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Terrapene carolina (Linnaeus 1758) – Eastern Box Turtle, Common Box Turtle

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Summary. – The Eastern Box Turtle, *Terrapene carolina* (Family Emydidae), as currently understood, contains six living subspecies of small turtles (carapace lengths to ca. 115–235 mm) able to close their hinged plastrons into a tightly closed box. Although the nominate subspecies is among the most widely distributed and well-known of the world's turtles, the two Mexican subspecies are poorly known. This primarily terrestrial, though occasionally semi-terrestrial, species ranges throughout the eastern and southern United States and disjunctly in Mexico. It was generally recognized as common in the USA throughout the 20th century, but is now threatened by continuing habitat conversion, road mortality, and collection for the pet trade, and notable population declines have been documented throughout its range. In the United States, this turtle is a paradigm example of the conservation threats that beset and impact a historically common North American species. In Mexico, the greatest need for the subspecies that occur there is to further assess their distribution, habitat requirements, economic status, and conservation threats.

Distribution. – Canada (extirpated), Mexico, USA. Broadly distributed in eastern and southern USA from southern Maine and New Hampshire to Florida and west to Michigan, Kansas, Oklahoma, and Texas, and disjunctly in Mexico in San Luis Potosi, Tamaulipas, and Veracruz, and also disjunctly in Yucatán, Campeche, and western Quintana Roo.

Synonymy. – *Testudo carolina* Linnaeus 1758, *Terrapene carolina, Emys (Cistuda) carolinae, Cistuda carolina, Cistudo carolina, Terrapene carolina carolina*, *Testudo carinata* Linnaeus 1758, *Terrapene carinata, Cistudo carinata*, *Testudo brevicaudata* Lacépède 1788 (nomen suppressum), *Testudo incarcerata* Bonnaterre 1789, *Testudo incarceratostriata* Bonnaterre 1789, *Testudo clausa* Gmelin 1789, *Emydes clausa, Emys clausa, Didicla clausa, Terrapene clausa, Cistudo clausa, Cinosternon clausum, Pyxidemys clausa, Cinosternum clausum*, *Testudo virgulata* Latreille *in* Sonnini and Latreille 1801, *Emys virgulata, Terrapene virgulata*; *Emys schneideri* Schweigger 1812, *Monoclida kentukensis* Rafinesque 1822 (nomen suppressum), *Terrapene maculata* Bell 1825, *Terrapene carolina maculata*, *Terrapene nebulosa* Bell 1825, *Terrapene carolina nebulosa*, *Testudo irregulata* Daudin *in* Gray 1830 (nomen nudum), *Emys kinosternoides* Gray 1830, *Terrapene kinosternoides, Emys cinosternoides* Duméril and Bibron 1835 (nomen novum), *Cistudo carolina cinosteroides, Cistudo cinosternoides, Terrapene cinosternoides, Cistudo virginea* Agassiz 1857, *Cistudo eurypygia* † Cope 1870, *Terrapene eurypygia*, *Toxaspis anguillulatus* † Cope 1899, *Terrapene anguillulatus*, *Testudo munda*† Hay 1920.

Subspecies. – Six subspecies are currently recognized: 1) *Terrapene carolina carolina* (Linnaeus 1758) (Woodland Box Turtle) (distribution: eastern USA from southern Maine to northern Florida, New York and Michigan, west to southern Illinois, Kentucky, Tennessee, northern Mississippi and Alabama; also historically southern Ontario, Canada); 2) *Terrapene c. bauri* Taylor 1895 (Florida Box Turtle) (synonymy: *Terrapene bauri* Taylor 1895, *Pariemys bauri, Cistudo bauri, Terrapene carolina bauri*, *Terrapene innoxia* † Hay 1916a, *Trachemys nuchocarinata* † Hay 1916a (nomen dubium), *Terrapene singletoni* † Gilmore 1927 (distribution: peninsular Florida, USA); 3) *Terrapene c. major* (Agassiz 1857) (Gulf Coast Box Turtle) (synonymy: *Cistudo major* Agassiz 1857, *Cistudo carolina major, Terrapene major, Toxaspis major, Terrapene carolina major*, *Cistudo marnochii* † Cope 1878, *Terrapene marnochii*, *Terrapene putnami* † Hay 1906, *Terrapene carolina putnami*, *Terrapene canaliculata* † Hay 1907, *Terrapene formosa* † Hay 1916a, *Terrapene antipex* † Hay 1916) (distribution: along the Gulf of Mexico, USA, panhandle of Florida, southern Georgia, Alabama, Mississippi, Louisiana, and southeast Texas); 4) *Terrapene c. mexicana* (Gray 1849) (Mexican Box Turtle) (synonymy: *Cistudo (Onychotria) mexicana* Gray 1849, *Onychotria mexicana, Cistudo*

***mexicana, Cistudo carolina mexicana, Chelopus mexicanus, Terrapene mexicana, Terrapene mexicana mexicana, Terrapene carolina mexicana*, *Terrapene goldmani* Stejneger 1933) (distribution: eastern Mexico in San Luis Potosi, Tamaulipas, and Veracruz); 5) *Terrapene c. triunguis* (Agassiz 1857) (Three-toed Box Turtle) (synonomy: *Cistudo triunguis* Agassiz 1857, *Cistudo carolina triunguis, Terrapene triunguis, Onychotria triunguis, Terrapene carolina triunguis, Terrapene mexicana triunguis*, *Terrapene whitneyi* † Hay 1916b, *Terrapene bulverda* † Hay 1920, *Terrapene impressa* † Hay 1924, *Terrapene llanensis* † Oelrich 1953) (distribution: southern and central USA, Alabama, Arkansas, Illinois, Louisiana, Mississippi, Missouri, eastern Kansas, Oklahoma, and Texas); 6) *Terrapene c. yucatana* (Boulenger 1895) (Yucatan Box Turtle) (synonymy: *Cistudo yucatana* Boulenger 1895, *Terrapene yucatana, Terrapene mexicana yucatana, Terrapene carolina yucatana*) (distribution: Yucatán peninsula, Mexico, Campeche, Quintana Roo, and Yucatán).**

Status. – IUCN 2014 Red List: Vulnerable (VU A2bcde+4bcde, assessed 2011); CITES: Appendix II (as *Terrapene* spp.)

