# CONSERVATION BIOLOGY OF FRESHWATER TURTLES AND TORTOISES

## A Compilation Project of the
## IUCN/SSC Tortoise and Freshwater Turtle Specialist Group

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*Terrapene ornata* (Agassiz 1857) –
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Desert Box Turtle, Tortuga de Caja Ornamentada

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# *Terrapene ornata* (Agassiz 1857) – Ornate Box Turtle, Plains Box Turtle, Western Box Turtle, Desert Box Turtle, Tortuga de Caja Ornamentada

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**SUMMARY. – The Ornate Box Turtle, *Terrapene ornata* (family Emydidae), a terrestrial species of North American prairies and grasslands, is recognized by its brown to black shell with light yellow to orange radiating lines on each scute. This species inhabits mostly open, semiarid to xeric environments; forest, desert, and cropland habitats can be used, but prairies are preferred, and soft substrates are critical for burrowing and nesting behaviors. Males can be distinguished by a thickened, inwardly curved inner hindtoe and a generally smaller adult body size, reaching a maximum straight-line carapace length (SCL) of 157 mm, while females can attain 170 mm SCL, but most mean sizes of adults are <130 mm SCL. Sexual maturity is reached in males at 8–9 years and 100–109 mm SCL, while females mature at 10–11 years and 110–119 mm SCL, with some geographic variation noted for these patterns. Male home ranges are, on average, 6% larger than those of females. Home-range philopatry is common, with mean yearly overlap often exceeding 40%, and some individuals with over 80% overlap between years. Above-ground activity extends from March to November in most populations, but individuals from southern sites may be surface-active in winter months. Copulations have been observed from April to October with peaks during ingress and egress from overwintering sites. Daily activity is maximal in the morning and afternoon, with reduced mid-day activity and increased activity after rain. Males are generally more active than females, especially during mate-seeking in spring and fall. Nesting occurs seasonally from mid-May through mid-July. Clutch size ranges from 1 to 8 eggs, with most mean estimates of 2–4 eggs. Production of a second clutch within a season occurs but is uncommon, and not all females nest annually. Hatchlings typically overwinter below the nest. Peripheral populations, particularly the fragmented ones across the Upper Midwest, are the most vulnerable to extirpation. Habitat modifications, especially grassland succession to forests, prairie conversion to agriculture, and road construction, pose the primary threats to this species. Populations in the core of its range (Nebraska to Texas), are likely more stable, but poaching for illegal trade, collecting for turtle races, and vehicle collisions remain serious concerns. Conservation efforts should focus on maintaining, expanding, and properly managing prairie habitats with *T. ornata*, especially in the Midwest.**

**DISTRIBUTION. – USA, Mexico. *Terrapene ornata* occurs in the Great Plains ecosystem throughout the central and midwestern USA with the core range from Nebraska south to Texas. In the northern reaches of the Midwest (Great Plains), the species is known from south central South Dakota, southwestern Wisconsin, and northwestern Indiana; in the eastern Midwest, it is known from southern Illinois, southwestern Indiana, eastern Iowa, Missouri, central Arkansas, and southern Louisiana; and in the west central USA, it is known from southeastern Wyoming, eastern Colorado, and southeastern Arizona. The southern extent of the species range in the USA occurs in southern Texas and along the Gulf Coast to Louisiana. In Mexico, the species is

found in the northern reaches of the northern states of Chihuahua and Sonora, and its range is presumed to extend through southwestern Texas into Coahuila.

SYNONYMY. – *Cistudo ornata* Agassiz 1857, *Terrapene ornata, Terrapene ornata ornata, Terrapene carolina ornata, Terrapene ornata cimarronensis* Cragin 1894, *Terrapene longinsulae* † Hay 1908, *Terrapene ornata longinsulae, Terrapene whitneyi* † Hay 1916, *Terrapene ornata luteola* Smith and Ramsey 1952.

SUBSPECIES. – Two have been described, but are not currently uniformly recognized: 1) *Terrapene ornata ornata* (Plains or Western Box Turtle) (Agassiz 1857), distributed in the USA from South Dakota and Wisconsin in the North, Indiana in the East, Colorado in the West, and Texas to the border with Mexico in the South (possibly in Coahuila); and 2) *Terrapene ornata luteola* (Desert Box Turtle) Smith and Ramsey 1952, distributed in the USA from central New Mexico and western Texas to southern Arizona and in northern Mexico from the states of Chihuahua and Sonora.

STATUS. – IUCN 2024 Red List: Near Threatened (NT, assessed 2011). CITES: Appendix II, as *Terrapene* sp. (1995). NatureServe Global Conservation Status Rank: G5–Secure. USA: Arizona (Species of Greatest Conservation Need; S2—Imperiled); Arkansas (Species of Greatest Conservation Need; S2—Imperiled); Illinois (Threatened; S2—Imperiled); Indiana (Endangered; S1—Critically Imperiled); Iowa (Threatened and Species of Greatest Conservation Need; S2—Imperiled); Louisiana (S1—Critically Imperiled); South Dakota (Species of Greatest Conservation Need; S3—Vulnerable); Texas (S3—Vulnerable); Wisconsin (Endangered; S1—Critically Imperiled); Wyoming (S1—Critically Imperiled). No threatened designation exists for Colorado, Kansas, Nebraska, Missouri, New Mexico, or Oklahoma.

**Taxonomy**. — The Ornate Box Turtle (*Terrapene ornata*) was originally described as *Cistudo ornata* (Agassiz 1857) and was later reclassified into the genus *Terrapene* (Baur 1891, 1893). The early taxonomic work distinguished *T. ornata* from its congeners primarily based on differences in skeletal structure and distinct phalangeal formula (Taylor 1895). These studies also highlighted the distinct habitat preferences of *T. ornata* compared to those of other members of the genus *Terrapene*. Numerous morphological studies have since provided deeper insights into the relationships between *T. ornata* and its congeners (Legler 1960; Milstead and Tinkle 1967; Milstead 1967, 1969; Minx 1992, 1996). Most of these studies recognized the Sonoran Box Turtle (*T. nelsoni* Stejneger 1925) as the sister species to *T. ornata* (Thomson et al. 2021). The species status of *T. ornata* has not been questioned and has been consistently upheld by studies of both morphology (Milstead 1967, 1969; Milstead and Tinkle 1967; Minx 1992, 1996) and genetics (Feldman and Parham 2002; Stephens and Wiens 2003; Martin et al. 2013, 2020, 2021).

Indeed, both fossils and genes indicate a Miocene divergence date around 18 million years ago between *T. ornata* / *T. nelsoni* and *T. carolina* / *T. mexicana* / *T. triunguis,* and a divergence date of about 10 million years between *T. ornata* and its sister species *T. nelsoni* (Holman and Corner 1985; Holman and Fritz 2005; Martin et al. 2013, 2021). However, a recent dated nuclear DNA



**Figure 1.** Adult female *Terrapene ornata ornata* from Johnson County, Iowa, USA. Photo by Daniel F. Hughes.

phylogenetic analysis of most turtle species (Thomson et al. 2021) estimated divergence times among *Terrapene* lineages to be earlier than those above, with the divergence between *T. ornata* and *T. carolina* / *T. mexicana* / *T. triunguis* at about 12 million years ago (Miocene) and between *T. ornata* and its sister species *T. nelsoni* at about 3 million years ago (Pliocene). Although hybridization between *T. ornata* and its congeners occurs, genomic evidence suggests that this happens infrequently and without subsequent backcrossing or introgression into the parental populations (Martin et al. 2020; but see Cureton et al. 2009, 2011). The fossil record for *T. ornata* extends into the Miocene (Milstead 1967; Holman and Fritz 2005; TEWG 2015), with fossils into the late Pliocene for Arizona (Moodie and Van Devender 1978). *Terrapene ornata* has been considered a permanent resident of the Great Plains since at least the mid-Pliocene (Preston 1979).

Within *T. ornata*, two subspecies have been described and both have been historically recognized: *Terrapene ornata ornata* (Agassiz 1857) and *Terrapene ornata luteola* Smith and Ramsey 1952. A third alleged subspecies, *Terrapene ornata longinsulae* † Hay 1908, was described based on fossils. However, this extinct taxon likely represented either *T. o. ornata* or *T. o. luteola* as the morphological characters used for its classification were deemed unreliable (Dodd 2001; but see Holman and Fritz 2005). Milstead (1969) suggested that *T. o. longinsulae* was morphologically indistinguishable from *T. o. luteola*, which was later corroborated by Joyce et al. (2012).

The taxonomic status of the subspecies *T. o. ornata* and *T. o. luteola* remains a topic of considerable interest and debate (Herrmann and Rosen 2009). Recent phylogenetic studies have cast doubt on the distinction of these subspecies (Martin et al. 2013, 2020, 2021), since the genetic differences were not as pronounced as previously thought, suggesting that the morphological and ecological differences between them may be more apparent than real. As a result, TTWG (2021) recently agreed that *T. o. luteola* belonged in the synonymy of a monotypic *T. ornata,* based largely on molecular data of Martin et al. (2021) and the morphological data provided by Minx (1996), which was contrary to the taxonomy in their previous listing (TTWG 2017). TTWG (2021) made this taxonomic change with the caveat "that more complete genetic sampling may revise this decision." We note that The Reptile Database has not recognized this taxonomic change (Uetz et al. 2024). Given the lack of consensus among taxonomic authorities, the historical recognition of both subspecies, and the taxonomic freedom sanctioned by the International Code of Zoological Nomenclature (ICZN 1999), we have elected to continue to recognize *T. o. luteola* in this account.
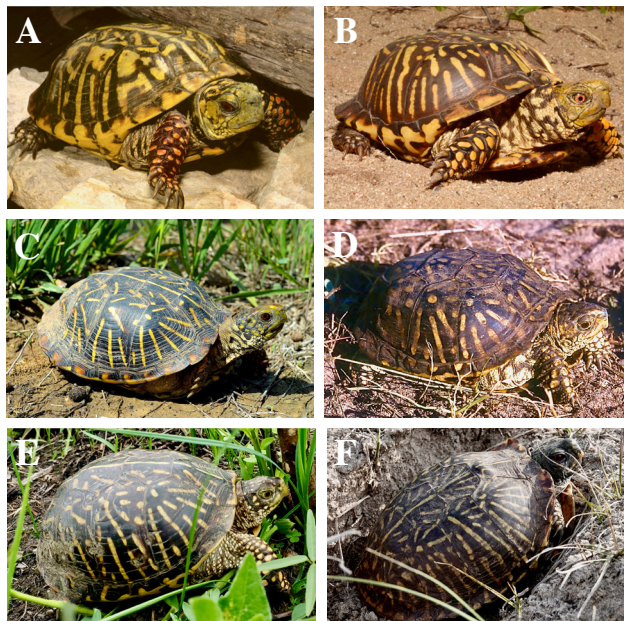


**Figure 2.** *Terrapene ornata ornata* from various localities across its range. **A**. Rooks County, Kansas. Photo by Suzanne Collins. **B**. Johnson County, Iowa. Photo by Daniel F. Hughes. **C**. Barton County, Kansas. Photo by Jeffrey E. Dawson. **D**. Garden County, Nebraska. Photo by John B. Iverson. **E**. Shawnee County, Kansas. Photo by Benjamin M. Reed **H**. Cherry County, Nebraska. Photo by Colin Croft.
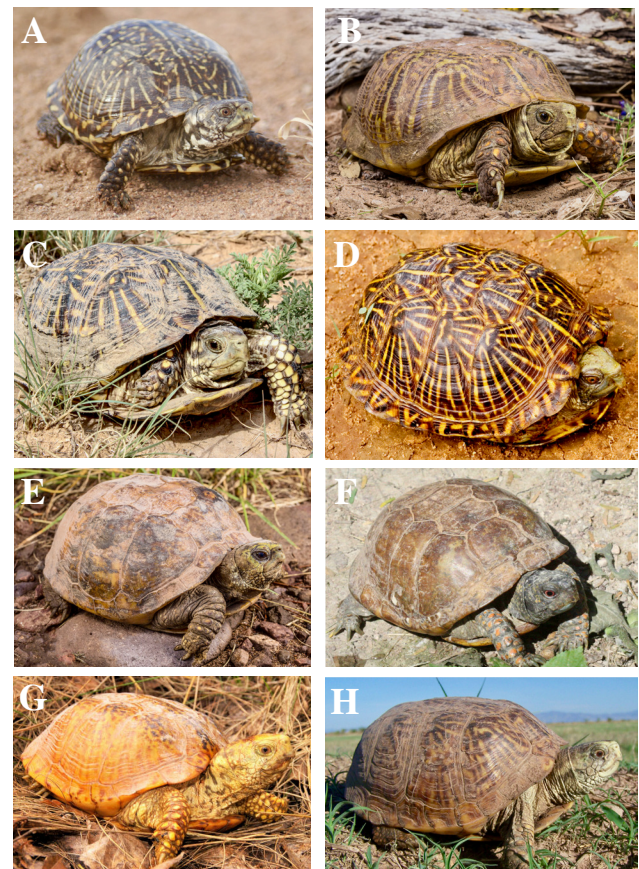


**Figure 3.** *Terrapene ornata luteola* from various localities across its range. **A**. Socorro County, New Mexico. Photo by David J. Germano. **B, C**. Hudspeth County, Texas. Photos by Frank Portillo. **D**. Hidalgo County, New Mexico. Photo by Patrick Alexander. **E**. Jeff Davis County, Texas. Photo by Frank Portillo. **F, G**. Cochise County, Arizona. Photos by Scott Loarie (F) and Brian D. Horne (G). **H**. Chihuahua, Mexico. Photo by Ana Colima.
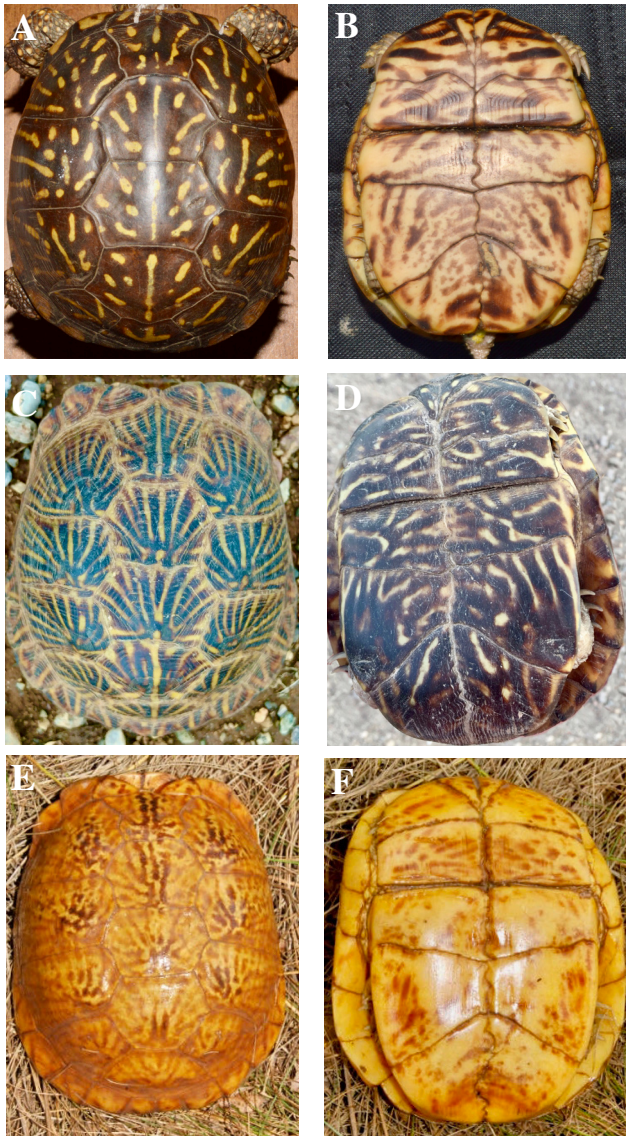
**Figure 4.** *Terrapene ornata ornata* (A, B) and *Terrapene ornata luteola* (C, D, E, F). **A, B**. Johnson County, Iowa. Photos by Daniel F. Hughes. **C, D, E, F**. Cochise County, Arizona. Photos by Casey Richart (C), C.K. Kelly (D), and Brian D. Horne (E, F).

While genetic and morphological data indicate a close relationship between the subspecies, *T. o. ornata* and *T. o luteola* may represent important conservation, ecological, and/or Evolutionarily Significant Units (ESUs) or Management Units (MUs) (i.e., ecotypes) in which recognizing localized or regional population distinctions could be crucial to understanding the adaptive capacity and variation within the species as a whole. Given very recent origins and distinct habitat preferences, these subspecies (or ecotypes) would be ideal systems for exploring ecological drivers of divergence in closely related groups, an infrequently studied topic for long-lived vertebrates generally and for terrestrial chelonians specifically. Our perspective emphasizes the need for integrative conservation strategies that are sensitive to such fine-scale ecological and evolutionary differences, acknowledging that even recently diverged populations can possess distinction. Ongoing research in this question is vital for informing conservation efforts, ensuring that both of these ecologically distinctive populations are adequately protected and managed in the face of environmental changes and habitat fragmentation.

*Phylogeography*. — Despite differences in habitat use, distribution, and coloration between the subspecies of *T. ornata*, there is weak genetic differentiation, as evidenced from both mitochondrial DNA and broader genomic studies, which generally recover the subspecies as paraphyletic (Martin et al. 2013, 2021; but see Herrmann and Rosen 2009). These results suggest that *T. o. ornata* and *T. o. luteola* may be in the midst of divergence, driven by parapatric adaptation to different habitats with lagging genetic separation. Phylogeographically, *T. ornata* populations likely closely tracked grasslands during the Pleistocene that expanded and contracted between shifts in pluvial periods, which would have allowed individuals to cross the Rocky Mountains Corridor several times (Auffenberg and Milstead 1965). Perhaps, *T. o. luteola* originated from a relict population that became isolated after a climatic shift expanded forests across the Rocky Mountain Corridor, thus limiting its connectivity to other populations of *T. o. ornata* (Auffenberg and Milstead 1965). This scenario could account for its recent divergence in the respectively distinct habitats. Today, there is a wide intergradation zone through suitable habitat across much of New Mexico that could be contributing to the limited morphological and genetic divergence of *T. o. luteola* from the nominate subspecies (i.e., Legler 1960), but more genetic sampling across this contact zone would improve our understanding of the divergence process in this long-lived ectotherm.

There do not appear to be any distinct or isolated populations that are genetically divergent and require special consideration (Martin et al. 2021), which is likely due to long lifespans in a previously homogenous habitat across much of the Great Plains and the Prairie Peninsula. In a small, relictual Illinois population, Kuo and Janzen (2004) detected a recent genetic bottleneck, which had little effect on the level of genetic diversity in the population. Subpopulations in Iowa were within a normal range of heterozygosity, but the level of genetic divergence indicated that they had separated from a once larger population that is now fragmented (Richtsmeier 2005; Richtsmeier et al. 2008). In Texas, Cureton et al. (2014) found that an apparently isolated population experiencing moderate levels of road mortality exhibited high genetic diversity and modest inbreeding, but was not genetically distinct from nearby populations.

