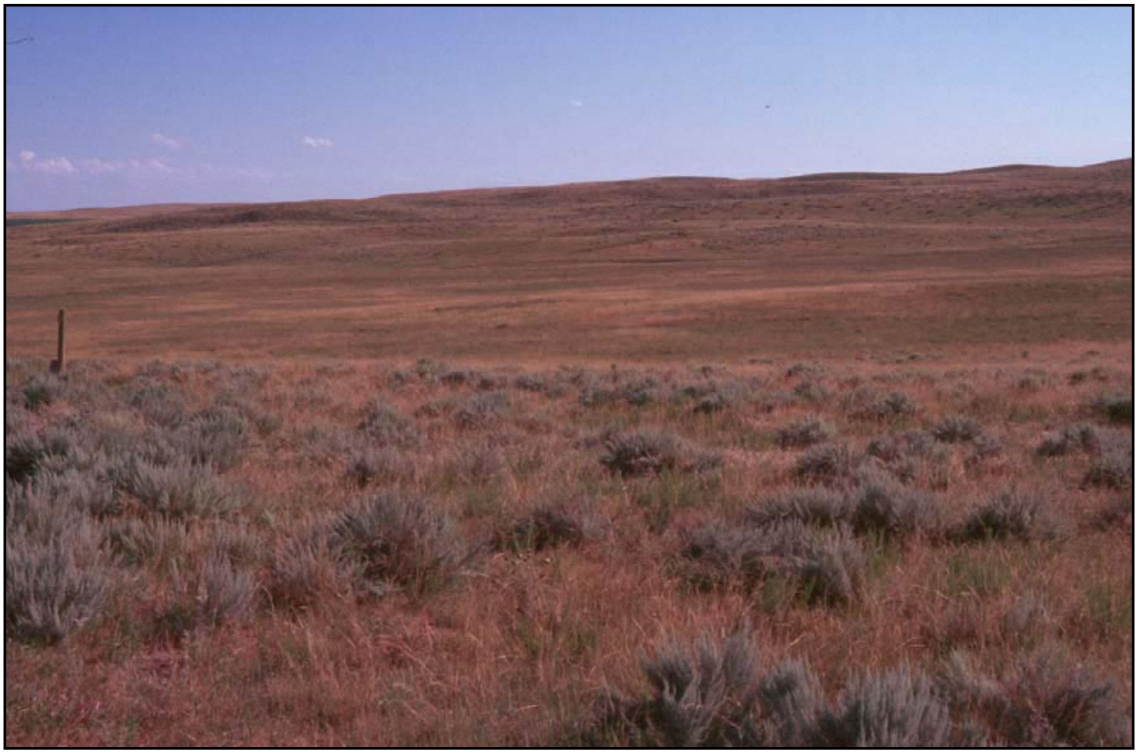

Figure 3. Typical habitat of ornate box turtle in the Nebraska Sandhills. Photograph taken south of the Crescent Lake National Wildlife Refuge in Garden County, Nebraska by A.J. Redder.

1961, Degenhardt et al. 1996) and for hibernation (Norris and Zweifel 1950, Ernst and Barbour 1972). It is not known whether ornate box turtles use prairie dog (*Cynomys*) burrows. Overwintering in water has rarely been observed by this species (Clarke 1956); it is more common for other species of box turtles.

Females dig a nesting cavity, usually away from tree or shrub cover (Vogt 1981). Many turtles, including ornate box turtles, usually avoid ecotones between forests and grasslands, preferring nesting sites in unfragmented habitat (Temple 1987). Preferred nesting sites are "open, well-drained, and have a soft substrate" (Ernst and Barbour 1972, p. 100). Soil texture is an important characteristic because of the propensity of hatchlings and adults to move to varying depths during hibernation depending on soil temperature (Grobman 1990, Costanzo et al. 1995). Soils in nesting areas must be loose and friable, preferably sandy, well-drained, with no bedrock near the surface. Since hatchlings typically burrow deeper into their natal nest cavity to overwinter, suitable soil characteristics must extend deeper than the depths to which the females dig the nests (as deep as 1.8 m; Hammerson 1999).

Nesting and overwintering sites are usually within an individual turtle's home range, so no migration corridor is usually required. However, Iverson (personal communication 2005) observed at his western Nebraska site that after spring emergence, some individuals make extensive movements to small ponds or other open water to rehydrate, thus risking death when roads intersect this path. Individual female box turtles often use the same locations for nesting and overwintering in successive years, so the preservation of these particular sites is especially important for both survival and reproduction (Doroff and Keith 1990, Hay personal communication 2004).

Area requirements

Ornate box turtles had home ranges of approximately 2.2 to 2.3 ha (Fitch 1958, Legler 1960) in Kansas, where no territoriality was observed in the overlapping home ranges. Other home range estimates from Nebraska come from three studies. Claussen et al. (1997) estimated home ranges of box turtles in the Sandhills of Nebraska to range from 0.12 to 0.57 ha, although animals were tracked for very short time periods (1 to 5 days). Trail (1995) generated home ranges of 2.2 to 15.8 ha, based on a small sample size (3). Holy (1995) reported home ranges of 4.6 to 36.4 ha (mean = 13.2 ha in 1993 and 18.8 ha in 1994). In Wisconsin, Doroff and Keith (1990) found considerable variation among individuals (0.2 to 58.1 ha, mean = 8.7 ha); and home ranges for subadults were much smaller (mean = 1.5 ha) than for adults. In Texas, home ranges were roughly circular, with diameters between 67 and 122 m, with very few observations outside of these areas. The mean home range diameter for males (111 m) was slightly larger than for females (94 m) (Blair 1976). These estimates were much smaller than the mean diameter of 169 m (Legler 1960) and 177 m (Fitch 1958) in Kansas turtles. By comparison, ornate box turtles had much larger home range diameters (mean = 276 m) in the much drier and resource-sparse New Mexico desert (Nieuwolt 1996). Judging from these data, the home range of this species varies in response to different levels of available resources (Auffenberg and Iverson 1979).

The measurement of home range size and/or population density estimates can be complicated by various factors:

- ❖ seasonal temperatures and rainfall events that can increase primary productivity and thus reduce the required size of the home range
- ❖ body size of individuals (Doroff and Keith 1990) since young are likely to remain near burrow entrances in their natal areas for years until reaching a size that makes longer movements survivable
- ❖ the time period over which movements were tracked (Claussen et al. 1997), with longer tracking periods more likely to reveal an occasional, but relatively rare, very long movement beyond the edge of the home range (Kiester et al. 1982)
- ❖ the presence of roads, which can result in expanded home ranges because of the reduced costs of locomotion on a smooth, unobstructed surface (Nieuwolt 1996)
- ❖ the statistical method used to calculate home range
- ❖ the difficulties involved in conducting a complete census of even small areas, due to a combination of movement and burrowing behavior, and perhaps the presence of transients (Iverson personal communication 2005).

Homing behavior occurs in ornate box turtles (Legler 1960, Germano 1999b) and might be useful for returning to home ranges of good habitat quality situated in patchy landscapes dominated by lower quality habitat. However, the small proportion of turtles that successfully return to their original home ranges (31.3 percent in Metcalf and Metcalf 1970, 1979) and the short distances traveled by most animals (less than 1 km) provide evidence that some individuals are more adept than others at homing, and that there are limits to the propensity to home. The timing of translocation may affect homing since animals translocated in autumn tend to stay for hibernation and then return to previous home ranges the following spring. Turtles appear to recognize and remember landmarks and the location of food sources and shelter within and near their home ranges (see maps in Metcalf and Metcalf 1970).

There is as yet no evidence of long-distance migration or dispersal by ornate box turtles, but some dispersal of juveniles and sub-adults probably occurs. Some animals, probably males, could be frequent or permanent transients as part of a mate search strategy (Duvall et al. 1985); however, this has not been documented in turtles. Transience by males would have important effects on gene flow and metapopulation dynamics, as well as the population structure of local populations. Large proportions of translocated *Terrapene carolina carolina* emigrated from large preserve areas, demonstrating that box turtles are capable of significant movements (Kiester et al. 1982, Belzer 2000).

Food habits

Ornate box turtles appear to have no specific food preferences and will consume locally and temporally abundant items whenever encountered; they are omnivorous but opportunistic. Thus reports from different localities vary widely. They eat a variety of plants such as grasses, blackberries (*Rubus* spp.), ground cherries, and prickly pear (*Opuntia*) in Wisconsin, as well as various insects and invertebrates, such as caterpillars, grasshoppers, beetles, and earthworms (Vogt 1981). In Kansas, Metcalf and Metcalf (1970, 1979) listed mulberries, blueberries, strawberries, cantaloupe, tomatoes, green beans, dandelions, fish, and carrion. Consumption of five types of carrion has been observed: mammals, birds, amphibians, snakes (*Thamnophis*) (Kolbe 1998), and even other box turtles (Legler 1960). Eggs of ground-nesting birds are occasionally eaten (Legler (1960), as are persimmons and insects associated with cow dung (Blair 1976, Fitch 2006), mushrooms (Moore 1943), and the flowers of a pincushion cactus (*Coryphantha vivipara*) in Kansas (Thomasson 1980). Cahn (1937) reported a strictly vegetarian diet in Illinois, with no trace of insects or other animal remains. Ornate box turtles readily captured *Scaphiopus* tadpoles in captivity, suggesting that tadpoles might form a significant part of their diet when turtles find them in temporary pools after thunderstorms (Norris and Zweifel 1950). Metamorphosed *Scaphiopus* were not acceptable prey because of the toxicity of their skin secretions. In captivity, ornate box turtles also have consumed a horned lizard (*Phrynosoma*) (Eaton 1947) and baby domestic chickens (Black 1987). Ernst and Barbour (1972) state that insects make up 90 percent of their prey, with dung beetles being a very important prey item. Fitch (2006) also pointed out the significance of dung beetles. The consumption of small stones, gravel, and soil by ornate box turtles has also been observed (Legler 1960, Skorepa 1966, Kramer 1973) although the function of geophagy is unknown (Sokol 1971). Food is located by sight (Degenhardt et al. 1996) and possibly by other cues (e.g., color, motion, olfaction) (Dodd 2001).

Breeding biology

Breeding phenology

Rapid follicular growth begins after emergence from hibernation and continues until ovulation and the beginning of the beginning of the ovarian cycle in midsummer. Spermatogenesis begins in May, peaks in September, and is completed in October. Copulation can occur any time during the active season. Sperm are stored over the winter and eggs are fertilized the following summer (Legler 1960). Breeding phenology and clutch-related life history parameters for ornate box turtles are summarized in **Table 2**.

Nesting is generally in the spring or early summer with hatching in the fall. Females can retain eggs for as long as 50 days (Nieuwolt 1996); this allows oviposition to occur under relatively optimal conditions. Oviposition occurs in the evening or at night (Doroff and Keith 1990). Egg size is inversely proportional to clutch size (Caldwell and Collins 1981). See **Table 3** for egg size data for ornate box turtles.

Duration of incubation varies strongly with temperature, as demonstrated by Legler (1960). Under laboratory conditions, he found that eggs had mean incubation times of 59 days at 33 ºC, 70 days at 28 ºC, and 125 days at 24 ºC. Hatching usually occurs in the fall, but it may be delayed until spring if nest conditions are dry (Caldwell and Collins 1981). Eggs

Table 2. Summary of breeding phenology for the ornate box turtle at various locations across its range.

Location	Copulation	Nesting	Incubation Period (days)	Hatching	Citations
Wisconsin	May 28 – Sept 6	May-June	79 - 87		Vogt 1981, Temple 1987, Doroff and Keith 1990
Texas	Apr 5 – Oct 13				Blair 1976
Kansas			65	fall	Caldwell and Collins 1981
Indiana			59 - 70		Minton 1972, Collins 1993, Vogt 1981
Kansas		June			Collins 1993
Kansas	May	June			Brumwell 1940

Table 3. Egg size data for the ornate box turtle.

Location	Egg Length	Egg Width	Egg Weight	n	Citations
Kansas	36.1 mm (31.3-40.9)	21.7 mm (20.0-26.3)	10.1 g (8.0-14.3)	42	Caldwell and Collins 1981
New Mexico	31-41 mm	20-26 mm		?	Nieuwolt 1993

are also moisture-sensitive and can die from desiccation (Belzer 2002).

Hatchlings range from 28.8 to 37 mm (Marr 1944, Minton 1972), and they are about 7 g in body mass. Maximum growth occurs in early spring-emerging hatchlings, which are usually those that overwinter in the nest as eggs (Ernst and Barbour 1972). High precipitation and correspondingly high grasshopper numbers are associated with rapid growth of hatchlings (Legler 1960).

Breeding behavior

Successful mate searching by male eastern box turtles relies heavily on vision, and especially on detection of motion by females, rather than other sensory modes (Belzer 2000). Olfactory capabilities apparently do not allow for long-distance chemosensory mate searching. As a consequence, males must be in relatively close physical proximity to potential mates. Limited mate detection capability implies that mating opportunities might be very limited for all members of a population, although this problem may be ameliorated by sperm storage. It is not known if limited mating opportunities contribute to the low percentage of females nesting annually in the Wisconsin populations studied by Doroff and Keith (1990).

Males display agonistic behavior (e.g., shell bumping, attempted biting) while in pursuit of a female (Nieuwolt 1996), but it is unclear if these behaviors affect reproductive success. There is no evidence that males keep harems, guard recently mated females, or exhibit territoriality as a means of increasing mating opportunities. Strongly philopatric males may be limited to mating opportunities that occur on overlapping portions of their home ranges (Stickel 1978). The male initiates copulation. He holds the female with the recurved inner claw on the hind feet while inserting his feet between her carapace and plastron to prevent her from excluding him; coitus may last for as long as 4 hours (Vogt 1981).

Females can store sperm for periods of at least the duration of a winter following mating (Legler 1960) and perhaps for as long as several years. However, sperm fertility probably declines with time since insemination. Female choice may play a part in courtship and mating behavior (Brumwell 1940). Both males and females have multiple partners, both within and across years (Blair 1976).

There are no reports of territoriality or social structure in ornate box turtles beyond the limitations on mating outlined above. However, they may be aggressive toward conspecifics when in close proximity during feeding.

Population demography

Life history parameters

In Kansas, male ornate box turtles mature at 8 to 9 years of age at a plastron length (PL) of 10 cm, whereas females mature at 10 to 11 years at 11 cm PL (Legler 1960). In Oklahoma, males mature sexually at 5 years and 10 cm curved carapace length (CCL), and females mature at 8 years and 12.8 cm CCL in captive animals held under natural conditions (St. Clair 1998).

In Colorado, the age of first reproduction for females is probably no earlier than 11 years of age (Hammerson 1999). The smallest copulating female in an Austin, Texas population was 97 mm carapace length (CL) where the largest females were less than 114 mm CL (Blair 1976). Blair also found a large range of annual growth increments, from 1.0 to 15.5 mm per year, which he explained as the result of confusing major and minor growth rings and the undependable formation of growth rings after sexual maturity. Converse (1999) estimated that females older than 13 winters were reproductive adults.

The lifespan of ornate box turtles can be at least 32 years and could be as long as 37 years (Blair 1976, Christiansen et al. 2004). Ornate box turtle populations in Texas may undergo complete turnover every 32 years (Blair 1976). Metcalf and Metcalf (1985) presented data from a long-term study of 115 turtles in Kansas largely in agreement with Blair: a maximum age in the low 30's with a population turnover within that span of time.

Reported sex ratios suggest that females predominate: 0.58 males:1 female (or 37:63) in Kansas (Legler 1960), 0.7:1 in Illinois (Bowen et al. 2004), 0.64:1 in Wisconsin (Doroff and Keith 1990), and 0.58: 1 (Converse 1999) and 0.51:1 in western Nebraska (Converse et al. 2002). Recent data from Wisconsin populations suggest that sex ratios are approximately even (Hay personal communication 2004). Sex determination in turtles is temperature-dependent, with females usually resulting from incubation temperatures above 29 ºC (Bull 1980, Packard and Packard 1986). The temperature at which differentiation occurs in ornate box turtles is unknown, but eggs incubated at 29 ºC produce 100 percent females (Packard et al. 1985). Observed box turtle sex ratios probably vary among years because of the interacting effects of weather, environmental temperature and humidity, nest site location and depth, and oviposition dates (Vogt and Bull 1982) and recruitment. Primary sex ratios and other biological information on young turtles have been difficult to obtain because hatchlings and juveniles are usually found in low numbers. Rodeck (1949) speculated that the low numbers of juveniles seen in the wild is due to the tendency of turtles to spend their early years underground in rodent burrows.

Fecundity, survivorship, and recruitment

Ornate box turtle females are limited in their annual reproductive output by their small size, energy intake limitations imposed by primary production of occupied habitat, and life history constraints (i.e., long lifespan coupled with late age of first reproduction). Females deposit between two and eight eggs per clutch throughout their range (**Table 4**). In Kansas, two clutches per year are possible in a third of the population (Legler 1960). By contrast, in Wisconsin only 50 to 63 percent of females deposited eggs in a given year (Doroff and Keith 1990). Since sperm storage is possible in this species, this disparity between localities in the number of breeding females and the number of clutches per year per female is likely due to energy intake and/or thermoregulatory limitations (Redder 1994).