Taxonomy. — The Eastern Box Turtle, also known as the Common Box Turtle, *Terrapene carolina* (Linnaeus 1758), is currently considered to contain six living subspecies: *T. c. carolina* (Linnaeus 1758, Woodland Box Turtle), *T. c. triunguis* (Agassiz 1857, Three-toed Box Turtle), *T. c. major* (Agassiz 1857, Gulf Coast Box Turtle), *bauri* (Taylor 1895, Florida Box Turtle), *T. c. mexicana* (Gray 1849, Mexican Box Turtle), and *T. c. yucatana* (Boulenger 1895, Yucatan Box Turtle). The subspecies intergrade where their ranges overlap and the species hybridizes in some instances with *T. ornata* where their ranges overlap (Blaney 1968; Cureton et al. 2011). Until recently, the species had a stable nomenclatural history since the work of Milstead (1969). Ditmars (1934), Smith and Smith (1979) and Ernst and McBreen (1991) provided complete accounts of the taxonomy and nomenclatural history of this species throughout the 20th century. Milstead (1969) included the present Mexican subspecies in *T. carolina* and saw the species as containing the six living and one extinct subspecies, *T. c. putnami* † (Hay 1906), and although the subspecies *yucatana*, *mexicana,* and *bauri* have at times been treated as distinct species (e.g., Smith

Figure 1. Adult male *Terrapene carolina carolina* from Virginia, USA. Photo by Peter Paul van Dijk.

Figure 2. Adult males of the six living subspecies of *Terrapene carolina*. Clockwise from top left: *T. c. carolina*, New Jersey (photo by Michael T. Jones); *T. c. triunguis,* Missouri (photo by Michael T. Jones); *T. c. mexicana,* Mexico (photo by Collette Adams); *T. c. yucatana,* Yucatán (photo by Michael T. Jones); *T. c. bauri,* peninsular Florida (photo by Michael T. Jones); *T. c. major,* Florida panhandle (photo by Michael T. Jones). Carapace patterns are variable within each subspecies. Note the horn-colored shell of *T. c. triunguis* and "fire-marked" pattern of *T. c. mexicana*; the carapace of the *T. c. major* example is scarred by fire.

et al. 1996; Stephens and Wiens 2003; Butler et al. 2011; Crother 2012; Legler and Vogt 2013), Minx (1996), Dodd (2001), Fritz and Havas (2007), van Dijk (2011), and the Turtle Taxonomy Working Group (2014) considered them subspecies of *T. carolina,* as we do here.

Recently, however, phylogenetic relationships among the subspecies have been a matter of debate. The relationship between *putnami* and *major* has long been a confusing one (Minx 1996), with the two taxa considered equivalent by several authors (Blaney 1971). Butler et al. (2011) suggested that *major* is the result of *carolina* and *putnami* introgression and therefore not a distinct subspecies, as was also suggested by Auffenberg (1967) using fossil examination, and the relationship continues to be problematic (Minx 1996; Martin 2012). Butler et al. (2011) also concluded that *bauri* should be elevated to full species status, and Crother (2012) agreed. Recently, Martin (2012) used mitochondrial, cyt-b, and nuclear DNA to conclude that *triunguis* is paraphyletic with *T. carolina* and *T. ornata* and therefore should be a full species (as *mexicana*), with *triunguis*, *mexicana,* and *yucatana* as subspecies within it, as had been suggested by Minx (1996). Few representatives of the latter subspecies were examined, however, and DNA barcoding suggested divergence distances for all *T. carolina* subspecies were at interspecific levels (>2%) with the exception of *triunguis* and *mexicana*. In response, Fritz and Havaš (2014) echoed Shen et al. (2013), who noted that there should be no standard level of interspecific divergence levels using DNA barcoding. Fritz and Havaš (2014) also argued that *T. c. triunguis* and *T. c. carolina* should remain a single species

Figure 3. Ventral view of adults of the six living subspecies of *Terrapene carolina*. Clockwise from top left: male *T. c. carolina*, Massachusetts (photo by Michael T. Jones); male *T. c. major*, Florida (photo by Michael T. Jones); male *T. c. bauri*, Florida (photo by Michael T. Jones); male *T. c. yucatana*, Yucatán (photo by Michael T. Jones); female *T. c. mexicana* (photo by Patty Scanlan); male *T. c. triunguis*, Missouri (photo by Michael T. Jones). Note the characteristic hinge in all subspecies, the pronounced axillary scute in *T. c. major*, and the lack of concavity in the male *T. c. triunguis* and *T. c. yucatana*.

because the individuals observed by Butler et al. (2011) in the contact zone between *T. c. carolina* and *T. c. triunguis* represent a "true genetic melting pot" with no distinct forms of either subspecies, a situation which should be viewed as intergradation between subspecies, in contrast to the area of sympatry between the species *T. carolina* and *T. ornata,* where distinct forms of each are maintained in addition to hybrid forms. On the whole, relationships within the genus and species are problematic and will require a great deal more information to fully resolve (Spinks et al. 2009), and additional work may warrant a recognition of several species and/or subspecies within the *T. carolina* complex.

The most closely related living species to *T. carolina* (sensu lato), is *T. coahuila*, an isolated species in the Cuatro Cienegas basin of Coahuila, Mexico. The other species within *Terrapene* (*ornata* and *nelsoni*) occur in more western locations of North America. The genus *Terrapene* has now been dated back to the Miocene (Holman and Corner 1985; Holman 1987) and Pleistocene fossils are common in various locales (Oelrich 1953; Auffenberg 1959; McClure and Milstead 1967; Gillette 1974; Jackson and Kaye 1974; Moodie and Van Devender 1978; Preston 1979; Bentley and Knight 1998).

Description. — *Terrapene carolina* has often been described in the literature. Ernst and McBreen (1991) listed 21 references to general descriptions, and the genus was profiled in a comprehensive book by Dodd (2001). The subspecies, where they do not intergrade, are generally distinct (Figs. 1–3), but each contains considerable variation. Milstead (1969) and Dodd (2001) gave differential diagnoses and complete descriptions of the subspecies and their variation. The U.S. subspecies are generally, often delightfully, described by

Figure 4. Hatchling box turtles often have a single yellow dot at the center of each carapacial scute; *T. c. carolina* hatchling from Massachusetts. Photo by Michael T. Jones.