**Description**. — The Ornate Box Turtle (*Terrapene ornata*) is a small, terrestrial turtle in the family Emydidae with apparently different maximum straight-line carapace
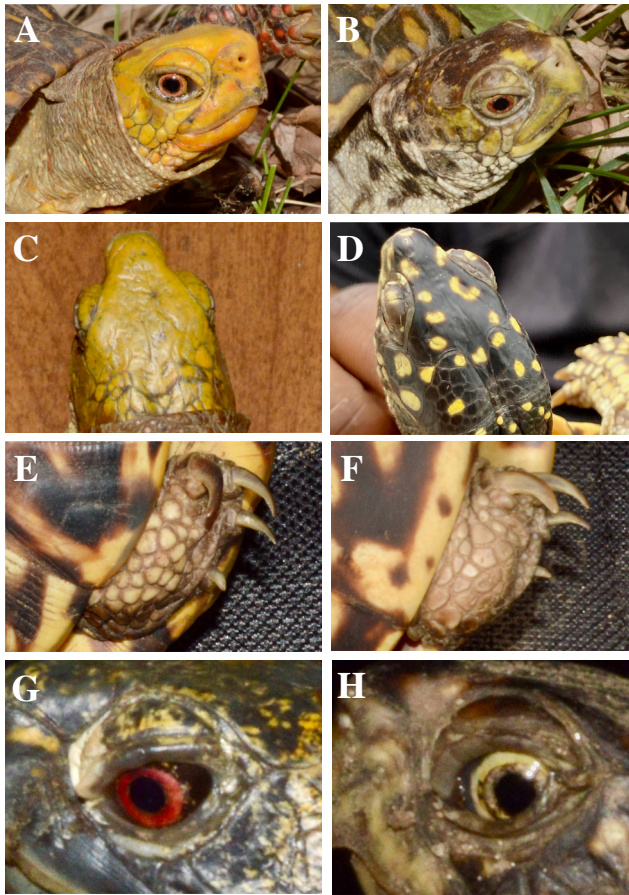
**Figure 5.** Comparison of secondary sexual characteristics that aid in discriminating between adult male (*left column*) and adult female (*right column*) *Terrapene ornata ornata*. Male traits include generally more yellow-green coloration on the top of the head (A, C). Females usually have more brown coloration on the head with yellow speckling (B, D). Males have a larger and more curved inner (medial) toenail on the hind feet (E) compared to females (F). Males tend to have a redder iris (G) compared to females (H), but this is variable (compare A and B). All individuals from Johnson County, Iowa. Photos by Daniel F. Hughes.

lengths (SCL) for the two subspecies. Ernst and Lovich (2009) recorded maximum SCLs in USA populations of 154 mm in females and 130 mm in males, but Legler and Vogt (2013) provided maximum SCLs in Mexican populations of 170 mm in females and 157 mm in males for the generally larger subspecies (*T. o. luteola*).

However, mean SCL values for studied populations are often significantly smaller than these maximum values, and even the values provided by Ernst and Lovich (2009) seem large, compared to the numerous the studies that we examined which encompass measurements of thousands of individuals (see References). For example, Iverson (2024) reported a mean female SCL of 107.6 mm (range, 84.5–132.0 m, $n = 714$) and a mean male SCL of 106.5 mm (range, 88.2–126.8 mm, $n = 386$) at his study site in Nebraska, and also reported mean female SCLs from several studies across the species' range which varied from 126 mm in Arizona to 103.5 mm in Illinois.

In general, the carapace of *T. ornata* has brown to black background coloration with light yellow to orange lines arranged in a radiating pattern on each pleural and vertebral scute. The lines are sometimes complete but can also be fragmented or even appear to be mottled. There is usually a complete middorsal yellow stripe on the domed carapace, which sometimes has a slight middorsal keel. The carapace is occasionally flattened, at least partially, especially at its most dorsal aspect. The plastron also has a dark background coloration with similar radiating lines on each scute, but the lines are usually thicker than those on the carapace.

The skin is usually deep brown or black on the limbs and a lighter brown, yellow, or cream in places between the carapace and plastron. Individual scales on the limbs are frequently adorned with a bright, circular color patch that can be red, orange, or yellow and is more common on scales of the forelegs than those on the hindlegs.

The plastron is hinged at the junction between the pectoral and abdominal scutes. The plastron is usually as long, or slightly longer, than the carapace. Flaring of the posterior marginal scutes occurs in both sexes, often more obvious in older individuals.

There has been one report of albinism in a wild individual from Oklahoma (Bigham 1976) and another of kyphoscoliosis (Fox 1941). A synopsis of major osteology, type specimens, and distribution records was provided by Ward (1978).

The species has 24 microchomosomes and 26 macrochromosomes ($2n = 50$), 16 of which are metacentric, 6 submetacentric, and 4 telocentric (Bickham 1981; Bickham and Baker 1976; Killebrew 1977; Stock 1972).

*Subspecies Distinctions*. — The two subspecies, *T. o. ornata* (Figs. 1–2, 4) and *T. o. luteola* (Figs. 3–4), are nearly indistinguishable morphologically and genetically, but differ in geographic distribution and somewhat in shell pattern. For example, the most comprehensive morphological and genetic analyses indicated only weak differentiation between these two subspecies (Minx, 1992, 1996; Martin et al. 2013, 2020, 2021). Nevertheless, the radiating light-colored lines on carapace scutes are usually more numerous, thinner, and of a lighter shade in populations of *T. o. luteola*, which is restricted to the southwestern portion of the species' range. Furthermore, there are typically 5–9 radiating lines on the pleural scutes in the nominate subspecies (Figs. 1–2, 4), whereas there are usually 10–16 lines present on *T. o. luteola* (Figs. 3–4). Further distinctions are related to the size dimensions of the plastron (Ward 1978). In addition to a geographic restriction to the areas within the northern Chihuahuan Desert and the greater number of radiating lines on its scutes, *T. o. luteola* can sometimes be distinguished by a propensity to have a more uniform coloration on the carapace in older adults, which can be almost fully brown, pale yellow, or straw-colored (Figs.

**Figure 6.** Carapace and plastron of two hatchling *Terrapene ornata ornata* from Johnson County, Iowa. Photos by Daniel F. Hughes.



**Figure 7.** Hatchlings of *Terrapene ornata* subspecies. *Left*: *Terrapene ornata ornata* with egg tooth, Garden County, Nebraska. Photo by John B. Iverson. *Right*: *Terrapene ornata luteola*, Socorro County, New Mexico. Photo by David J. Germano.

3–4). In fact, the subspecies name *luteola* is Latin for yellowish, in reference to the general shell coloration.

*Sexual Dimorphism*. — Adult males of *T. ornata* can be differentiated from adult females through the presence of a combination of traits (Fig. 5). Males are most effectively identified by the presence of a larger, inwardly curved inner (medial) hindfoot toenail, a slightly concave plastral hindlobe, and a thicker tail with the cloaca extending past the distal end of the plastron. In addition, males tend to have a uniformly yellow-green dorsum on the head (usually brown with yellow spots in females), red iris (yellow, brown, or orange in females, but occasionally red), and a smaller body size (females are generally larger). Females also tend to have a more domed carapace (Legler 1960) and a proportionally larger pelvic canal than males (Long and Rose 1989). When extruded, the penis is a dark color, extends beyond the tail tip and has a tapered shape with two lighter spots on its posterior aspect. Iris color changes have been noted (Bernstein, pers. obs.) in a similar manner to that observed in *T. carolina* (Carlson et al. 2020).

*Hatchlings*. — Hatchling appearance is generally more muted in color with less striking patterns than juveniles and adults (Fig. 6). For example, compared to adults, the typically yellow markings on the carapace and plastron are more cream in color, the background pattern is a lighter

brown, and the radiating lines on scutes are fewer, rounder, and less clearly defined. The middorsal stripe is usually apparent on the carapace of hatchlings. The umbilical scar on the plastron is distinct but usually fades by the second year. Hatchlings are more rounded in shell proportions compared to the eggs from which they hatched. Hatchlings of *T. o. luteola* appear similar in coloration to those of *T. o. ornata* (Fig. 7).

**Distribution**. — *Terrapene ornata* is distributed in mostly prairie habitats across the central, midwestern, and southwestern USA and northern Mexico (Fig. 8), with northern occurrences in south central South Dakota (Ballinger et al. 2000), Nebraska (Hudson 1985; Ballinger et al. 2010), southwestern Wisconsin (Vogt 1981; Kapfer and Brown 2022), Iowa (LeClere 2013; VanDeWalle and Bernstein 2024); eastern occurrences in western Indiana (Minton 2001), Illinois (Smith 1961), Missouri (Johnson 2000), central Arkansas (Trauth et al. 2004), and western Louisiana (Boundy and Carr 2017); and western occurrences in southeastern Wyoming (Redder et al. 2006), eastern Colorado (Hammerson 1999), and eastern New Mexico (Degenhardt et al. 1996). Its southern range extends west from central Texas and Oklahoma (Sievert and Sievert 2021) to southeastern Arizona (Plummer 2003), east to southwestern Louisiana, and south to Mexico, where it is found in northern Chihuahua and northeastern Sonora (Legler and Vogt 2013). It also possibly occurs in far northwestern Coahuila, Mexico, via contiguous habitat extending from Big Bend National Park in Texas (Lazcano et al. 2019), but empirical records are needed to confirm its presence. The species ranges from sea level up to nearly 2,200 m elevation (Brennan and Feldner 2003).

**Habitat and Ecology**. — Across the geographic range of *T. ornata*, the ecology and life history of the nominate subspecies has received more attention than has *T. o. luteola* (Degenhardt et al. 1996). In addition, northern populations of the species have received the most attention, with the notable exceptions of Texas (Blair 1976) and Arizona (Plummer 2003, 2004, 2014). The most comprehensive studies are the historical work of Legler (1960) from Kansas and the recent work of Iverson (2024) from Nebraska. The most robust reviews of the species, beyond the abovementioned studies, are found in Ernst and Lovich (2009), Dodd (2001), Redder et al. (2006), and van Dijk and Hammerson (2011). We note that there is a large amount of gray and other obscure literature on *T. ornata* available online and in print, such as abstracts of conference presentations (e.g., https://www.boxturtleconservation.org/workshops) and unpublished graduate theses, most of which was not subjected to peer review. In order to provide the most inclusive summary of the species to date, we opted to include selected unpublished works, but we note that priority was given to peer-reviewed sources whenever possible, such as only referencing published versions of studies that were initially presented in a non-refereed form. Lastly, we also
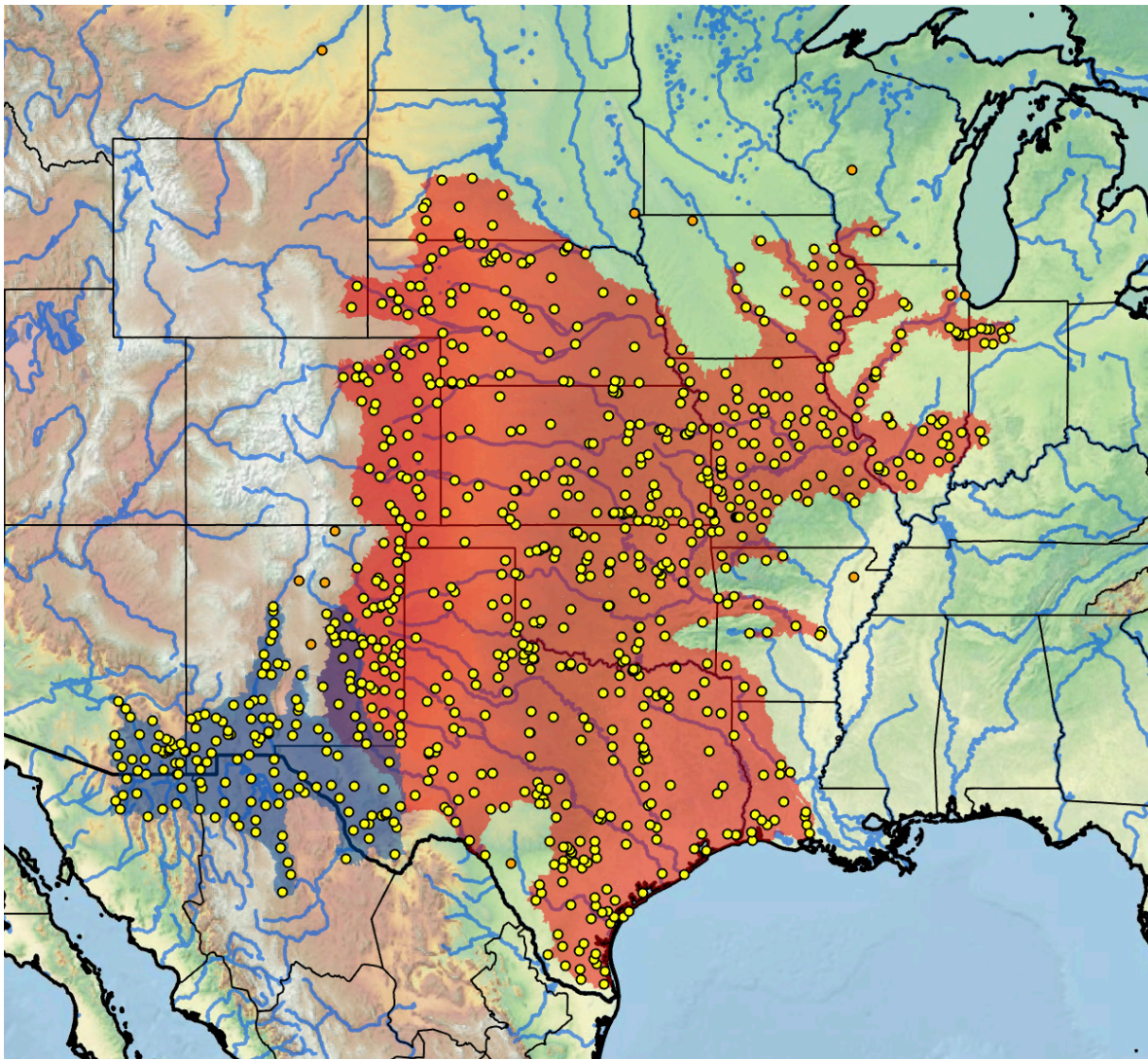
**Figure 8.** Distribution of *Terrapene ornata* in the USA and Mexico. Yellow dots = museum and occurrence records of native populations based on literature records (Iverson 1992; TTWG 2021; TTWG, in press); orange dots = introduced or possibly historically relict populations or individual trade or translocated specimens; colored shading = estimated historical indigenous ranges of: 1) *T. o. ornata* = red, and 2) *T. o. luteola* = blue; purple-colored overlap areas = presumptive intergrades. Distribution is based on fine-scaled GIS-defined level 12 HUCs (hydrologic unit compartments) constructed around verified localities and then adding HUCs that connect known point localities in the same watershed or physiographic region, and similar habitats and elevations as verified HUCs based on Buhlmann et al. (2009), TTWG (2017, 2021), and data from authors and other sources.

prioritized sources that were available for us to assess. The following summaries of various ecological aspects reflect these prior accounts and the overall geographic bias inherent in the literature for the species.

 *Habitat Preferences. — Terrapene ornata* is most commonly found in open habitats with friable, often sandy, soils. Core habitats used by *T. o. ornata* are prairies, grasslands, pastures, and wooded plains (Fig. 9). Habitats used by *T. o. luteola* are primarily Chihuahuan Desert grasslands and prairies (Fig. 10). The wide distribution of the species includes a continuum between semi-arid and xeric habits, but soft substrate is critical to its ability to burrow for estivation and overwintering, and in which to construct nests. Shrubby, wooded habitats and shallow, open water are used, especially during the summer. Hard substrates

and rocks are generally avoided (Norris and Zweifel 1950); however, when used, the turtles generally move to sandy areas to nest, estivate, and overwinter. Mammal burrows can be used as retreats, estivation sites, and for overwintering, as they are found generally throughout the species' range. *Terrapene ornata* can move through water bodies, especially shallow wetlands and drainages, which is usually accomplished by walking on the substrate but occasionally by swimming (Clarke 1958). For example, Clarke (1950) observed an adult male *T. ornata* swimming across the nearly 20 m (60 ft) wide Marais Cygnes River in Kansas, which he first found by boat in the middle of the river with most of the carapace above the water, with the head submerged, while it swam toward the opposite shore. In Iowa, an adult was filmed swimming and walking
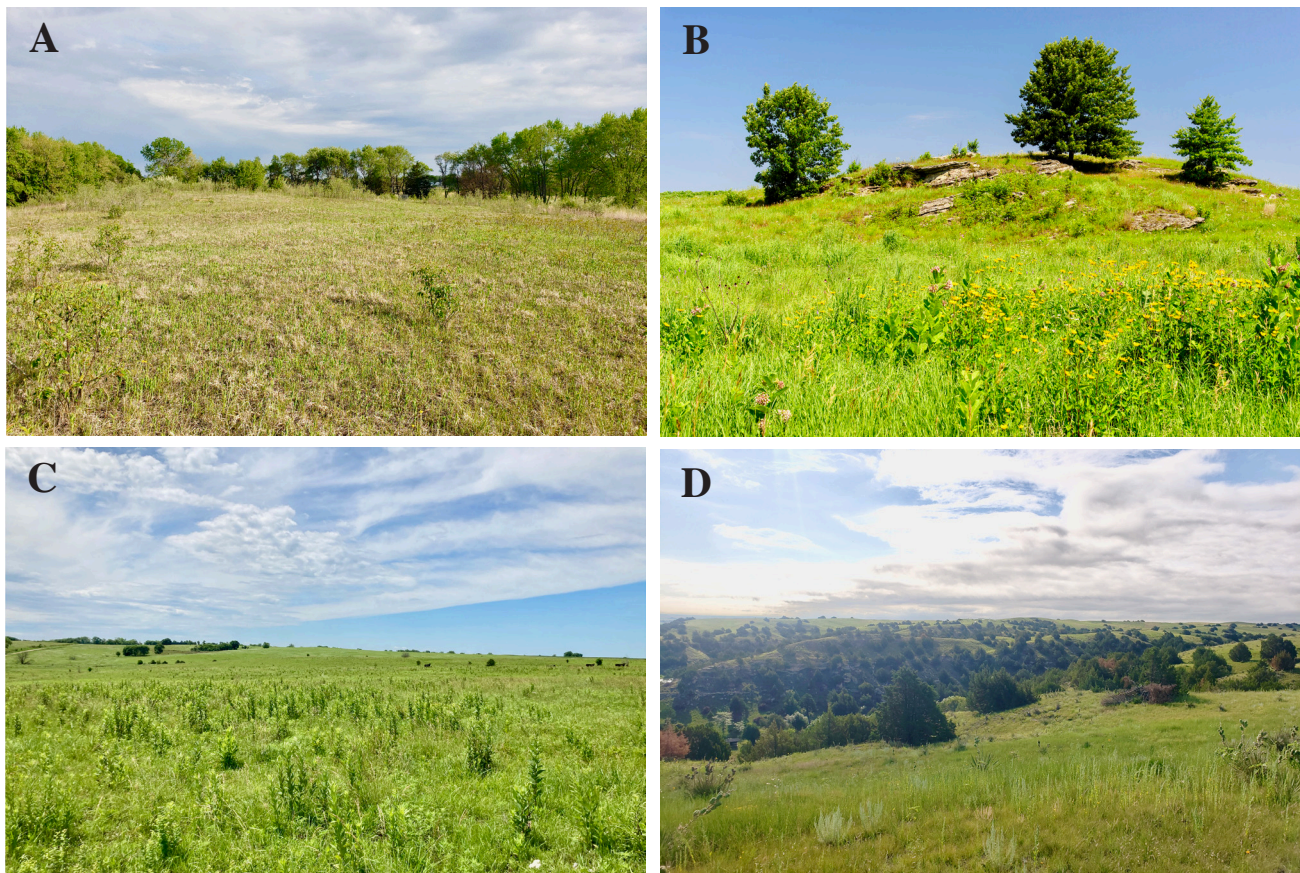
**Figure 9.** Representative habitats of *Terrapene ornata ornata*. **A**. Johnson County, Iowa. Photo by Daniel F. Hughes; **B**. Lee County, Illinois. Photo by Tom Gill; **C**. Shawnee County, Kansas. Photo by Daniel F. Hughes; **D**. Keith County, Nebraska. Photo by Benjamin M. Reed.

on the bottom of a shallow wetland, and several individuals regularly crossed a steep drainage ditch during annual movements (Bernstein, pers. obs.). Dodge and Folk (1963) reported that *T. ornata* had a maximum tolerance of time submerged underwater of 12 hours based on laboratory studies. Free water may be essential for drinking (Ernst and Lovich 2009), but empirical evidence in support of this claim is lacking. Several studies suggest individuals obtain moisture from plants such as cacti and succulents (e.g., Blair 1976; see also Diet below).

According to Redder et al. (2006), *T. ornata* requires three main types of microhabitat: 1) feeding areas consisting primarily of grassland or prairie habitat, but with some access to free water and occasional use of other habitat types; 2) nesting sites, which are often in the same soils used for overwintering; and 3) soft soil or litter used for thermoregulation and resting (colloquially called "forms") in which partial or total burial of the body is used to avoid extreme temperatures, to maintain water balance, avoid predators, and rest overnight (Dodd 2001; Converse and Savidge 2003; Ernst and Lovich 2009).