Survivorship and recruitment are limited by a series of factors: infertility and low rate of embryonic development, predation, and environmental stresses. Doroff and Keith (1990) reported only 42 to 58 percent hatching success in Wisconsin. In Kansas, 75 percent of eggs were fertile, and 80 percent of those eggs hatched (Legler 1960). In the congeneric *Terrapene carolina carolina*, clutch size ranged from one to seven, averaging four eggs (n = 42) (Belzer 2000). Belzer also reported a very low degree of embryonic development (six of 30) of *in situ* eggs that were shielded from predators. Only 8 percent of eggs that did not receive supplemental watering during a drought showed signs of successful development.

Table 4. Clutch-related life history parameters for the ornate box turtle at various locations across its range.

Location	Clutch Size Range (mn) [n]	# Clutches / Yr	% Hatching Success	Citations
Wisconsin	(3.5-4.1)	0-1	42-58	Vogt 1981, Temple 1987, Doroff and Keith 1990
Texas	Apr 5 - Oct 13			Blair 1976
Kansas	2 - 8 (4.7) [23]		65	Caldwell and Collins 1981)
Indiana			59 - 70	Minton 1972
Kansas	2-6	2	80	Legler 1960
Pennsylvania	1 - 7 (4) [42]		20	Belzer 2000 (for congeneric T. c. carolina)

Survivorship in turtles fits a Type III survivorship curve (Gotelli 1995) in which mortality decreases with age (Iverson 1991). The following survivorship estimates for ornate box turtles are annual estimates for adults:

- 0.816 (95% CI = 0.69 to 0.94) for females, and 0.813 (95% CI = 0.70 to 0.93) for males in disturbed habitat in Wisconsin (Doroff and Keith 1990),
- 0.81 to 0.96 in Texas (Blair 1976),
- 0.83 in disturbed habitat in Kansas (Metcalf and Metcalf 1985),
- 0.99 (95% CI = 0.87 to 1.00) for females, and 0.90 (95% CI = 0.75 to 1.00) for males in disturbed habitat in Illinois (Bowen et al. 2004),
- 0.932 (SE = 0.014) for females, and 0.883 (SE = 0.021) for males in undisturbed habitat in western Nebraska (Converse et al. 2005).

These values are typical for adult and sub-adult terrestrial turtles (Iverson 1991, Heppell 1998).

Doroff and Keith (1990) provided annual survivorship estimates by sex for 10 years from their severely disturbed Wisconsin sites. Using those data and the optimistic assumption that females were producing the maximum number of female offspring observed in clutches on their site, their estimates of juvenile and sub-adult survival rates that would be necessary for a stable population were higher than actually observed adult survival rates. They also calculated that the observed rate of survival among adults (0.81) was not sufficient for a stable or increasing population. As a point of reference, Congdon et al. (1993) estimated that a minimum annual juvenile survivorship of 0.6 is needed to sustain Blanding's turtle (*Emydoidea blandingii*) populations. Doroff and Keith attributed the low survivorship to recent rapid habitat destruction and other serious anthropocentric mortality factors.

Converse et al. (2005) also presented annual adult apparent survivorship estimates by sex for 10 intervals between 1981 – 1999 from their relatively undisturbed site in western Nebraska. Their data showed considerable variation in annual survival and the standard errors for those estimates. Their models indicated that minimum winter temperature was the only significant climatic factor affecting survival.

Metcalf and Metcalf (1985) estimated overall mortality at 19.1 percent for a sample of 115 ornate box turtles that they tracked for more than 15 years. Twenty-seven percent of the fatalities resulted from human action.

In a recent study of an ornate box turtle population in isolated fragmented habitat in Illinois, Bowen et al. (2004) reported the highest known survivorship estimates (see above) and estimated annual recruitment at 1.02 (SE = 0.06). A similarly positive assessment of population growth rate, $\lambda = 1.006$ (SE = 0.065), was reported by Converse et al. (2005). Using stochastic simulations of λ and its variability, they estimated that the mean population growth rate would be 12 percent over a 20-year period. However, the ranked results of their simulations revealed that 58 percent of the simulations produced negative population changes. Bowen et al. (2004) cautioned that despite apparently positive estimates, these populations are still likely to be sensitive to the loss of reproductive females (see matrix model results below). Small population size might still endanger such apparently growing populations. They also mention that the lower limit of their estimates puts these populations in a range close to those of endangered populations, such as those studied by Doroff and Keith (1990). They also caution that their estimates of variation in these statistics are underestimates.

The primary defense of box turtles is to withdraw the head and feet and tightly close the hinged plastron. This is not possible for hatchlings and juveniles (Caldwell and Collins 1981) until their fourth year and probably affects the survival of young (Norris and Zweifel 1950). Adult survivorship rates are not attained until 8 to 10 years old when the shell completely hardens.

It should be noted that all of the preceding survivorship estimates resulted from mark-recapture studies, which tend to underestimate survival because some marked animals are likely to leave the study area. The most reliable survivorship estimates result from radio-telemetry studies. Unfortunately, the only radio-telemetry studies on ornate box turtles completed to date examined only home range, movement, and habitat selection.

Summary of matrix population demography models

We used the matrix modeling techniques of McDonald and Caswell (1993) and Caswell (2000), together with the basic life history parameters from Ernst et al. (1994) to construct a model of ornate box turtle demography. Two types of stage-specific parameters are presented: estimates of the sensitivity of the population growth rate, λ, to *absolute* changes in the vital rates at the various stages in the life cycle; and estimates of the elasticity (sensitivity of λ to *proportional* changes in the vital rates) for those life history stages. Calculation of sensitivities and elasticities allows managers to assess the relative importance of reproduction and survival for the various life history stages. Managers can then target management actions toward those transitions most likely to have a significant impact on population dynamics or avoid actions that would adversely affect a particularly sensitive stage. We extended this technique by performing stochastic simulations of changes to reproduction and survival rates at various life stages to reveal the possible effects of these changes on long-term population persistence. The result is a range of possible outcomes for assessing the viability of populations. In this way, the life history stages that most critically affect population persistence can be modeled. We present the details of the modeling procedures in **Appendix A**.

1) The major conclusion from the sensitivity and elasticity analyses is that *protection of older reproductive females is the key to population growth rate, λ, and to long-term viability.* Further analyses suggest that ornate box turtles are most susceptible to habitat degradation and other sources of mortality that affect the survival of older reproductive females.

2) In an ornate box turtle population with a stable stage distribution, eggs represent 41 percent of the population, juvenile stages represent 42 percent, and adult stages represent 18 percent. The cohort generation time for ornate box turtles is 29.2 years (SD = 19.5 years). The mean age of females in the final mixed-age stage (consisting of all reproductive females between the 4th-5th reproductive year and the end of life) is 33.0 years (SD = 19.5 years).

3) *Altering only the "oldest adult" survival rate had a much more dramatic effect on λ than did altering the entire set of fertility transitions*. As an example of the contrasting effects of varying fertilities versus survival rates, the stochastic modeling of alternative scenarios revealed that the median ending population size due to changing fertilities was essentially the same as the starting size. In contrast, varying the survival of the oldest females resulted in a median ending size of only half the starting size. λ was much more sensitive and elastic to changes in the survival of the oldest females than it was to the entire set of fertilities. *These results suggest that populations of ornate box turtles are relatively tolerant of stochastic fluctuations in egg production (due, for example, to annual climatic change or to human disturbance) but extremely vulnerable to variations in the survival of adult females*.

4) Large-effect stochasticity has a negative effect on population dynamics. The magnitude of fluctuation has a potentially large impact on the detrimental effects of stochasticity. Thus, decreasing the magnitude of fluctuation also decreased the severity of the negative impacts. The number of extinctions dropped by 89 percent when the magnitude of fluctuation was halved.

5) To refine this matrix demographic analysis, the survival rates, especially those of older reproductive females, are the data elements that most merit careful monitoring.

A word of caution about the model results: the model assumes a stable stage distribution in which the proportions in the (st)age classes do not vary over time. This is unlikely to be met in populations that have been seriously impacted by external threats. In particular, the estimate that reproductive females should comprise approximately 18 percent of the overall female population could be an overestimate if collection or mortality have differentially affected adult females, as is likely the case.

Density estimates

The scientific literature provides few estimates of abundance in terms of population size estimates for particular areas. Even in areas that have been intensively studied over many years with mark-recapture methods, density estimates are unreliable because new, unmarked turtles appear often (Dodd 2001, Iverson personal communication 2005). Various difficulties with sampling and encounter probabilities (e.g., sex differences in activity, the presence of transients, reliability of marking techniques, the survey methods employed) result in unreliable and incommensurate density and population size estimates (Dodd 2001). Given those caveats, **Table 5** summarizes density estimates reported in the literature. These are

Table 5. Density estimates for ornate box turtle populations at various locations across its range.

Location	Density Estimate (per ha)	Citation
Kansas	5.8 - 13.9	Legler 1960
Texas	4.5	Rose 1978
Texas	0.53 - 0.89	Blair 1976
Kansas	0.5 (statewide)	Collins 1993
Wisconsin	2.9 - 5.0	Doroff and Keith 1990

comparable with densities of other box turtle species (summarized in Dodd 2001). Density estimates on the order of those reported by Legler (1960) could reasonably be interpreted as indicating that ornate box turtles are "common" to "abundant" at his Kansas site. However, because of differences in habitat quality and other factors relevant to density estimates made at various sites, such qualitative descriptions applied to other sites will necessarily be imprecise and should be interpreted cautiously. Truly comparable density estimates and home range size estimates (see below) will have to rely on intensive radio-telemetry studies in the future.

Metapopulation dynamics

Nothing is known about the metapopulation dynamics of ornate box turtles, but information about other aspects of their life history gives some hints. As discussed above, box turtles have a significant homing ability and tend to maintain the same home ranges and hibernation and nesting sites over their extended lifespans. Movements outside those home ranges appear to be uncommon and may not be extensive, but the use of sun clocks by turtles makes long-distance straight-line navigation possible (Auffenberg and Iverson 1979). Kiester et al. (1982) have found that males (*Terrapene carolina triunguis*) can make relatively long uni-directional movements many multiples of the size of the home range diameter. The frequency of occurrence of transient *T. o. ornata* individuals is currently unknown, but even a few in a population may have an important role in gene flow between populations.

Doroff and Keith (1990) estimated that the minimum size for a prairie reserve in Wisconsin necessary for a small box turtle population would be 100 ha of roadless habitat, assuming no human disturbance. In recent work on a relict population of ornate box turtles in Illinois, Kuo and Janzen (2004) suggested that a minimum population size of 700 turtles would be necessary to maintain a level of 90 percent of the genetic diversity currently found in that population. In their study of road mortality, Gibbs and Shriver (2002) concluded that, given the generally low densities of land turtles (0.5 to 2 per ha as estimated by Iverson 1982), sizeable populations (500 to 1000 individuals) of land turtle species would need at least 1000 ha of suitable, unfragmented habitat for long-term persistence.

Community ecology

Predators and competitors

Raptors, crows, domestic cats, ravens, canids (i.e., foxes, coyotes, domestic dogs), opossums, raccoons, skunks (*Mephitis mephitis*), snakes, and even adult ornate box turtles will prey on young ornate box turtles (Legler 1960, Ernst and Barbour 1972, Vogt 1981). Raccoons (*Procyon lotor*) are particularly common predators in disturbed habitats where they are attracted by garbage and other refuse (Garber and Berger 1995, Line 1998). Doroff and Keith (1990) noted the destruction of a nest by a prairie vole (*Microtus ochrogaster*). Germano (1999a) recorded attempted predation by a turkey vulture (*Carthartes aura*). Box turtle remains have been found in bald eagle (*Haliaeetus leucocephalus*) nests, but the absence of fresh flesh suggested that they were taken as carrion (Clark 1982). The high proportion of injured animals found in some populations (Metcalf and Metcalf 1970, Rose 1977, Line 1998) suggests many encounters with predators. Defensive behaviors beyond retreat inside the shell are not well developed although occasional individuals will bite or defecate when handled. Cahn (1937) stated that the ornate box turtle "seems to have complete and absolute control of its temper and to have developed a completely fatalistic attitude."

Because of their omnivorous and opportunistic feeding habits, ornate box turtles probably face little direct competition for food. However, because ornate box turtles so closely depend on grasslands, cattle could be considered competitors if overgrazing occurs. Berry and Jones (2004) mentioned that desert tortoises (*Gopherus agassizii*) rely on certain plants with a high PEP (potassium excretion potential) index to survive, even if they are able to consume these plants only in wet years with abundant primary production. It is not known if ornate box turtles have similar dietary requirements, but if they do, cattle would be competitors for that forage.

The nesting requirements of ornate box turtles do not appear to conflict with those of other species.

Parasites and disease

Until recently, knowledge of diseases and parasites that affected terrestrial turtles and tortoises has been minimal. Most known instances were not harmful to box turtles (Bilsing and Eads 1947, Metcalf and Metcalf 1979, Collins 1993). However, flies of the genus *Sarcophaga* have been known to infest the limbs of ornate box turtles (Rodeck 1949), sometimes to the point of severely inhibiting movement, resulting in death by starvation (Rainey 1953).

It is now known that a variety of respiratory tract, infectious, metabolic, and shell diseases affect the desert tortoise and other tortoises and terrestrial turtles (Berry and Jones 2004, Jacobson and Johnson 2005), some of which are present in both captive and wild turtle populations. The extent of infection and mortality in wild populations of turtles is less well known, but Berry and Jones (2004) reported high incidence of mortality in wild desert tortoise populations due to *Mycoplasma agassizii*, a bacterium known to be one of the causes of symptoms of upper respiratory tract disease (URTD). URTD is spread by direct contact, and outbreaks in wild populations are strongly suspected of having originated in captive populations and spread by the escape or release of infected captives. Berry and Jones (2004) also mention that herpes virus is present in captive desert tortoises and has the potential for lethal infection, as is known from other vertebrate species. Jacobson and Johnson (2005) found that iridovirus infections were linked with four mass mortality events (Georgia 1992, Texas 1998, Pennsylvania 2003, Florida 2004) in turtles. They also documented chronic bacterial pneumonia and URTD infections.

Shell disease has also been found in wild populations of desert tortoises, but its causes are not clear. Shell diseases may make turtles more susceptible to other infections (Berry and Jones 2004). Nutritional deficiencies may play a role in increasing the susceptibility of turtles to these various diseases, especially shell diseases (Berry and Jones 2004).

Symbiotic and mutualistic interactions

Parker (1982) reported repeated intensive foraging by a box turtle under the nests of Mississippi kites (*Ictinia mississippiensis*) where high density of prey “litter” from the nests was dropped, suggesting possible commensalism. The preponderance of dung beetles in the diet of ornate box turtles, and the frequent signs of dung pile disturbance by turtles, suggests that they might rely on the presence of large ungulates (i.e., cattle now, and possibly bison before their disappearance from the High Plains). Fitch (2006) reported the gradual disappearance of ornate box turtles on originally grazed pasture because the removal of cattle eliminated both the grazing pressure that kept the pasture free of tall, dense vegetation, but also the absence of cattle dung eliminated the concentrated sources of dung beetles on which the turtles fed heavily. Thus, at least on the Kansas site that Fitch has monitored for over five decades, the presence of cattle was a definite advantage for ornate box turtles. This may not be true in other grazed areas where succession after the cessation of grazing would not necessarily result in wooded areas, as in Fitch’s Kansas site.

Grassland habitats are structured by the burrowing activities of rodents in ways that are probably essential to ornate box turtles. Hatchlings and juveniles probably rely on burrows for shelter and food for the first few years of life; this may explain why hatchlings and subadults are rarely seen. When available, *Dipodomys* and *Geomys* burrows are frequently used for shelter by adults as well (Vaughn 1961, Degenhardt et al. 1996, Nieuwolt 1996). Use of prairie dog burrows by ornate box turtles is possible where towns still exist, but actual use by ornate box turtles has not been documented. The distribution, behavior, and population status of these mammals could significantly influence the distribution and status of ornate box turtles, especially for the successful recruitment of young.

Envirogram for ornate box turtle

Andrewartha and Birch (1984) recommended the construction of an envirogram as a graphical summary of the factors affecting turtle survival and reproduction, both positively (Resources) and negatively (Malentities). We present such an envirogram in **Appendix B**.

CONSERVATION OF THE ORNATE BOX TURTLE

Threats

Intrinsic vulnerability and life history constraints

The fundamental vulnerability of the ornate box turtle is, ironically, its long lifespan with associated life history traits. As is typical of long-lived species, ornate box turtle populations are intrinsically vulnerable due to a combination of delayed age of first reproduction, low reproductive output, and high nesting and juvenile mortality. In western and northern populations, females may not first reproduce until they are 10 or 11 years of age (Doroff and Keith 1990, Converse 1999, Hammerson 1999). Resource limitations appear to limit the proportion of reproductive age females who actually lay eggs in a given season to as little as half the population (Doroff and Keith 1990). The few females who do reproduce have low annual reproductive potential: two to eight eggs per clutch, and no more than one clutch per season. Thus each reproductively active female must reproduce repeatedly over a period of many years merely to ensure her own replacement in the population, as well as to provide for the high losses to recruitment due to low juvenile survival. High nesting and juvenile mortality result in very few turtles reaching reproductive age. Thus every female who reaches reproductive age becomes essential for population viability.