Carr (1952), while the Mexican subspecies have been further described by Smith and Smith (1979), Buskirk (1993), and Legler and Vogt (2013).

The most obvious feature of Eastern Box Turtles is their kinetic plastron (Fig. 3), which allows them to close the shell completely and securely. The mechanisms of this remarkable adaptation are described by Bramble (1974) who compared box turtles to other genera of emydid turtles and noted that *Terrapene* has the most advanced form of closure mechanism. The *T. carolina* group can be differentiated from the *T. ornata* group by a keeled carapace, a steeply angled first vertebral and rectangular first marginal scute, and having the greatest carapace depth posterior to the plastral hinge (Milstead 1969; Dodd 2001).

The living subspecies of *T. carolina* range in adult straight carapace length (CL) size from about 115 mm for *triunguis* to over 200 mm in the aptly named *major*. The now extinct *putnami* reached CL sizes of greater than 300 mm. While each subspecies has a characteristic size range (Milstead 1969), there can be occasional individuals that are much larger; Pritchard (1980) recorded a *bauri* with 187 mm CL, Cook et al. (1972) described a *carolina* with 198 mm CL from a population in New York that averaged only 133 mm CL, and Jackson and Brechtel (2006) reported a 235 mm captive *major* and a 190 mm captive *bauri*.

Color patterns of both the shell and skin of Eastern Box Turtles range from riotously colorful to dull, and defy easy description because of variation within and between subspecies. Shells may be brown to black with a variety of yellow, orange, or white stripes or splashes, but can become almost uniform black in older *major*, a uniform horn color in older *triunguis*, or "fire marked", to use Milstead's (1969) term for a horn-colored shell, with each lamina outlined in black, in older *mexicana*. Skin color ranges from dark brown and black to various mixes of red, orange, and yellow and even blue, purple, and white. Schwartz et al. (1984) presented color plates of several individuals of *triunguis* showing both genetic and ontogenetic variation. The other subspecies are similarly variable and their patterns are described in detail by Milstead (1969). Hatchlings often have a single light-colored dot centered on the dark background of each carapacial scute (Fig. 4).

Subadults are generally impossible to sex without internal examination. Sex differences are described generally by Carr (1952) and have been discussed in detail for *triunguis* by Schwartz et al. (1984). Males are usually more brightly colored than females, but this is not true for *bauri* and *major*, though males may have white or blue heads in these two subspecies. Males often have larger tails with a more posterior cloaca and a more concave plastron than females (Fig. 5), though the male concavity seems to be reduced in *triunguis* and absent in *yucatana*. Males may have a bright red iris while those of females are usually brown, though this is not a definitive characteristic as females may also have red eyes on occasion (Nichols 1940), and male *yucatana* do not have red eyes. Evans (1953) thought that the red eye of males was significant in sex identification and courtship. This may be true for some subspecies or populations, but the great variation among individuals and subspecies means that this feature may not always be diagnostic. As with sex characteristics, size dimorphism varies by subspecies (Nichols 1939a; Stickel and Bunck 1989; Ernst et al. 1998; St. Clair 1998).

Distribution. — The maps for this species show a wide distribution within the eastern and southern United States with over 1100 localities (Fig. 6). Some range-edge states and provinces (i.e., Maine, New Hampshire, and Ontario) no longer have any known functioning populations, though historic records and/or archaeological evidence exist for the

Figure 5. Plastron of female (left) and male (right) *T. c. bauri* from Florida. Note the size dimorphism and the concavity in the posterior plastral lobe of the male. The female appears to be older than the male with ontogenic traits typical in older *bauri*, including a plastron that is free of dark markings and worn smooth (note the dark coloration and lines of arrested growth visible on the male, by contrast). Photo by Lisabeth Willey.