The eastern populations of *T. ornata* in Illinois, Indiana, Wisconsin, and Iowa are largely fragmented and mainly located in remnant sand prairies adjacent to agricultural land, meadows, woodlands, and shrublands (Doroff and

Keith 1990; Curtin 1997; Bowen et al. 2004; Bernstein et al. 2007, 2023). In Indiana, *T. ornata* is disjunct and very rare, being found in the northwest and southwest (Minton 2001), with just a few historical records in Marshall, Starke, Daviess, Jasper, and Pulaski counties (Evermann and Clark 1930; Grant 1935; List 1951), and more recent records from only a few sandy sites in southern Indiana (Lodato and Hulvershorn 2001). In southwestern Wisconsin, an 8 sq. km area studied by Doroff and Keith (1990) contained a mixture of deciduous and planted conifer woodlands (59%), wetland (12%), remnant prairie (6%), and cropland (22%). All nests found by Doroff and Keith (1990) were on remnant or disturbed prairie; all turtles overwintered in loose sandy soil, nine within woodlands and 20 on native prairie; and all age classes primarily used prairie habitat and avoided croplands.

Numerous studies have documented the historic distribution of *T. ornata* in Iowa, and in some areas, the species was abundant and widespread (Anonymous 1881; Osborn 1892; Somes 1911; Brumfiel 1919; Platt 1973 (misidentified species name); Christiansen and Bailey 1988, 1997; Christiansen 1981, 1998). One of two large populations in Iowa is found within and around a private sand prairie preserve in southeastern Iowa near the Mississippi River that is dominated by sandy soils
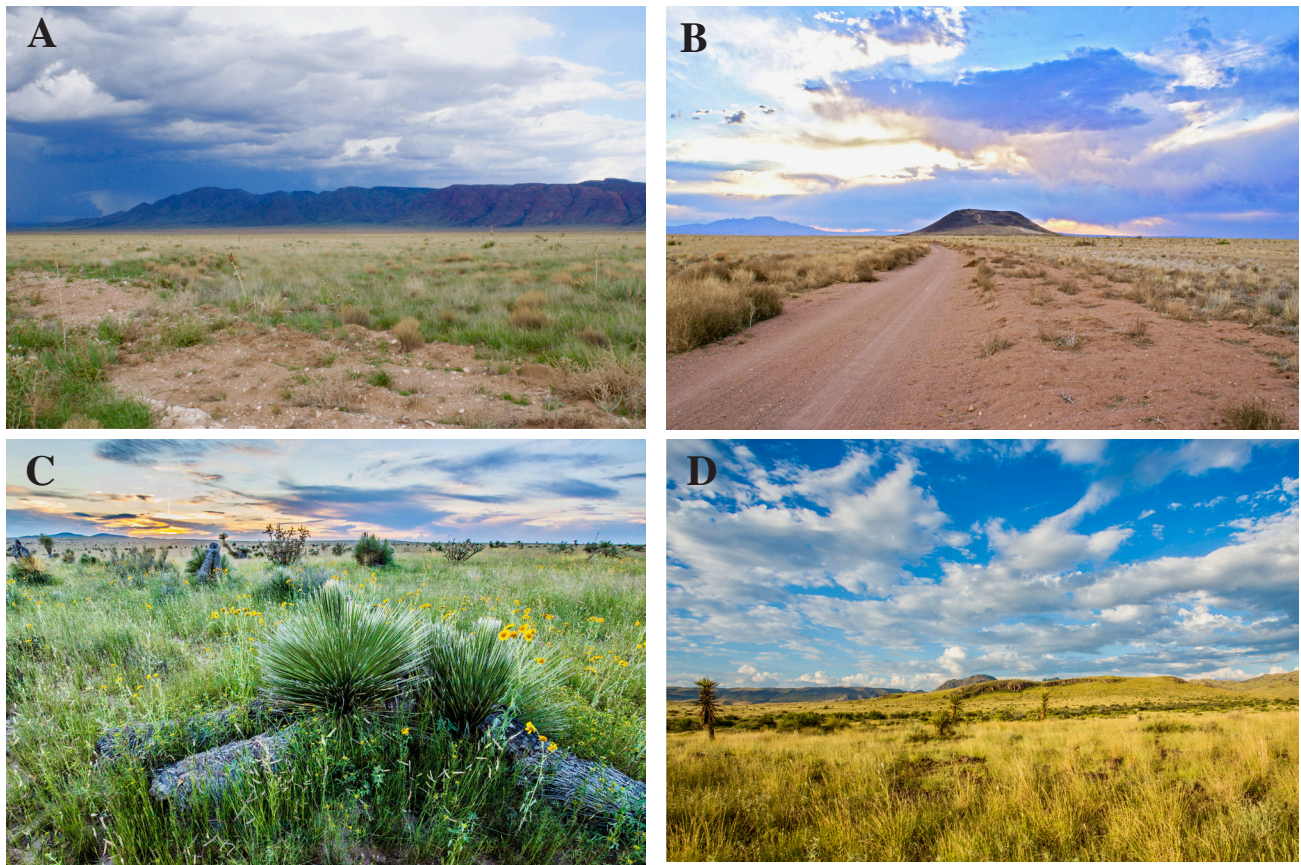
**Figure 10.** Representative habitats of *Terrapene ornata luteola*. **A–B**. Socorro County, New Mexico. Photos by David J. Germano. **C**. Hudspeth County, Texas. Photo by Frank Portillo. **D**. Davis County, Texas. Photo by Frank Portillo.

with sparse vegetation (LeClere 2013; VanDeWalle and Bernstein 2024). The area is adjacent to backwater Mississippi River habitats and subjected to increasing woody succession (*Rhus aromatica*, conifers [especially cedar trees], and deciduous trees). The second large population from east-central Iowa also exists on former sand dunes, many of which have been invaded by woody succession (*R. glabra*, *Elaeagnus angustifolia*, *Rubus* sp., conifers including cedars, and deciduous trees) or converted to agriculture (Bernstein et al. 2007, 2023). In both areas, turtles overwinter, breed, and nest largely in the sandy areas, but most turtles avoid the exposed, open prairie during the summer by dispersing to shaded low-lying woodlands near wetlands or, less frequently, to the cover of neighboring cultivated areas (Bernstein et al. 2023a). A few small Iowa populations live in the southern portion of the rocky Paleozoic Plateau of northeastern Iowa where calcareous bedrock is close to or on the surface. Populations along Iowa's Western Loess Hills Landform, the eastern edge of the Great Plains, are largely extirpated except for perhaps in extreme southwestern Iowa. The same is true for most populations in southern Iowa (LeClere 2013; VanDeWalle and Bernstein 2024). Blanchard (1923) reported a single individual in northwestern Iowa which was probably introduced.

In Missouri, *T. ornata* is known from all but the southeastern counties, although it is more common in former grasslands in the north and west (Johnson 2000). At a site of sympatry with *Terrapene triunguis* in Missouri, Sammartano and Moll (1994) found that *T. ornata* was most commonly found in grasses (92% of captures), whereas *T. triunguis* was most commonly found in woods (62% of captures). Arkansas and Louisiana populations are fragmented and inhabit open, grassy areas and prairies (England 1979; Trauth et al. 2004; Witsell and Warriner 2013).

More contiguous populations exist through southern South Dakota, Nebraska, Kansas, Colorado, Oklahoma, and Texas, and several studies describe habitat requirements in these states (e.g., Clarke 1958; Fitch 1958; Legler 1960; Metcalf and Metcalf 1970; Cadwell and Collins 1981; Nieuwolt 1996; Dixon 2000; Platt et al. 2005; Redder et al. 2006; Germano 2014). However, many of these populations are also increasingly fragmented (see Fig. 4 in Redder et al. 2006).

In their primary study area of southwestern South Dakota, Quinn et al. (2014) described two types of habitats (upland habitat with deep sandy soils and lowland habitat with clay soils); however, they did not specify which habitats the turtles used most. Timken (1969) noted the South Dakota grassland habitat developed via the synergistic effects of

warm climate on sandy substrates that developed following the Dust Bowl years (Redder et al. 2006); however, Quinn et al. (2014) noted records away from the sandhill habitat, as did Platt et al. (2005). Also in South Dakota, a more detailed habitat study by Uresk and Higa (2019) indicated that *T. ornata* chose habitats with high visual obstruction readings and (relatively) high canopy cover, with an apparent preference for Sand Sagebrush (*Artemesia filifolia*) that provided both shade in the summer and sites for overwintering.

Nebraska, Kansas, and Colorado populations are also more common in open areas. Converse et al. (2002, 2005) studied populations in the Nebraska Sandhills which consisted of mixed-grass prairie on grass-stabilized sand dunes with a high density of lakes and wetlands. In Nebraska, sedentary turtles also sheltered under vegetation or at the edge of wetlands (Converse et al. 2002; Converse and Savidge 2003). Near the Flint Hills of Kansas, Metcalf and Metcalf (1970) tracked turtle movements among gardens, farmyards, an orchard, pasture, and native grassland habitats. While there were some shade trees and access to a pond, the turtles spent much of their time in cultivated gardens.

In southwest Nebraska, Trail (1995) found that turtles were frequently shaded from above and the side by vegetation when relatively stationary but used more open areas with shorter vegetation when moving, a finding similar that of Uresk and Higa (2019) in South Dakota. In far eastern Kansas, Brumwell (1951) considered the species rare on Fort Leavenworth, which was dominated by hardwood forest habitats.

In contrast, much of Legler's (1960) study in Kansas was conducted on cattle-grazed pastures, which were treeless habitats. Additional studies from Kansas indicate a preference for open grasslands and pastures (Brennan 1937; Clarke 1958); however, Fitch (1958), also in Kansas, noted that box turtles preferred grazed pastures, woodlands, open fields with disturbed prairie vegetation, and fallow fields.

Similarly, *T. ornata* inhabits open grasslands and pastures in eastern Colorado (Rodeck 1949; Hammerson 1999; Redder et al. 2006). In Oklahoma, Ortenburger and Freeman (1930) indicated that *T. ornata* was most common in the western portion of the state, where they were most often taken from tufts of grass or sage, and many were collected in sedges along the bank of a river. Redder et al. (2006) noted a single population in southeastern Wyoming, but this population may be extirpated.

In Texas, Blair (1976) studied *T. ornata* in an area that included a residence, a single *Morus rubra* tree, a woody ravine, a mowed area, and a farm pond. As in other studies, turtles congregated around fallen ripe mulberry fruit, so Blair (1976) speculated that some hydration also came from eating both fruit and pads of the Prickly Pear Cactus (*Opuntia lindheimeri* = *O. cespitosa*). Minton (1958) found *T. ornata* to be restricted to short grass habitats in the Big

Bend Region of western Texas. Franklin (2003) found a male sheltering in a small pool of water under a shelved layer of limestone in Texas. In Louisiana, Rossman (1965) was the first to report *T. ornata* from the state, where it was restricted to prairie soils.

From 34 sites in Arkansas during 2018–2020, *T. ornata* was detected at nine sites with a mean occupancy of 0.48 (0.09–0.89 95% CI) and a mean detection of 0.04 (0.03–0.08 95% CI) (Royal et al. 2023), where occupancy is the probability that a species occurs at site and detection is the probability of finding a species if it is present at a site. The species exhibited strong positive relationships with prairie mound density, a proxy measure indicating historical land use, suggesting the importance of this habitat feature for its presence in the state (Royal et al. 2023). Also in Arkansas, Yerdon et al. (2023) found that sympatric *T. triunguis* (called *T. carolina* in the paper) was observed under canopy cover 50% of the time, in shaded prairie 50% of the time, and never in the open, while *T. ornata* was found in the open 16% of the time, in shaded prairie 84% of the time, and never under canopy cover. Further, *T. ornata* was located on prairie mounds twice and within 1.5 m of an open trail edge five times (Yerdon et al. 2023).

Several habitat studies have been conducted in New Mexico (Nieuwolt 1996; Germano 2014; Suriyamongkol et al. 2021). Nieuwolt (1996) noted that turtles favored microhabitats with lower surface temperatures, higher atmospheric temperatures, and slightly lower relative humidities when compared to nearby sites; however, specific vegetation was not defined. Germano (2014) conducted road surveys and found the number of turtles detected was positively correlated with air temperature but not precipitation. Suriyamongko et al. (2021) found that turtles used areas with little ground cover that facilitated movement and provided better basking, but they did not quantify overhead vegetation as a factor.

In Arizona, Plummer (2003) studied a population inhabiting semi-arid grasslands in an area of transition between the Sonoran and Chihuahuan Deserts. A single adult was found near an exposed tributary in the Huachuca Mountains of Arizona at an elevation of 2180 m in pine forest (Brennan and Feldner 2003); however, the note does not speculate whether the turtle could have been translocated. Plummer et al. (2003) found that dehydrated *T. o. luteola* had a lower critical thermal maximum by 2°C than normally hydrated individuals. Along with sheltering under tall grasses and shrubs (mainly *Prosopis* sp.), turtles actively used mammal burrows mainly from *Dipodomys spectabilis* in Arizona (Plummer 2004) and *D. ordii* in Nebraska (Iverson, pers. obs.). *Terrapene ornata* also sheltered in burrows of *Cynomys ludovicianus* in the panhandle of Oklahoma (Lomolino and Smith 2004). In Mexico, Axtell and Webb (1963) described an individual that was active in a grassy area on a dry playa with scattered mesquite, catclaw, and herbs in the area.

*Home Range.* — Habeck et al. (2019) conducted a meta-analysis of home range studies of *T. ornata* and noted the difficulty of drawing comparisons due to the various analytical methods employed. Methodologies of locating turtles vary among the techniques of thread-trailing, hand mark-recapture, dog tracking, and radiotelemetry, and variation exists among area/unit time estimates (i.e., annual versus monthly), ages of turtles tracked, amount of time individuals were tracked, and sample sizes (Redder et al. 2006). Because *T. ornata* is relatively sedentary during much of the year, is rarely on the surface, and is cryptically patterned, how turtles are located can strongly influence results. For example, Refsnider et al. (2011) found that visual-encounter surveys were not sufficient to detect turtles with transmitters, and Tucker et al. (2014) found that automated radiotelemetry was effective at locating nocturnal nesting females. Movement and activity can also be affected by microclimate (Tucker et al. 2015), body size of individuals (Doroff and Keith 1990), surrounding habitats, and presence of transients (Redder et al. 2006). Activity tends to vary across the active season, with more and longer movements occurring in the spring and fewer during mid-summer (Bernstein et al. 2007; Struecker et al. 2023). Some studies also investigated linear distance moved while recognizing that turtles do not necessarily travel in straight lines; all analyses introduce biases and errors into conclusions (e.g., Iglay et al. 2006). Consequently, we have taken a holistic view of movements and home ranges that permits nuanced examination of comparisons among habitats, geography, sexes, times of year, and age classes.

Males tend to be more active than females (Tucker et al. 2015); however, mean differences in mean home-range size by sex are rarely observed within individual studies (Doroff and Keith 1990; Grant 2010; Refsnider et al. 2012; Bernstein et al. 2023a; Struecker et al. 2023; but see Bernstein et al. 2007). Nevertheless, a recent synthesis of home-range studies based on 22 home-range estimates found that males (mean = 4.67 ha, SE = 1.63 ha) tend to have home ranges that are on average 6% larger than those of females (mean = 4.37 ha, SE = 1.63 ha) (Habeck et al. 2019).

Fitch (1958) studied 14 turtles at the same location as Legler's (1960) landmark study of *T. ornata* in Kansas and reported an average home range radius of 83.5 m (274 ft) and an area of 21,853 m² (5.4 ac). Fitch (1958) also reported a single female (presumably gravid) that traveled almost 558 m (1,830 ft) in 53 days. Using thread trailers, Legler (1960) reported average daily distances of females as 68.9 m (226 ft) in June and 79.2 m (260 ft) in July and of males as 88.1 m (289 ft) in June. In agreement with Fitch (1958), Legler (1960) noted a gravid female that traveled approximately 213.4 m (700 ft) along a rock fence and then travelled in a nearly straight line for another 365.8 m (1,200 ft) across a cultivated field before the thread on her trailer ran out. Legler (1960) also reported a male that

travelled 682.8 m (2,240 ft) between 16 October and 20 November 1954. The home ranges calculated for 44 adults by Legler (1960) using both thread trailers and recaptures resulted in an average radius of 84.7 m (278 ft; 21.6–278.3 m) and an average home range of 22,662 m² (5.6 ac; 2.27 ha). Males and females did not differ significantly in these estimates, and Legler (1960) noted habitat differences as a major factor affecting distances travelled. On the Ross History Reservation in eastern Kansas, Rose (1984) estimated home ranges to be 5.27 ac (2.13 ha). In northeastern Kansas, Hodge et al. (2022) compared movement metrics between sympatric *T. ornata* and *T. triunguis* and found that while they used similar habitat types, *T. triunguis* (*n* = 4) had significantly larger home ranges and lower year-to-year philopatry than *T. ornata* (*n* = 19).

In southwest Nebraska, Trail (1995) radio-tracked three females and estimated annual home range sizes of 2.2, 2.4, and 15.8 ha. Also in Nebraska, Holy (1995) found no sexual differences in home range size, although in 1993, she only compared three males (mean = 12.16 ha) to four females (mean = 12.67 ha) and, in 1994, eight males (mean = 18.52 ha) and seven females (mean = 19.1 ha). During both years, Holy (1995) found that daily movement ranged 0–200 m. In western Nebraska, Iverson (2024) reported nesting forays up to 1,024 m from the normal home range. Using thread trailing in Nebraska, Claussen et al. (1997) found that *T. ornata* exhibit minimal or no directional preferences, and that increased vegetation cover led to trails of a more winding nature, higher temperatures led to greater distances traveled per day, and injuries impacted all movement metrics measured.

In Wisconsin, Doroff and Keith (1990) found high variability in individual annual home ranges (0.2–58.1 ha) in degraded habitats. Home ranges were almost four times larger than those used in less degraded habitats (8.7 ha versus 2.5 ha, respectively). Turtles travelled farther between habitat remnants in the degraded habitats, which could potentially expose individuals to more threats, such as roadkill. Curtin (1997) also suggested that turtles in fragmented, disturbed habitats could have shorter activity seasons and longer incubation periods. In Illinois, Refsnider et al. (2012) estimated home ranges for females to be 4.3 ha (± 5 ha SD) and males to be 3.1 ha (± 2 ha SD).

Studies in Iowa examined annual, monthly, and weekly home ranges of different age classes and sex as well as linear distance travelled. Average home-range size was reported to be 3.96 ha (Bernstein et al. 2007). Males had higher annual estimated home ranges based on 100% minimum convex polygons (MCP) and 95% kernel density (K) than females, but monthly between-sex comparisons of MCP and K were not significantly different (Bernstein et al. 2007). Home ranges were highly variable in size, with one female having moved < 25 m radius in a year (Bernstein et al. 2007), and such high variation likely obscured statistical comparisons among individuals or between sexes. In Iowa,

a male turtle moved 1 km in less than 48 hrs over shrubs, logs, and through a drainage ditch; the individual remained in this summer range, barely moving until returning to the spot where it was first encountered in September, again, covering the distance in less than 48 hrs (VanDeWalle and Bernstein 2024).

In an examination of home range comparisons between age classes and sex in Iowa, Bernstein et al. (2023a) compared weekly 95% MCPs of two size classes of juveniles, subadult, and adult turtles for three time periods. Age class was the only significant factor explaining differences, where home range size significantly increased with age during May and June–July, but there were no significant differences between ages and sexes during August–September. In examining age differences in linear distance travelled, significant differences between age classes were present during all time periods with the overall tendency that distance travelled increased with age class. Bernstein et al. (2023a) found that younger turtles (neonates and juveniles) have smaller day-to-day home-range areas compared to adults in early-to-mid summer but not in August–September.

In Texas, Blair (1976) followed five females and six males over multiple years and estimated an average home range diameter of 105 m (ca. 0.86 ha) for males and 94 m (ca. 0.69 m) for females. Also in Texas, Holm (2003) found that home-range estimates ranged between 0.73 and 3.28 ha in one population, whereas Grant (2010) found that home ranges averaged 4.04 ha (females) and 8.30 ha (males) in another Texas population.