This is confirmed by our matrix population model, which shows that the greatest impact to viability results from increased mortality at the stage of reproductive-age females. Since they comprise less than 20 percent of the total female population (see matrix model results above), the loss of even a few older females during their reproductive years combined with the low egg and hatchling survival rates can result in populations that appear to be stable and viable (i.e., adults continue to be observed), but that in fact are not putting enough recruits into the population to make up for the reproductive potential lost with those females. This situation may not be apparent except with careful, long-term demographic research. It is possible that the current, inadequate level of monitoring and population research, which is essentially presence/not detected data, would not reveal a potentially very serious demographic disaster in the making in these turtle populations.

Another potential intrinsic vulnerability is due to temperature-dependent sex determination in this species (Dodd 2001). Managers could be faced with a variety of problems resulting from extreme environmental conditions, especially temperature extremes during incubation, that skew sex ratios of hatchlings. Climatic effects of drought, extreme winter temperatures during successive winters, or sudden climate change are all unpredictable factors that could result in successive unisex cohorts of animals in which reproduction is minimal or non-existent. On a regional scale, if changes in climatic conditions are sufficiently widespread relative to the range of this species, single-sex cohorts might result over large areas and across successive years, resulting in a prolonged, widespread episode of reduced recruitment. This would be an especially serious prospect for small, isolated populations in which mating opportunities would already be limited. On a landscape scale, spatial variation in soil temperatures of relatively nearby nesting sites could result in a mosaic of single-sex clutches, which when combined with limited mate search capabilities (Belzer 2000), would diminish recruitment.

Another potential aspect of intrinsic vulnerability of ornate box turtles is the tendency of individuals to establish home ranges that are maintained in successive years. While this highly conservative behavior probably enhances survival and reproduction in various ways, this direct link of individual turtles to specific locations also limits their mating opportunities and probably has meta-population-level effects on gene flow and population viability. Small, localized populations with little likelihood of interaction with neighboring populations are more likely to be subject to stochastic factors as shown by our matrix model.

More significantly in the short-term, philopatry subjects them to site-specific extrinsic threats while reducing the likelihood of migration in response to those threats. The effects on fitness for individuals forced to leave long-occupied territories are unstudied, but likely to be detrimental.

Extrinsic threats

Most extrinsic threats to ornate box turtle populations across their range are direct results of human actions. Most natural mortality occurs in early years whereas most anthropocentric mortality occurs in older, reproductively active life stages.

Non-anthropocentric threats are often exacerbated by human actions.

Agriculture

Certainly the massive conversion of millions of hectares of Great Plains habitats from grasslands to farms and ranches has been the greatest single factor affecting ornate box turtle populations over the past century across most of their range in the West. To the extent that such conversion continues, and along with it the inevitable correlates of highway construction and increased traffic, invasive weeds, and fragmentation of habitat, massive habitat change is probably the most significant factor affecting current and future distribution and abundance. Areas of undisturbed prairie are smaller and more isolated, with fewer potential corridors between them than was the case a century ago. Although serious, the other extrinsic threats discussed below are subsidiary to this historic and ongoing threat.

Disturbance to native, unplowed prairie is a primary, long-term, region-wide threat to ornate box turtle populations. The degree of destruction of the various grassland habitats inhabited by ornate box turtles has been severe. Grasslands west of the Mississippi River decreased in area by an annual average of 2.6 million acres between 1850 and 1950 (World Wildlife Fund 2006). Estimates of the extent of loss of grassland habitat types across the Great Plains since 1830 range from 82 to 99.9 percent of tallgrass prairie to 77 percent of mixed-grass prairie in states in Region 2 inhabited by box turtles (Samson and Knopf 1994). Grassland types that have been affected most severely are those found in the eastern part of this turtle's range where human impacts have been greatest, in particular the tallgrass prairie types. Only shortgrass prairie and, to some extent, mixed-grass prairie remain in public ownership. These remnants are primarily on national grasslands managed by the USFS.

Not only is habitat being lost, but remaining habitat is becoming increasingly fragmented, resulting in physical isolation of surviving populations and increased mortality from most of the factors causing the fragmentation. Isolated populations are more vulnerable to stochastic events, whether resulting from natural or demographic processes, than are contiguous populations. If habitat patches are too small or isolated, populations will be extirpated over time, unless immigration rates are high. Animals moving between isolated habitat patches also are exposed to increased probability of collection, predation, or exposure to unfavorable conditions.

Fragmentation results in an increase in ecotonal areas, leading to sharp demarcations between habitats. Turtles that nest close to habitat edges suffer increased levels of nest predation, similar to the increases in predation observed in nesting birds in such habitats (Wilcox 1985, Johnson and Temple 1986, Temple 1987). The edge mortality effect results from an increase in the number of potential turtle nest predators (e.g., raccoons) near habitat edges.

Prevalent human-related activities contributing to edge generation are the encroachment of agriculture on previously undisturbed prairie and the construction of roads and other public rights-of-way through turtle habitat. The effects of fragmentation are on at least the same magnitude as the degree of destruction of grassland habitats, and therefore pose serious threats to turtles. A map by EarthTrends (2006) illustrates extensive fragmentation of Great Plains grasslands by roads alone and that the predominant grassland patch size in the western Great Plains has contracted over the last century. In the absence of roads, 90 percent of habitat blocks exceeded 10,000 km^2 in area. With roads present, none of the blocks were greater than 10,000 km^2 in area, and 70 percent were reduced to between 100 and 1,000 km^2 in area. Unfortunately, we are unaware of any studies that would allow even basic estimation of the effects of fragmentation on turtle populations at scales greater than the very local scale of the research cited above. Clearly, habitat fragmentation is a significant threat to turtle populations in the Great Plains and nationwide.

Other human structures and activities related to fragmentation are harmful to ornate box turtles. Turtles have become entangled in wire fences and died due to exposure (Blair 1976). Box turtles have drowned in stock tanks where the wind can form drifts of sand on the lee side of the tank, providing access to the tank (Iverson personal communication 2005). Caldwell and Collins (1981) reported trampling by cattle to be an important cause of death. Mowing grass in turtle habitat and using other farm machinery can also be fatal (Metcalf and Metcalf 1985, Doroff and Keith 1990, Dodd 2001, Hay personal communication 2004); however, mortality of turtles from mowing can be reduced (see Management tools below). Sink holes and other pits from which turtles cannot climb out are a common cause of turtle mortality generally (Auffenberg and Iverson (1979).

Development

Urban sprawl (i.e., housing developments, commercial construction, civic spaces, industrial parks, roads) has become an ever-increasing encroachment on western landscapes in recent decades (Dunay et al. 2000). Like agriculture, sprawl contributes to habitat loss, habitat fragmentation, and increased road mortality. It also exacerbates other threats, by increasing the likelihood of collection, mowing, biocide exposure, and infection of native turtles by disease transmitted from captive turtles released into the wild.

Sometimes the mere presence of humans using an area for recreational purposes, without any obviously significant habitat alteration, is correlated with terrestrial turtle declines. Garber and Burger (1995) documented the decline of wood turtle (*Glyptemys insculpta*) populations over a 20-year period after their previously undisturbed site was opened to human recreation. The predominant mechanism causing the decline was unknown, but these authors listed five possibilities: removal, roadkill, handling by recreationists, disturbance by dogs, and increased predation, due to an increase in the abundance of predators, particularly crows and raccoons, that are attracted to the increased food waste.

Road mortality

Over the last 50 years, various authors have commented on the destruction of large numbers of turtles on roads (Rodeck 1949, Legler 1960, Ernst and Barbour 1972, Blair 1976, Ballinger et al. 1979, Doroff and Keith 1990, Collins 1993, Mackessy personal communication 2005), to the point where roadkill is clearly a major cause of mortality (Hammerson 1999, Hay personal communication 2004, Converse personal communication 2005, Iverson personal communication 2005). Highway mortality was noted as early as the 1940's in Nebraska (Hudson 1942).

For various reasons, road mortality is often concentrated in specific areas. Box turtles in sandhills habitats are likely to cross and recross roads during spring movements from a hibernaculum to the nearest body of reliably occurring standing water (Iverson personal communication 2005). The proximity of roads to occupied habitat occurs in some areas, such as along the South Platte River (Wagner personal communication 2003, Jackson personal communication 2006), on specific lengths of highway in the Nebraska panhandle (Redder unpublished data), along the Loup River in central Nebraska (Eddy personal communication 2004), and in Cheyenne County, Colorado (Mackessy personal communication 2005). During recent box turtle surveys in western Nebraska, local residents invariably referred to the locations of extant populations by citing stretches of highway where turtle mortality was severe (Redder unpublished data).

While no numerical estimates exist for the effects of roads on box turtle mortality, a very conservative estimate of the effects of roads on desert tortoises in the Mojave Desert suggested that one tortoise death per year occurred every 3.3 km of highway (Boarman 2004). Estimates of roadkill effects on other turtle populations indicate that it is a serious mortality factor (Dodd 2001), especially for females of freshwater species who cross roads looking for well-drained upland sites for nesting. Given the incidence of ornate box turtle mortality on roads in anecdotal reports, quantitative estimates of direct road mortality are likely to be much higher for ornate box turtles, at least locally (Wagner personal communication 2003, Eddy personal communication 2004).

Habitat quality also suffers because of the increased number and extent of roads in ornate box turtle habitat. Boarman (2004) indicated that a zone of reduced desert tortoise occurrence exists for at least 400 m from highways but may extend as far as 1.6 km (Sazaki et al. 1995), probably due to the various combined detrimental effects of roads. A similar effect of roads on ornate box turtle populations is likely.

Road mortality could be a problem as the result of two other observed box turtle behaviors. Because ornate box turtles are known to eat carrion of various types (see Food habits section above), an abundance of carrion on roadways may entice box turtles onto roads for an easily-acquired, relatively calorie-intensive meal. Use of roads for movement (Degenhardt et al. 1999), presumably to reduce energy expenditure during long movements compared to surrounding landscape with impediments to movement, also is likely to be a factor in road mortality.

A recent series of papers has documented male-biased sex ratios in turtle populations in proximity to roads throughout North America (Aresco 2005, Gibbs and Steen 2005, Steen and Gibbs 2004, Steen et al. 2006). Skewed sex ratios result from differential mortality of females as roadkills, presumably as they disperse to nesting sites or nest on road rights-of-way. Given the importance of females to the long-term viability of box turtle populations, differential female mortality along transportation corridors may exacerbate existing problems of habitat fragmentation and disrupt metapopulation dynamics.

Indeed, roads may not be the only problem in terms of transportation. Research being conducted on *Terrapene carolina carolina* in North Carolina suggests railroad tracks also serve as barriers to dispersal and as traps for turtles unable to cross. Box turtles enter the median between tracks at railroad crossings, and move along the rails seeking a way across. Caught by rising temperatures in the direct sun, the turtles quickly succumb to heat stress (Kornilev et al. in press). Preliminary observations suggest substantial mortality can occur in some areas (M. Dorcas, Davidson College, personal communication, 2006). Because railroads were constructed in the West long before roads became common, there is the possibility that railroad tracks have had serious long-term consequences for ornate box turtle population abundance and metapopulation dynamics.

Collection

Two types of collection activities have affected box turtle populations: collection for commercial trade and collection for pets by individuals. Of the two types, commercial collection has had the more serious impacts. The collection of large numbers of box turtles in recent years for shipment abroad and for the domestic pet trade has certainly had a significant effect on turtle populations. Like road mortality, commercial collection has pronounced local effects on particular populations where relatively high densities make possible the collection of many individuals. Instances are known where entire truckloads of ornate box turtles have been collected in a small area in a single day (Wagner personal communication 2003). Collection is made easier by roads (Converse 1999). Collection of small numbers of box turtles by individuals probably has less local impact, but undoubtedly it occurs at a relatively constant level across the range.

Information concerning precise numbers collected is seldom available or reliable. Law enforcement is unlikely to be effective because of too few personnel, inadequate funding, and the extensive areas in the Great Plains where box turtles occur. Converse (1999) used simulation models to predict the impact of various levels of collection on box turtle populations. She found that serious declines (26.4 to 56.4 percent) would occur over the next 200 years at harvest levels typical of the 1990's in Nebraska.

Collection of adult individuals, whether by commercial collectors or by individuals, is a seriously damaging human activity generally affecting box turtle populations in Region 2 (Wagner personal communication 2003, Converse personal communication 2005, Iverson personal communication 2005). The loss of even one or two reproductive females per year from small populations can result in the extinction of those populations (Doroff and Keith 1990, Congdon et al. 1993, Belzer 2000, Gibbs and Shriver 2002).

Biocides

Exposure to biocides is a suspected cause of mortality and adverse, sublethal effects on population dynamics (Meyers-Schöne and Wilson 1994). However, most reports of adverse side-effects are anecdotal and lack sufficient empirical testing. Effects of four types of exposure have been investigated in reptiles:

- direct exposure to skin
- the relatively immediate effects of indirect exposure by ingesting poisoned food
- long-term bioaccumulation effects on health and reproduction (Sparling et al. 2000)
- effects on disruption of the endocrine system with concomitant effects on maturation and reproduction (Crain and Guillette 1998, Guillette 2000).

Freshwater turtles are affected mostly by the bioaccumulation of chemicals, usually in fat tissues and embryos. There are no studies on the effects of chemicals specifically on ornate box turtles, but it is likely that they are locally impacted by chemicals through all four modes. Although box turtles have been found with high levels of various contaminants in their tissue and eggs, the prevalence of such contamination and the ultimate consequences for box turtle populations are unknown (Dodd 2001). But herbicides and insecticides are known to have various adverse effects on turtles (Hall 1980, Sparling et al. 2000), and their continued and even increasing use could pose a threat to both the vegetation and the insects that are the major prey of ornate box turtles.

Parasitism and disease

Parasitism and disease occasionally cause deaths in ornate box turtles, but the extent to which either are significant mortality factors in wild populations is unknown. A greater threat probably is the introduction of disease into wild populations from released or translocated captive turtles. This is known to be a problem in desert tortoise populations (Berry and Jones 2004).

Invasive species

As far as is known, ornate box turtles have no significant interactions with any exotic species in Region 2. However, it is possible that the increasing occurrence of invasive weeds could affect box turtle habitat in various detrimental ways, including the replacement of palatable plant species by unpalatable ones, changes in fire regime (especially with invasions of cheatgrass [*Bromus* spp.]), changes in thermal characteristics of nesting and burrow sites (Curtin 1997), and increased encounters with predators (McDougal 2000).

Fire

No firm conclusions can be reached about the effects of fire on box turtles. While Scott (1996) mentioned the vulnerability of box turtles, Russell at al. (1999) referenced many reports that various turtle species, including box turtles, often avoid the direct effects of fire by burrowing. Nonetheless, prairie wildfires can result in significant mortality (Legler 1960). In a survey of wildlife mortality after an August fire in a 160 ha grassland, 25 of 28 box turtles were found dead (Bigham et al. 1965). Fire intensity, the rapidity with which a fire passes over a turtle, and the immediate availability of shelter all affect survivorship. Individual turtles have been known to survive, and burned scutes have regenerated (Legler 1960, Rose 1986). Fire would also threaten food sources, at least temporarily, especially if it were large enough to force turtles into a long, stressful migration to find sufficient food.

Climate change

As with all reptiles inhabiting cold climates, overwinter survival of ornate box turtles can be affected by extreme winter temperatures. Modelling efforts by Converse et al. (2005) using almost two decades of data from their western Nebraska site revealed that only minimum winter temperature was a significant climatic factor for survival. Surprisingly, survival and minimum winter temperature were negatively correlated. They suggested that warmer winters might produce higher metabolic rates during hibernation, resulting in depletion of lipid reserves that adversely affected subsequent survival.

Conservation Status of the Ornate Box Turtle in Region 2

NatureServe and the Natural Heritage Programs in the states of USFS Region 2 (NatureServe 2006) assess the conservation status of the ornate box turtle as “Not very threatened range-wide”; S5 (secure) in Nebraska, Kansas, and Colorado; S2 (imperiled) in South Dakota; and S1 (critically imperiled) in Wyoming. The S1 rank in Wyoming is a result of a single historical record at the western edge of the taxon’s range and the subsequent absence of observations in eastern Wyoming. The S5 ranks in Nebraska, Kansas, and Colorado may be in need of revision since most of the records of box turtle occurrence in those states currently available to the authors were historical. The occurrence data assembled for the Region 2 range map (**Figure 4**) indicate that this species continues to be observed in many widely scattered locations throughout Region 2, but relatively few recent data concerning locations or abundance were available beyond informal assessments by biologists throughout the region.

Most reports from Nebraska indicate that in most sandhills habitat ornate box turtles are commonly seen and widely distributed, especially in northern Nebraska (Bogan 1995, Nenneman personal communication 2006). However, they do not appear to be as common farther south on the Nebraska National Forest near Halsey (Griffin personal communication 2006) despite occurrences in surrounding areas of the Sandhills (**Figure 4**), or in the Fort Niobrara National Wildlife Refuge (Bogan 1995). Iverson (personal communication 2005) indicated that box turtles are apparently extirpated in locations in eastern Nebraska north of Omaha. The population at Crescent Lake National Wildlife Refuge in Garden County may be increasing (Converse personal communication 2005, Iverson personal communication 2005, Converse et al. 2005), and Converse (1999) considered them to be abundant at Crescent Lake National Wildlife Refuge. The westernmost populations in the panhandle do not appear to extend west beyond a line from Sydney to Chadron (Redder personal observations 2004- 2005), which roughly coincides with the western extent of the Sandhills.