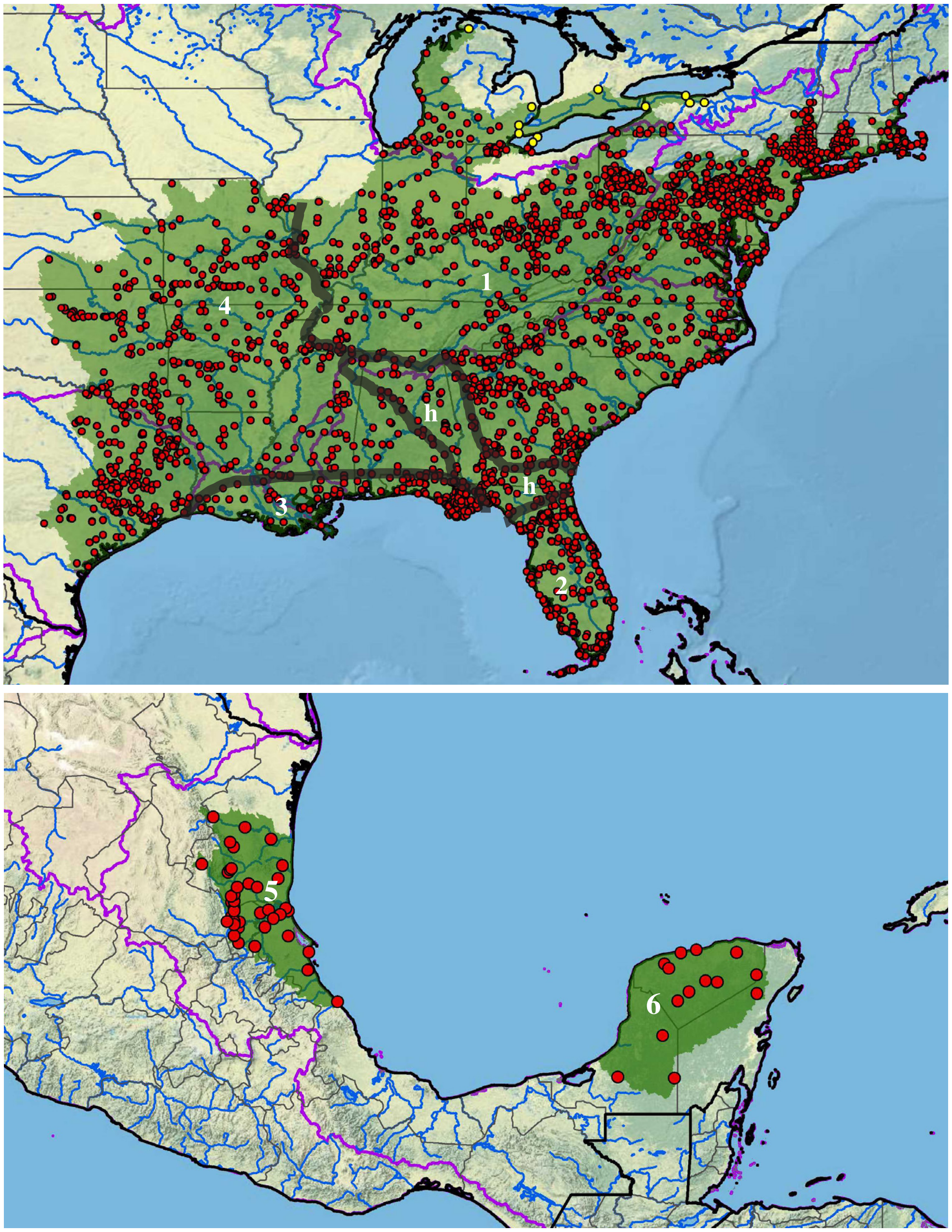

Figure 6. Distribution of *Terrapene carolina* in the United States and Canada (now extirpated) (upper map) and in Mexico (lower map). Purple lines = boundaries delimiting major watersheds (level 3 hydrologic unit compartments – HUCs); red dots = museum and literature occurrence records based on Iverson (1992) and Kiester and Bock (2007) plus more recent data, including specific information from Pennsylvania Amphibian and Reptile Survey (a joint project of the Mid-Atlantic Center for Herpetology and Conservation and the Pennsylvania Fish and Boat Commission), the New York State Herp Atlas Project, and the authors' personal data; yellow dots = historic observations where populations have likely been extirpated; broad gray lines = approximate boundaries between the U.S. subspecies as delineated by Dodd (2001), with *T. c. carolina* (**1**) in the northeast, *T. c. bauri* (**2**) in peninsular Florida, *T. c. major* (**3**) along the Gulf Coast, *T. c. triunguis* (**4**) in the west, and a broad zone of hybridization (**h**) between the four subspecies in the southeast; *T. c. mexicana* (**5**) in eastern Mexico and *T. c. yucatana* (**6**) on the Yucatán Peninsula in Mexico; green shading = projected native distribution based on GIS-defined HUCs 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 (Buhlmann et al. 2009; TTWG 2014), and adjusted based on authors' subsequent data.

species there (Josselyn 1672; Fogg 1862; Babcock 1919; Bleakney 1958; Adler 1968, 1970). The northern distribution of the species has been a matter of debate for some time; Bleakney (1958) suggested several shells found in Ontario were likely traded there, and recent sightings of the species in the province have been single individuals, likely released pets. Consequently, COSEWIC (2014) recently changed the species' designation to extirpated in Canada.

In Mexico the subspecies *T. c. mexicana* has a range that is fairly well defined, with many localities, but the range for *T. c. yucatana* is much less well known, with fewer recorded localities (Fig. 6). In the United States the subspecies *T. c.*

carolina and *T. c. bauri* sometimes occur on offshore islands where appropriate habitat is present (Lazell 1976; Cablk 1991; Dodd et al. 1994; Verdon and Donnelly 2005).

The range of the Eastern Box Turtle may have been partially altered by native Americans prior to the arrival of Europeans (Bleakney 1958; Adler 1968, 1970). Holman and Claussen (1984) presented evidence that *T. c. putnami*, which is now extinct, was used as food by prehistoric people in Florida. Today, the Maya use *T. c. yucatana* to treat asthma (Carr 1991) and Yucatan Box Turtles are often transported between pueblos. Adler (1970) argued that *T. carolina* was extirpated from western New York state by overexploitation prior to the arrival of Europeans. While the case he makes is not conclusive, it is persuasive.

Eastern Box Turtles continue to be moved throughout the landscape by humans today and recently the Eastern Box Turtle's entry into the pet trade with its associated escapees has probably confused the range of this species, particularly at range boundaries, by introducing animals outside of the species' natural range, and within the main range by mixing individuals from different populations and subspecies.

Habitat and Ecology. — Because of its relative availability, particularly throughout the 20th century, *T. carolina* has been used for a wide-range of both experimental and observational studies, including growth (Nichols 1939a; Stickel and Bunck 1989; Ernst et al. 1998; St. Clair 1998), bioenergetics (Penick et al. 2002), heat production (Elghammer and Johnson 1976), heating and cooling rates (Spray and May 1972), freeze tolerance (Claussen 1990; Costanzo and Claussen 1990; Costanzo et al. 2008), evaporative water loss (Morgareidge and Hammel 1975), water absorption of eggs (Cunningham and Huene 1938), odor stimulation (Tonosaki 1993), chemosensory behavior (King et al. 2008), auditory response (Wever and Vernon 1956; Zeyl and Johnston 2014), sensory mate finding (Belzer 2002), color discrimination and cognitive function (Leighty et al. 2013), space perception (Yerkes 1904), competitiveness (Boice 1970; Boice et al. 1974), sleep (Flanigan et al. 1974), stress and preference for environmental enrichment when in captivity (Case et al. 2005), locomotion (Adams et al. 1989; Muegel and Claussen 1994; Marvin and Lutterschmidt 1997), lung ventilation (Landberg et al. 2003), sensitivity to X-ray irradiation (Altland et al. 1951; Cosgrove 1965), lead uptake in tissue (Beresford et al. 1981), color development (Belzer and Seibert 2010; Rowe et al. 2014), and material and mechanical properties of the shell (Rhee et al. 2009). Here, we review those aspects that are most pertinent to the conservation of the species.

Figure 7. Examples of habitat of five of the six living subspecies of *Terrapene carolina*. From top: *T. c. carolina* habitat in North Carolina, *T. c. triunguis* habitat in Missouri, *T. c. major* habitat in the Florida panhandle; *T. c. bauri* habitat in peninsular Florida, and *T. c. yucatana* habitat in the Yucatán. Photos by Michael T. Jones.