In New Mexico, most studies have focused on the effects of the desert climate on movements of *T. o. luteola*. On average, individuals exhibited larger home ranges (1.6 ha) than conspecifics in more mesic habitats because patchy habitats prompted longer distances travelled to reach kangaroo rat (*Dipodomys* spp.) burrows needed for thermoregulation in otherwise drier habitats (Nieuwolt 1996). New Mexico home-range sizes ranged between 0.73 and 2.3 ha in a study by Suriyamongkol et al. (2021). In one Arizona study, the average home-range size was 5.2 ha and was variable across three sites in close proximity to one another (2.8 ha to 9.0 ha), which the authors attributed to the availability of standing water (Hall and Steidl 2003). Plummer (2014) documented similar findings in another study in southeastern Arizona with an average home range size of 9.8 ha (± 2.63 ha), and there were no sexual differences in home-range size or daily distance travelled as well as no individual differences in annual distance traveled. However, Plummer (2014) did find that some individuals travelled toward stock water tanks and suggested, somewhat in contrast to Nieuwolt (1996), that supplemental anthropogenic water may influence individual movements and home range with smaller home ranges in areas without a constant water source. As noted in previous studies, Plummer (2014) found that a few individuals made long distance daily movements that ranged 431–1,485 m away

from their usual home ranges, but most turtles returned to the same burrow each day within their home range.

*Philopatry.* — *Terrapene ornata* is highly philopatric and will often travel "home-ward" if translocated (e.g., Metcalf and Metcalf 1978; Bernstein et al. 2007; Richtsmeier et al. 2008; Refsnider et al. 2012; Sosa and Perry 2015). Evidence indicates that some females repeatedly use the same location for nesting and many individuals overwinter in the same location (Doroff and Keith 1990; Redder et al. 2006; Bernstein et al. 2007). In Illinois, three of five *T. ornata* displayed overwintering site fidelity (Schmidt and Hellgren 2014). *Terrapene ornata* displays consistent home-range philopatry (year-to-year overlap in home range) with average overlap estimates typically around or exceeding 40% (Bernstein et al. 2007; Refsnider et al. 2012) with some individuals exceeding 80% (Struecker et al. 2023), but there is within-population and across-population variation. Average percent overlap between 2021 and 2022 within a population in northeastern Kansas exceeded 80% for both males ($n = 8$) and females ($n = 12$) (Lewis et al. 2022). However, in another study during 2020–2021 on a population in western Nebraska, the average percent year-to-year overlap was less than 50% for both males ($n = 11$) and females ($n = 12$) (Kim et al. 2021).

Individuals of *T. ornata* are mostly non-territorial (Legler 1960; Trail 1995), exhibiting a high degree of home-range overlap with conspecifics, which is often described as "extensive overlap" (Nieuwolt 1996; Refsnider et al. 2012), or at least appears that way from mapped plots of annual home ranges (Plummer 2014). The lack of territoriality in *T. ornata*, combined with their relatively low metabolic rate (Ultsch 2013), minimal costs of locomotion (Zani and Kram 2008), and physical performance across a range of conditions (Claussen et al. 2002) can promote high population densities in small areas. Such overlap in home ranges could increase competition, but *T. ornata* is a dietary generalist, and higher population densities increase the likelihood of finding mates. Therefore, the seasonal peaks of mating (spring and fall) coincide with the greatest among-individual overlap in home ranges (e.g., Hughes et al. 2023).

*Activity Patterns.* — The species is most active from March to November, depending on the location and both microclimate and overall climate, but annual fluctuations in local weather can also affect activity. At northern locations, *T. ornata* tends to be surface-level active between the months of April and October (Legler 1960) and has been observed mating throughout this entire active season (e.g., Hughes et al. 2023). However, based on visual encounters in Texas, Blair (1976) found turtles on the surface year-round except in January and February; females were most active in the spring, while males exhibited two peaks of seasonal activity, one in June and another in September–October. Blair (1976) compared his population in Texas to Legler's (1960) in Kansas and found an extended activity season

compared to those farther north, which corroborated later findings that *T. ornata* may have different preferred or selected body temperatures across latitudes (Ellner and Karasov 1993). For example, Wisconsin turtles were found to select cooler temperatures than did those from Kansas, and Wisconsin turtles also had a tolerance for a broader range of temperatures, which may serve as a mechanism to maximize total daily activity (Ellner and Karasov 1993). In one Kansas study, turtles were active from 1 April to 24 October with observations from a temperature range from 12.8°C to 38.9°C (Clarke 1958). In Iowa, there are above-ground records of activity for every month except December (VanDeWalle and Bernstein 2024), although turtles are most active from mid-April to early October (Bernstein and Black 2005).

Overall, above-ground daily activity in 24 hrs as a percentage of time ranges from 20 to 30% (Nieuwolt 1996; Converse et al. 2002), but is presumably higher in populations with a shorter overall active season (Hall and Steidl 2003). Under favorable conditions, *T. ornata* generally exhibits a peak of activity in the morning and a secondary peak in the afternoon (Converse et al. 2002; Plummer 2003; Sievers 2015). In Illinois, males were generally more active than females, especially when searching for mates in spring and late summer, and activity of both sexes decreased during mid-day (i.e., a bimodal distribution of activity), and increased with higher humidity and rain (Tucker et al. 2015). Average activity exceeded 6 min/hr at 21–32°C, >7 min/hr at 25–31°C, and peak activity (7.9 min/hr) occurred at 26–27°C (Tucker et al. 2015). In turn, activity was less than 2 min/hr at temperatures below 15°C. From this pattern, Tucker et al. (2015) concluded that thermal constraints dictated activity, that warm, dry years inhibited movement, and that relative humidity, reproductive status, and time of day and year also influenced activity. Similarly, in western Nebraska, temperature was again inversely correlated with activity levels (Converse and Savidge 2003), and total April–July captures in a given year were related to rainfall in May and June (Iverson 2024).

In New Mexico, Nieuwolt (1996) found *T. o. luteola* is most active at substrate temperatures ranging from 31 to 36°C and air temperatures ranging from 13 to 24°C, coinciding with early morning and late afternoon. Turtles mainly selected habitats with lower substrate temperature, higher ambient temperature, and lower humidity compared to a local meteorological station (Nieuwolt 1996). Microclimatic extremes were avoided, and turtles were more active during low to medium temperatures, low to medium solar intensity, and high humidity (Nieuwolt 1996). Suriyamongkol et al. (2021) found that time of day, humidity, and temperature were all significant predictors of activity in a population of box turtles in eastern New Mexico. In Arizona, near the southwestern range limit of the species, seasonal and daily activity were found to positively coincide with the monsoon season (July–September) and inversely with temperature

(Plummer 2003, 2004). In addition, Plummer (2003, 2004, 2014) also looked at microclimatic effects on activity and again found that turtles were most active just after dawn and later in the afternoon as mediated by ambient temperature with precipitation having a positive impact on both daily and seasonal activity. Hatchlings appear to exhibit plasticity in their thermal preference based on the temperatures at which they are reared (Curtin 1998), which may help explain the differences in preferred body temperatures that have been documented across the range. In Texas, Rose (1988) found that *T. ornata* was most active between 0600–0800 hrs, that body temperature was on average lower than the sympatric *Gopherus* tortoise species, and that *T. ornata* was more active at lower body temperatures than *Gopherus*. Bethea (1972) found that *T. ornata* can have 20 heartbeats/min at 20°C, whereas Rose (1988) found that sympatric *Gopherus* had about 6 heartbeats/min at the same temperature.

In laboratory studies based on animals confiscated from the illegal pet trade in Oklahoma, Sousa do Amaral et al. (2002) found that *T. ornata* exhibited significantly higher mean body temperatures compared to *T. triunguis* (identified as *T. carolina* in the paper), although they displayed similar diel thermoregulatory cycles within an approximate 24-hour period. No distinct variations in the absolute thermoregulatory precision of body temperatures (percent match between observed body temperature and preferred range) were observed between the species, despite distinctly different habitat choices. In Arkansas, Yerdon et al. (2023) found the average rate of water loss for *T. ornata* was lower (range = 1.5 to 3.1 g/day, mean = 2.33 g/day) compared to *T. triunguis* (range = 1.96 to 4.94 g/day, mean = 3.24 g/day), but the rate of loss was not different between the two species after adjusting for differences in body size, though the rate of loss increased with increasing body mass in both. Yerdon et al. (2023) found differences between the two species in average daytime temperature, average daily maximum temperature, and average daily minimum temperature; though not significantly different, *T. ornata* showed an average daily maximum temperature 1.68°C higher and an average daily low 0.58°C lower than in *T. triunguis*. Degraded prairies apparently provided suboptimal thermal conditions for *T. ornata*, with agricultural areas and those with encroaching canopy cover being identified as degraded habitats that limit thermoregulatory opportunities for the species in Arkansas (Yerdon et al. 2023).

According to Yerdon et al. (2023), human encroachment and fire suppression in Arkansas's historic prairies have led to increased forestation, which is more suitable for *T. triunguis* due to its lower preferred body temperature (Sousa do Amaral et al. 2002). This may explain the prevalence of *T. triunguis* in Arkansas, its range expansion, and its hybridization with *T. ornata*, underscoring the need for active management, including prescribed burning and restoration efforts, to provide optimal thermal conditions

for the remaining populations of *T. ornata* in Arkansas and beyond. Aiming to better understand how to reduce mortality associated with prescribed prairie fires, Edmonds et al. (2023) generated surface activity models for a population in Illinois and found that temperature and precipitation, in combination, were best for predicting activity and that turtles were likely to be above-ground between April 1 and November 1.

*Overwintering.* — *Terrapene ornata* usually burrows below the frostline to avoid freezing temperatures in a progressive manner (Legler 1960; Doroff and Keith 1990; Bernstein and Black 2015). Length of time spent below the surface over the winter appears to positively correlate with winter length and cold. The Iowa overwintering period was similar to that in Nebraska (Converse et al. 2002), but more than that estimated in Kansas (Metcalf and Metcalf 1970). The overwintering period lasted 209–216 days in Wisconsin (Doroff and Keith 1990), and 166–201 days in Iowa (Bernstein and Black 2005). Moriarty (2016) recorded an overwintering estivation of 117 days in Arizona, which was apparently the longest recorded for the subspecies *T. o. luteola* by 24 days (Plummer 2004). Hatchlings usually burrow below the natal nest during the winter (Costanzo et al. 1995).

In Kansas, Fitch (1956) recorded the latest dates of surface activity in various years as 25 September – 25 October, and the dates of emergence from overwintering as 21 April – 31 May. In Missouri, Grobman (1990) recorded the dates of emergence from overwintering across years as 21 March – 18 April (mean date, 4 April). In Nebraska, Iverson (2024) observed the earliest male on 18 April – 12 May over 12 years (mean, 30 April), and the earliest female between 21 April – 20 May (mean, 4.5 May) over the same period.

In eastern Iowa, there are five records of emergence between 1–2 April (four females and one male) (Bernstein, pers. obs.). In southeastern Iowa, a male was found above the surface on 7 March 2024 following above normal high temperatures for February, but the individual appeared emaciated and died three days later (J.G. Otten, pers. comm.). Grobman (1990) found that the emergence from overwintering is preceded by five days of subsurface temperatures of at least 7°C. However, Bernstein and Black (2005) found that subsurface temperatures alone could not predict emergence in Iowa and suggested precipitation might also be a factor.

Over two winters in Iowa, most adults never burrowed below 0.75 m, but a detached radio transmitter was recovered at a depth of 1.67 m (Bernstein and Black 2005). In Wisconsin, Doroff and Keith (1990) estimated winter burrowing depths of 0.5–1.8 m. Freeze tolerance has been demonstrated in hatchlings of *T. o. ornata* by Costanzo et al. (1995), who also suggested that adults may be freeze-tolerant, similar to *T. carolina*, which burrows just below the surface in the winter (Costanzo and Claussen 1990;

Costanzo et al. 1993). Legler (1960) stated that winter body temperatures approximate soil temperatures. Bernstein and Black (2005) documented two adults, presumably buried at a relatively shallow depth, which underwent three weeks of freezing underground temperatures (range −1.0 to −8.0°C) and emerged the following spring. Over a three-year study in Illinois, Schmidt and Hellgren (2014) found that turtles mainly overwintered in remnant prairie, and the majority of turtles (95.8%) overwintered in the same land cover type with none utilizing agricultural fields. Moreover, Schmidt and Hellgren (2014) found that *T. ornata* predominantly self-excavated overwintering burrows (73.1% of observed individuals) rather than utilizing abandoned mammal burrows (22.4%) or local features (4.5%), and overwintering survival was high, with only one male observed deceased and two females suspected to have perished. On 8 March 1953, Clarke (1956) found three *T. ornata* in an outdoor well filled with 1.5 ft of water, where two turtles were floating and the third was under the water on the bottom. All quickly began activity after being placed in a warm basement (Clarke 1956). From groups of turtles physiologically measured before vs. after overwintering, Peters (1959) reported increases in red and white blood cells, and decreases in blood sugar, fat in the liver, and overall weight.

In Kansas, Reed and Hobelman (2023) recorded both overwintering site fidelity and communal overwintering sites (2–3 individuals per burrow for six unique burrows). In Nebraska, Converse et al. (2002) found all 18 of their tracked turtles burrowed individually, although they could not confirm that turtles without transmitters were not sharing burrows with their turtles with transmitters. Given these reports, it is unclear whether communal overwintering is rare, geographically variable, or simply not well documented, given the challenge of investigating burrow occupancy without compromising burrow structure or the turtles therein. Converse et al. (2002) also found that all 18 of their turtles overwintered in burrows within their typical summer home-range area. Reed and Hobelman (2023), on the other hand, found that one turtle moved >330 m away from the edge of their summer home range to overwinter, which it repeated for three consecutive winters. Also in Iowa, four individuals, each with six growth rings, were found clustered together on 22 April (Bernstein, pers. obs.), thus it was possible, albeit unlikely, that they were nest mates that overwintered together. Multiple turtles overwintering together (usually no more than three) were observed several times in Iowa, even though they dig their own burrows at this site (Bernstein, pers. obs.).

*Mating Season.* — Across its geographic range, copulations in *T. ornata* have been observed in every month from April to October, never during November to March, and mating was most common during spring and fall, corresponding to ingress and egress from overwintering (Hughes et al. 2023). In Nebraska, Iverson (2024) observed courtship on 4 and 15 May and copulation on 13, 16, and 22 (two pairs)

May, 28 June, and 14 August. Forrester et al. (2020) observed mating in Nebraska in July, which is noteworthy in having occurred in water by a species otherwise known to usually mate on land. Fogell (2010) reported that in Nebraska, mating begins in May and extends through September. In Kansas, most mating occurs in the spring and fall (Legler 1960). Field observations of mating in May (Brumwell 1940; Smith 1950) and one between two turtles in April (Brumwell 1940) are also reported for Kansas. Mating occurred during April–September in South Dakota (Quinn et al. 2014), June (Hammerson 1982) and August (Smith et al. 1965) in Colorado, and May–September (Doroff and Keith 1990), or anytime in captivity, in Wisconsin (Vogt 1981). A pair was seen mating in May in Indiana (Minton 2001). In Missouri, most mating occurred in the spring, tapered off in summer, and possibly increased again in early autumn (Johnson 2000). In Texas, *T. ornata* mated throughout April to October, with both sexes having multiple partners within and among years (Blair 1976). Another pair in Texas was observed in copulation in October (Marr 1944). Reed et al. (2022) documented same-sex mounting between two males in May from Kansas.

Legler (1960), based on 40 male *T. ornata* specimens collected across the active season, found that the testes exhibited the greatest size during the spring and fall months. Notably, there was a progressive increase in testis size from April through early June, followed by a decline from late June to July, and then there was a renewed increase in size during August, reaching maximum dimensions from September through October. Additionally, he noted that mature sperm within the epididymis were most abundant during the spring and fall seasons, coinciding with the peaks of the spermatogenic cycles. Furthermore, sperm retention persisted over the winter months, as also documented by Fogell (2010).

Similarly, Legler (1960) also analyzed 68 female *T. ornata* specimens collected through an entire active season and observed the seasonal variation in the occurrence of females with enlarged ovarian follicles. The highest frequency of enlarged ovarian follicles was observed during October and from March to May, which were notably reduced during June and July, reaching the smallest in August and September. In addition, Legler (1958) found extra-uterine migration in *T. ornata* because counts for ovary and oviduct on the same side of the animal often differed, indicating that ova had passed from one ovary into the oviduct of the opposite side.

*Personality*.—Recently, Reed et al. (2023) documented clear and consistent behavior types at levels comparable to other vertebrates within and across four separate populations of *T. ornata* ranging from Iowa to Nebraska with some of the same turtles studied from 2016 to 2022. They found that personality variation in three behavioral traits (boldness, exploration, and activity) did not differ between males and females, despite females being larger on aver-

age than males, and that body size variation did not relate to behavioral variation. The finding that mean personality differences exist between populations suggests that selection is variable across habitat types, but within-population variation indicates that selection may not be strong enough to eliminate all behavior types. They postulated that such within-population variation can promote population persistence, because environmental conditions are dynamically changing, which will favor different behavior types at different times. Hughes et al. (in review) found that these three personality traits form behavioral syndromes, where more active turtles are also bolder, and the directionality of trait co-variation was consistent across four populations. Boldness, activity, and exploration behaviors have been quantified in wild *T. ornata*, but future work is needed to investigate the remaining two main personality axes (aggression and sociality). Historically, Rosenbaum (1968) described an eight-year-old female *T. ornata* that he "trained" to respond to visual cues, suggesting that this species can learn during its lifetime. Also, Harless and Lambiotte (1971), found that 36 *T. ornata* trained in a laboratory setting had no sex-based differences in latency to move, running speed, turnover latencies, or time to walk after release.

Findings of variation in boldness, exploration, and activity within and across *T. ornata* populations are still emerging and here we attempt to summarize preliminary evidence from these continuing studies because they have potentially transformative implications for the ecology, evolution, and conservation of the species. For example, Suboh et al. (2021) linked home-range size to personality variation among 17 individuals over one active season (seven males and 10 females) in Iowa and found initial evidence that home-range size was not correlated with personality variation in females, but males with larger home ranges were the boldest.

A potential ecological outcome of variation in personality types may relate to the timing of nesting behavior. In western Nebraska, Guldner et al. (2023) found preliminary results that showed no link between nesting date and personality, suggesting that variation in the timing of nesting may be more driven by environmental conditions. Variation in personality types may also relate to thermoregulatory precision. In Iowa, Norris et al. (2023) compared the relationship between personality and thermoregulation in 15 individuals with temperature loggers affixed to their shells set to record temperature every 20 minutes during June to August in 2021. Preliminary results from Norris et al. (2023) revealed that bolder turtles stayed within their preferred temperature range (27–31°C) more than shyer turtles and had higher mean temperatures; however, the relationship was strongest in June (especially for females) and August, and only significant in males for mean temperature from June to August. Lastly, personality also has implications

for translocation efforts that attempt to rescue *T. ornata* populations from habitat destruction. For example, Kim et al. (2021) found preliminary evidence that more active turtles displayed higher levels of year-to-year philopatry to their core area, whereas bolder turtles showed lower levels of year-to-year core area philopatry.

*Nesting Season, Timing, and Sites.* — For most populations of *T. ornata*, June and July are the peak months associated with oviposition. Nesting in South Dakota was reported in June (Quinn et al. 2014) and during May–June (Kiesow 2006). In Wisconsin, nesting was restricted to June (Vogt 1981; Kapfer and Brown 2022) or mainly in June during a May–June nesting season (Doroff and Keith 1990). A June–July nesting season was reported for Illinois (Baker et al. 2010), and a single nesting event was noted in Indiana in July (Minton 2001), although that may have been based on a captive because it produced only one egg. In Iowa, nesting occurs from late May to late June, peaking during the first two weeks of June (VanDeWalle and Bernstein 2024). Field observations in Kansas determined that nesting occurred evenly throughout June (Legler 1960), and a report from August by Smith (1950) seems questionable. Nesting in June (Trail 1995) and in the "summer" (Fogell 2010) were reported for Nebraska. In western Nebraska, Iverson (2024) found gravid females (*n* = 58) from 21 May to 26 June and observed nesting (*n* = 22) from 22 May to at least 18 June. In New Mexico, *T. o. luteola* was gravid during May–August; however, most eggs were laid by late-July (Nieuwolt-Dacanay 1997). Also in New Mexico, nesting appeared to occur during June–July, although one nesting event occurred on 8 August (Germano 2014). Clearly the timing in the Southwest is later than in northern populations, presumably due to the later annual commencement of rains in the former.