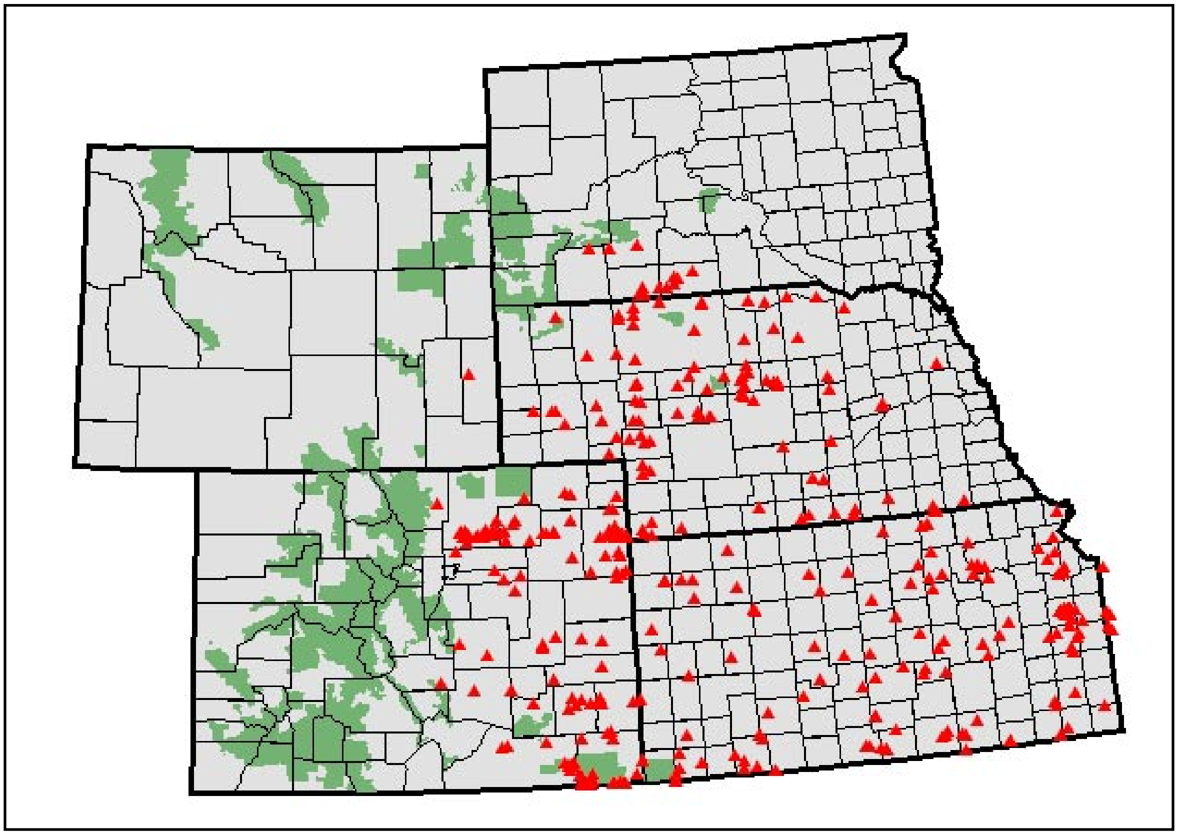

Figure 4. Distribution of the ornate box turtle (red triangles) in USDA Forest Service Region 2, with National Forest System units in green.

The ornate box turtle range extent and abundance in Colorado have declined during the last century, due largely to the conversion of native prairie to farmland and urban and residential development along the Front Range (Hammerson 1999). Hammerson stated that the most viable Colorado populations occur in conjunction with the last large remnants of undisturbed prairie. Preliminary surveys by Redder (personal observations 2004-2005) suggest that some populations on the western fringes of the distribution in western Nebraska and eastern Colorado may no longer exist. Interviews with local residents near rapidly developing areas in northern Colorado sometimes elicited statements to the effect that "sand turtles" had sometimes not been seen "in twenty years" in some locations indicated by historical records. The westernmost records along the Colorado Front Range are probably no longer extant as a result of extensive development in these locations, but thorough survey work has not yet confirmed this. Although **Figure 4** shows an occurrence just south of the Pawnee National Grassland, Wagner (personal communication 2003) reported that ornate box turtles are not present on the Pawnee National Grassland itself, probably due to unsuitable soil characteristics. Absence on the Pawnee National Grassland is confirmed by Patton (personal communication 2006) who also observed that they did not appear to be present in the more heavily tilled parts of Logan, Sedgewick, and Phillips counties in northeastern Colorado, areas for which our data indicate an historical presence.

However, Wagner, Patton and Jackson all recently reported their presence in sandhill, sage, and mixed-grass habitats along and south of the South Platte River through northeastern Colorado. Our data suggest that the sandhills near the Republican and Arikaree rivers in eastern Colorado and southwestern Nebraska have historically been a hotspot for ornate box turtles, but we have no recent collections or observations from that area allowing an assessment of current status. Both the Cimarron (Collins and Collins 1991) and Comanche national grasslands are in areas where box turtles have occurred in the past. Mackessy (personal communication 2005) reported high ornate box turtle mortality in Prowers and Kiowa counties, just north of these grasslands. Apparent abundance of box turtles on the Cimarron National Grassland (Anonymous 2002) and in other western Kansas locations (Anonymous 2001b) was recently reported. The more scattered occurrences in east-central Colorado have not recently been surveyed, so their status awaits future survey efforts.

The U.S. Fish and Wildlife Service (1996) documented declines in Kansas. Metcalf and Metcalf (1979) suggested that population numbers may vary cyclically in Kansas, depending on the harshness of the winters and mortality associated with overwintering. Caldwell and Collins (1981) considered the ornate box turtle the most common reptile in Kansas, inhabiting all but a few counties; they mentioned no declining populations. Ornate box turtles are reported as common on Fort Riley and vicinity in east-central Kansas (Busby et al. 2005). Ken Brunson (personal communication 2006) also reported that populations of this species are widespread and abundant in Kansas.

Only two documented occurrences of box turtles exist in Wyoming. One is from several decades ago near the North Platte River in Goshen County, possibly as far north as Ft. Laramie National Historical Site; the second is a picture taken at an unknown time and location in Wyoming by wildlife photographer LuRay Parker and published in a recent wildlife brochure by the Wyoming Game and Fish Department (2004). Recent fieldwork by one author (Redder personal observations 2004-2005) has not confirmed the presence of ornate box turtle populations at any location in eastern Wyoming, despite the apparent presence of suitable habitat. Thus, eastern Wyoming populations appear to have been diminished, if not extirpated.

Data indicate that sandhills habitats in southern South Dakota on the Pine Ridge and Rosebud Reservations may have “large populations” in “select few areas” (Backlund personal communication 2004), as well as in other locations in Bennett County off tribal lands. Occurrences in northern Jackson County suggest that box turtles may also be present on the Buffalo Gap National Grassland north of the White River. Two sightings along the Missouri River near Pierre (not shown on **Figure 4**) are probably released specimens (Backlund personal communication 2004) since these locations are much farther north than any current or historical sightings in South Dakota.

Most of these grassland units and their box turtle populations are at or near the northern or western edges of their range and perhaps up against an altitude-related climate limit. Monitoring these populations is likely to provide the first indications of change in population size, extent, and structure, due to either natural or human-related factors, that could eventually affect other areas.

Management of the Ornate Box Turtle in Region 2

Implications and potential conservation elements

Implications

The demographic consequences of the factors discussed above, together with inherent life history traits of the ornate box turtle, should be of prime importance for managers. Yet, the interaction of these demographic parameters and extrinsic threats can make turtle conservation difficult (Congdon et al. 1993, 1994).

The following implications to ornate box turtle conservation are especially noteworthy:

- ❖ Annual reproductive output tends to be low, especially at the edges of their range where resource limitations, including thermoregulatory constraints and activity season length, sometimes prevent annual reproduction by females by limiting energy intake sufficient for egg production.

- ❖ Hatching success tends to be low due to high incidence of nest predation and soil conditions unfavorable to completion of embryonic development and survival.

- ❖ Juvenile mortality is high because an abundance of predators find young turtles easy prey, partly because of their relative immobility, softer shells that do not completely close, and incomplete development of their defensive behavioral strategy. Complete shell closure is not possible until approximately 4 years of age, and complete shell hardening does not occur until approximately 10 years.

- ❖ A long lag time exists between management actions that affect the early life stages and expected demographic results (e.g., increased reproductive capacity and productivity in the adult stage) because an affected cohort of females does not attain reproductive capacity until approximately 10 to 11 years of age in northern and western populations.

- ❖ Nests are difficult to locate, increasing the effort and difficulty of management actions focused on the early life stages. However, since ornate box turtles have been observed to hibernate and nest very near to each other (within 0.5 m), if such a situation is found, protection of such semi-communal sites from human disturbance and predation might prove worthwhile (Hay personal communication 2004). *The consequence of the preceding implications is that an effective management strategy will most likely not focus heavily on early life stages*.

- The strongly philopatric habits of ornate box turtles make them both more susceptible to local disturbance and less likely to successfully respond to such disturbances. Overwintering sites are crucial to survival, yet little is known about the characteristics of these sites. Doroff and Keith (1990) noted that some turtles used burrows within 1 m of previous burrows in successive years. Similar specificity of overwinter burrow location in consecutive years was also observed by Converse et al. (2002) and in *Terrapene carolina carolina* (Dodd 2001). These sites merit special protection when known.

- The wide range of actual and potential effects on ornate box turtle populations from human contact, the major source of mortality, implies that minimizing human contact with extant populations should be an essential part of any management strategy. When that is not possible, taking specific measures that would ameliorate the effects of human activity might be required. A range of possible solutions are necessary to consider, not only because the types and extent of human impacts vary with location, but because human impacts hit hardest at the adult life stages most necessary for the persistence of this species. *Even partial amelioration of adverse effects on a critical and sensitive stage (larger, older adult females) is likely to be more effective than substantial efforts directed at less sensitive stages (eggs and juveniles).*

Potential conservation elements

- The immediate requirement for adequate conservation of the ornate box turtle is the collection of current distribution and population status data. Until surveys have clarified the distribution and status of extant populations and provided evidence of population structure sufficient to ensure population viability, prudence would suggest that *all harvest and collection of ornate box turtles should be prohibited, except by permit for research and conservation purposes*. Congdon et al. (1993) state bluntly that “[t]he concept of sustainable harvest of already-reduced populations of long-lived organisms appears to be an oxymoron.”

- Along with current distribution and abundance data, sufficient life history data are required for truly understanding the population dynamics of these long-lived animals. Management decisions on regional and local scales require such data from multiple localities. Proper and efficient collection of detailed life history data requires spatially-explicit, long-term monitoring in various parts of the species’ range. For a useful perspective on rangewide status and the effects of the various factors discussed above, research site localities should include both the current apparent strongholds of box turtle abundance and sites at the limits of its range and in already, or soon-to-be, heavily impacted areas.

- The combination of high annual adult survival, delayed age of first reproduction, and the apparent scarcity of hatchlings and adults in ornate box turtle surveys makes the detection of long-term trends in population status difficult for biologists and managers. Some extant ornate box turtle populations in Region 2 states, although apparently healthy and common, could in fact be geriatric remnants with sufficiently low densities of reproductively active females that population viability could be in doubt. This is the danger of reliance on the “we see them everywhere” assessment method. Unfortunately, this is the current, widely-used ornate box turtle population assessment method.

- The matrix model points out that older reproductive females are the most sensitive and elastic stage in the life history of this species. Natural history data suggest that it is precisely that most sensitive stage that is most affected by human causes of mortality, especially highway mortality. Thus any management actions undertaken to reduce turtle mortality would most profitably focus on adult females. For instance, minimizing road mortality and collection are more desirable than headstarting, nest protection, or predator control on egg and juvenile stages. Because locations of high adult mortality are readily determined, and in many cases already known, current experimental methods of mortality reduction should be attempted in those areas.

- Diseases have the potential to severely impact populations of box turtle and other turtle species, especially those populations that experience frequent or heavy exposure to humans. Release of infected captive turtles into wild populations is the likely vector of respiratory diseases. Prohibition of collection of ornate box turtles from wild populations and prohibition of commercial sale, together with education of the public to the dangers of turtle release, are likely to be the most effective steps to minimizing this problem. Because of the threats posed by diseases in box turtle populations, biologists and managers should be encouraged to participate in Dr. April Johnson's study of iridovirus in box turtles using road-killed specimens (A. Johnson, pg. 11 in Swarth and Hagood 2005). Dr. Johnson can be contacted at the College of Veterinary Medicine at the University of Florida in Gainesville (JohnsonA@mail.vetmed.ufl.edu) for the details of the project and collection methods.

- Maintenance of appropriate habitat structure could be crucial to long-term ornate box turtle persistence. Management practices that result in successional changes or microhabitat alteration (Curtin 1995, 1997, Fitch 2006), destruction of shrubs essential for thermoregulation (Converse and Savidge 2003), or elimination of rodents whose burrows are used for thermoregulation or hibernation (Nieuwolt 1996) could be harmful to ornate box turtle populations.

- Because additive annual mortality rates of as little as 2 to 3 percent are probably not sustainable by most turtle populations (Doroff and Keith 1990, Brooks et al. 1991, Congdon et al. 1993, 1994, Gibbs and Shriver 2002), any amelioration of anthropocentric mortality sources should be seriously considered.

Tools and practices

Inventory and monitoring

This conservation assessment provides a first step toward a comprehensive inventory of ornate box turtle occurrences in the Great Plains states, which comprise the northwestern portion of the range of this species. Unfortunately many of the data used for the Region 2 range map have various problems associated with them, so our current knowledge is limited. The imprecision of some records, especially some of the older observations and collections, is substantial, in many cases many times greater than the mean home range size of most turtles. Important biological information is sparse and often absent. Thus the most important first step toward achieving sufficient knowledge of this species to allow for informed management decisions would be the establishment of an inventory and monitoring program at the regional level to provide the overall context for decisions at the local level and to eventually illuminate meta-population dynamics throughout its range.

With one exception, monitoring programs for ornate box turtles in Region 2 states are either non-existent or rudimentary at best. This is clearly demonstrated by the fact that only a few observations in the dataset for the regional distribution map (**Figure 4**) are dated within the last 10 years. All but a few observations available for this project from Kansas are historical and thus may tell us little about the existence or status of turtle populations in those locations today. The majority of data are from observations that were not made as part of systematic survey work by biologists equipped to record relevant biological variables and reasonably precise location information. Thus any monitoring program established locally or regionally for this species would be a major improvement over the current situation. The one exception is a 25-year study conducted by John Iverson at Crescent Lake National Wildlife Refuge in the Sandhills of western Nebraska, the data for which are currently being analyzed (Converse personal communication 2005, Iverson personal communication 2005).

Initial survey efforts would best be focused on areas of historical occurrence that have been heavily impacted or are likely to be impacted in the near future by the threats discussed above or that might be at increased risk from the relative extremes of environmental conditions on the edges of their range. Searches in areas that appear to satisfy the basic habitat requirements of ornate box turtles but from which we have no current data would form a second tier of inventory effort. Such surveys would help to provide essential population data for distributional, trend, and demographic analyses. It is especially important that surveys be conducted in areas where ornate box turtles were known to be abundant both recently and historically, as well as in occurrence areas likely to be affected by human activity in the future.

Initial inventory efforts, as well as long-term monitoring, will be facilitated by the eventual addition to this report of predictive range maps for box turtles in Region 2. Such maps are currently under development by the Wyoming Natural Diversity Database (Beauvais and Smith 2005, Beauvais et al. in preparation). By synthesizing current and historical presence data, absence data from surveys, and a wide variety of physical and biological data over the range of this species, these models produce valuable predictions about the possible, and likely, geographic distribution of a taxon. These predictive range maps are testable, data-driven hypotheses that promote the efficient use of field survey resources in the search for additional occurrences.

As noted here and elsewhere (Dodd 2001), only a few detailed research projects have been undertaken on the ornate box turtle. These projects have been carried out in widely scattered locations, not all of which were in Region 2 or even within the Great Plains, and in some cases decades ago. Whereas the older work provides invaluable background data, land-use practices and other changes since then have almost certainly affected the populations studied. The replication of these studies at or as near the original locations as possible would provide invaluable snapshots capable of revealing long-term effects on previously well-studied populations. Along with assessments of current habitat conditions at these locations, replication of work on home range size would result in quantitative estimates of changes in turtle population densities and habitat use (home range size changes) in those areas as well as other biological data collection that were not done originally.

Because these turtles appear to be widely distributed in areas containing various state and federal agency jurisdictions, inter-agency and multi-jurisdictional cooperation is essential. Future monitoring and research should focus on both protected areas, such as National Forest System units, state parks, state and federal wildlife refuges, and Nature Conservancy lands and easements, as well as reservation lands and private holdings, especially areas slated for urban and residential development and road construction. Relatively undisturbed USFS and other federal lands would make a good control for the comparison of active management strategies applied to other, possibly more impacted areas.

Knopf and Samson (1996) recommended including the ornate box turtle, as well as other reptile and amphibian species native to the Great Plains, as an important component species in a program for monitoring grassland ecosystem health. Considering that biologists may soon be facing a similarly grim situation with reptiles as with the current status of amphibian extinction (Gibbons et al. 2000), an integrated, multi-taxon effort may be necessary. Ideally, monitoring of turtles and other vertebrates by the USFS would be coordinated with other state and federal agency rangeland monitoring efforts so that the maximum amount of habitat data can be associated with box turtle occurrences. Ultimately, for purposes of analysis and dissemination, it is essential that data be assembled and edited by a central database facility, such as the various state Natural Heritage Programs and NatureServe.