Habitat Use. — Any species that ranges from Ontario to Yucatán obviously has a fair degree of habitat tolerance and regional variability in its habitat preferences (Fig. 7). Habitat use of the U.S. subspecies is generally described in Carr (1952), and more specifically in a number of more recent studies (Dolbeer 1969, 1971; Reagan 1974; Yahner 1974; Madden 1975; Stickel 1978, 1989; Strass et al. 1982; Schwartz et al. 1984; Williams and Parker 1987; Dodd et al. 1994; Cook 2004; Donaldson and Echternacht 2005; Rossell et al. 2006; Jennings 2007; Quinn 2008; Fredericksen 2014).

Eastern Box Turtles occupy a mix of forest, open forest, fields, and riparian areas, but there is a good deal of variation from place to place and among individuals within a single population. Dodd et al. (1994) gave a detailed account of habitat use by *T. c. bauri* on Egmont Key in a habitat type not available to *T. c. carolina* or *triunguis*. Milstead (1967) and Auffenberg (1959) characterized *T. c. major* as marsh-inhabiting as well as occurring in pine-palmetto forests. Milstead (1967) further showed that habitat selection differences between *triunguis* and *major* could be found where their ranges were close to each other. Though often considered a forest, forest gap, or edge species, early successional and grassland habitat has been identified as seasonally important for *T. carolina* by a number of authors (Reagan 1974; Madden 1975; Nazdrowicz et al. 2008; Willey 2010; Fredericksen 2014). Despite the range of studies, multi-site comparisons have only recently been undertaken (Iglay et al. 2007; Rittenhouse et al. 2008; Hagood 2009; Willey 2010; Currylow et al. 2012, 2013a), most of which illustrate great variation between populations, and one (Rittenhouse et al. 2008) specifically noted that habitat selection may be population-specific.

Juveniles are often under-represented in habitat analyses (but see Jennings 2003; Felix et al. 2008) and results from Jennings (2007) suggest this may be because they are using different habitats, and often habitats with higher vegetation cover that may be more difficult to survey.

Eastern Box Turtles, particularly *T. c. major* (Penn and Pottharst 1940), are also known to be aquatic in some instances, and use of aquatic habitat has been noted throughout the species' range (Englehardt 1916; Allard 1948; Dickson 1953; Donaldson and Echternacht 2005, Rossell et al. 2006), though more frequently in warmer climates and during hotter, drier weather (Donaldson and Echternacht 2005; Weiss 2009).

Diet. — Eastern Box Turtles are probably as omnivorous as any reptile. They eat an extraordinary variety of food (Allard 1948; Klimstra and Newsome 1960; Dodd et al. 1994; Platt et al. 2009): berries, fruits (Stone and Moll 2009), mushrooms (Latham 1968), carrion (Alsop and Wallace 1978; Jensen 1999), gastropods, insects, earthworms, slugs, snails, salamanders (Anton 1990), mammals (Moore 1953), birds (Anton 1990), and a host of other oddities (Latham 1972; Walde and Christensen 2007). Their diet varies seasonally and may vary ontogenetically. Eastern Box Turtles may play an important coevolutionary role in their habitats as seed and fungi dispersers (Rust and Roth 1981; Braun and Brooks 1987; Liu et al. 2004; Jones et al. 2007).

Hibernation. — In most of the United States, Eastern Box Turtles become dormant during the winter, with northern populations active from April to October or November (Barbour 1968; Madden 1975; Cook 1996; Currylow et al. 2013*a*); southern populations have a longer active season (Dolbeer 1971), and *T. c. bauri* has been observed active in every month in Florida (Dodd et al. 1994). The location of hibernation sites may not be within the normal summer activity area, and many individuals may aggregate in areas suitable for hibernating (Kiester 1985; Congdon et al. 1989; Claussen et al. 1991). Emergence is thought to be related to subsurface soil temperatures (Grobman 1990). Woodley (2013) observed that overwintering adult box turtles in southwest Michigan surfaced at carapace temperatures averaging 7.1°C and emerged at 14.3°C, with 90% of the 44 adults emerging when growing degree days reached 100.

Overwintering habitat has been fairly well characterized, but is also variable throughout the range. Most *T. carolina* overwinter in forested areas (Carpenter 1957; Dolbeer 1971; Carr and Houseal 1981; Claussen et al. 1991; Cook 2004; Currylow et al. 2013a), select microhabitats that are warmer than the surrounding area (Currylow et al. 2013a), and burrow down in the leaf litter and soil, which stays much warmer than the air (Claussen et al. 1991; Savva et al. 2010). Overwintering locations are often associated with areas of structure where leaf litter will accumulate, and their use of "stump holes" or "tree tip-ups" has been noted throughout the species' range (Carpenter 1957; Dolbeer 1971; Willey 2010).

Eastern Box Turtles have the ability to withstand a fair amount of freezing (Costanzo and Claussen 1990; Costanzo et al. 1993, 1995; Storey et al. 1993). Despite this ability, individuals in populations throughout the range sometimes die in association with winter conditions (Carpenter 1957; Schwartz and Schwartz 1974; Harding 1997; Cook 2004; Nazdrowicz et al. 2008; Currylow et al. 2010), and 17 neonates tracked through their first winter in Illinois lost 11–12% of their body weight (Luca and Moore 2014).

Terrapene carolina has been known to successfully overwinter underwater in captivity in Illinois (Cahn 1933), and hatchlings immediately moved to water, suggesting this may be one reason they are difficult to find. The species does not build up fat storage prior to overwintering (Brisbin 1972) and Costanzo et al. (1993) suggested glucose may be used for cryoprotection (though levels were not as high in *T. carolina* as in anurans) in conjunction with dehydration of organs. They also noted that heart rate ceased for 25 hrs, at -2.1°C, 47 hrs after freezing, but resumed during thawing.

Activity Patterns. — Field studies suggest a diurnal behavioral pattern, and this has been confirmed in lab experiments (do Amaral et al. 2002a). Eastern Box Turtles tend to be more active during times of warm temperatures and high humidity (Stickel 1950; Reagan 1974; Madden 1975; Dodd et al. 1994), and movements tend to be larger in association with rain events (Madden 1975; Strang 1983; Donaldson and Echternacht 2005), though temperatures vary geographically and seasonally.