Nest construction can begin at night or, more often, shortly before dark and extend into the night. In Kansas, females commenced digging early in the evening and laid eggs after dark (Legler 1960). In Wisconsin, females nested from two hours before sunset to two hours after sunrise (Vogt 1981). In Illinois, nesting activities occurred at night (Tucker et al. 2017), with specific nesting times of 2110 and 2123 hrs (Baker et al. 2010). In both Kansas (Legler 1960) and Illinois (Tucker et al. 2017), digging activity could precede the night of oviposition. Air temperatures associated with nesting are available for Wisconsin (22.3°C; Vogt 1981) and Illinois (23.2 and 26.4°C; Baker et al. 2010). A study in Iowa suggested that heavy rainfall and thunderstorms can trigger nesting in *T. ornata* (Bernstein et al. 2015); however, Iverson (2024) in Nebraska found no evidence that rainfall stimulated nesting as no rain fell during the 24 hrs prior to nesting observations in 18 of the 22 documented cases.

Open habitat typifies nesting sites for *T. ornata*. In Kansas, eggs were laid in open habitat having a well-drained and soft substrate (Legler 1960). Likewise, nests were excavated in upland prairie in Nebraska (Fig. 11A; Converse et al. 2002) and loose sandy prairie soil in Wisconsin (Vogt 1981; Doroff and Keith 1990). In Iowa, multiple nests were clustered on top of an exposed sand dune (Fig. 11B; Bernstein et al. 2015). In Illinois, nesting sites were found on the slope of open-canopied old fields or edges of small closed-canopied old fields (Baker et al. 2010).

All females in Nebraska dug a vertical body pit before excavating an egg chamber (Iverson 2024; photos in Jost and Jost 2000 and Artner 2007). The construction of a body pit was also reported in New Mexico (Murray 2013), Arizona (Legler and Vogt 2013), and Wisconsin (Kapfer and Brown 2022). Tucker et al. (2014, 2015) also reported body pit construction in Illinois, but found that 65% of females produced shallow nests without a body pit. One study even reported subterranean oviposition (Tucker et al. 2017). The basis for this variation in nest construction is unknown.

*Body Size and Age at Sexual Maturity.* — Sexual maturity in both sexes of *T. ornata* appears to be related to body size. In South Dakota, adults of both sexes matured at 100 mm SCL (Kiesow 2006). However, the smallest male from South Dakota with secondary sexual characteristics was 103 mm SCL, and females were found to be mature at 110 mm SCL (Quinn et al. 2014). In Nebraska, females matured at about 100 mm SCL (Iverson 2024). However, Trail (1995) reported that males matured at 90 mm SCL and females at 95 mm SCL. In Kansas, most males were sexually mature at 100–109 mm SCL and all were sexually mature at 110–119 mm SCL (Legler 1960). Sexual maturity occurred at a larger carapace length in females, with most females having reached maturity between 110–119 mm SCL, and nearly all when 120–129 mm SCL (Legler 1960). Also in Kansas, minimum adult size of both sexes was reported to be 100 mm SCL (Collins 1974, 1993). In Wisconsin, sexual maturity was reached at 100 mm SCL in males and 110 mm SCL in females (Vogt 1981). In Illinois, females reached sexual maturity at 94–96 mm SCL (Edmonds 2020; Edmonds et al. 2020), and in adjoining Indiana, sexual maturity was reached at 87 mm SCL in males and 95 mm SCL in females (Minton 2001). In a Texas population, males were sexually mature when at least 107 mm SCL, and females were mature at 97 mm SCL (Blair 1976). Minimum body size at sexual maturity of both sexes was 100 mm SCL in a New Mexico population (Germano 2014). We note that the wide variation in size at maturity may be a result of small sample sizes in some studies and/or lack of strict criteria for identifying adults across studies.

Age at sexual maturity varied among sites and often between sexes. In South Dakota, both sexes matured at 7–8 years (Kiesow 2006) or 9 years (Quinn et al. 2014). In Wisconsin, males matured at 8–9 years and females at 10–11 years (Vogt 1981). In western Nebraska, females matured after 12–16 years (Iverson 2024). In a Kansas

**Figure 11.** Nests of *Terrapene ornata ornata.* **A**. Typical covered single nest, Garden County, Nebraska. Photo by John B. Iverson. **B**. Multiple clustered nests, Johnson County, Iowa. Photo by Daniel F. Hughes.

population, sexual maturity was reached at 8–9 years in males and at 10–11 years in females (Legler 1960). Sexual maturity was reached by at least 11 years in males and at 11 years in females in Colorado (Hammerson 1999). Among captive turtles in Oklahoma, sexual maturity was reached at 5 years in males and 8 years in females (St. Clair 1998). In Texas, sexual maturity was reached at 7 years in males and 8 years in females (Blair 1976). Sexual maturity in both sexes of *T. o. luteola* in New Mexico occurred at 6.9 years (Germano 2014).

The species generally exhibits ontogenetic changes in coloration (plastron and carapace) and evidence of scute growth rings (i.e., annuli) associated with age. Hatchlings often exhibit indistinct coloration, juveniles and subadults have sharp radiating lines and obvious growth rings (Fig. 12), adults have distinct but sometimes variable lines and somewhat indistinct growth rings, and older adults can have a nearly complete loss of pattern on an almost completely smooth plastron.

*Longevity*. — Legler (1960) speculated that *T. ornata* could live over 50 years in Kansas. Metcalf and Metcalf (1985) observed individuals at least 28 years old in Kansas. In Illinois, Edmonds (2020) suggested that the oldest *T. ornata* was at least 31 years old. Blair (1976) found two 31-yr-old males and a 32-yr-old female in Texas. Christiansen et al. (2005) documented a female in Iowa that was at least 37 years old. Germano (2014) estimated that three individuals lived over 40 years in New Mexico. Lewis and Iverson (2018), based on ages estimated at first capture of 609 individuals in Nebraska, estimated at least five survived to 33 years, four to 36 years, and 11 lived to between 45 to 57 years. Recently, in Iowa, Bernstein et al. (2023b) used photographs at first capture to estimate ages of 374 marked turtles and found that at least 44% of turtles lived into their 30s, at least 3.5% survived into their 40s, and the oldest turtle was a minimum of 42 years. Females tended to survive longer than males in both Nebraska and Iowa (Lewis and Iverson 2018; Bernstein et al. 2023b).

Nonetheless, published ages may be an underestimation of the true maximum lifespan in *T. ornata* as suggested by the capture history of a female from Nebraska documented by Iverson (pers. obs.): turtle #138 was first caught in 1983 as a mature adult with an SCL of 117 mm, plastral length of 121 mm, and smooth carapace (e.g., growth rings uncountable), and last captured 34 years later in 2017 with the same measurements (Fig. 13), i.e., at least about ≥50 years old.

*Growth*. — Legler (1960) identified four growth stages from turtles in Kansas: juvenile 1 at SCL < 50 mm, juvenile 2 at SCL 50–69 mm, subadults at SCL 70–100 mm, and adults at SCL > 100 mm. In Iowa, Bernstein et al. (2018) fit growth models to 226 female *T. ornata* and defined the following size at age classes: juvenile 1 at SCL < 43.5 mm (<3 growth rings), juvenile 2 at SCL 43.6–69.7 mm (4–8 growth rings), subadults at SCL 69.8–94.5 mm (8–9 growth rings), and adults at SCL > 94.6 mm (>9 growth rings). For 231 males, Bernstein et al. (2018) defined the following size at age classes: juvenile 1 at SCL <31.9mm (<1 growth ring), juvenile 2 at SCL 32.0–62.2 mm (1–4 growth rings), subadults at SCL 62.3–91.8 mm (4–9 growth rings), and adults at SCL >91.9 mm (>9 growth rings). Bernstein et al. (2018) found similar growth patterns as Legler (1960), except that the growth stages were at smaller SCLs, which is perhaps related to different environments between Iowa and Kansas, or an artefact of the different methodological approaches.

Growth is most rapid during early life stages and continues past maturity until about 15 years of age, where growth slows and becomes almost non-existent (Ernst and Lovich 2009). From long-term capture histories (12–37 yrs) of 37 full adults in Nebraska, Iverson (2024) found positive slopes for growth rate for 37 adults, although only 13 slopes were significantly greater than zero. In Iowa, Bernstein et al. (2023b) re-measured 30 turtles between 2021 and 2022 that were initially captured between 1993 and 1996, and just two females showed noticeable growth (1–3 mm).

**Figure 12.** Juvenile and subadult *Terrapene ornata ornata* of different ages. *Top*: Two-year-old from Shawnee County, Kansas. Photo by Benjamin M. Reed. *Bottom*: Nine-year-old from Johnson County, Iowa. Photo by Daniel F. Hughes.

In South Dakota, Quinn et al. (2014) found that males were larger than females until age 8 years, but growth rates were apparently not statistically different between sexes, despite females attaining overall larger sizes. In Kansas, males tended to grow faster than females (Legler 1960), as was the case in Iowa (Bernstein et al. 2018). In New Mexico, Germano (2014) found no difference in the growth rates between males and females, with females being larger in two of his three surveys. In Oklahoma, St. Clair (1998) also found no difference in the growth rate between sexes despite females reaching a much larger adult mean size than males. In fact, most studies found that adult females attain larger mean body sizes than males (Legler 1960; Dodd 2001; Ernst and Lovich 2009; Reed et al. 2023; Iverson 2024) with at least one exception where males were slightly larger (Iowa: Bernstein et al. 2018). The plastron has been noted to exhibit a differential growth rate than the carapace (Legler 1960; Bernstein et al. 2018).

*Survival.* — Nest survival and neonatal overwinter survival are highly variable but generally higher than in aquatic turtles (Iverson 1991). In Wisconsin, Hay (in Kapfer and Brown 2022) estimated egg fertility to be 97%, Temple (1987) found nest survival to be 36.4% from predation, and Doroff and Keith (1990) found hatching success to range 42–58%. In Illinois and Indiana, hatching success was 80–87% and 59–70%, respectively (Tucker

et al. 2017; Minton 2001). In Nebraska, Iverson (2024) found nest survival before winter to be only 42.9% (i.e., post hatching), but overall survival from egg deposition to post-overwintering emergence the following spring was only 9.4%. In late autumn, turtles could get caught above ground if temperatures drop rapidly, and then may become immobile and possibly perish in the winter (Bernstein and Black 2005).

Juvenile survival rates are available from Iverson's (2024) study in Nebraska: survival during the first full year of activity (after overwintering emergence) was 86%, and then 93% annually for the next two years, and 90% annually for the following eight years. In Texas, McVay (2017) found annual survival of subadults to young adults (8–17 years of age based on scute growth ring counts) was 79.4%.

An exceptional mortality event was documented in New Mexico after several major flooding events that followed three years of extreme drought; Rodriguez et al. (2022) found 83 dead juvenile *T. ornata* with a mean SCL of 53.8 mm in a depression near a patch of Eastern Cottonwoods (*Populus deltoides*) among open sand dunes. There was no physical evidence of predation (e.g., claw, beak, or tooth marks), and hence, these turtles may have been attracted to the shallow water table in this swale due to the severe drought, and then drowned during the ensuing rainstorms. The area experienced significantly low precipitation levels (D4 exceptional drought index from November 2020 to April 2021), indicating that drought contributed to the observed mass die-off. The absence of adults in the sample was puzzling, but perhaps some combination of concentrated avian predation that removed carcasses as observed in other turtle species (e.g., Holcomb et al. 2021) and water stress contributed to this event.

Estimates of adult survival are available from several studies. At undisturbed sites, annual survival was 93.2% (Converse et al 2005) and 96.3% (Iverson 2024) at the same site in Nebraska, and 99% (Bowen et al 2004) and 97% (Mitchell et al. 2016) at two sites in Illinois. From two other sites in Illinois, survival estimates for adult females and juveniles were 97.4% and 86.7%, respectively (Ayers Sand Prairie), and 89.7% and 84.4%, respectively (Nachusa Grasslands) (Edmonds et al. 2023). However, at disturbed sites (e.g., with road mortality) annual adult survival rates were 81.6% in Wisconsin (Doroff and Keith 1990), 66% in Illinois (Mitchell et al. 2016), 83% in Kansas (Metcalf and Metcalf 1985), and 86.9% in Texas (Blair 1976). Mitchell et al. (2016) found survival was lowest at a disturbed location with road mortality, especially for juveniles, indicating potential impacts of vehicular disturbance on populations, and they advised against heavy development activities like building construction and vegetation mowing, as persistent human presence in the environment significantly reduces adult survival in *T. ornata*.

**Figure 13.** A female *Terrapene ornata ornata* that was first caught in 1983 as a mature adult with a smooth carapace and had no measurable shell growth when last caught in 2017 (34 years between first and last captures), Garden County, Nebraska. Photo by John B. Iverson.

*Clutch Frequency.* — Multiple clutch production in a season is generally uncommon in *T. ornata*; however, up to one-third of females in Kansas could have produced a second clutch (Legler 1960). In Nebraska, only one in 25 females produced a second clutch (Converse 1999). In an expanded study at that same site (Iverson 2024), seven of 113 females skipped reproduction in a given year and five apparently produced a second clutch (overall frequency = 1.07%). In Wisconsin, one clutch was produced annually (Doroff and Keith 1990), and a second annual clutch was rare in Illinois (Edmonds et al. 2020). No direct evidence of multiple clutch production was evident in a population of *T. o. luteola* in New Mexico (Nieuwolt-Dacanay 1997), but would be expected, since gravid females were found from May to August.

In neither *T. o. ornata* nor *T. o. luteola* have all females been found to be gravid in a given year, and the percent of gravid females varies among years within a site. In South Dakota, 64% of adult females were gravid (Quinn et al. 2014). Gravid females accounted for 50 and 63% (mean, 57%) in Wisconsin (Doroff and Keith 1990). In Illinois, the percentage of gravid females was widely variable across two sites, ranging from 24 to 63% (mean, 40%) (Edmonds 2020), and across all sites and years documented in Illinois, an overall average of 34% of females were gravid (Edmonds et al. 2020). For another Illinois population, 67% were gravid (Tucker et al. 2015), corroborating an

apparent absence of annual reproduction in all *T. o. ornata* in any given population. In Nebraska, females that did not nest one year could retain sperm of that year's mating for nesting the following year (Fogell 2010). In western Nebraska, 11% of 27 adult females were gravid in 2022, but 85% of 27 females were gravid in 2023, an increase which was apparently related to drought conditions and extended above-average temperatures in 2022 (Munsell 2023).

The frequency of gravid females of *T. o. luteola* in New Mexico also ranges widely over the years; values of 10, 42, and 61% (mean, 58%) were reported among years (Nieuwolt-Dacanay 1997), as well as values of 31, 38, and 44% over three years of a long-term study (Germano 2014), with some females skipping two successive seasons. Rainfall volume in the spring was positively correlated with that year's frequency of gravid females (Nieuwolt-Dacanay 1997), but the average clutch size was not related to precipitation in the year of oviposition or precipitation in the preceding year (Germano 2014).

*Clutch Size.* — Across its geographic range, mean clutch size of *T. ornata* does not exceed 5 eggs, but there is considerable variability within a season, among years, and among sites. In South Dakota, clutch size averaged 4.3 eggs (range, 2–5; Quinn et al. 2014) and ranged 4–6 eggs for the state in general (Kiesow 2006). In Wisconsin, 6 eggs were reported as the usual clutch size (but this number is dubious) and ranged 2–8 eggs (Vogt 1981). Mean clutch sizes over two years in Wisconsin were 2.8 and 4.1 eggs (3.5 eggs combined), with up to 7 eggs in a clutch (Doroff and Keith 1990). Mean clutch sizes from two locations in Illinois were 2.5 eggs (range, 1–4), 4.2 eggs (range, 3–6), and 2.4 eggs (range, 1–4) for the entirety of the study (Edmonds 2020). Average clutch sizes were 2.6 eggs (range, 1–4) and 4.6 eggs (range, 3–6) from two sites in Illinois (Edmonds et al. 2020). In Kansas, clutch size averaged 4.7 eggs (range, 2–8); however, second clutches in the same season averaged 3.5 eggs (Legler 1960). The eggs that were laid each year were produced from oogenesis during the previous year (Legler 1960). A single clutch of four nearly ovulatory-sized follicles was reported for southwest Nebraska (Iverson 1977). In western Nebraska, Converse (1999) reported that clutch size averaged 3.4 eggs (range, 2–6). A subsequent study at that site estimated a mean clutch size of 2.6 eggs (range, 2–4), which was suspected by the authors to have been an artifact of a small sample size (Converse et al. 2002). Further study revealed a mean clutch size for 102 females as 3.6 eggs (range, 1–6; Iverson 2024), and clutch size was positively correlated with body size. A clutch of six eggs was noted in Kansas (Collins 1993).

In New Mexico, *T. o. luteola* produced an average of 2.7 eggs (range, 1–4) over three consecutive years (annual means = 2.5, 2.8, and 2.7 eggs), and clutch size was not affected by rainfall (Nieuwolt-Dacanay 1997). Mean clutch size of 16 females in Arizona was 3.1 eggs (Legler and Vogt

2013). Annual mean clutch sizes of 2.7 eggs (range, 1–4), 2.8 eggs (range, 2–3), and 3.6 eggs (range, 2–5) showed variation among years in New Mexico (Germano 2014). For all six years combined, Germano (2014) found the mean clutch size to be 2.9 eggs (range, 1–5), and the mode was three eggs. Although Germano (2014) found a significant relationship between the number of eggs per clutch and SCL of females, body size only explained 10.8% of the variation in clutch size.

*Egg Dimensions.* — Eggs are elliptical in shape, pliable-shelled, and can be large. Ernst and Lovich (2009) reported means and ranges for 65 eggs, presumably laid from captive animals of *T. o. ornata*, as: 34.2 mm in length (range, 25.7–41.0), 24.5 mm in width (range, 20.0–29.0 mm), and 10.5 g in mass (range, 8.0–14.3 g). In Nebraska, 160 eggs averaged 37.6 mm in length, 23.0 mm in width, and 11.95 g in mass (Iverson 2024). In Kansas, 42 eggs of *T. ornata* averaged 36.1 mm length, 21.7 mm width, and 10.1 g mass, with the largest and heaviest eggs coming from smaller clutches (Legler 1960). Based on 11 eggs for *T. ornata* in Iowa, mean egg length was 36.7 mm (range, 30–40.6 mm) and mean egg width was 22.4 mm (20.7–23.8 mm) (Christiansen and Parmelee 2003). Mean egg width of *T. o. luteola* in New Mexico was the largest recorded (26.7 mm; range, 23.8–29.0 mm) (Nieuwolt-Dacanay 1997). Using samples from Nebraska, *T. ornata* was found to produce larger eggs relative to its body size than other turtles (Ewert 1979), which was thought to represent an adaptation for box turtles (genus *Terrapene*) for embryonic development in terrestrial settings because larger eggs are more likely to hatch under a wider range of conditions than smaller ones (Packard et al. 1985).

*Nest Dimensions.* — One shallow nest (with no body pit) in Kansas measured 7.6 cm deep and 7.6 cm wide with a smaller opening at the surface (Legler 1960). Depth of nests (with body pits) averaged 16.8 cm below the ground surface (range, 14–20 cm) in Nebraska (Costanzo et al. 1995). Nests from Wisconsin were described as flask-shaped (Vogt 1981; Doroff and Keith 1990), with a neck measuring 5–8 cm across and the nest cavity depth averaging 13 cm (Doroff and Keith 1990), presumably without a body pit. Soil temperatures of nests are available for Wisconsin (26.3 and 26.4°C) (Vogt 1981) and Illinois (23.2 and 23.9°C) (Baker et al. 2010). Two relative humidity readings of nests are available for Illinois (70 and 83%) (Baker et al. 2010).

*Relative Clutch Mass.* — Relative Clutch Mass (RCM) is a measurement of the proportion of the gravid female's body mass incorporated into the clutch. Dividing the clutch mass, estimated as the difference between pre- and post-oviposition masses of females, by the pre-oviposition body mass provided a mean estimate of 13.6% in South Dakota (Quinn et al. 2014). For females in Nebraska with measured gravid mass and clutch mass data (*n* = 51), RCM averaged 11.3% (range, 6.3–17.0%) (Iverson 2024).