Standardization of data collection (Foscarini and Brooks 1997) and analysis techniques is important. To put collected data to the most effective and scientifically valid use, coordination of sampling efforts and techniques among cooperating agencies would require some initial planning for the most powerful yet practical statistical experimental design. In the absence of such consideration, the resulting expensive and hard-earned data are rendered less valuable for scientifically valid and managerially useful conclusions. Such large-scale and long-term planning will be especially important if valid inference is to be made concerning metapopulation data on multiple spatial and temporal scales. Ideally future studies will combine multiple data sources in an integrated, multi-disciplinary approach to assess turtle population health (e.g., Rubin et al. 2001, 2004, Kuo and Janzen 2004, Bowen et al. 2004).

Obtaining detailed, long-term life history parameter estimates of turtle populations for construction of complete life tables in support of informed management decisions may appear to be very demanding of research resources, especially considering the difficulty in finding nests and juveniles. But Heppell (1998) noted that only three estimates are essential: age at maturity for females, adult female annual survival, and λ, the annual population multiplication rate. Estimating λ may also appear problematic since it is usually calculated from the life table, but Dodd et al. (in preparation) have measured λ using mark-recapture methods with long-term datasets. However, for initial management decisions, a multi-year census of adult females may provide a sufficient indication of population trends until more detailed and complete demographic data are available. Heppell also suggested that in the absence of detailed demographic data on an unstudied turtle species, life history data from other turtle species with similar basic demographic characteristics are more likely to be relevant than comparisons with phylogenetically close species (e.g., congenerics).

Methods. Various methods are available to inventory and monitor terrestrial turtles. Intensive visual encounter searches on foot would be a first step in areas of known or suspected abundance. However, repeated intensive searches of specific areas have often continued to find new individuals (Dodd 2001, Converse personal communication 2005, Iverson personal communication 2005), so the results of a single search should be considered a tentative first estimate. The use of detector dogs for desert tortoise and ornate box turtle surveys has proven successful (Converse and Savidge 2003, Iverson personal communication 2005) and would greatly aid researchers in finding box turtles as juveniles and while in their burrows (Bjurlin et al. 2004).

More formalized methods, such as the use of transects, are somewhat inefficient and are likely to underestimate turtle abundance due to burrowing behavior, which is used for hibernation, escape from predators, and for management of daily ambient temperature extremes. Nevertheless, the use of standardized transects could produce much useful data about population sizes and densities in particular localities, as well as allow for meaningful comparisons of relative population densities between localities and to estimate the effectiveness of search effort.

Driving roads through turtle habitat is another effective method for finding ornate box turtles and would be especially useful for initial, large-scale inventory efforts. Because of the propensity of turtles (as well as other desert and grassland reptiles) to be active during and after thunderstorms, driving surveys could take advantage of this easily observable (and predictable) correlate of turtle behavior to greatly increase the probability of encountering turtles in unsurveyed areas. Unfortunately, many turtles found on roads are flattened and reveal little useful biological information. Road surveys that recorded mortality data itself are useful both for population estimates and for estimation of the effects of road mortality on those populations, and thus eventually perhaps for the evaluation of turtle road mortality prevention measures.

A variety of methods exist for more intensive, more specialized, or longer-term research. Notching marginal scutes is the classic method for long-term marking of turtles (Dodd 2001). Labels and tags of various types are easily affixed to turtles, and if carefully done, these tags can remain harmlessly attached for years, facilitating long-term population studies as well as focal animal research. Thread trailing has been used for studying box turtle movements for short time periods and short travel distances (Claussen et al. 1997, Loehr 2004). The technique is well-suited to turtles since the additional weight of the spool and thread is a small proportion of the body mass for adult turtles and does not interfere with movement or defense. Thread trailing also works well in most of the grassland habitats favored by ornate box turtles and has been shown to be more accurate than telemetry for quantifying distance travelled (Islay et al. 2006). In addition to their use in scientific studies, the implantation of PIT tags (Buhlman and Tuberville 1998) also has a potential use in detection of illegal trafficking in turtles and could be a deterrent if the use of such tags becomes widely known among commercial collectors. Some deterrence to collectors is also provided by any marking method that harmlessly but permanently defaces the carapace.

Although it is costly and labor-intensive, radio-telemetry is a very useful and productive technique to track turtles and can be applied to the study of many aspects of turtle biology. With the current availability of small, temperature-sensitive transmitters, studies could be carried out, for example, on the thermal biology of hibernation, a critical time period in the cold climates of Region 2. Tracking individual female turtles might also permit data collection on nesting success, a poorly understood stage in this species' life cycle. Sufficiently small transmitters would even permit the study of juveniles, about which virtually nothing is known. Telemetering wandering males, in conjunction with mark-recapture efforts, is probably the only method likely to reveal the extent of movements beyond home ranges (Kiester et al. 1982), essential data if metapopulation dynamics are to be understood.

Spatially-explicit mark-recapture sampling should be an essential aspect of any study because of the demographic data it would produce and because of the ease of use of marking techniques. Juveniles were tagged with tabs from aluminum cans and successfully relocated with a metal detector (Doroff and Keith 1990). The use of PIT tags has also been successfully tested on small turtles (Buhlman and Tuberville 1998).

Long-term studies are essential for various reasons. Lack of knowledge about early life stages, error introduced by uncertainty in distinguishing growth rings (and hence, inferring age, especially in the oldest specimens), low fecundity, and late age of first reproduction combine to make the detection of changes in ornate box turtle population status difficult. Long-term, spatially-extensive mark-recapture studies, ideally combined with population genetics studies, are the ideal way to obtain the necessary data for this species (Bowen et al. 2004).

Depending on the status of various populations, as revealed by the basic demographic work recommended above, further research using molecular genetic techniques, such as genetic fingerprinting and assessment of genetic variability within and between populations (e.g., Kuo and Janzen 2004), would provide the following types of data that could be essential for further conservation work:

- Ascertaining the degree of inbreeding or establishing paternity (Galbraith et al. 1995);
- Aiding in understanding the role of transient males for gene flow and metapopulation dynamics;
- Distinguishing possible management areas (Britten et al. 1997);
- Understanding the nature and extent of variation between populations;
- Helping inform management decisions involving reintroduction or translocation (Petit et al. 1998).

A word of caution: Averill-Murray (2002), Berry et al. (2002), and Berry and Jones (2004) cautioned that handling desert tortoises can cause them to urinate and thus increase their risk of mortality, due to the loss of essential water and electrolytes. Ornate box turtles are also known to urinate when handled, so any field techniques used for handling and marking should be as non-traumatic as possible.

Management tools

The combined effects of roadkill, collecting, habitat loss and degradation, and biocides pose ever increasing risks for ornate box turtles. Risks are greatest in or near areas with high human population densities, since the various risk factors affecting turtles are strongly linked to human activity. In general, finding ways to minimize human contact with turtles is the best tool (Garber and Burger 1995). While other short-term, "technological" solutions may be locally applicable, over the long term, maintaining large areas of high-quality, unfragmented habitat subject to a minimum of human disturbance is the only effective strategy.

Management activities such as weed or pest control should be undertaken only after information on the effects of a particular chemical on box turtles or other reptiles is obtained. Carrion can comprise a significant part of ornate box turtle diet; thus carcasses resulting from the use of poisons for pest or predator control pose a risk to box turtles. Use of controlled burns or mowing as management tools also should follow assessment of the likelihood of adversely affecting local turtle populations. The timing of these activities can be critical. For instance, the use of controlled burning of grasslands would be best carried out in early spring or late fall, before or after the activity season of turtles, both to protect them and for purposes of fire control. Mowing in occupied habitat should be done during the heat of the day when turtles will be inactive and under cover. The mower blade should be set no lower than necessary, preferably higher than 8 inches, to avoid contacting any turtles present. Planning for these activities, including searches of the affected areas, could be done in conjunction with turtle and other herpetological surveys to collect data for the area of proposed treatment.

Since box turtles possess a particular attractiveness that makes them susceptible to collection for the pet trade and by individuals, educational programs and public relations efforts can take advantage of this attraction to enlist public support in conservation efforts. Public relations efforts by USFS and other agency personnel might be a cost-effective way to inform the public about the dangers facing turtles and other reptiles from commercial collection and other human interactions. With the cooperation of local biology teachers, high school biology classes can be involved in projects studying local populations (Anonymous 1999); this would result in both the production of scientific data and increased publicity and awareness of turtle conservation issues.

Predator removal is a possible management strategy in limited circumstances. Christiansen and Gallaway's (1984) experimental removal and reintroduction of raccoons in turtle habitat clearly showed that turtle recruitment increased in the absence of these particularly effective turtle predators.

In an attempt to minimize roadkill, the state of Nebraska has recently constructed over a mile of roadside fencing to direct Blanding's turtles into culverts (Anonymous 2001a). This project is located in the Valentine National Wildlife Refute in the Sandhills of north-central Nebraska, where it appears to be working well (Nenneman personal communication 2006). A similar program could be considered for other lengths of highway where significant numbers of box turtle deaths have been observed to occur.

Managers should consider the consequences to ornate box turtles and reptiles generally of management practices that could affect successional processes and structural changes in microhabitat characteristics. Fitch (2006) found that succession from grassland to a more wooded stage occurred after cattle were removed from his Kansas site, resulting in a collapse of ornate box turtle and other reptile populations. Curtin (1995, 1997) showed that successional changes that affected microhabitat adversely affected ornate box turtles in Wisconsin.

Translocation and reintroduction of turtles from healthy populations to areas in which they are endangered or extirpated is a possible management strategy. However, such a program would require considerable detailed knowledge of both the characteristics of the population from which the turtles are to be taken and the area into which they are to be translocated. Such a program is in progress in Wisconsin until at least 2012. However, we caution managers that reestablishment of populations through translocation is typically difficult to implement successfully. Consequently, it is best viewed as a tactic of last resort when populations have been extirpated from areas where habitat quality and quantity appear to remain. See and Dodd and Siegel (1991), Dodd (2001) and Cook (2004) for in-depth discussions of this option.

Information Needs

Ornate box turtle data collection in the future should focus on the estimation of basic population parameters and important life history variables, the estimation of human impacts on turtle populations, and the possible effect of various management practices. It is essential to survey locations and sizes of extant ornate box turtle populations in Region 2 states. Demographic profiles of these extant populations, with an emphasis on the age and size structure, are required to estimate the viability of current populations and to estimate the effects of loss of reproductive females on future population viability and recruitment, with special reference to the effects and extent of commercial collection on populations in various parts of its range. Understanding the effects of road mortality on turtle populations is also very important. The effectiveness of roadside barriers and ecopassages on the reduction of turtle mortality in grassland habitats needs to be assessed quantitatively.

When basic distribution and abundance data as well as detailed local demographic data have been assembled, the role of metapopulation dynamics will be better understood. Synthesis of these data is essential to estimate the likelihood that declining populations can be sustained by immigration from neighboring populations, to quantify the extent of gene flow between populations, and to estimate the minimum size for an unfragmented habitat parcel capable of sustaining a box turtle population.

Repeating previous in-depth studies of activity, reproduction, and survivorship in additional locations would provide both temporal and spatial replication of important studies.

Concurrent collection of DNA samples during basic distribution and demographic sampling would help to estimate the population genetic structure and genetic diversity across the species' range, and to determine the possible genetic uniqueness of peripheral or isolated populations.

The quality of habitat currently occupied by extant populations should be surveyed, and the local and regional threats to those habitats should be appraised using standard assessment methods. The role of habitat structure, especially mammal burrows, on the survivorship of hatchlings and juveniles needs to be clarified, and the changes in habitat quality in those areas where historical data indicate turtles once lived, but where they are no longer found, need to be examined.

The collection of focal-animal data for individual females would provide a better understanding of nesting habitat requirements and aid in the estimation of nesting success.

Information about the types, amounts, and locations of herbicide and pesticide application should be collected to estimate potential exposure of turtles and the effects of such exposure. These data would be most relevant in the case of substances used to deal with invasive weeds and well as animal pest control poisons.

REFERENCES

Andrewartha, H. G. and L. C. Birch. 1984. The Ecological Web: More on the Distribution and Abundance of Animals. University of Chicago Press, Chicago, IL.

Anonymous. 1999. Tracking turtles slow endeavor- students hope project will help preserve animals' environment. Internet newsgroup article, 3 May 1999. Kansas Herpetological Society Newsletter 117:9. Kansas Herpetological Society, Lawrence, KS.

Anonymous. 2001a. Keeping Blanding's turtles from being roadkill. Omaha World-Herald, 9/11/01. Cited at http: //www.chelonian.org/ttn/archives/ttn5/pp24-27.shtml.

Anonymous. 2001b. Results of the KHS spring field trip west. Kansas Herpetological Society Newsletter 125:10. Kansas Herpetological Society, Lawrence, KS.

Anonymous. 2002. Results of the spring 2002 field KHS field trip. Journal of Kansas Herpetology 3:6. Kansas Herpetological Society, Lawrence, KS.

Aresco, M.J. 2005. The effect of sex-specific terrestrial movements and roads on the sex ratio of freshwater turtles. Biological Conservation 123:37-44.

Auffenberg, W. and J.B. Iverson. 1979. Demography of terrestrial turtles. Pages 541-570 *in* M. Harless and H. Morlock, editors. Turtles: Perspectives and Research. J. Wiley and Sons, New York, NY.

Averill-Murray, R.C. 2002. Effects on survival of desert tortoise (*Gopherus agassizii*) urinating during handling. Chelonian Conservation Biology 4(2):430-435.

Backlund, D. 2005. Biologist, South Dakota Game and Fish Commission, Pierre, SD. Personal communication.

Ballinger, R.E., J.W. Meeker, and M. Thies. 2000. A checklist and distribution maps of the amphibians and reptiles of South Dakota. Transactions of the Nebraska Academy of Sciences 26:29-46.

Baxter, G.T. and M.D. Stone. 1985. Amphibians and Reptiles of Wyoming. Wyoming Game and Fish Department, Cheyenne, WY.

Beauvais, G.P. and R. Smith. 2005. Predictive distribution maps for 54 species of management concern in the Rocky Mountain Region of the USDA Forest Service. Report prepared for the USDI Geological Survey – Gap Analysis Program by the Wyoming Natural Diversity Database, University of Wyoming, Laramie, WY.

Beauvais, G.P., N. Brown, and L. Master. *In preparation*. Element distribution modeling to prioritize field inventories of sensitive species in western forests. Report prepared for NatureServe (Arlington, Virginia) by the Wyoming Natural Diversity Database, University of Wyoming, Laramie, WY.

Belzer, B. 2000. A nine year study of eastern box turtle courtship with implications for reproductive success and conservation in a translocated population. Turtle and Tortoise Newsletter 6:17-26.

Berry, K.H. and R. Jones. 2004. Highlights from the November 2002 workshop on desert tortoise health and disease. 14-17 November, Soda Springs, CA.

Berry, K.H., E.K. Spangenberg, B.L. Homer, and E.R. Jacobson. 2002. Deaths of desert tortoises following periods of drought and research manipulation. Chelonian Conservation Biology 4(2):436-448.

Bigham, S.R., J.L. Hepworth, and R.P. Martin. 1965. A casualty count following a fire. Proceedings of the Oklahoma Academy of Science 45:47-50.

Bilsing, S.W. and R.B. Eads. 1947. An addition to the tick fauna of the United States. Journal of Parasitology 33:85-86.

Bjurlin, C.D., W.J. Vanherweg, P. Mackay, R. Long, S. Weigley, and B. Davenport. 2004. Scenting abilities of detector dogs for desert tortoise surveys: pilot study results. [abstract] 29th Annual Meeting and Symposium of the Desert Tortoise Council, February 20-23.

Black, J.H. 1987. Do ornate box turtles prey on birds? Bulletin of the Maryland Herpetological Society 23:130-131.

Black, J.H. and J.N. Black. 1971. Montana and its turtles. International Turtle and Tortoise Society Journal 5(3):10-11, 34-35.

Blair, W.F. 1976. Some aspects of the biology of the ornate box turtle, *Terrapene ornata*. Southwestern Naturalist 21: 89-104.

Boarman, W.I. 2004. Road effect zone for desert tortoises: problems and solutions. [abstract] 29th Annual Meeting and Symposium of the Desert Tortoise Council, February 20-23.

Bogen, M.A., editor. 1995. A biological survey of Fort Niobrara and Valentine National Wildlife Refuges. 0227MESC #15126, USDA National Biological Service: Fort Collins, CO.

Bowen, K.D., P.L. Colbert, and F.J. Janzen. 2004. Survival and recruitment in a human-impacted population of ornate box turtles, *Terrapene ornata*, with recommendations for conservation and management. Journal of Herpetology 38:562-568.

Brattstrom, B.H. 1965. Body temperatures of reptiles. American Midland Naturalist 73:376-422.

Breckenridge, W.J. 1944. Reptiles and Amphibians of Minnesota. University of Minnesota Press, Minneapolis, MN.

Britten, H.B., B.R. Riddle, P.F. Brussard, R. Marlow, and T.E. Lee, Jr. 1997. Genetic delineation of management units for the desert tortoise, *Gopherus agassizii*, in northeastern Mojave Desert. Copeia 1997(3):523-530.

Brooks, R.J., G.P. Brown, and D.A. Galbraith. 1991. Effects of a sudden increase in natural mortality of adults on a population of the common snapping turtle (*Chelydra serpentina*). Canadian Journal of Zoology 69:1314-1320.