A rough summary of activity (especially for *T. c. carolina* and *triunguis*) follows. During the times of the year when Eastern Box Turtles are active, they spend the night in a "form" or "pallet" (Stickel 1950), which is a temporary resting site created by settling down into vegetation, leaf litter, or soil, so as to become hidden and partially buried (Strass et al. 1982). Often forms are located in structurally diverse areas where they are more concealed and leaf litter and soil collection is larger (e.g., downed logs, shrubs, or next to rocks) (Stickel 1950), and may have higher humidity than the surrounding area (Rossell et al. 2006). Activity begins in the morning and may include some basking. Turtles may rest during the middle of the day if it is hot (Penn and Pottharst 1940; Dodd et al. 1994) and then have another period of activity in the late afternoon, but during cooler times of the year, they may only be active during the hottest part of the day (Stickel 1950). Activity patterns vary from day to day and not all turtles are active on any given day. During hot, dry weather few turtles are active. When active, turtles may range over almost all of the microhabitats in their immediate area.

In the lab, Eastern Box Turtles given a thermal gradient choose similar temperatures to those in the field (19.95–28.88°C, do Amaral et al. 2002a), significantly lower than those chosen by *T. ornata*, and active temperatures are lower than resting temperatures. Eastern Box Turtles are able to walk faster at warmer temperatures, reaching a maximum velocity of 0.49 m/sec at 31.9°C (Adams et al. 1989).

Monagas and Gatten (1983) have described the phenomenon of behavioral fever for *T. c. carolina*. This occurs when Eastern Box Turtles suffering a bacterial infection voluntarily thermoregulate to a higher temperature than is normal using behavioral means, and do Amaral et al. (2002b) observed that turtles regulate their body temperatures depending on the dose of toxin administered. The existence of this behavior is indirect evidence that basking must play an important role in the life of this species.

Orientation and Homing. —Eastern Box Turtles are known to home (Nichols 1939c; Gould 1957, 1959; Posey 1979). They are capable of orienting themselves (DeRosa and Taylor 1980, 1982), and although the mechanisms by which they do this are not yet understood, DeRosa and Taylor (1982) suggested they rely on celestial cues available under clear, daylight sky, while Madden (1975) suggested that smell may play a role. The fact that Eastern Box Turtles have these abilities is important, however, because it implies that they have the behavioral capability to move long distances outside of a normal home range, and return, if they choose to do so. Therefore, the complex movement patterns that we suspect Eastern Box Turtle to have (see below) have a definite behavioral basis. Additionally, having a complex understanding of the landscape may help them to exploit new resources as they become available, which has been seen on a variety of scales, from congregating around a local food resource (Dolbeer 1969) to adjusting habitat use based on recent forest management (Currylow et al. 2012).

Movement and Transients. — The home range of Eastern Box Turtles has been estimated for populations throughout the range using techniques from mark-recapture, often with the assistance of dogs (Schwartz and Schwartz 1974, 1991; Kiester et al. 1982; Schwartz et al. 1984; Kapferet al. 2012), to thread trailing and radiotelemetry. Home range estimates vary throughout the species' range, though variation in home range size estimation methods makes comparisons difficult. Although estimates have largely increased with the advent of radiotelemetry, home range sizes also increase with latitude and habitat homogeneity. Range size based on the minimum convex polygon (MCP) method is the most common standard metric recorded, and these estimates for individuals range from 0.22 (Davis 1981) to 187.6 ha (Currylow et al. 2012). Average MCP estimates across populations range from less than 2 ha in West Virginia (Aall 2011, n = 9) and Tennessee (Donaldson and Echternacht 2005, n = 13), to 2–7 ha in North Carolina (Hester et al. 2008, n = 10; Kapfer et al. 2013, n = 11), 4.7 ha in Maryland (Lentz 2005, n = 100), 4–8 ha in New York (Madden 1975, n = 23; Capitano 2005, n = 7), 5.0 ha in Connecticut (Quinn 2008, n = 14), and greater than 7 ha in Illinois (Baker 2009, n = 24), Indiana (Currylow et al. 2012, n = 50), and Massachusetts (Willey 2010, n = 86). The length of time observed and number of locations per animal vary widely across studies, however, making comparisons difficult. Home range size estimates for males and females are consistently not significantly different (Stickel 1950; Dolbeer 1969; Cook 2004; Baker 2009; Aall 2011; Kapfer et al. 2013).

Though most animals maintain a similar home range from year to year (Stickel 1950; Williams and Parker 1987), observed changes in centroids between years have ranged from 7 to 1345 m (Cook 2004, n = 25; Willey 2010, n = 64). Turtles in more diverse habitats and more developed areas move smaller distances than those in less fragmented, more homogenous landscapes (Kipp 2003; Iglay et al. 2007; Willey 2010).

The existence of true transients in Eastern Box Turtle populations had been long suspected (Stickel 1950), and their existence was confirmed by Kiester et al. (1982). They used a thoroughly marked population to screen for potential transients that were then radiotracked. Transient individuals were all males, and moved in remarkably straight lines through habitable and uninhabitable areas. One individual was followed for 18 months and covered 10 km. Mating was observed on a number of occasions, indicating that these individuals play an important role in the genetic structure of the metapopulation.

Hagood (2009) and Kimble et al. (2014) suspected that the broadscale genetic connectivity they observed between distant populations may have been, in part, a result of historical connectivity via transients. Kimble (2012) found that although direct siblings were rare in the population (<1% of his sample), they averaged geographic distances of 11.6 km apart, suggesting that dispersal is much greater in this species than traditionally assumed. We do not yet know whether transients eventually settle down, or what their frequency is in populations, though estimates have been made based on mark-recapture studies (Stickel 1950; Schwartz and Schwartz 1991), and recent work in Indiana suggests that animals may use "typical home ranges" for one or more seasons before, during, or after exhibiting transient behavior (Kimble 2012). Transients clearly make use of whatever orientation mechanisms that Eastern Box Turtles have.

Intermediate Disturbance Hypothesis and Metapopulation Dynamics. — Eastern Box Turtles generally may be said to live in landscapes that are a dynamic mosaic of forests, riparian areas, and open fields. They do not seem to be adapted to extensive closed canopy forest, rather, they prefer forests that have natural or man-made openings. Downed trees that provide access to sun and coarse woody debris are important habitats for hatchlings and juveniles.