*Clutch Relationships.* — In Kansas, the positive relationship between clutch size and female size in *T. ornata* was not strong, but the largest and heaviest eggs occurred in the smallest clutches (Legler 1960). However, in Illinois and Nebraska, larger females produced larger clutches (Edmonds 2020; Edmonds et al. 2020; Iverson 2024), and in New Mexico (*T. o. luteola*), larger clutches were associated with larger females (Nieuwolt-Dacanay 1997; Germano 2014), though weakly. Also in New Mexico, heavier females laid wider eggs, but egg width was not related to female SCL or carapace width, and no trade-off was detected between clutch size and egg size (Nieuwolt-Dacanay 1997; but see Iverson 2024).

*Clutch Size and Egg Size vs. Latitude.* — Clutch size in *T. ornata* does not vary with latitude (Edmonds et al. 2020; Iverson 2024). However, it remains to be understood why the largest clutch sizes were in the north (South Dakota and Kansas, excepting Nebraska), and the lowest were in the east (Illinois) and southwest (New Mexico). To that end, a larger clutch size was found in New Mexico compared to Kansas populations (Nieuwolt-Dacanay 1997). However, egg size does not appear to vary with latitude, although eggs are bigger in New Mexico and Arizona than those on the Great Plains (Iverson 2024).

*Incubation Time.* — Under favorable conditions in the wild, incubation lasted about 65 days for *T. ornata* in Kansas (Legler 1960). In that same study at varying temperatures, incubation in the field lasted 125 days at 23.9°C and 70 days at warmer temperatures. In the lab, hatching occurred at 56–125 days (Legler 1960). In Nebraska, eggs hatched in August and September (Converse et al. 2002) after approximately 49 days of incubation (Fogell 2010). In Wisconsin the incubation period ranged 59–70 days from captive animals (Vogt 1981) versus an average of 80 days in the wild (Doroff and Keith 1990). Eggs from Nebraska incubated in the lab at 29°C hatched in 51 days (Packard et al. 1985). The studies addressing hatching success in *T. ornata* report values of 67% in Nebraska (Converse et al. 2002), and 42 and 58% in Wisconsin (Doroff and Keith 1990).

Overwintering below the natal nest has been reported for both subspecies of *T. ornata*. In Kansas, hatchlings overwintered below their natal nest if the soil was dry in autumn (Legler 1960). In Nebraska, hatchlings overwintered underground below the nest at a mean soil depth of 64.7 cm (range, 17–98 cm) (Costanzo et al. 1995, 2002). In Wisconsin, overwintering of hatchlings was reported at burrow temperatures ranging from -8 to 11.8°C, with survivorship of 20% (Doroff and Keith 1990). Germano (2014) did not find evidence of overwintering below nests in New Mexico because most periods of inactivity were spent in enlarged kangaroo rat burrows, as observed by Legler and Vogt (2013). Murray (2013), also in New Mexico, found two hatchlings (SCL = 38.1 mm and 36.3 mm) that overwintered in the natal nest for at least 266 days at a

*Diet.* — *Terrapene ornata* is an opportunistic omnivore that primarily uses visual cues to detect moving prey, but will also employ olfactory senses to discriminate among still prey (Fitch 1965). The species generally varies its diet depending upon what is seasonally available in the local habitat, which can vary extensively throughout the year, from near exclusive consumption of mulberries (Moraceae) to dung beetles (Scarabaeidae). Turtles will often congregate at concentrated resources to forage, such as fruiting trees (e.g., *Morus rubra*) waiting for ripe fruit to fall (Legler 1960; Metcalf and Metcalf 1970; Blair 1976), and even under bird nests, such as the Mississippi Kite (*Ictinia mississippiensis*), which frequently drop prey items (Parker 1982). Much of Legler's (1960) study was conducted on cattle-grazed pastures where the turtles appeared to co-exist well with the cows (Fig. 14) by eating primarily dung beetles associated with cow manure. Legler (1960) even speculated that large mammals and their manure were needed for *T. ornata* to thrive. In fact, from similar habitats in Kansas, *T. ornata* has been observed frequently using cow patties for food (coprophagy) and protection (forms), in both fresh and old manure piles (Fig. 14), which could possibly also protect them from thermal and drought-related stresses. Suriyamongko et al. (2022) made direct observations of juvenile and adult *T. ornata* exhibiting coprophagy of cow dung in New Mexico. Parandhaman and Forstner (2018) observed an adult purported *T. o. luteola* × *T. o. ornata* intergrade in Texas feeding on a fresh cow patty lacking insects, which shrank in size after a >3-hr interval, presumably from coprophagy. This reliance on dung piles should not be surprising given the diversity of ungulates across the Great Plains during the entire evolutionary history of *T. ornata*.

Arthropods are known to comprise the bulk of the diet in *T. ornata* (Legler 1960; Blair 1976; Sievers 2015; Worthington et al. 2017; Forrester et al. 2019; Grose et al. 2021), including beetles (Cantharidae, Carabidae, Cerambycidae, Chrysomelidae, Curculionidae, Dryophthoridae, Geotrupidae, Histeridae, Lampyridae, Phengodidae, Scarabaeidae, Silphidae, and Staphylinidae), caterpillars (Arctiidae, Noctuidae, Pyralidae, and Sphingidae), dipteran larvae (Sarcophagidae), robber flies (Asilidae), harvestmen (Phalangidae), spiders (Araneidae), ants (Formicidae), bees (Apidae), cicadas (Cicadidae), grasshoppers (Acrididae), thrips (Phlaeothripidae), planthoppers (Caliscelidae), fireflies (Lampyridae), stick insects (Phasmatodea), and crickets (Gryllidae). Other invertebrates consumed include snails (Planorbidae, Polygyridae, Gastrodontidae, and Succineidae), earthworms (Lumbricidae), millipedes (Diplopoda), woodlice (Armadillidiidae), and crayfish (Cambaridae). Sievers (2015) examined the diet of reintroduced *T. ornata* at two sand prairies in western Illinois across two years and found that ants, dung beetles, grasshoppers, and weevils (Curculionidae) were in many of the 33 fecal samples in 2013, and those same arthropods were prominent in the



**Figure 14.** Grazed, treeless habitat co-occupied by *Terrapene ornata ornata* and Domestic Cattle (*Bos taurus*) with observations of manure use in Shawnee County, Kansas. *Top*: Cattle-grazed habitat. Photo by Benjamin M. Reed. *Middle*: Juvenile in a fresh manure patty. Photos by Daniel F. Hughes. Bottom: Adult in an old manure patty. Photos by Benjamin M. Reed.

depth of at least 25 cm. Further, Murray (2013) also had semi-captive hatchlings (i.e., kept in a fenced backyard) that overwintered in the nest cavity in Albuquerque, New Mexico.

*Hatchling Size and Sex.* — Ernst and Lovich (2009) reported sizes for hatchling *T. ornata,* presumably from captive animals (*n* = 21), as: 29.7 mm SCL (range, 28–32), 24.0 mm CW (range, 22.9–29.0), and 7.5 g mass (range, 6–9). A single wild neonate measured 28.8 mm SCL in Indiana (Minton 2001), and hatchlings were apparently 30 mm SCL in Wisconsin (Vogt 1981), and 32.6 mm SCL (8.6 g mass) in Iowa (*n* = 5; Hughes, unpubl. data). Hatchlings (*n* = 74) in Nebraska averaged 32.2 mm SCL, 32.1 mm PL, and 9.94 g (Iverson 2024).

*Terrapene ornata* exhibits temperature-dependent sex determination (Vogt and Bull 1982; Ewert and Nelson 1991). One study found that all females were produced at incubation temperatures of 29°C, and larger hatchlings were produced from eggs incubated on moister substrates (Packard et al. 1985).

25 samples from 2014, with the addition of click beetles (Elateridae) and stink bugs (Pentatomidae). Overall, Sievers (2015) found that arthropods and plant matter were found in >90% of all fecal samples, and that the Strawberry Root Weevil (*Otiorhynchus ovatus*) was the most common insect (48% of samples in 2014 and 73% of samples in 2013). Platt et al. (2012) examined fecal samples of 14 *T. o. luteola* from Arizona (mean SCL = 121 mm; range, 89–147) and found the remains of dung beetles, lady beetles (Coccinellidae), millipedes (*Orthoporus* spp.), grasshoppers (Caelifera), the molar of a small mammal (likely eaten as carrion), small stones, and unidentified leaves and seeds. Lange and Alarcon (2020) described *T. ornata* consuming spittlebug nymphs (superfamily Cercopoidea, order Hemiptera) and their froth, which contains chemicals that act as irritants. Detailed lists of invertebrate taxa found in the diet of *T. ornata* can be found in Sievers (2015: Appendix), Worthington et al. (2017), and Ernst and Lovich (2009:436).

Plant taxa in the diet, mostly fruits, include blackberries, cantaloupes, prickly pear cactus, dandelions, green bean pods, groundcherries, melons, mulberries (false fruits), persimmons, spiderworts, strawberries, and tomatoes (Legler 1960; Blair 1976; Stone 2002; Ernst and Lovich 2009; Stone and Moll 2006, 2009; Sievers 2015). Consumption of cow dung, which is mostly made up of plant matter, has also been documented extensively (see above). In areas of the sandhills of eastern Colorado and western Nebraska lacking standing water, *T. ornata* readily consumes Prairie Spiderwort (*Tradescantia occidentalis*), which was speculated as a potentially significant source of moisture (Nash and Gangloff 2010a, 2010b; Iverson, pers. obs.). Blair (1976) described a similar situation in Texas with the Prickly-pear Cactus (*Opuntia lindheimeri = O. cespitosa*) serving as a source of hydration for *T. ornata*. In Iowa, *T. ornata* readily consumes the pads of *O. humifusa* on sand prairies (Hughes, pers. obs.). In Kansas, Thomasson (1980) found *T. ornata* ate the flowers of the Pincushion Cactus, *Coryphantha vivipara*. Sievers (2015) found that monocot plants were more common than dicots in fecal samples from Illinois. Worthington et al. (2017) and Stone and Moll (2006) also documented consumption of fungi by *T. ornata*. Murray (2013) found hatchling *T. o. luteola* consuming petals of Thread-leaf Groundsel (*Senecio flaccidus*). Murray et al. (2014) documented *T. o. luteola* eating flower buds of a Hot Springs Globemallow (*Sphaeralcea polychrome*) and pads of the Purple Prickly Pear Cactus (*O. macrocentra*). Detailed lists of plant taxa found in the diet of *T. ornata* can be found in Sievers (2015: Fig. 12), Stone and Moll (2009), and Ernst and Lovich (2009:436).

Vertebrate taxa are mostly consumed by *T. ornata* as carrion, and include fish and the following amphibians and reptiles: Plains Leopard Frog (*Lithobates blairi*), American Bullfrog (*L. catesbeianus*), Northern Leopard Frog (*L. pipiens*), Western Spadefoot (*Spea hammondi*), Mexican Spadefoot (*S. multiplicata*), Great Plains Toad (*Anaxyrus cognatus*), Eastern Collared Lizard (*Crotaphytus collaris*), Texas Horned Lizard (*Phrynosoma cornutum*), Greater Short-horned Lizard (*P. hernandesi*), Round-tailed Horned Lizard (*P. modestum*), Spot-tailed Earless Lizard (*Holbrookia maculata*), Red-sided Gartersnake (*Thamnophis sirtalis parietalis*), Long-nosed Snake (*Rhinocheilus lecontei*), and *T. ornata*; the following birds were reported in the diet as carrion: Blue-winged Teal (*Anas discors*), Northern Bobwhite (*Colinus virginianus*), Chicken (*Gallus gallusdomesticus*), and Mississippi Kite (*Ictinia mississippiensis*); and the following mammals were reported as carrion in the diet: Ord's Kangaroo Rat (*Dipodomys ordii*), Eastern Woodrat (*Neotoma floridana*), Black Rat (*Rattus rattus*), Eastern Cottontail (*Sylvilagus floridanus*), and unidentified small mammals (Legler 1960; Blair 1976; Black 1987; Kolbe 1998; Dodd 2001; Ernst and Lovich 2009; Germano 2009; Murray et al. 2014; Forsberg and Geluso 2017). There is a report of *T. ornata* hunting and eating a live Texas Horned Lizard which was placed in the same cage with it for four days (Eaton 1947).

*Terrapene ornata* may be an important agent of seed and spore dispersal (chelonochory) for a variety of plants and fungi (Stone 2002; Stone and Moll 2006, 2009). In Iowa, Dukuly et al. (2023), observed a substantial decline of 2,905% in seed count and 4.83% in fecal weight of *T. ornata* fecal samples from spring to fall in Iowa, which was primarily due to mulberry seeds from fruiting trees in spring. Dukuly et al. (2023) noted enhanced germination of seeds passing through the digestive tract of *T. ornata*, with an average germination rate of 13.9% across 13 fecal samples (range, 0–39.8% seeds germinated per sample) with a total of 411 seeds germinating out of 3,699 seeds planted. A single female's fecal sample contained 926 mulberry seeds, likely from around 47 fruits (mean, 19.75 seeds per fruit). *Terrapene ornata* dispersed an average of 99.3 seeds per fecal sample (205.5 seeds per fecal sample in spring vs. 3.7 in fall), yielding an average of 0.28 seeds per unit body mass (g) (0.59 in spring vs. 0.01 in fall), surpassing dispersal rates relative to body mass in Brown Bears (*Ursus arctos*) (0.051), Mallard Ducks (*Anas platyrhynchos*) (0.0013), and Lowland Tapirs (*Tapirus terrestris*) (0.045), but second only to Painted Turtles (*Chrysemys picta*) (0.77) in the published literature (Dukuly et al. 2023).

Several researchers have found stones (lithophagy) to be included in the diet of *T. ornata*, which may be associated with dietary or mineral deficiency, or could function as a crop to grind food (Ernst and Lovich 2009). Legler (1960) found stones (up to 7 mm) in the stomach of dissected turtles, and Skorepa (1966) observed captives deliberately eating stones (3–5 mm), as did Kramer (1973).

*Predators.* — Documented predators consist of a wide diversity of vertebrates and even other *T. ornata* (Ernst and Lovich 2009). Eggs, hatchlings, and juveniles are the most at-risk for predation in comparison to adults. Adults have a highly ossified shell with a closable hinge capable

of protecting vulnerable soft tissues from predators (Dodd 2001; Redder et al. 2006). However, eggs and juveniles lack the ossification necessary to prevent crushing or complete ingestion by predators. A detailed list of predators, most involving nests and hatchlings can be found in Ernst and Lovich (2009:437).

In Kansas, confirmed predators of eggs were the Striped Skunk (*Mephitis mephitis*) and the Gopher Snake (*Pituophis catenifer*) (Legler 1960). Striped Skunks were also reported as nest predators in Illinois (Smith 1961). Western Hognose Snakes (*Heterodon nasicus*) commonly ate box turtle eggs in Illinois (Barten 1980; Durso and Mullin 2017); however, Iverson and Auth (2024) did not find eggs or young of *T. ornata* in the diet of 92 *H. nasicus* in western Nebraska, even though turtle eggs of other species were the most common dietary item and box turtles were common in the area. Raccoons (*Procyon lotor*) and other mammalian mesopredators were the most common predators of nests in Iowa (Bernstein et al. 2015). Temple (1987) documented increased nest depredation closest to habitat edges, presumably corridors used by mammalian mesopredators. However, Bernstein et al. (2015) found no edge effect in experimental nests and noted that the primary cue predators used to find nests was soil disturbance (see also Geller and Parker 2022). Because females often cluster nests in suitable habitat and do not lay eggs on the same night, mesopredators have a predictable and reliable location to forage over several weeks. Other known predators of nests include the Prairie Vole (*Microtus ochrogaster*; Doroff and Keith 1990) and Prairie Mole (*Scalopus aquaticus*; Converse et al. 2002). The Eastern Copperhead (*Agkistrodon contortrix*), White-necked Raven (*Corvus cryptoleucus*), and Raccoon were confirmed predators of hatchlings in Kansas (Legler 1960), and Bernstein et al. (2023a) found hatchlings with limbs nibbled and one depredated with tooth markings suggestive of damage by a Short-tailed Shrew (*Blarina brevicauda*). Rose (1984) stated that nearly a third of the 175 *T. ornata* captured in Kansas exhibited some form of injury.

Predators of subadults and adults are mostly medium-sized mammal species, such as the American Badger (*Taxidea taxus*), Raccoon, Virginia Opossum (*Didelphis virginiana*), Nine-banded Armadillo (*Dasypus novemcinctus*), Feral Hog (*Sus scrofa*), Red Fox (*Vulpes vulpes*), Coyote (*Canis latrans*), and Domestic Cat (*Felis catus*) (Legler 1960; Dodd 2001; Redder et al. 2006; Ernst and Lovich 2009). Avian predators include Crows (*Corvus* spp.), Common Raven (*Corvus corax*), Turkey Vulture (*Carthartes aura*), Golden Eagle (*Aequila chrysaetos*), and Red-tailed Hawk (*Buteo jamaicensis*) (Legler 1960; Dodd 2001; Redder et al. 2006; Ernst and Lovich 2009). Germano (1999) described an attempted predation by a Turkey Vulture on a female *T. o. luteola* (128 mm SCL and 480 g) in New Mexico; the turtle was recaptured less than a year later and the damaged epidermal material on

the carapace had regrown. Most attempted predation of *T. ornata* appears to be directed at the limbs, head, or tail, as these are the most common injuries observed in living box turtles in Iowa (Hughes, pers. obs.) and Kansas (Legler 1960). Bernstein et al. (2023a) reported 8 of 799 healthy adult turtles with healed amputations of a front limb or digits. Metcalf and Metcalf (1979) discovered 163 dead *T. ornata* in late February and March near an overwintering site in Kansas with the head and front legs missing on all specimens, but no tooth marks visible on the shells. They attributed these deaths to coyotes based on canid-like holes that were dug to unearth the turtles. In Illinois, Adamovicz (2019) found shell lesions from attempted predation to occur at a rate of 51–59% annually. Bullfrogs are the only amphibian recorded as a predator, and *T. ornata* is reported to exhibit cannibalism (Ernst and Lovich 2009). *Terrapene carolina* has been depredated by Red Imported Fire Ants (*Solenopsis invicta*; Mount 1981) and *T. triunguis* has died from stings of this species (Montgomery 1996). Thus, *T. ornata* likely could also potentially be depredated by this species.

Most defensive behaviors by *T. ornata* against predators involve closing the hinged plastron tightly against the carapace, biting, and thrashing the limbs to get away (Dodd 2001). Gangloff and Nash (2010) reported musking behavior in 14 wild and two captive *T. ornata*, where a strong odor was produced, which was distinct from urine or feces and was apparently similar in odor to the musk of the Common Musk Turtle (*Sternotherus odoratus*).

Many aspects of predation on *T. ornata* are understudied, and many of the currently known predators of this species are based on Legler (1960), which is one of the few studies that included first-hand sightings of active predation. However, with the paucity of direct predation sightings, it is possible there are other more unassuming or cryptic predators.

Recent studies investigating predator-prey ecology utilized camera traps to record direct predation attempts and added prey models to increase predation records (e.g., Akcali et al. 2019). For example, Tetzlaff et al. (2020) used 3D printed models of juvenile *T. carolina* paired with camera traps in Illinois to document predation attempts by Raccoon (*n* = 22), Virginia Opossum (*n* = 2), Eastern Chipmunk (*Tamias striatus*) (*n* = 3), Fox Squirrel (*Sciurus niger*) (*n* = 1), and Wild Turkey (*Meleagris gallopavo*) (*n* = 1). The use of cameras with models in the field has the potential to provide greater insight into the full suite of predators of *T. ornata*. For example, Kolthoff and Hughes (2023) in Iowa applied the same methodology as Tetzlaff et al. (2020), but with models that were made to resemble adult *T. ornata* (Fig. 15). Surprisingly, the Eastern Cottontail (*Sylvilagus floridanus*) was recorded as the most frequent mammal biting on the heads, limbs, and shells of the models (possibly to sharpen their incisors or some other non-predatory reason), with various rodent species

and Raccoons also investigating or attacking the models (Fig. 15). With the application of these new technologies, it is likely that our knowledge of the predation ecology for *T. ornata* will expand.