Brumwell, M.J. 1940. Notes on the courtship of the turtle, *Terrapene ornata*. Transactions of the Kansas Academy of Science 43:391-392.

Brunson, K. 2006. Wildlife Diversity Coordinator, Kansas Department of Wildlife and Parks. Personal communication.

Buhlman, K.A. and T.D. Tuberville. 1998. Use of Passive Integrated Transponder (PIT) tags for marking small freshwater turtles. Chelonian Conservation Biology 3:102-104.

Bull, J.J. 1980. Sex determination in reptiles. Quarterly Review of Biology 55:3-21.

Busby, W.H., J.T. Collins, and G. Suleiman. 2005. *The Snakes, Lizards, Turtles, and Amphibians of Fort Riley and Vicinity*. Second revised edition. Kansas Biological Survey, Lawrence, KS. 76 pp.

Cahn, A.R. 1933. Hibernation of the box turtle. Copeia 1933(1):13-14.

Cahn, A.R. 1937. The Turtles of Illinois. Illinois Biological Monographs. 16:1-218.

Caldwell, J.P. and J.T. Collins. 1981. Turtles in Kansas. AMS Publishing, Lawrence, KS.

Capron, M. 1987. Selected observations on south-central Kansas turtles. Kansas Herpetological Society Newsletter 67:13-15.

Carr, A. 1952. Handbook of Turtles: The Turtles of the United States, Canada, and Baja California. Cornell University Press, Ithaca, NY.

Caswell, H. 2000. Matrix Population Models: Construction, Analysis, and Interpretation. Second Edition. Sinauer Associates, Sunderland, MA.

Christiansen, J.L. 1998. Perspectives on Iowa's declining amphibians and reptiles. Journal of the Iowa Academy of Science 105:109-114.

Christiansen, J.L. and R.M. Bailey. 1988. The Lizards and Turtles of Iowa. Iowa Department of Natural Resources, Des Moines, IA. 19 pp.

Christiansen, J.L. and B.J. Gallaway. 1984. Raccoon removal, nesting success, and hatchling emergence in Iowa turtles with special reference to *Kinosternon flavescens* (Kinosternidae). Southwestern Naturalist 29:343-348.

Christiansen, J.L., J.M. Grzybowski, and B.P. Rinner. 2004. Facial lesions in turtles, observations on prevalence, reoccurrence, and possible origin. Journal of Herpetology 37(3):293-298.

Clarke, R.F. 1950. Notes on the ornate box turtle. Herpetologica 6:54.

Clarke, R.F. 1956. A case of possible overwintering of *Terrapene ornata* in a well. Herpetologica 12:131.

Clarke, R.F. 1958. An ecological study of reptiles and amphibians in Osage County, Kansas. Emporia State Research Studies 7(1):1-52.

Claussen, D.L., M.S. Finkler, and M.M. Smith. 1997. Thread trailing of turtles: methods for evaluating spatial movements and pathway structure. Canadian Journal of Zoology 75:2120-2128.

Claussen, D.L., R. Lim, M. Kurz, and K. Wren. 2002. Effects of slope, substrate, and temperature on the locomotion of the Ornate Box Turtle, *Terrapene ornata*. Copeia 2002:411-418.

Collins, J.T. 1993. Amphibians and Reptiles in Kansas. Third Edition. University Press of Kansas. Lawrence, KS.

Collins, J.T. and S.L. Collins. 1991. *Reptiles and Amphibians of the Cimarron National Grasslands Morton County, Kansas*. Cimarron National Grasslands, Elkhart, KS. 60 pp.

Congdon, J.D., A.E. Dunham, and R.C. van Loben Sels. 1993. Delayed sexual maturity and demographics of Blanding's turtles (*Emydoidea blandingii*): implications for conservation and management of long-lived organisms. Conservation Biology 7:826-833.

Congdon, J.D., A.E. Dunham, and R.C. van Loben Sels. 1994. Demographics of common snapping turtles (*Chelydra serpentina*): implications for conservation and management of long-lived organisms. American Zoologist 34: 397-408.

Constanzo, J.P., J.B. Iverson, M.F. Wright, and R.E. Lee, Jr. 1995. Cold hardiness and overwintering strategies of hatchlings in an assemblage of northern turtles. Ecology 76:1772-1785.

Convention on the International Trade in Endangered Species in Flora and Fauna (CITES). Appendix 2. Available online at http://www.cites.org/eng/disc/text.shtml.

Converse, S.J. 1999. Habitat selection and population response to commercial harvest of Nebraskan ornate box turtles. Unpublished M.S. Thesis, University of Nebraska, Lincoln, NE.

Converse, S.J. 2005. Ph.D. Candidate, Colorado State University, Ft. Collins, CO. Personal communication.

Converse, S.J. and J.A. Savidge. 2003. Ambient temperature, activity, and microhabitat use by ornate box turtles (*Terrapene ornata ornata*). Journal of Herpetology 37:665-670.

Converse, S.J., J.B. Iverson, and J.A. Savidge. 2002. Activity, reproduction and overwintering behavior of ornate box turtles (*Terrapene ornata ornata*) in the Nebraska Sandhills. American Midland Naturalist 148:416-422.

Costanzo, J.P., J.B. Iverson, M.F. Wright, and R.E. Lee, Jr. 1995. Cold hardiness and overwintering strategies of hatchlings in an assemblage of northern turtles. Ecology 76(6):1772-1785.

Cook, R.P. 2004. Dispersal, home range establishment, survival, and reproduction of translocated eastern box turtles, *Terrapene c. carolina*. Applied Herpetology 1:197-228.

Crain, D.A. and L.J. Guillette, Jr. 1998. Reptiles as models of contaminant-induced endocrine disruption. Animal Reproduction Science 53:77-86.

Cristoffel, R. 1999. Ornate box turtle (*Terrapene ornata*) recovery in Wisconsin: headstarting and hatchling turtle telemetry program in Iowa county: 1999. University of Wisconsin, Department of Wildlife Ecology, Madison, WI.

Cristoffel, R. and R. Hay. 1995. Effectiveness of placing turtle mortality barriers and crossing signs along highways to reduce turtle mortality. Wisconsin Endangered Resources Report # 107; Bureau of Endangered Resources, Wisconsin Department of Natural Resources; Madison, WI.

Crother, B.I., editor. 2000. Scientific and Standard English Names of Amphibians and Reptiles of North America North of Mexico, with Comments Regarding Confidence in Our Understanding. SSAR Herpetological Circular 29. iii + 82 pp.

Curtin, C.G. 1997. A biophysical analysis of the cost and consequences of changing land-use on ornate box turtles (*Terrapene ornata*), Wisconsin, USA. Pages 31-36 *in* J. van Abbema, editor. Conservation, Restoration and Management of Tortoises and Turtles. New York Turtle and Tortoise Society, New York, NY.

Curtin, C.G. 1998. Plasticity in ornate box turtle thermal preference. Journal of Herpetology 32:298-301.

Degenhardt, W.G., C.W. Painter, and A.H. Price. 1996. Amphibians and Reptiles of New Mexico. University of New Mexico Press, Albuquerque, NM. 431 pp.

Diller, A. 1955. James Mackay's journey in Nebraska in 1796. Nebraska History. 36:123-128.

Dodd, C.K., Jr. 2001. North American Box Turtles. A Natural History. University of Oklahoma Press, Norman, OK.

Dodd, C.K., Jr. 2006. A Working Guide to the Literature on Box Turtles (*Terrapene*). Life History, Evolution, Fossil Record, External Morphology, Conservation. Available online at http://cars.er.usgs.gov/Center_Publications/box_turtle_bib1/box_turtle_bib1.html.

Dodd, C.K., Jr. and R. Franz. 1993. The need for status information on common herpetofaunal species. Herpetological Review 24:47-50.

Dodd, C.K., Jr. and R.A. Siegel. 1991. Relocation, repatriation and translocation of amphibians and reptiles: Are they conservation strategies that work? Herpetologica 47(3):336-350.

Dodd, C.K, Jr., R. Franz, and S.A. Johnson. 1997. Shell injuries and anomalies in an insular population of box turtles (*Terrapene carolina bauri*). Herpetological Natural History 5:66-72.

Doroff, A.M. and L.B. Keith. 1990. Demography and ecology of an ornate box turtle (*Terrapene ornata*) population in south-central Wisconsin. Copeia 1990:387-399.

Duany, A., E. Plater-Zyberk, and J. Speck. 2000. Suburban Nation: The Rise of Sprawl and the Decline of the American Dream. North Point Press, New York, NY.

Dunder, J. 2003. Biologist, U.S. Bureau of Land Management. Rock Springs, WY. Personal communication.

Duvall, D., M.B. King, and K.J. Gutzwiller. 1985. Behavioral ecology and ethology of the prairie rattlesnake. National Geographic Research 1(1):80-111.

EarthTrends. 2006. Grassland fragmentation by roads in the Great Plains. Available online at http://earthtrends.wri.org/text/forests-grasslands-drylands/map-253.html [Accessed March 2006].

Eaton, T.H., Jr. 1947. Box turtle eating a horned toad. Copeia 1947:270.

Eddy, J. 2004. Biologist, WEST Inc. Laramie, WY. Personal communication.

Ellner, L.R. and W.H. Karasov. 1992. Latitudinal variation in the thermal biology of ornate box turtles. Copeia 1992: 387-399.

Ernst, C.H. and R.W. Barbour. 1972. Turtles of the United States and Canada. University Presses of Kentucky, Lexington, KY.

Ernst, C.H. and J. McBreen. 1991. *Terrapene* Merrem: Box turtles. Catalogue of American Amphibians and Reptiles 511.1-511.6.

Ernst, C.H., J.E. Lovich, and R.W. Barbour. 1994. Turtles of the United States and Canada. Smithsonian Institution Press, Washington, D.C.

Farrar, J. 2001. Tracking turtles. NEBRASKAland (Nebraska Game & Parks Commission) (Mar):40-45.

Fitch, H.S. 1956. Temperature responses in free-living amphibians and reptiles of northeastern Kansas. University of Kansas Publication of the Museum of Natural History 8(7):417-476.

Fitch, H.S. 1958. Home range, territories, and seasonal movements of vertebrates of the Natural History Reservation. University of Kansas Publication of the Museum of Natural History 11(3):63-226.

Fitch, H.S. 2006. Collapse of a fauna: reptiles and turtles of the University of Kansas Natural History Reservation. Journal of Kansas Herpetology 17(March):10-13.

Foscarini, D.A. and R.J. Brooks. 1991. A proposal to standardize data collection and implications for management of the wood turtle, *Clemmys insculpta*, and other freshwater turtles in Ontario, Canada. Pages 203-209 *in* Proceedings: Conservation, Restoration, and Management of Tortoises and Turtles – An International Conference. New York Turtle and Tortoise Society, NY.

Fritz, M. 2003. Biologist, Nebraska Game and Parks Commission, Lincoln, NE. Personal communication.

Galbraith, D.A., B.N. White, R.J. Brooks, J.H. Kaufman, and P.T. Boag. 1995. DNA fingerprinting of turtles. Journal of Herpetology 29:285-291.

Garber, S.D. and J. Berger. 1995. A 20-year study documenting the relationship between turtle decline and human recreation. Ecological Applications 5:1151-1162.

Gaston, K.J. 2003. The Structure and Dynamics of Geographic Ranges. Oxford University Press, Oxford, UK.

Germano, D.J. 1999a. *Terrapene ornata luteola* (Desert Box Turtle). Attempted Predation. Herpetological Review 30: 40-41.

Germano, D.J. 1999b. *Terrapene ornata luteola* (Desert Box Turtle). Homing Behavior. Herpetological Review 30: 96.

Gibbons, J.W., D.E. Scott, T.J. Ryan, K.A. Buhlman, and T.D. Tuberville. 2000. Global decline of reptiles, déjà vu amphibians. BioScience 50:653-666.

Gibbs, J.P. and W.G. Shriver. 2002. Estimating the effects of road mortality on turtle populations. Conservation Biology 16(6):1647-1652.

Gibbs, J.P. and D.A. Steen. 2005. Historic trends in sex ratios of turtle populations in the United States. Conservation Biology 19:552-556.

Gotelli, N.J. 1995. A Primer of Ecology. Sinauer Associates, Sunderland, MA.

Graul, W.D., and S.J. Bissell. 1979. Lowland river and stream habitat in Colorado: a symposium. Colorado Division of Wildlife, Denver, CO.

Griffin, T. 2006. Biologist, Nebraska National Forest, Halsey, NE. Personal communication.

Grobman, A.B. 1990. The effect of soil temperatures on emergence from hibernation of *Terrapene carolina* and *T. ornata*. American Midland Naturalist 124:366-371.

Guillette, L.J., Jr. 2000. Contaminant-associated endocrine disruption in reptiles. Pages 595-615 *in* D.W. Sparling, G. Linder, and C.A. Bishop, editors. Ecotoxicology of Amphibians and Reptiles. SETAC Press, Pensacola, FL.

Hall, R.J. 1980. Effects of environmental contaminants on reptiles: a review. USDI Fish and Wildlife Service Special Scientific Report -- Wildlife No. 228. Washington, D.C.

Hammerson, G.A. 1999. Amphibians and Reptiles in Colorado. University Press of Colorado and Colorado Division of Wildlife, Denver. Niwot, CO.

Hatch, K. 1996. Translocation, reintroduction, and habitat use of ornate box turtles – results and summary of 1995 research. Report to Wisconsin Department of Natural Resources; Madison, WI.

Hay, R. 2003. Endangered Resources Coordinator, Wisconsin Department of Natural Resources, Madison, WI. Personal communication.

Heppell, S.S. 1998. Application of life-history theory and population model analysis to turtle conservation. Copeia 1998:367-375.

Holy, L.L. 1995. Home range, homing ability, orientation and navigational mechanisms of the western box turtle (*Terrapene ornata*) from western Nebraska. Unpublished. M.S. Thesis, University of Nebraska, Lincoln, NE.

Islay, R.B., J.L. Bowman, and N.H. Nazdrowicz. 2006. Comparison of two methods for studying box turtle movements. Wildlife Society Bulletin 34(1):208-210.

Iverson, J.B. 1982. Biomass in turtle populations: a neglected subject. Oecologia 55:69-76.

Iverson, J.B. 1991. Patterns of survivorship in turtles (Order Testudines). Canadian Journal of Zoology 69:385-391.

Iverson, J.B. 2005. Professor, Department of Biology, Earlham College, Richmond, IN. Personal communication.

Jackson, T. 2006. Biologist, Colorado Division of Wildlife, Denver, CO. Personal communication.

Jacobson, E.R. and A. Johnson. 2005. Ranavirus, An Emerging Pathogen of Tortoises and Box Turtles in the United States. Morris Animal Foundation website: http://www.morrisanimalfoundation.org/learn/animals/wildlife/QAEasternBoxTurtle.asp [Accessed Feb 2006].

Johnson, R. and S.A. Temple. 1986. Assessing habitat quality for birds nesting in fragmented tall grass prairies. Pages 245-249 *in* J. Verner, M.L. Morrison, and C.J. Ralph, editors. Wildlife 2000: Modeling Habitat Relationships of Terrestrial Vertebrates. University of Wisconsin Press, Madison, WI.

Kazmaier, R.T. and R.J. Robel. 2001. Scute anomalies of ornate box turtles in Kansas. Transactions of the Kansas Academy of Science 104:178-182.

Kiester, A.R., C.W. Schwartz, and E.R. Schwartz. 1982. Promotion of gene flow by transient individuals in an otherwise sedentary population of box turtles (*Terrapene carolina triunguis*). Evolution 36:617-619.

Knopf, F.L. and F.B. Samson. 1996. Conservation of grassland vertebrates. Pages 273-290 *in* F.L. Knopf and F.B. Samson, editors. Ecology and Conservation of Great Plains Vertebrates. Springer, New York, NY.

Kolbe, J.J. 1998. *Terrapene ornata ornata* (Ornate Box Turtle), Diet. Herpetological Review 29:235.

Kornilev, Y.V., S.J. Price, and M.E. Dorcas. In press. Between a rock and a hard place: responses of eastern box turtles (*Terrapene carolina*) when trapped between railroad tracks. Herpetological Review.

Kramer, D.C. 1973. Geophagy in *Terrapene ornata ornata* Agassiz. Journal of Herpetology 7:138-139.

Küchler, A.W. 1964. Manual to accompany the map of potential vegetation of the conterminous United States. Special Publication No. 36. New York: American Geographical Society. 77 p.

Kuo, C.H. and F.J. Janzen. 2004. Genetic effects of a persistent bottleneck on a natural population of ornate box turtles (*Terrapene ornata*). Conservation Genetics 5:425-437.

LeClere, J. 2006. Ornate Box Turtle *Terrapene ornata*. Iowa Herpetology website: http://www.herpnet.net/Iowa-Herpetology/reptiles/turtles/box_turtle.html [Accessed March 2006].

Legler, J. M. 1960. Natural history of the ornate box turtle, *Terrapene ornata ornata* Agassiz. University of Kansas Publication of the Museum of Natural History 11(10):527-669.

Levell, J.P. 1997. A Field Guide to Reptiles and the Law. Second edition. Serpent's Tale Books, Lanesboro, MN.

Line, L. 1998. Fast decline of a slow species. National Wildlife 36(6):22-31.

Livo, L. 1996. Shell game. Colorado Outdoors 45(5):487-495.