In general, the species seems to be adapted to intermediate disturbance regimes (Connell 1978; Huston 1979). Too much disturbance results in only open areas, and too little disturbance leads to closed canopy forests that are too dark. This generalization may not apply to the Mexican subspecies, although *T. c. yucatana* also appears to inhabit mosaics of forested and open habitats.

Within this landscape, Eastern Box Turtles exhibit a complex metapopulation structure (for a general discussion of this topic see Hanski and Gilpin 1991). Individuals tend to aggregate around favorable habitat, depending on the locally limiting resource. In more open habitats, they may congregate in the fall when they may move to sites most favorable for hibernation, dispersing out to summer home ranges (Kiester 1985). In more forested areas, winter habitat is more dispersed and they may congregate around habitat openings in the spring and summer to thermoregulate and nest. Such site-specific habitat preference was observed by Rittenhouse et al. (2008), and ontogenetic habitat selection might exist as well (Jennings 2003, 2007; Felix et al. 2008).

Dodd et al. (2006) noted that an island population of *T. c. bauri* responded to disturbance by moving to less disturbed parts of the island, and disturbance events affected the growth rates of animals on the island (Dodd and Dreslik 2008), though there were no long term effects on the population size (Dodd et al. 2012). Currylow et al. (2012) also noted changes in movement as a result of disturbance, suggesting that larger reserve areas may be necessary for turtles to cope with changes in habitat as a result of natural or anthropogenic disturbance processes and succession.

Nazdrowicz et al. (2008) found that population densities were higher at less forested sites, but these areas also had lower adult survival rates, suggesting a threshold or "tipping point" relationship may exist, and rough population estimates at five sites in Massachusetts suggested a potential unimodal response between population density and percent forest cover (Willey 2010). Turtles in forested areas were also observed to grow more slowly but may reach adult size sooner and live longer (Budischak et al. 2006), and move greater distances than those in more open habitat (Kipp 2003; Iglay et al. 2007; Willey 2010). Large movements may be related to egg laying, thermoregulation, or foraging, since females, males, and juveniles all make such excursions. As mentioned above, some individuals are transient, moving long distances in a straight line (Kiester et al. 1982).

As a result of these movements, populations appear to be relatively well connected under natural circumstances, and this has been borne out in molecular work (Hagood 2009; Kimble 2012; Kimble et al. 2014). Habitat conversion and increased mortality on roads likely has the effect of isolating populations from each other to a greater degree. An important open question is whether roads operate as sinks, drawing turtles from forested areas in search of open habitat. If this is the case, it is likely that road mortality could have a much more serious effect on population and metapopulation structure.

Reproduction. — Reproduction in *T. carolina* has been well studied throughout the species' range, with more than 25 studies evaluating some aspect of reproductive output. Mating (Cahn and Conder 1932; Evans 1953) and nesting (Ewing 1933, 1935; Congello 1978) behaviors have been described on a number of occasions. Mating can occur at any time during the active season, and though most subspecies mate on land in accordance with their generally terrestrial behavior, Evans (1968) noted that *T. c. major* customarily mates in water. Nesting typically occurs in the evening under variable weather conditions (Allard 1948; Congello 1978; Messinger and Patton 1995; Kipp 2003; Baker 2009). Using radiographs, Dodd (1997) determined that eggs were calcified in Florida from late March through early August, though late May through early July is more typical for nest deposition elsewhere in the species' range. Nesting habitat has also been well documented throughout its range (Allard 1948; Barbour 1968; Kipp 2003; Flitz and Mullin 2006; Burke and Capitano 2011); the species prefers areas of open canopy, minimal vegetation and leaf litter, and sandy soils, and often makes use of anthropogenic openings.

Clutch sizes range from 1 to 10, and average clutch size increases with latitude (Kipp 2003; Cook 2004; Wilson and Ernst 2005; Burke and Capitano 2011; Willey and Sievert 2012) as annual clutch frequency decreases. Average clutch size ranges from less than 3 for *T. c. bauri* in Florida (Dickson 1953, n = 83; Dodd 1997a, n = 98) and *T. c. triunguis* in Texas (Buchman et al. 2010, n = 15), to greater than 5 for *T. c. carolina* in New York (Cook 2004, n = 11), Illinois (Baker 2009, n = 18), and Massachusetts (Willey and Sievert 2012, n = 31). Though several authors have found a correlation between body size and clutch size (Dodd 1997a; Tucker 1999; Miller 2001; Kipp 2003; Wilson and Ernst 2005; Buchman et al. 2010; Willey and Sievert 2012), the relationship is often not significant, and the pattern is not consistent (Cook 2004; Burke and Capitano 2011). Females remain reproductively active well past 50 yrs old (Henry 2003) and may even lay larger, more frequent clutches as they age (Miller 2001).

Double and triple clutching has often been reported (Ewing 1935; Dickson 1953; Reimer 1981; Jackson 1991; Dodd 1997a; Kipp 2003), and six clutches were laid by a captive female in Louisiana in one year (Messinger and

Patton 1995). Females near the northern limit of their range have not been observed laying multiple clutches in a year (Cook 2004; Willey and Sievert 2012), and this has been confirmed by analyzing hormone levels in a population in Indiana (Currylow et al. 2013b).

Egg mass ranges from 6.8–11 g (Allard 1948; Messinger and Patton 1995), and egg dimensions range greatly from 15.5 x 9.5 mm to 40 x 21 mm (Allard 1948). Hatchlings typically emerge from late August to early September after 57–136 days (Allard 1948; Iverson 1977), though hatchlings have been known to overwinter in the nest chamber (Madden 1975). Depredation rates vary across space and time and range from 0–100%. Egg and nest success rates also vary considerably, from 55% (Messinger and Patton 1995; Willey and Sievert 2012) to 95% (Burke and Capitano 2011).

Ewert and Nelson (1991) found that *T. c. carolina* from Indiana showed temperature-dependent sex determination, with males produced at lower egg incubation temperatures and females at higher temperatures. They also showed that this species' pattern of dependency on temperature did not closely correspond to that of any other turtle, including *T. ornata*. Ewert and Nelson (1991) and Burke (1993) reviewed possible explanations for this phenomenon, but agreed that we simply do not fully understand it yet.