*Parasites*. — Myiasis is often reported in *T. ornata*, and several sources have identified sporadic occurrences in various locations (e.g., Legler 1960; McMullen 1940; Rainey 1953; Rodeck 1949), and at least one long-term study described occurrence records in approximately 2% of individuals (12 of 609 turtles) (Iverson 2023). Dipteran larvae have been reported as parasites of *T. ornata*, especially in the genus *Cistudinomyia* (*Sarcophaga*) (Rodeck 1949), where they infest limbs and other areas of exposed skin, limiting movement, and sometimes resulting in death (e.g., Rainey 1953; Smith et al. 2024). The flesh fly species *C. cistudinis* is a turtle-specific parasite, and McMullen (1939) reported the infestation of larvae inducing myiasis in the skin of a *T. ornata* from Oklahoma. Iverson (2023) documented that at least 2% of captured individuals over 38 years in western Nebraska were infected by sarcophagid botflies, primarily in late spring following warm temperatures in the previous September; thus, they may be a cause of mortality in some years.

Gauntt et al. (2021) found *C. cistudinis* infections in three of four *T. ornata* populations across Nebraska ($n$ = 1), Kansas ($n$ = 2), and Iowa ($n$ = 1), with at least two deaths attributable to infections; however, in two of the three infected populations only one turtle was found to have flesh flies in each (1 of 81 turtles in Nebraska; 1 of 49 turtles in Kansas). More recently, Smith et al. (2024) found that the two infected populations in Kansas were less than 40 miles apart but varied dramatically in their infection rate. The infection rate near Lawrence, Kansas (11/42 = 26%) was 11.5 times higher than the infection rate in North Topeka, Kansas (2/88 = 2%). The average number of larvae for all infected turtles ($n$ = 20) across all years was 16.2 flesh flies, with an infection intensity ranging between 1 and 56 flesh flies. The highly infected population near Lawrence was in a habitat with more human activity, a higher density of invasive plant species, and more irregular habitat management practices compared to the less infected population. Smith et al. (2024) also found that females were more likely to be infected than males by a ratio of 2 to 1.

O'Toole et al. (2021) described cutaneous myiasis via computed tomography of six sarcophagid larvae infecting the neck and limbs of a captive-bred 26-g juvenile female *T. ornata* from Kansas. Recently, Otten and Becker (2023) described two incidences of the Smooth Turtle Leech (*Placobdella parasitica*) parasitizing *T. ornata* in Iowa by attaching to the carapace.

Two species of apicomplexan, coccidian parasites in the genus *Eimeria* have been described from the feces of *T. ornata* in Texas (*E. ornata*; McAllister and Upton 1989) and Arkansas (*E. doddi*; McAllister et al. 2017). *Eimeria*
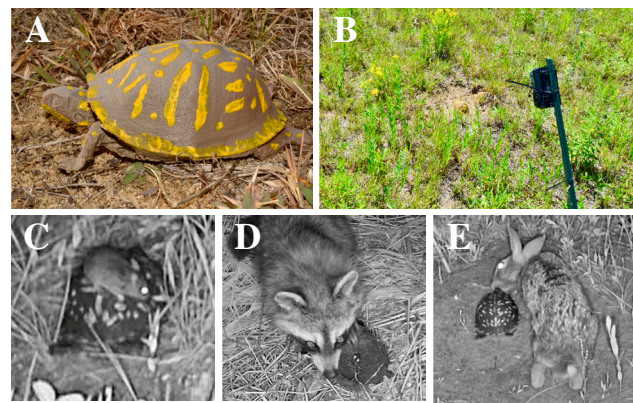


**Figure 15.** Images showing the setup and findings from the *Terrapene ornata* predation study by Kolthoff and Hughes (2023) using camera traps and 3D printed turtle models, Johnson County, Iowa. **A**. 3D-printed and hand-painted model of *T. ornata*. **B**. Deployed model and associated camera trap. **C–E**. Camera-trapped mammals investigating / attacking the turtle models, including a rodent (C), a raccoon (D), and a rabbit (E).

species can cause the disease coccidiosis, but it is unclear whether the host turtle's health was negatively affected by infestation by these parasites. Mosquitos (*Aedes* spp.; Crans and Rockel 1968) could be considered parasites as they have been found feeding from the exposed skin of other box turtles. In Kansas, Rose (1984) found *T. ornata* to be infected with chiggers, and a single wild individual in Kansas was found to be infected with hundreds of unidentified mites covering its shell, head, forelimbs, and hindlimbs (Reed, pers. obs.). In addition, *T. ornata* has been shown to have nematodes (Harwood 1930; Hill 1941; May 1960) and trematodes (May 1960).

**Population Status**. — Annual rates of population growth ($\lambda$, lambda) for *T. ornata* are available from Nebraska (1.006, Converse et al. 2005; 1.007, Iverson 2024), Illinois (1.02, Bowen et al. 2004), and Kansas (1.02; Metcalf and Metcalf 1985), all of which indicate somewhat stable and slightly growing populations. In contrast, Edmonds et al. (2024) recently found lambda estimates of less than 1.0 for two populations in Illinois, indicating that they are declining, albeit at slightly different rates. However, when analyzed under different, more liberal demographic assumptions, the populations could also be increasing (Edmonds et al. 2024).

Two life table studies are available for *T. ornata*. Based on previously published life history traits, Redder et al. (2006) generated an estimated life table assuming a stable age class distribution and a matrix model projection. Their model estimated generation time at 29.2 ± 19.6 years, and their sensitivity analysis determined that lambda was most affected by changes in adult female mortality (as demonstrated by Converse et al. 2005 and Edmonds et al. 2024). Based on a complete suite of the life history traits for a single population in Nebraska, Iverson (2024) produced a life table that estimated generation time at 28.4 years, very similar to the estimate of Redder et al. (2006) and

**Figure 16.** Observed threats to the survival of *Terrapene ornata*. **A**. Injury from a presumed predation attempt by an unidentified predator, Johnson County, Iowa. Photo by Daniel F. Hughes. **B**. Partially burned carapace from a previous fire, Shawnee County, Kansas. Photo by Benjamin M. Reed. **C**. Female stuck in root system during attempted emergence from overwintering, Johnson County, Iowa. Photo by Daniel F. Hughes. **D**. Dead-on-road female with eggs, Garden County, Nebraska. Photo by John B. Iverson. **E**. Dead female due to disking from heavy machinery in a corn field, Johnson County, Iowa. Photo by Daniel F. Hughes.

close to the estimate of 32 years by Blair (1976) based on a complete turnover of his population in Texas.

*Age-Class Distribution.* — The proportion of juveniles was 20% in South Dakota (Quinn et al. 2014), 16% in Nebraska (Converse et al. 2002), 16% in Kansas (Legler 1960), ca. 12% in Texas (Blair 1976), and 18.2% and 6.0–10.6% (<100 mm PL) in New Mexico (Nieuwolt 1996 and Germano 2014, respectively). While similar, these proportions may well underestimate the actual proportion of cryptic juveniles in each of these populations. For example, at a Nebraska site, Iverson (2024) used drift fences between wetlands and uplands and found 45.3% of 1,535 total captures were immature turtles (<110 mm PL), and 30.6% were juveniles <100 mm PL. These higher proportions reflect the greater effectiveness of drift fences for sampling juveniles, compared to typical visual encounter surveys (e.g., Refsnider et al. 2011). From over 34 years in Illinois, Edmonds et al. (2023) had 583 captures of 392 individuals (42.3% male, 34.7% female, and 23% juvenile at Ayers Sand Prairie), with a population estimate of 578 turtles in 2022. In addition, they made 407 captures of 224 individuals (with similar size-class proportions) at Nachusa Grasslands over eight years with a population estimate of 185 turtles in 2023.

*Sex Ratio.* — Sex ratios in populations of *T. ornata* are typically female dominated, even when not statistically different (but see Illinois populations by Edmonds et al. 2023 and also Schmidt and Hellgren 2013): 1.03F/1M (South Dakota, Quinn et al. 2014), 1.56F/1M (Wisconsin, Doroff and Keith 1990), 1.43F/1M (Illinois, Bowen et al. 2004), 1.49F/1M (Nebraska, Iverson 2024), 1.72F/1M (Kansas, Legler 1960), 1.4F/1M (Kansas, Rose 1984), 1.31F/1M (New Mexico, mean of three surveys, Germano 2014), and 1.12F/1M (Arizona, Hall and Steidl 2003). This pattern may be related to the species' temperature-dependent sex determination (warm incubation producing females and cool temperatures producing males; Ewert and Nelson 1991, Packard et al. 1985); however, it might also reflect increased movements by females (e.g., for nesting migrations) and thus relatively higher capture rates (Iverson 2024). It could also be related to the fact that females tend

to live longer than males as observed in Nebraska (Lewis and Iverson 2018) and Iowa (Bernstein et al. 2023b).

*Density and Biomass.* — In Wisconsin, Doroff and Keith (1990) found 2.9–5.0 adults per ha, and if average body mass was similar to that in Nebraska (323 g; Iverson 2024), then standing crop biomass would have been 0.9–1.6 kg/ha. In eastern Kansas, Legler (1960) reported densities of 6.4–15.6 turtles per ha, and from those data, Iverson (1982) estimated a standing crop biomass of 1.8–4.3 kg/ha. In Kansas, Clarke (1958) and Rose (1984) estimated densities of 4.6/ha and 10.4/ha, respectively. In Texas Blair (1976) found 0.53–0.81 adults per ha, but in his core study area (0.93 ha), he found 16–22 adults each year (17.2–23.7/ha). If average body mass was 323 g (as in Nebraska), estimated biomass in his core area would have been as high as 5.6–7.7 kg/ha.

**Threats to Survival**. — Direct threats to survival in *T. ornata* include predation on adults, wildfires and controlled burns, succession to woody vegetation, road mortality from vehicle collisions, damage from agricultural machinery, nest and hatchling depredation, and commercial exploitation (Fig. 16). Below we detail these specific threats and others that manifest in more indirect ways.

*Commercial Exploitation.* — The species has been poached for the international pet trade, but the amount of such evidence is less than that for *T. carolina* (e.g., Kiester and Olson 2011; Sevin et al. 2022). Thus, most trafficking incidents involving *T. ornata* likely go unreported. For example, Easter et al. (2023) found 54 cases in the media of illegal trade between 1998 and 2021 involving at least 24,000 trafficked turtles of 34 different species, with only four cases mentioning *T. ornata* compared to 22 for *T. carolina* (*sensu lato*). Maron (2019) described poaching of thousands of turtles from the wild for sale into the illegal wildlife trade, including specific incidents involving the Florida Box Turtle (*T. bauri*) and *T. carolina*, but it was not clear how many involved *T. ornata*. Recently, Easter and Carter (2024) found that the number of exported box turtles (*Terrapene* spp.) increased over the last 20 years to a peak in 2018 with the top importing region being eastern Asia and the top exporting US port being Miami, Florida.

A reptile dealer in Nebraska who began collecting for the trade in 1981 reported selling 4,813 *T. ornata* from the Sandhills region in 1997 alone (Farrar 1998). He single-handedly may have removed over 100,000 *T. ornata* during his years of trading. In 1993, Nebraska introduced legislation to track commercial trading in reptiles, which revealed that 5,814 *T. ornata* were sold in 1994 and 8,705 in 1995 (Farrar 1998).

In Oklahoma, a man was arrested in 2020 for conspiring to purchase, transport, and sell more than 1,000 box turtles collected in the state (Brown 2020). The individual facilitated the purchase and transport of unlawfully collected *T. triunguis* and *T. ornata* from Oklahoma on to New Jersey, and was sentenced to two years' probation, ordered to pay $250,000 to the Oklahoma Department of Wildlife Conservation and $100,000 to the U.S. Fish and Wildlife Service (U.S. Attorney's Office 2020).

In Iowa, an individual was encountered while in the act of poaching at one of the only two large populations left in the state (Bernstein, pers. obs.), and conservation officers confiscated living and dead *T. ornata* from a poacher in eastern Iowa in 1999. In Kansas, a newspaper article by Petterson and Dvorak (1997) stated that two men had been indicted for illegally buying and selling 1,000 *T. ornata* taken from the state.

In Texas, Smith (2004) noted that the pet trade negatively impacted populations of *T. ornata* and congeners. Petterson and Dvorak (1997) quoted the late herpetologist Joseph T. Collins who stated that *T. ornata* could sell for $5 to $10 in the US, but that could increase to $300 when sold internationally. A recent report by the Kansas Chapter of the Sierra Club stated that prices for individual *T. ornata* from online sources ranged from $200 to $400 and that one could sell for as much as $3,000 in parts of Asia (Revello and Giessel 2023).

*Road Mortality*. — Overall, terrestrial turtles such as *T. ornata* are strongly affected by road density, with more than 5% of individuals at risk of road mortality annually (Gibbs and Shriver 2002). As far back as the 1930s, it was estimated that thousands of *T. ornata* were killed on highways each year (Burt and Hoyle 1934). In Arizona, Hall and Steidl (2003) reported that 38 of 54 *T. ornata* found on paved roads were dead. A roadkill survey conducted by Langley (2018) found that a total of 424 *T. ornata* were killed by traffic in 1984 and 1985 in Kansas. Another study done in Kansas in 2004 and 2005 found that 144 out of 352 documented *T. ornata* were roadkill (Taggart 2006). In a historical study across rural Iowa, only two *T. ornata* (or 0.004 causalities/mile, both in August) were found during roadkill surveys (Scott 1938). In Nebraska, Ballinger et al. (2010) reported 40 dead and 12 live *T. ornata* from a road on 12 June 1986. There are also observations of *T. ornata* being run over by farm machinery when they enter crop fields in Iowa (Fig. 16E; Bernstein et al. 2007). Collins et al. (2006) found 61%

of 41 *T. ornata* were found dead on roads in contiguous grassland habitat in New Mexico, Oklahoma, and Texas. In Oklahoma, Richter et al. (2013) found that female box turtles were more likely to be killed than males, including *T. ornata*, and that the population at a more developed site was more impacted by road mortality.

Prenosil and Klosterman (2020) described many instances of *T. ornata* that fell into cattle guards on Nebraska roads, which had to be rescued. White (2018) found a desiccated adult *T. ornata* lodged in a fence gate on a Texas ranch. Collins et al. (2006) found several dead individuals in New Mexico that were apparently trapped in man-made water tanks, as did Iverson (2024) in western Nebraska. Tuegel and Weise (2006) found an adult *T. o. luteola* in Arizona with a large, healed puncture injury to its carapace, but offered no explanation for the damage. However, Iverson (pers. obs.) has noted similar damage and even death to *T. ornata* in western Nebraska which was attributed to hoof strikes by pronking Mule Deer (*Odocoileus hemionus*).

*Turtle Races*. — Populations of *T. ornata* have experienced historical and contemporary conservation challenges stemming from turtle races conducted at county fairs and other forms for community entertainment because such events involve the capture and utilization of hundreds to thousands of wild individuals per year. The practice of turtle races persists today which poses ongoing threats to local populations and could lead to population declines (e.g., Lee 2012). For example, media reports documenting over 25,000 turtle races, the large majority of which occurred in states from the core range of *T. ornata*, specifically Kansas, Nebraska, and Oklahoma, have been documented by Heeb (2007; https://www.turtletaskforce.org/map).

Conservation concerns from such events include habitat disturbance from collecting events, stress and injury to individual turtles, translocation if turtles are not returned to where they were collected, and the disruption of essential behaviors such as nesting, foraging, and mating. Anecdotal observations have revealed that participants usually released the turtles near the race site and even local conservation officers usually allowed these activities to proceed (Bernstein, pers. obs.). Effective conservation measures should involve public outreach and education to discourage the use of wild turtles in races and enforcement of regulations to safeguard the well-being of *T. ornata* and their ecosystems (https://www.youtube.com/watch?v=kAwGK2OqAe8).

*Hybridization*. — Reports show that *T. ornata* readily hybridizes with sympatric species of *Terrapene* in Illinois (*T. carolina*; Smith 1955), Indiana (*T. carolina*; Clark 1935), Missouri (*T. triunguis*; Shannon and Smith 1949; Ward 1968), Texas (*T. triunguis*; Lutterschmidt et al. 2007, Cureton et al. 2011), and Louisiana (*T. triunguis*; Blaney 1968), but Martin et al. (2020) did not detect any hybrids between these taxa beyond the F1 generation in the contact zone in southern Illinois. In Kansas, Reed (pers. obs.)

has observed a male *T. triunguis* mounted on a female *T. ornata* at a site of sympatry where both species have been routinely observed mating with conspecifics, suggesting that cross-species mating behaviors may not be simply due to a lack of conspecifics.

*Population Declines*. —Populations of *T. ornata* are apparently decreasing across much of the species' range, but the most detailed studies (Bowen et al. 2004; Converse et al 2005; Iverson 2024) document at least some degree of population stability (or even slight growth in some populations as indicated by lambda >1). Populations outside of the species' core range, however, often documented declines, especially in regions along the distribution margins (e.g., Wisconsin: Doroff and Keith 1990).

In Illinois, Edmonds et al. (2023) determined that the Ayers Sand Prairie turtle population was declining at a rate of 1.7% annually ($\lambda = 0.983$), while the Nachusa Grasslands population was declining at a higher rate of 5.9% annually ($\lambda = 0.941$). However, under optimistic scenarios using maximum demographic rates, both populations showed potential growth (Ayers $\lambda = 1.033$; Nachusa $\lambda = 1.050$), while minimum rates projected rapid population declines (Ayers $\lambda = 0.935$; Nachusa $\lambda = 0.784$), with adult survival identified as the factor most influencing population growth (Edmonds et al. 2023). These data suggest that conservation management could reverse the decline in at least the Ayers populations. Also in Illinois, Adamovicz (2019) found that removing just two adult female turtles from the population dramatically increased the probability of population extinction in the next century, highlighting how vulnerable seemingly stable populations are because of their low intrinsic growth rate, long generation time, and low probability of survival to adulthood. Ultimately, it is likely that many of the populations that have declined, or have been already extirpated, went unnoticed (see Fitch 2006), and many populations that were studied historically with enough detail to properly document changes over time (e.g., Legler 1960) have not been revisited to determine their current status.

*Rarity Due to Habitat Loss and Climate Change*. — In Iowa, there are two main populations remaining in the eastern part of the state, with sporadic records elsewhere (VanDeWalle and Bernstein 2024). In Illinois, *T. ornata* is uncommon to rare in much of the state, with at least two well-studied populations that are apparently in decline (Edmonds et al. 2023). In Indiana, the species is found in just six counties, with most observations limited to historical records (Minton 2001). In Arkansas and Louisiana, *T. ornata* is rare and restricted to a few localized areas with historically sandy soils (Boundy and Carr 2017), where land-use legacy is a better predictor of occurrence than current prairie vegetation (Royal et al. 2023). In Wyoming, the species may have already been extirpated from the state (Redder et al. 2006). In Kansas, Fitch (2006) documented the complete loss of a *T. ornata* population at a site due to

succession from open grasslands to closed forests over a 50-year period.

Citizen-science observations of *T. ornata* show general agreement with the literature for locations where the species is rare, or in some cases, possibly extirpated due to habitat loss. For example, as of 8 February 2024, there are 6,353 observations of *T. ornata* from 3,073 observers on iNaturalist (https://www.inaturalist.org), an online platform that started in 2008, which included the following states with <100 observations: Wyoming ($n = 0$), Louisiana ($n = 0$), Indiana ($n = 2$), Wisconsin ($n = 16$), South Dakota ($n = 22$), Iowa ($n = 27$), Arkansas ($n = 28$), and Illinois ($n = 95$).

Climate change is certain to affect *T. ornata* populations that already occupy habitats whose climates are challenging to their physiology. Prowant (2014) modeled the current and future climatic distribution of *T. ornata* and predicted that the potential range would expand northward over the next 60 years. Whether this species, with a generation time of 28 years can redistribute northward rapidly enough to stave off the impact of climate change seems unlikely. Furthermore, Converse et al. (2005) reported that winter mortality increased in a Nebraska population during warmer winters. In such cases, turtles may begin to overwinter, but warming can induce emergence from shallow burrows. When the temperature rapidly drops, these individuals are often immobilized on the surface and perish over the winter, which are only to be discovered the following spring. This weather-induced mortality raises more concerns about the impact of global warming.

**Conservation Measures Taken**. — *Terrapene ornata* has been assessed as Near Threatened on the IUCN Red List with decreasing population trends since 2011 (van Dijk and Hammerson 2011; Iverson, in press) and has been included on CITES Appendix II (as *Terrapene* sp.) since 16 February 1995. The CITES Appendix II listing led to significant decreases in US exports of box turtles (Reed and Gibbons 2003), which are now exported in higher volumes from Europe than from the US (Easter and Carter 2024). The species has been the official state reptile in Kansas since 1986 and in Nebraska since 2022.