Loehr, V.J.T. 2004. A new thread-trailing method for small tortoises in densely structured habitats. Turtle and Tortoise Newsletter 7:13-14.

Lynch, J.D. 1985. Annotated checklist of amphibians and reptiles of Nebraska. Transactions of the Nebraska Academy of Sciences 13:33-57.

Mackessy, S. 2005. Professor of Natural and Health Sciences, University of Northern Colorado, Greeley, CO. Personal communication.

Marr, J.C. 1944. Notes on amphibians and reptiles from the central United States. American Midland Naturalist 32: 478-490.

Mays, M.L. 1960. A survey of helminth parasites of box turtles in central Oklahoma. Unpublished M.S. Thesis, University of Oklahoma, Norman, OK.

McDonald, D.B. and H. Caswell. 1993. Matrix methods for avian demography. Pages 139-185 *in* D. Power, editor. Current Ornithology. Vol. 10. Plenum Press, New York, NY.

McDougal, J. 2000. Conservation of tortoises and terrestrial turtles. Pages 180-206 *in* M.W. Klemens, editor. Turtle Conservation. Smithsonian Institute Press, Washington, D.C.

Metcalf, A.L. 1978. An experiment with homing in ornate box turtles (*Terrapene ornata ornata* Agassiz). Journal of Herpetology 12:411-412.

Metcalf, A.L. and E.L. Metcalf. 1985. Longevity in some ornate box turtles *Terrapene ornata ornata*. Journal of Herpetology 19:157-158.

Metcalf, E.L. and A.L. Metcalf. 1970. Observations on ornate box turtles *Terrapene ornata ornata* Agassiz. Transactions of the Kansas Academy of Science 73:96-117.

Metcalf, E.L. and A.L. Metcalf. 1979. Mortality in hibernating ornate box turtles, *Terrapene ornata*. Herpetologica 35:93-96.

Meyers-Schöne, L. and B.T. Watson. 1994. Turtles as monitors of chemical contaminants in the environment. Review of Environmental Contaminants and Toxicology 135:93-153.

Minnesota Herpetological Society . 1985. Distribution maps for reptiles and amphibians of Minnesota. Bell Museum of Natural History. Minneapolis, MN.

Minton, S.A., Jr. 1972. Amphibians and Reptiles of Indiana. Indiana Academy Science Monographs 3. V + 346 pp.

Moore, G.E. 1943. Food habits of the box tortoise. Missouri Conservationist 4(7):12.

NatureServe. 2006. NatureServe Explorer: An online encyclopedia of life [web application]. 2001. Version 1.6. Arlington, VA: NatureServe. Available: http://www.natureserve.org/explorer [Accessed: March 2006].

Nenneman, M. 2006. Biologist, Valentine National Wildlife Refuge, Valentine, NE. Personal communication.

Nieuwolt, P.M. 1996. Movement, activity, and microhabitat selection in the western box turtle, *Terrapene ornata luteola*, in New Mexico. Herpetologica 52:487-495.

Nieuwolt-Dacanay, P.M. 1997. Reproduction in the western box turtle, *Terrapene ornata luteola*. Copeia 1997:819-826.

Norris, K.S. and R.G. Zweifel. 1950. Observations on the habits of the ornate box turtle, *Terrapene ornata* (Agassiz). Natural History Miscellanea (58):1-4.

Oldfield, B. and J.J. Moriarty. 1994. Amphibians and Reptiles Native to Minnesota. University of Minnesota Press, Minneapolis, MN.

Packard, G.C. and M.J. Packard. 1986. Physiological ecology of reptilian eggs. Pages 523-605 *in* C. Gans and R.B. Huey, editors. Biology of the Reptilia. Volume 16. Ecology B. Defense and Life History. A.R. Liss Inc., New York, NY.

Packard, G.C. and M.J. Packard. 1997. Overwintering strategies of neonatal turtles. Herpetology '97; Abstracts of the Third World Congress of Herpetology, 2-10 August 1997, Prague, Czech Republic. Page 157.

Packard, G.C., M.J. Packard, and W.H.N. Gutzke. 1985. Influence of hydration of the environment on eggs and embryos of the terrestrial turtle *Terrapene ornata*. Physiological Zoology 58:564-575.

Parker, J.W. 1982. Opportunistic feeding by an ornate box turtle under the nest of a Mississippi kite. Southwestern Naturalist 27:365.

Patton, G. 2005. Species Conservation Project Manager, USDA Forest Service, Region 2, Lakewood, CO. Personal communication.

Peters, J.A. 1948. The box turtle as a host for dipterous parasites. American Midland Naturalist 40:472-474.

Peters, K. 1959. A physiological study of the effect of hibernation on the ornate box turtle. Transactions Kansas Academy of Science 62:15-20.

Petit, R.J., A. El Mousadik, and O. Pons. 1998. Identifying populations for conservation on the basis of genetic markers. Conservation Biology 12:844-855.

Platt, S.G., J.L. Stover, and E.J. Stover, III. 2005. An additional record of the ornate box turtle from western South Dakota. Prairie Naturalist 37:123-124.

Rabb, G.B. 1961. Natural history of the ornate box turtle, *Terrapene ornata ornata* Agassiz. Copeia 1961:123-124.

Rainey, D.C. 1953. Death of an ornate box turtle parasitized by dipteran larva. Herpetologica 9:109-110.

Redder, A.J. 1994. Daily and seasonal activity patterns of prairie rattlesnakes (*Crotalus viridis viridis*) in Wyoming. Unpublished M.S. Thesis, University of Wyoming, Cheyenne, WY.

Reichard, K., T. Duncan, H.M. Smith, and D. Chiszar. 1995. Herpetological microbiogeography of Kansas. I: Quantitative summary. Kansas Herpetological Society Newsletter 102:6-10.

Rodeck, H.G. 1949. Notes on box turtles in Colorado. Copeia 1949:32-34.

Rokosky, E.J. 1948. A bot-fly parasite in box turtles. Natural History Miscellanea (32):1-2.

Rose, F.L. 1986. Carapace regeneration in *Terrapene* (Chelonia: Testudinidae). Southwestern Naturalist 31:131-134.

Rose, R. 1978. Observations on natural history of the ornate box turtle (*Terrapene o. ornata*). Transactions of the Kansas Academy of Science 81:171-172.

Rubin, C.S., R.E. Warner, J.L. Bouzat, and K.N. Paige. 2001. Population genetics structure of Blanding's Turtles (*Emydoidea blandingii*) in two suburban Chicago forest preserves. Biological Conservation 99:323-330.

Rubin, C.S., R.E. Warner, D.R. Ludwig, and R. Thiel. 2004. Survival and population structure of Blanding's Turtles (*Emydoidea blandingii*) in two suburban Chicago forest preserves. Natural Areas Journal 24:44-48.

Russell, K.R., D.H. Van Lear, and D.C. Guynn, Jr. 1999. Prescribed fire effects of herpetofauna: a review and management implications. Wildlife Society Bulletin 27(2):374-384.

Samson, F.B. and F.L. Knopf. 1994. Prairie conservation in North America. BioScience 44:418-421.

Sazaki, M., W.I. Boarman, G. Goodlet, and T. Okamoto. 1995. Risk associated with long-distance movement by desert tortoises. Proceedings of the Desert Tortoise Council Symposium 1994:33-48.

Schmidt, K.P. 1938. Herpetological evidence for the postglacial eastward extension of the steppe in North America. Ecology 19:396-407.

Scott, N.J., Jr. 1996. Evolution and management of the North American grassland herpetofauna. Pages 40-53 *in* D.M. Finch, editor. Ecosystem disturbance and wildlife conservation in western grasslands, a symposium proceedings; 22-26 Sept. 1994; Albuquerque, NM. General Technical Report RM-GTR-285 USDA Forest Service, RMFRES, Fort Collins, CO.

Skorepa, A.C. 1966. The deliberate consumption of stones by the ornate box turtle *Terrapene ornata ornata*. Journal of the Ohio Herpetological Society 5:108.

Smith, H.M. and L.W. Ramsey. 1952. A new turtle from Texas. Wasmann Journal of Biology 10:45-54.

Smith, M. 2004. A plea for help from the coordinator of the box turtle partnership of Texas. (8/31/04) Reported in HerpDigest.org 5(1), published by Allen Salzberg.

Sokol, O.M. 1971. Lithophagy and geophagy in reptiles. Journal of Herpetology 5:69-71.

St. Clair, R.C. 1998. Patterns of growth and sexual size dimorphism in two species of box turtles with environmental sex determination. Oecologica 115:501-507.

Sparling, D.W., G. Linder, and C.A. Bishop, editors. 2000. Ecotoxicology of Amphibians and Reptiles. SETAC Press, Pensacola, FL.

Stebbins, R.C. 1985. A Field Guide to Western Reptiles and Amphibians. Houghton Mifflin, Boston, MA.

Stebbins, R.C. 2003. A Field Guide to Western Reptiles and Amphibians. Houghton Mifflin, Boston, MA.

Steen, D.A. and J.P. Gibbs. 2004. The effects of roads on the structure of freshwater turtle populations. Conservation Biology 18:1143-1148.

Steen, D.A., M. Aresco, S.G. Beilke, B. Compton, C.K. Dodd, Jr., H. Forrester, J.W. Gibbons, J. Greene-McLeod, G. Johnson, T. Langen, M.J. Oldham, D.N. Oxier, R. Sammure, F. Schueler, J. Sleeman, L.L. Smith, J. Tucker, and J.P. Gibbs. 2006. Relative vulnerability of female turtles to road mortality. Animal Conservation 9:1-5.

Stickel, L.F. 1978. Changes in a box turtle population during three decades. Copeia 1978: 221-225.

Swarth, C. and S. Hagood. 2005. Summary of the Eastern Box Turtle Regional Conservation Workshop. Humane Society of the United States.

Taggart, T.W. 2006. Kansas Herpetofaunal Atlas. Ornate Box Turtle *Terrapene ornata*, (Agassiz, 1857). Available online at http://webcat.fhsu.edu/ksfauna/herps/index.asp?page=species&species_id=445-982&dots=yes&tributaries=yes&isAnura=&map=ks [Accessed March 2006].

Temple, S.A. 1987. Predation on turtle nests increases near ecological edges. Copeia 1987:250-252.

Thomasson, J.R. 1980. Ornate box turtle, *Terrapene ornata* (Testudinae), feeding on pincushion cactus, *Coryphantha vivipara* (Cactaceae). Southwestern Naturalist 25:483.

Timken, R. 1969. Ornate box turtle distributions in South Dakota. Herpetologica 25:70.

Trail, C.D. 1995. Natural history and habitat use of the ornate box turtle *Terrapene ornata ornata* at a mixed grass prairie in southwest Nebraska. Unpublished M.S. Thesis, University of Nebraska, Omaha, NE.

U.S. Fish and Wildlife Service. 1996. Export of box turtles from the United States in 1996. Federal Register 61(23): 3,894-3,898 (2 February).

Vaughn, T.A. 1961. Vertebrates inhabiting pocket gopher burrows in Colorado. Journal of Mammalogy 42:171-174.

Vogt, R.C. 1980. Natural History of Amphibians and Reptiles in Wisconsin. Milwaukee Public Museum, Milwaukee, WI.

Vogt, R.C. and J.J. Bull. 1982. Temperature controlled sex-determination in turtles: ecological and behavioral aspects. Herpetological 38:156-164.

Wagner, J. 2003. Biologist, Colorado Division of Wildlife, Eaton, CO. Personal communication.

Ward, J.P. 1978. *Terrapene ornata* (Agassiz). Ornate box turtle. Catalogue of American Amphibians and Reptiles 217.1-217.4.

Wilcox, D.S. 1985. Nest predation in forest tracts and the decline of migratory songbirds. Ecology 66:1211-1214.

World Resources Institute. 2004. Grassland fragmentation by roads in the Great Plains. Available online at http://earthtrends.wri.org/text/forests-grasslands-drylands/map-253.html. Page 2000. Washington, D.C.

World Wildlife Fund. 2006. World Wildlife Fund website, Northern Great Plains – Threats. Available online at http://worldwildlife.org/wildplaces/ngp/threats.cfm [Accessed March 2006].

Wyoming Game and Fish Department. 2004. Wild Times. 3(Winter issue):1. Wyoming Game and Fish Department, Cheyenne, WY.

APPENDIX A

Matrix Population Model for the Ornate Box Turtle

Life history model

The life history described by Ernst et al. (1994) provided the basis for a lifecycle graph (**Figure A1**) and a matrix population analysis with a post-breeding census (Cochran and Ellner 1992, McDonald and Caswell 1993, Caswell 2000) for ornate box turtles. The original life table had 31 age classes. Using a self-loop for an "adult" reproductive stage at Stage 15 (arc from Node 15 back to itself in **Figure A1**) greatly simplifies the graph, matrix, and analysis without sacrificing information (McDonald and Caswell 1993). The model has three kinds of input terms: P_i describing survival rates, m_i describing fertility, and B_i describing the probability of reproduction (**Table A1**).

Table A1a shows the symbolic terms in the projection matrix corresponding to the lifecycle graph. **Table A1b** gives the corresponding numeric values. **Table A1c** provides the parameter values for the component terms in the projection matrix. The model assumes female demographic dominance so that, for example, values for fertility are given as female offspring per female. The population growth rate, λ, is 1.000 based on the estimated vital rates used for the matrix. Although this suggests a stable population, the value is subject to the many assumptions used to derive the transitions and should not be interpreted as an indication of the general well-being and stability of the population. Other parts of the analysis provide a better guide for assessment.

Sensitivity analysis

A useful indication of the state of the population comes from the sensitivity and elasticity analyses. Sensitivity is the effect on λ of an absolute change in the vital rates (a_{ij}, the arcs in the life cycle graph [**Figure A1**] and the cells in the matrix, A [**Table A1**]). Sensitivity analysis provides several kinds of useful information (see Caswell 2000, p.118-119).

- ❖ First, sensitivities show "how important" a given vital rate is to λ or fitness. For example, one can use sensitivities to assess the relative importance of survival (P_i) and reproductive (F_i) transitions.

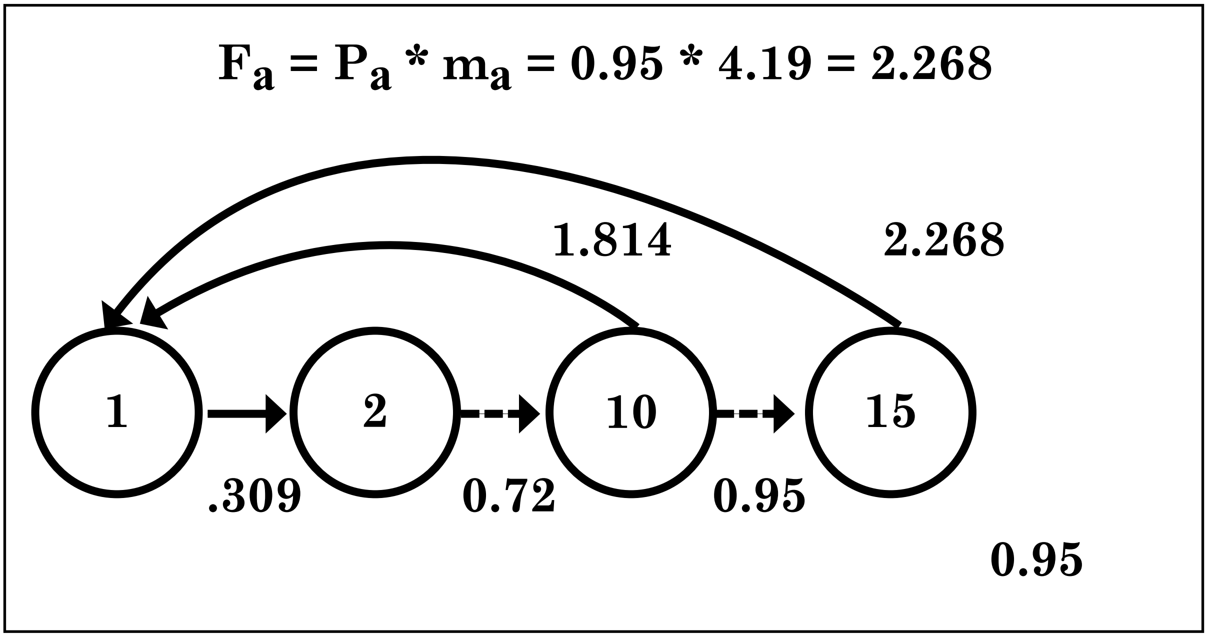

Figure A1. Age-classified life cycle graph for the ornate box turtle. The numbered circles (nodes) represent the 15 stages (including an age-heterogeneous "adult" stage at Node 15). The arrows (arcs) connecting the nodes represent the vital rates – transitions between age-classes such as survival (P_{ji}) or fertility (the arcs pointing back toward the first node from Nodes 10 through 15). Note that reproduction begins in the tenth year, and that the reproductive arcs include terms for survival of female parent (P_i) as well as number of female offspring per female (m_i). Note also the ellipsis of Nodes 2-10 (all with $P_i = 0.72$) for a prereproductive portion of the lifespan and of Nodes 10-15 for the "adult" reproductive stages (all with $P_i = 0.95$ and $F_i = 2.268$).

Table A1. Symbolic, numeric, and parameter values for the component terms that make up the vital rates, **A** (with cells a_{ij}) corresponding to the ornate box turtle lifecycle graph (**Figure A1**).

Table A1a. Symbolic values.

	1	2	3	4	5	6	7	8	9	10	11	12	13	14	15
1										P_aBm_{10}	P_aBm_a	P_aBm_a	P_aBm_a	P_aBm_a	P_aBm_a
2	P_1														
3		P_j													
4			P_j												
5				P_j											
6					P_j										
7						P_j									
8							P_j								
9								P_j							
10									P_j						
11										P_a					
12											P_a				
13												P_a			
14													P_a		
15														P_a	P_a

Table A1b. Numeric values.

	1	2	3	4	5	6	7	8	9	10	11	12	13	14	15
1										1.814	2.268	2.268	2.268	2.268	2.268
2	0.309														
3		0.72													
4			0.72												
5				0.72											
6					0.72										
7						0.72									
8							0.72								
9								0.72							
10									0.72						
11										0.95					
12											0.95				
13												0.95			
14													0.95		
15														0.95	0.95

Table A1c. Parameter values.

Parameter	**Numeric value**	**Interpretation**
m_{10}	3.35	Number of female offspring produced by a female in Stage 10
m_a	4.19	Number of female offspring produced by a fully-developed female
P_{21}	0.305	Annual survival rate of first-year individuals
P_j	0.76	Annual survival rate of prereproductives
P_a	0.95	Annual survival rate of reproductives
B	0.57	Probability of reproduction

- Second, sensitivities can be used to evaluate the effects of inaccurate estimation of vital rates from field studies. Inaccuracy will usually be due to paucity of data, but could also result from use of inappropriate estimation techniques or other errors of analysis. In order to improve the accuracy of the models, researchers should concentrate on transitions with large sensitivities.

- Third, sensitivities can quantify the effects of environmental perturbations, wherever those can be linked to effects on stage-specific survival or fertility rates.

- Fourth, managers can concentrate on the most important transitions. For example, they can assess which stages or vital rates are most critical to increasing λ of endangered species or the "weak links" in the life cycle of a pest. **Figure A2** shows the "possible sensitivities only" matrix for this analysis (one can calculate sensitivities for non-existent transitions, but these are usually either meaningless or biologically impossible – for example, the sensitivity of λ to moving from Age Class 3 to Age Class 2).

In general, changes that affect one type of age class or stage will also affect all similar age classes or stages. For example, any factor that changes the annual survival rate of Age-class 10 females is very likely to cause similar changes in the survival rates of other "adult" reproductive females (those in Stages 11 through 15). Therefore, it is usually appropriate to assess the summed sensitivities for similar sets of transitions (vital rates). For this model, the result is a summed "reproductive" survival sensitivity of 0.692 (57 percent of total), and a summed "prereproductive" sensitivity of 0.384 (32 percent of total), both considerably larger than the sensitivity of λ to the survival rate for eggs (0.11; 9 percent of total). Ornate box turtles show little sensitivity to changes in fertility (the first row of the matrix in **Figure A1**: 0.017 [1.0 percent of total]). *The major conclusion from the sensitivity analysis is that protection of older reproductive females is the key to population viability.*

Elasticity analysis

Elasticities are useful in resolving a problem of scale that can affect conclusions drawn from the sensitivities. Interpreting sensitivities can be somewhat misleading because survival rates and reproductive rates are measured on different scales. For instance,

Figure A2. Possible sensitivities only matrix, $\mathbf{S}_p$ (remainder of matrix consists of zeros). The three transitions to which the λ of ornate box turtles is most sensitive are highlighted: the survival of mature turtles ($s_{15\text{-}15}$ = 0.535), the survival of first-year individuals (Cell s_{21} = 0.111), and the survival of juvenile turtles ($s_{32} = s_{43} = s_{54} = s_{65} = s_{76} = s_{87} = s_{98} = s_{10\text{-}9}$ = 0.048).

	1	2	3	4	5	6	7	8	9	10	11	12	13	14	15
1										0.001	0.001	0.001	0.001	0.001	0.012
2	**0.111**														
3		**0.048**													
4			**0.048**												
5				**0.048**											
6					**0.048**										
7						**0.048**									
8							**0.048**								
9								**0.048**							
10									**0.048**						
11										0.035					
12											0.033				
13												0.031			
14													0.030		
15														0.028	**0.535**

a change of 0.5 in survival may be a large alteration (e.g., a change from a survival rate of 90 to 40 percent). On the other hand, a change of 0.5 in fertility may be a very small proportional alteration (e.g., a change from a clutch of 3,000 eggs to 2,999.5 eggs). Elasticities are the sensitivities of λ to proportional changes in the vital rates (a_{ij}) and thus largely avoid the problem of differences in units of measurement. The elasticities have the useful property of summing to 1.0. The difference between sensitivity and elasticity conclusions results from the weighting of the elasticities by the value of the original arc coefficients (the a_{ij} cells of the projection matrix). Management conclusions will depend on whether changes in vital rates are likely to be absolute (guided by sensitivities) or proportional (guided by elasticities). By using elasticities, one can further assess key life history transitions and stages as well as the relative importance of reproduction (F_i) and survival (P_i) for a given species.

Elasticities for ornate box turtles are shown in **Figure A3**. The λ of ornate box turtles is most elastic to changes in the survival of the "adult" reproductive females (the multi-age Stage 15 females and those in Age-classes 11 through 14), followed by the survival of "prereproductive" females (Age-classes 2 through 9) and of eggs. The sensitivities and elasticities for ornate box turtles correspond in the relative magnitude of the most important kinds of transitions, a phenomenon that is not always the case in other life histories (*cf.* Townsend's big-eared bat, plains killifish). Note, however, that the elasticities for survival are more even through the early age-classes than are the sensitivities, for which first-year survival dominates. *The survival rates, especially those of older reproductive females, are the data elements that warrant careful monitoring in order to refine the matrix demographic analysis*.

Partial sensitivity and elasticity

Partial sensitivity and elasticity analysis assesses the impact on λ of changes in "lower-level terms" (Caswell 2000, pp. 218 and 232). Some transitions (e.g., the F_i) include lower-level component terms (P_i, m_i, and B_i) related to the different kinds of transitions in the life cycle (e.g., survival, fertility, and breeding probability terms). Partial sensitivity results indicate that changes in the P_i (survival rates) will have by far the greatest impact on λ (94.2 percent of the total partial sensitivity). Changes in fertility (m_i) will have far less impact on λ (0.7 percent of the total partial sensitivity). Changes in probability of reproduction (Bi) will also have less impact on λ (5.1 percent of the total partial sensitivity). Similarly, P_i terms account for 93.1 percent of the total partial elasticity, with 3.5 percent accounted for by m_i terms, and the other 3.5 percent accounted for by B_i terms. Again, *every aspect of the analysis suggests that ornate box turtles are most susceptible*

Figure A3. Elasticity matrix, E (blank elements are zeros). The λ of ornate box turtles is most elastic to changes in the survival of adults ($e_{15\text{-}15}$ = 0.508) followed by the survival of first-year individuals and juveniles ($e_{21} = e_{32} = e_{43} = e_{54} = e_{65} = e_{76} = e_{87} = e_{98} = e_{10\text{-}9}$ = 0.034).

	1	2	3	4	5	6	7	8	9	10	11	12	13	14	15
1										0.0014	0.0016	0.0016	0.0015	0.0014	0.0268
2	**0.034**														
3		**0.034**													
4			**0.034**												
5				**0.034**											
6					**0.034**										
7						**0.034**									
8							**0.034**								
9								**0.034**							
10									**0.034**						
11										0.033					
12											0.031				
13												0.030			
14													0.028		
15														0.027	**0.508**

to habitat degradation that affects the survival of older reproductive females.

Other demographic parameters

The stable (st)age distribution (SSD; **Table A2**) describes the proportion of each Stage (or Age-class) in a population at demographic equilibrium. Under a deterministic model, any unchanging matrix will converge on a population structure that follows the stable age distribution, regardless of whether the population is declining, stationary or increasing. Under most conditions, populations not at equilibrium will converge to the SSD within 20 to 100 census intervals. For ornate box turtle at the time of the post-breeding annual census (just after the end of the breeding season), eggs represent 41 percent of the population, another 42 percent consists of juvenile stages, and the remaining 18 percent consists of adult stages.

Reproductive values (**Table A3**) can be thought of as describing the “value” of a stage as a seed for population growth relative to that of the first (newborn or, in this case, egg) stage. The reproductive value of the first stage is always 1.0. A female individual in Stage 2 is “worth” 3.2 female eggs, and so on (Caswell 2000). The reproductive value is calculated as a weighted sum of the present and future reproductive output of a stage discounted by the probability of surviving (Williams 1966). As in many species with large clutch sizes, the peak reproductive value (45.3 at Stage 11 and older) is considerably higher than that of the eggs (**Table A3**). Again, we see that "adult" reproductive females are the most important stage in the life cycle. The cohort generation time for ornate box turtles is 29.2 years (SD = 19.5 years). The mean age of females in the final mixed-age stage (Node 15 in the life cycle diagram) is 33.0 years (SD = 19.5 years).

Stochastic model

We conducted a stochastic matrix analysis for ornate box turtles. We incorporated stochasticity in several ways, by varying different combinations of vital rates or by varying the amount of stochastic fluctuation (**Table A4**). Under Variant 1 we altered the values for fertility (F_i). Under Variant 2 we varied only first-year survival, while under Variant three we varied all the survival rates. Under Variant 4 we varied only the survival of the "adult" female self-loop, $P_{15,15}$. Variants 5 and 6 consisted of other combinations of the various survival and fertility transitions (**Table A4**). Each run consisted of 2,000 census intervals (years) beginning with a population size of 10,000 distributed according to the Stable Stage Distribution (SSD) under the deterministic model. Beginning at the SSD helps avoid the effects of transient, non-equilibrium dynamics. The overall simulation consisted of 100 runs (each with 2,000 cycles). We varied the amount of fluctuation by changing the standard deviation of the random normal distribution from which the stochastic vital rates were selected. The default value was a standard deviation of

Table A2. Stable stage distribution (right eigenvector) for female ornate box turtles.

Stage	Description	Proportion
1	First-year individuals	0.405
2	Prereproductive	0.125
3	" "	0.090
4	" "	0.065
5	" "	0.047
6	" "	0.034
7	" "	0.024
8	" "	0.017
9	" "	0.013
10	First reproduction (m_i = 3.35)	0.009
11	Reproductive (m_i = 4.19)	0.009
12	" "	0.008
13	" "	0.008
14	" "	0.007
15	Reproductive (m_i = 4.19) ≥ Age Class 15	0.140

Table A3. Reproductive values for females. Reproductive values can be thought of as describing the "value" of an age class as a seed for population growth relative to that of the first (newborn or, in this case, egg) age class. The reproductive value of the first age class is always 1.0. The peak reproductive values are bolded.

Stage	Description	Proportion
1	Eggs	1.00
2	Prereproductive	3.24
3	" "	4.50
4	" "	6.24
5	" "	8.67
6	" "	12.05
7	" "	16.73
8	" "	23.24
9	" "	32.28
10	First reproduction (m_i = 3.35)	44.84
11	Reproductive (m_i = 4.19)	**45.29**
12	" "	**45.29**
13	" "	**45.29**
14	" "	**45.294**
15	Reproductive (m_i = 4.19) ≥ Age Class 15	**45.29**

one quarter of the "mean" (with this "mean" set at the value of the original matrix entry [vital rate], a_{ij} under the deterministic analysis). Variants 7 and 8 affected the same transition as Variant 4 ($P_{15,15}$) but with lower levels of variability (SD was one sixth or one eighth of the mean). We calculated the stochastic growth rate, *logλs*, according to Eqn. 14.61 of Caswell (2000), after discarding the first 1,000 cycles in order to further avoid transient dynamics.

The stochastic model (**Table A4**) produced two major results. First, altering only the "oldest adult" survival rate, $P_{15,15}$, had a much more dramatic effect on λ than did altering the entire set of fertility transitions. This "oldest adult" survival rate is the self-loop on the last node of **Figure A4**. As an example of the contrasting effects, the median ending size under the changed fertilities of Variant 1 (11,973) was essentially the same as the starting size of 10,000. In contrast, varying the survival of the oldest females under Variant 4 resulted in a median ending size of 502.9. This difference in the effects of stochastic variation is predictable from the sensitivities and elasticities. λ was much more sensitive and elastic to changes in $P_{15,15}$ than it was to the entire set of fertilities, F_i. Second, large-effect stochasticity has a negative effect on population dynamics. This negative effect occurs despite the fact that the average vital rates remain the same as under the deterministic model -- the random selections are from a symmetrical distribution. This apparent paradox is due to the lognormal distribution of stochastic ending population sizes (Caswell 2000). The lognormal distribution has the property that the mean exceeds the median, which exceeds the mode. Any particular realization will therefore be most likely to end at a population size considerably lower than the initial population size. For ornate box turtles under the adult survival Variant 4, 94 out of 100 trials of stochastic projection went to extinction vs. 0 under the fertility Variant 1. Variant 8 shows that the magnitude of fluctuation has a potentially large impact on the detrimental effects of stochasticity. Decreasing the magnitude of fluctuation also decreased the severity of the negative impacts -- the number of extinctions went from 94 in Variant 4 to 10 in Variant 8 when the magnitude of fluctuation was halved.

These results suggest that populations of ornate box turtles are relatively tolerant to stochastic fluctuations in production of eggs (due, for example, to annual climatic change or to human disturbance) but extremely vulnerable to variations in the survival of adult stages. Pfister (1998) showed that for a wide range of empirical life histories, high sensitivity or elasticity was negatively correlated with high rates of temporal variation. That is, most species appear to have responded to strong selection by having low variability for sensitive transitions in their life cycles. A possible concern is that anthropogenic impacts may

Table A4. Summary of stochastic projection for ornate box turtles. Eight variants of the stochastic models are projected.

	Variant 1	**Variant 2**	**Variant 3**	**Variant 4**	**Variant 5**	**Variant 6**	**Variant 7**	**Variant 8**
Input factors:								
Affected cells	F_i	P_{21}	P_i	$P_{15\text{-}15}$	$P_i + P_{15\text{-}15}$	$F_i + P_{21}$	$P_{15\text{-}15}$	$P_{15\text{-}15}$
S.D. of random normal distribution	1/4	1/4	1/4	1/4	1/4	1/4	1/6	1/8
Output values:								
Deterministic λ	1.00007	1.00007	1.00007	1.00007	1.00007	1.00007	1.00007	1.00007
# Extinctions / 100 trials	0	0	0	94	96	0	36	10
Mean extinction time	—	—	—	951.6	884.6	—	1,491.6	1,775.8
# Declines / # surviving populations	29/100	35/100	74/100	6/6	4/4	54/100	59/64	77/90
Mean ending population size	11,972.8	11,505.2	9,708.1	1,147.1	70.8	10,742.4	5,784.4	9,324.3
Standard deviation	3,988.2	4,484.7	19,163.0	1,781.9	72.9	7,149.0	26,602.9	39,947.2
Median ending popluation size	11,182.17	10,453.86	2,966.05	502.92	55.61	9,168.34	53.82	299.86
Log λ_s	0.0000478	0.0000572	-0.0006689	-0.009343	-0.01074	-0.0000513	-0.00396	-0.001667
λ_s	1.0000	1.0001	0.9993	0.9907	0.9893	0.9999	0.9960	0.9983
% reduction in λ	0.002497	0.00155719	0.07414	0.937117	1.076	0.0124062	0.402383	0.1740

induce variation in previously invariant vital rates (such as annual adult survival), with consequent detrimental effects on population dynamics.

Potential refinements of the models

Clearly, the better the data on survival rates, the more accurate the resulting analysis will be. Data from natural populations on the range of variability in the vital rates would allow more realistic functions to model stochastic fluctuations. For example, time series based on actual temporal or spatial variability would allow construction of a series of "stochastic" matrices that mirrored actual variation. One advantage of such a series would be the incorporation of observed correlations between variation in vital rates. Where we varied F_i and P_i values simultaneously, we assumed that the variation was uncorrelated, based on the assumption that factors affecting reproduction and, for example, overwinter survival would occur at different seasons or be due to different and likely uncorrelated factors (e.g., predation load vs. climatic severity or water levels). Using observed correlations would improve on this assumption by incorporating forces that we did not consider. Those forces may drive greater positive or negative correlation among life history traits. Other potential refinements include incorporating density-dependent effects. At present, the data appear insufficient to assess reasonable functions governing density dependence.

References

Caswell, H. 2000. Matrix Population Models: Construction, Analysis, and Interpretation. Second Edition. Sinauer Associates, Sunderland, MA.

Cochran, M.E. and S. Ellner. 1992. Simple methods for calculating age-based life history parameters for stage-structured populations. Ecological Monographs 62:345-364.

Ernst, C.H., J.E. Lovich, and R.W. Barbour. 1994. Turtles of the United States and Canada. Smithsonian Institution Press, Washington, D.C.

McDonald, D.B. and H. Caswell. 1993. Matrix methods for avian demography. Pages 139-185 *in* D. Power, editor. Current Ornithology. Vol. 10. Plenum Press, New York, NY.

Pfister, C.A. 1998. Patterns of variance in stage-structured populations: Evolutionary predictions and ecological implications. Proceedings of the National Academy of Sciences USA 95:213-218.

Williams, G.C. 1966. Natural selection, the costs of reproduction, and a refinement of Lack's principle. American Naturalist 100:687-690.

APPENDIX B

Envirogram for the Ornate Box Turtle