The species is officially listed by government agencies overseeing wildlife in several states: Iowa (Threatened), Illinois (Threatened), Indiana (Endangered), and Wisconsin (Endangered). In Arizona, Arkansas, Iowa, South Dakota, and Louisiana, it is listed as a Species of Greatest Conservation Need (SGCN), but some of these states still permit possession of individuals for "personal use". In Wyoming, the species is listed under Native Species Status Unknown (NSSU) and in Arkansas, it is protected from collection in the wild. Most states prohibit the collection of *T. ornata* for commercial uses, including Oklahoma, Colorado, Kansas, and Nebraska, but still allow non-commercial collection of less than five individuals, which may be related to the historical legacy of turtle races (Redder et al. 2006). In other

states, such as Texas, Oklahoma, and Missouri, a collection permit or fishing / hunting license is required to possess the species, which is apparently allowed for personal use. For a detailed list of other state regulations prior to 2001, see Table 10-1 in Dodd (2001); for more information on regulations prior to 2006, see Redder et al. (2006); and for more general information about state laws up to 2015, see the Nauti-Lass Ponds & Critters website (http://www.nauti-lasscritters.com/laws-by-state.html).

Many populations exist on large tracts of private ranches in Nebraska, Kansas, Oklahoma, and Texas, where some degree of protection exists due to ownership and land use. The species range overlaps with many areas under varying levels of protection across states: New Mexico (Lincoln National Forest, Carlsbad Caverns National Park, White Sands National Monument; Sevilleta National Wildlife Refuge; Bosque del Apache National Wildlife Refuge; Kiowa National Grassland); Colorado (Comanche National Grassland); Nebraska (Crescent Lake National Wildlife Refuge, Valentine National Wildlife Refuge, Scottsbluff National Monument, Nebraska National Forest, and Samuel R. McKelvie National Forest); Kansas (Quivira National Wildlife Refuge); Texas (Big Bend National Park, Big Bend Park Ranch, Davis Mountains State Park, Hueco Tanks State Park, Guadalupe Mountains National Park, Rita Blanca National Grassland, Sam Houston National Forest, Davy Crockett National Forest, Sabine National Forest, Angelina National Forest, and Big Thicket National Preserve); Oklahoma (Black Kettle National Grassland, Wichita Mountains National Wildlife Refuge, and Great Plains State Park); Arkansas (Ozark National Forest, Ouachita National Forest, and Ozark National Scenic Riverway); Arizona (Coronado National Forest); and Iowa (Hawkeye Wildlife Management Area and Big Sand Mound Preserve). The species is not yet known to occur in any protected area in Mexico.

*Translocation*. — When translocated to new areas, adults of *T. ornata* display variable philopatry. In Texas, 50% (4 of 8) of females remained where they were translocated, and 0% (0 of 9) of males remained where they were translocated, with many individuals that went missing entirely (Sosa and Perry 2015). In an intentional translocation in Iowa, 65 adults and a nest were relocated into 5 ha and 1.75 ha outdoor enclosures between 1998 and 2003, and 11 adults from the original population were later recovered during 2006–2007 along with three, five-year-old juveniles (Hill et al. 2009). In Wisconsin, Hatch (1997) found that 14 translocated adults held in a large, on-site enclosure for one or two years did not disperse from the area when released into the wild, but young juveniles may not need as much time in an enclosure before release. In Nebraska, Claussen et al. (1998) compared the post-release movements of *T. ornata* held in captivity for a year to those captured immediately using thread trailing for 200 m and found that captive animals exhibited more variance in movement

metrics than recent captures, but mean values were not different between groups. Germano and Nieuwolt-Dacanay (1999) reported an accidental displacement of a female *T. o. luteola* away from her home range in New Mexico, and the turtle travelled 9.15 km south and established a new home range, presumably her original range, within 8.1–8.75 km from the original release point. Hill et al. (2009) suggested relocations can be successful if the turtle is first released to a confined area to "restrict their philopatric instincts", which may mean 2–5 years in semi-captivity at the site of release. Thus, translocation of adult turtles may pose a challenge for the logistics and finances of reintroduction plans (Refsnider et al. 2012). Furthermore, the growing evidence that *T. ornata* exhibits distinct personalities (i.e., Reed et al. 2023) indicates that it will be important to select turtles with certain dispositions to maximize translocation success.

*Head-Starting*. — Sievers (2015) tested the success of reintroducing turtles to a site to support an already viable population, soft-released in a fenced enclosure at a site with few turtles, and hard-released at the same site without a fence, which revealed comparable outcomes for the treatments with no significant differences in home ranges, growth rates, diet, or mortality rates during the activity season. Sievers (2015) also found that head-started hatchlings reared in captive conditions reached 85–154 g (mean = 117 g) in 8–10 months and used transmitters representing 3.25–5.88% of their body mass at time of release. Karssen (2018) found growth was faster in head-started versus wild-hatched individuals, although home-range size, vegetation use, and shrub cover did not differ between groups; however, a large fence surrounding the population at the site likely impacted these comparisons. Buelow (2021) compared the plastral hinge-closing force, behaviors when threatened, and shell morphometrics between head-started and wild *T. ornata* and revealed that wild turtles typically closed immediately and with greater force than head-started turtles, whereas head-started turtles exhibited bolder behaviors and were often hesitant to seal themselves completely into their shells, perhaps because of longer plastrons. Buelow (2021) suggested that head-starting efforts should take steps to address maladaptive morphological and behavioral consequences of captivity to maximize anti-predator measures following release of turtles in the wild.

**Conservation Measures Proposed**. — To aid in the recovery of declining *T. ornata* populations, especially in the midwestern USA, wildlife managers should concentrate on mitigating mortality caused by three common prairie management practices: prescribed burns, vegetation mowing, and vehicle use in turtle habitats. Prescribed burns are advised to align with periods when turtles are underground for winter, while vegetation mowing should be timed to coincide with unfavorable conditions and inactivity, with specific measures such as raising mower blades and using

older sickle bar mowers. Rose (1969) found that *T. ornata* subjected to scute removal, such as after an injury or fire, experienced a significant decrease in weight, approximately 26% after six days of desiccation compared to those with scutes. Such injured turtles also exhibited slower warming rates and more rapid heat loss than controls (Rose 1969). Bigham et al. (1965), in Oklahoma, found that 25 of 28 box turtles (*T. triunguis* and *T. ornata*) were found dead after a fire. When conducting prescribed burns, the day of the year and current air temperature should be considered to assess the risk of fire to turtles. Edmonds et al. (2024) suggested that in Illinois, by March 1 at 15°C, there is a 10% likelihood of a turtle being above ground, rising to 20% by April 1 at the same temperature. In spring, Edmonds et al. (2024) recommended burning habitat before 1 April when air temperature is <10°C and in fall after 1 November when air temperature is <15°C, because above these temperatures, there was a >5% likelihood that turtles in northern populations would be above ground.

Edmonds et al. (2024) emphasized the need for managers to prioritize *T. ornata* in supervised habitats, particularly given the small, isolated, and likely declining nature of many populations. Additionally, controlling vehicle use and implementing measures like fencing roadways and building underpasses can reduce adult mortality. Further research is needed to explore the impacts of predation and road mortality, emphasizing the importance of maintaining high adult survival rates in isolated populations, which will help ensure the persistence of *T. ornata* along the periphery of its range.

Woody succession in sand prairies is an ongoing problem, and well-meaning land managers once planted conifers on sand prairies to prevent wind and water erosion. Maintenance and preservation of sand prairies and similar habitats is crucial for the preservation of *T. ornata*. Raccoons and other mammals are substantial nest predators (see above); thus, some areas may require controlling mesopredators to aid declining populations.

The construction of windmills for livestock and wildlife monitoring has been a great benefit to *T. ornata* because they regularly use the overflow wetlands for hydration and can expand their habitat deep into arid areas that otherwise lack surface water. However, windmills must be maintained to prevent soil build-up around the water tank, allowing turtles to climb up, fall in and drown (Collins et al. 2006; Iverson, pers. obs.).

**Captive Husbandry**. — Captive husbandry of turtles generally and *T. ornata* specifically is challenging due to dietary requirements, microhabitat preferences, and space needs. In fact, a captive care website for *T. ornata* describes it as "one of the most difficult species of North American turtle to successfully care for in captivity" (https://www.boxturtles.com/ornate-box-turtle/). Wappel and Schulte (2004) recommended a diet comprising 50% animal matter and 50% plant matter. Captive box turtles, especially

when housed communally, can develop anorexia (Barten 2005), highlighting the importance of individual access to food and adequate enclosure conditions. Barten (2005) described 10-gallon terraria to house turtles as "prison cells" and stated that proper lighting, heat, humidity, substrate, soaking areas, and shelter are crucial for box turtle health. Extreme temperatures can increase stress levels in captive turtles (Neyer 2018), emphasizing the need for temperature control, preferably with access to outdoor enclosures during summer months, but Boyer (1992) warned that outdoor pens must properly exclude mammalian mesopredators (e.g., raccoons). Overwintering temperatures are recommended to range 10–16 C° (Boyer 1992). More details of captive husbandry for box turtles, including *T. ornata*, are provided in Franklin and Killpack (2009). Descriptions of captive husbandry for *T. ornata* specifically are provided in Vinke and Vinke (2004), Wirth and Mattern (2001), Artner (2007), and Jost and Jost (2000). Guarisco (1983) described a successful method to repair the shell of *T. ornata* hit by a vehicle.

*Health*. — Hematologic, plasma biochemical, and pathogen prevalence data have been utilized as a means of determining the wellness of free-living *T. carolina* populations (Way Rose and Allender 2011). Sustainable wildlife populations depend on healthy individuals, and the approach to determine wellness of individuals is multifaceted. The health of free-living *T. ornata* is understudied, and the potential threats from disease to this species is largely uncharacterized (Christiansen et al. 2005; Harden et al. 2018; Legler 1960; Loomis 1956; Rainey 1953; Redder et al. 2006). Chelonian health status is affected by a variety of environmental, host, and pathogen factors, and understanding the multifactorial determinants of health requires a holistic approach (Hanisch et al. 2012). Comprehensive health assessments that simultaneously consider aspects of habitat quality, demographics, and spatiotemporal variation when interpreting diagnostic test results are uncommon in terrestrial reptiles and sparsely applied to *T. ornata* (Adamovicz et al. 2018). Many clinical features can be performed in awake animals, but an occasional need of an anesthetized exam or procedure is needed. A single study of an apparently healthy *T. ornata* population evaluated the efficacy of a three-drug protocol administered intramuscularly that provided light anesthesia but resulted in persistent palpebral response in 43% of animals (Rooney et al. 2021).

Baseline values for several blood analytes have been collected intermittently. Adamovicz and Allender (2022) reported safe venipuncture techniques, normal complete blood count and plasma biochemistry values, and interpretation in a review of all North America *Terrapene* spp; when combining all *Terrapene* results, numerous seasonal, sex, and age class differences were observed (Adamovicz and Allender 2022). Specifically, male *T. ornata* had higher packed cell volume (PCV) than females (Adamovicz et

al. 2018; Adamovicz 2019). Interestingly, an increasing red iris color positively correlates with PCV in male *T. carolina*, providing a subjective means of assessing patient status without repeated venipuncture, but this assay has not been evaluated in *T. ornata* (Cerreta et al. 2018). Few differences in white blood cell counts have been observed in *T. ornata*, but monocyte counts showed a relative (%) decrease in adults compared with juveniles (Adamovicz 2019; Adamovicz and Allender 2022). Seasonal changes were summarized for clinical pathology parameters in all species of *Terrapene*: increased PCV, total protein, albumin, albumin:globulin ratio, uric acid, creatine kinase, partial pressure of $CO_2$ and lactate concentrations in the summer, decreased heterophils, monocytes, heterophil:lymphocyte ratio, pH, bicarbonate, total carbon dioxide, and base excess in the summer along with increases in eosinophils, bile acids, and total calcium as the active season progresses (Adamovicz et al. 2018; Adamovicz and Allender 2022). A separate study in Illinois found few within-year differences in 20 free-living *T. ornata*, except for a positive association between blood glucose determined by a handheld analyzer and temperature (Harden et al. 2018). Acute phase proteins are highly conserved innate reactions in vertebrates and have been evaluated in *T. ornata* through characterization of erythrocyte sedimentation rate (ESR), hemoglobin binding protein (HBP), and fibrinogen (Parkinson et al. 2016; Adamovicz 2019), and ESR and HBP were positively associated with apparently unhealthy animals, and apparently healthy females had a higher baseline than apparently health males (Adamovicz 2019). Fibrinogen reference ranges were calculated and demonstrated a significant increase in animals deemed unhealthy, but the authors had a small sample size and recommended further work is needed before confidence in the method in determining health status is recommended (Parkinson et al. 2016).

Innate immune response was characterized by evaluating bactericidal capacity in both *T. ornata* and *T. carolina* (Adamovicz et al. 2020a). Bactericidal activity, presumed due to complement activity, was greater in *T. ornata* compared to *T. carolina*, and *T. ornata* plasma retained high antibacterial activities at a broader temperature range (20–40°C) compared to *T. carolina* (30–40°C) (Adamovicz et al. 2020a). Complement was then further characterized by evaluating plasma from both species; it demonstrated volume, time, and temperature-dependent SRBC hemolysis (SRBC = sheep red blood cells), with significantly greater hemolytic activity in *T. ornata* plasma (Adamovicz et al. 2020a). Two abundant mannan-binding proteins (presumed C-type lectins) were identified in *T. carolina* plasma using SDS-PAGE and MALDI-TOF, but *T. ornata* did not express either protein, suggesting *T. ornata* utilizes an alternative complement pathway (Adamovicz et al. 2020a). Adamovicz et al. (2020a, 2020b) described different immunological pathways in *T. carolina* and *T. ornata* in which hemolysis for both species was volume,

time, and temperature-dependent, and both species' plasma demonstrated antibacterial properties against eight bacterial pathogens. Although *T. ornata* demonstrated significantly greater hemolytic activity, *T. ornata* lacked two mannan-binding proteins associated with immune functions that were present in *T. carolina* (Adamovicz et al. 2020a). Adamovicz et al. (2020a, 2020b) noted that these immunological differences between closely related species could have conservation implications to environmental threats. In further immune system studies, Adamovicz et al. (2020c) noted erythrocyte sedimentation rate (ESR) was negatively correlated with packed cell volume and greater in unhealthy turtles; in addition, female *T. ornata* had significantly higher ESR values than males.

Morrow (2008) investigated oxygen consumption of captive *T. ornata* as related to meal size, composition, and time of the year and found that postprandial increases in oxygen consumption were shorter than in studies of other turtle species. Morrow (2008) postulated that the feeding strategy of *T. ornata* was to eat more frequent, smaller meals which stimulated the digestive system to be ready to process a steady supply of food; in addition, the tendency to take smaller bites of food rather than swallowing food whole sped digestion through increased surface area to volume ratio of the food. Oxygen consumption after feeding was higher in the mid-morning and afternoon compared to mid-night and early morning, and there were no seasonal effects on oxygen consumption following meals (Morrow 2008). At body temperatures of 30°C, Gatten (1974) found that aerobic metabolism was 1.75 times greater in the aquatic Red-eared Slider (*Trachemys scripta*) compared to *T. ornata*. Sturbaum and Riedesel (1974) found that exposure to 38 and 41°C air temperatures did not manifest as heat stress for *T. ornata*, and behavioral mechanisms, such as panting, allowed turtles to keep core temperatures well below stressful ambient air temperatures (48–51°C) for as long as l.5–3 hr. Further, Sturbaum and Riedesel (1977) found that when exposed to a 55°C environment, *T. ornata* produced saliva (frothing) that they spread over their heads and forelimb, but they continued to be active and exhibited mouth movements throughout the experiment.

*Diseases*. — Although rare for *T. ornata*, there are some historical reports of disease events (Christiansen et al. 2005; Farkas and Gal 2009) and physiological responses to temperature and other demographic factors (Bachman 2013; Bethea 1971). Johnson et al. (2007) experimentally inoculated *T. ornata* with *Ranavirus* via intramuscular injection and orally and found that oral inoculation failed to result in mortality, thus concluding that the natural route of transmission in the wild remains unknown. Intestinal parasites of unknown clinical disease or impact have been sparsely reported but include coccidians from Texas (McAllister and Upton 1989) and Arkansas (McAllister et al. 2017). Clinical signs of aural abscesses were observed in 3.47%

of *T. ornata* in an Iowa population over a 13-year period with reported bacterial growth, but no known impact on population health or structure (Christiansen et al. 2005). A current threat of shell disease involving 51–59% of turtles in an Illinois population has been minimally investigated but was found to be significantly associated with systemic changes in plasma proteins and circulating inflammatory cells indicating a broader impact beyond the shell (Adamovicz et al. 2018). Viral and bacterial infections in *T. ornata* are infrequently encountered, and an understanding of their presence is completely unknown. An adenovirus and *Mycoplasma*, two common pathogens of *T. carolina* that cause intermittent disease, were reported in Hungary in a captive animal (Farkas and Gal 2009). The same adenovirus and the recently described *Terrapene* herpesvirus 1 DNA were identified in a population of Illinois *T. ornata*, but neither was associated with any observed effect despite the prevalence changing between years (Adamovicz 2019). The causative bacterium of the zoonotic disease "Q fever" was detected from a PCR sampled *T. ornata* in Illinois (Sander et al. 2021).

**Current Research**. — Projects on *T. ornata* in Illinois are led by the researchers Michael J. Dreslik, Matthew C. Allender, and Devin A. Edmonds at the University of Illinois Urbana-Champaign, which are long-term studies on at least two populations with mark-recapture data as far back as 1988 (Edmonds 2020). One project on *T. ornata* in Iowa from Johnson County is currently led by Daniel F. Hughes at Coe College with mark-recapture data as far back as 1993 (Bernstein et al. 2023b). Another project in Iowa from Louisa County was initiated by James L. Christensen from Drake University and is now led by Joshua G. Otten at Cornell College with mark-recapture data as far back as the 1970s (Christensen 1998). One project in Nebraska at the Crescent Lake National Wildlife Refuge led by John B. Iverson recently concluded (due to cessation of permits) with mark-recapture data from 1981 to 2019 (Iverson 2024). Another project in Nebraska that is ongoing at the Cedar Point Biological Station is led by Benjamin M. Reed from Washburn University and has mark-recapture data from the early 2000s (Reed et al. 2023). Reed also has projects in Kansas near Lawrence and Topeka that began around 2018. There is recent unpublished work on *T. ornata* in Colorado by Franziska C. Sandmeier from Colorado State University Pueblo, but the origin and longevity of the research are unknown (Norton et al. 2022).

*Needed Research*. — Long-term data for *T. ornata* from the southern portion of its range are needed, especially Mexican populations and US populations in Texas and Oklahoma. Studies from Missouri and Colorado would also be very useful. Long-term monitoring projects in these regions are necessary to assess population trends and identify potential declines as has been documented from populations in the northern distribution. Populations historically documented along its range margins should be surveyed to determine their status, such as those in Louisiana, Wyoming, and Indiana. Research that revisits the study sites from the landmark papers of Legler (1960) in Kansas and Blair (1976) in Texas is needed to determine their status and whether any of those turtles are still alive and what has changed since the earlier studies. Given the intensity of marking and monitoring efforts on the Crescent Lake National Wildlife Refuge in Nebraska (Iverson 2024), a future researcher could continue the work there or at least follow-up at a later date to determine what has changed. Studies on populations in Mexico would provide an excellent southern endpoint for comparisons to other studies, and surveys to document the species' southern distribution limit would also be useful. Future studies should focus on the impact of environmental changes on population dynamics, habitat use, and reproduction. A compilation project that incorporates data across numerous populations that possess similar long-term data would go a long way toward that goal. More studies of reproductive biology that include nesting habits and factors influencing reproductive success are needed for the development of effective conservation strategies, especially for populations in decline. Additionally, research should focus on the impacts of potential threats such as predation, road mortality, turtle races, and disease. Collaborative efforts among researchers, conservationists, private landowners, and local communities can together contribute to a better understanding of this species that will help to ensure its long-term survival in the face of ongoing challenges.

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