Population Structure. — Throughout the range of *T. carolina*, population density estimates (Table 1) range from <1 adult turtle/ha in fragmented or range-edge populations of *T. c. carolina* (Nazdrowicz et al. 2008; Willey 2010) to well over 10 turtles/ha in populations of *T. c. bauri* (Langtimm et al. 1996; Verdon and Donnelly 2005), *T. c. carolina* (Stickel 1950; Wilson and Ernst 2005), and *T. c. triunguis* (Schwartz et al. 1984), but no population density estimates are available for *T. c. major*, *mexicana*, or *yucatana*.

Sex ratios range from even to heavily male-biased (Yahner 1974; Stickel 1978; Hall et al. 1999; Niederriter and Roth 2004; Chute 2007; Dodd et al. 2012). Although low density populations may pose problems for recruitment (Mosimann 1958; Belzer 2002), the ability of female Eastern Box Turtles to store sperm (Hattan and Gist 1975; Gist and Jones 1987) and to lay fertile eggs long after separation suggests that viable populations may persist at relatively low densities.

Juveniles are often under-represented in surveys and usually account for only a small fraction of the animals observed at a site, but juveniles (CL up to 115 mm) comprised up to 46% of a population in Missouri (Schwartz et al. 1984), 32% of a population in Maryland (Hall et al. 1999), 31% of a population in Delaware (Nazdrowicz et al. 2008), and 26.5% of a population in Florida (Dodd 1997b). Dogs have been observed to find a greater proportion of juveniles (Kapfer et al. 2012), and this difference in methodology may account for some of the differences in observed population structure.

Annual survival rates for adults typically range from 81% (Nazdrowicz et al. 2008) to 96% (Currylow et al. 2010), but were as low as 56% in a population in Florida (Verdon and Donnelly 2005), with sources of mortality including predation, disease, forest fire, prescribed burns, road mortality, mowing, and winterkill. Juvenile survival rates are less well known but have also been estimated in several studies (Yahner 1974; Schwartz et al. 1984; Dodd et al. 2012), and depredation may be a larger factor in their survival than that of adults (Madden 1975; Murphy 1976; Forsythe et al. 2004).

Though Eastern Box Turtles have a number of natural predators, including bald eagles (Clark 1982), hogs (Culbertson 1907), chipmunks (Belzer et al. 2000), snakes (Dickson 1953; Murphy 1964), and fire ants (*Solenopsis invicta*) (Montgomery 1996), predation rates are likely not a major factor in population declines except where populations are already stressed for other reasons, or predator densities are unusually high.

Many authors have reported longevity observations for this species. Observations made during long-term studies have been used to age animals to 50 and 73 years (Williams and Parker 1987; Schwartz 2001). More often, repeated observations of turtles with dates carved on their shells have been used to estimate longevity, with records ranging from 46 to over 100 years in several instances, and these observations have been reported in the scientific literature as well as in newspapers and other popular news sources (Townsend 1926; Babcock 1927; Deck 1927; Edney and Allen 1951; Price 1951; Oliver 1953; Belzer 2008).

Population Status. — Although *T. carolina* is apparently among the more widespread turtles of the United States, anecdotal evidence and long-term studies suggest that populations have declined, in some cases precipitously, throughout the species' range. In predominantly rural areas of the United States, Eastern Box Turtles appear to continue to exist in relatively high densities where the landscape has retained a mosaic of forest, open habitats, and riparian areas. Where the landscape has become urban or densely suburban, their numbers have dwindled, and in some cases they have disappeared altogether. Several states monitoring the distribution and population status in their jurisdiction have reported population declines or extirpation, including large portions of Michigan (Marsack and Swanson 2009) and Massachusetts (MNHESP 2011), and there are currently no known populations in Maine, New Hampshire, or Ontario, with only isolated reports of individuals.

Although most studies of population size and structure have been only a few years in duration, five long-term studies of *T. c. carolina, triunguis,* and *bauri* make these subspecies among the demographically best understood long-lived reptiles. Lucille Stickel began her studies of *T. c. carolina* at Patuxent in Maryland in 1945 and reported

Table 1. Population density estimates across the range of *Terrapene carolina*.

Author(s)	Subspecies	Location	Date of study	Turtles / ha	Range or Confidence Interval (if provided)
Langtimm et al. 1996	*bauri*	FL	1993	14.95	95% CI: 11.4–18.5
Verdon and Donnelly 1985	*bauri*	FL	2002–2003	10.20	95% CI: 6.65–19.07
Pilgrim et al. 1997	*bauri*	FL		16.30	
Nazdrowicz et al. 2008	*carolina*	DE	2001–2003	2.22	Range: 0.22–3.62
Williams and Parker 1987	*carolina*	IN	1958–1984	3.70	Range: 2.7–5.7
Willey 2010	*carolina*	MA	2005–2008	2.05	Range: 0.3–3.8
Stickel 1950	*carolina*	MD	1944–1947	10.63	Range: 9.9–12.4
Hallgren-Scaffidi 1986	*carolina*	MD	1984–1985	8.62	
Hagood 2009	*carolina*	MD	2005–2006	7.60	Range: 5.4–9.6
Kapfer et al. 2012	*carolina*	NC	2011	2.86	Range: 1.74–3.97
Chute 2007	*carolina*	NC	1999–2006	7.00	
Madden 1975	*carolina*	NY	1969–1972	3.71	
Dolbeer 1969	*carolina*	TN	1968	20.76	Range: 18.8–22.7
Wilson and Ernst 2005	*carolina*	VA	2000–2002	16.00	
Schwartz et al. 1984	*triunguis*	MO	1965–1983	22.52	Range: 18.4–26.9

demographic results up through 1975 (Stickel 1950, 1978). Additional work has been conducted at her site in the years since (Hallgren-Scaffidi 1986; Hall et al. 1999; Henry 2003; Hagood 2009). Eliot Williams, Jr. followed a population of *T. c. carolina* in Indiana from 1958 to 1984 (Williams 1961; Williams and Parker 1987). Several generations of biologists have studied a site in Delaware from 1965 to 2000 (Niederriter and Roth 2004; Nazdrowicz et al. 2008). Charles and Elizabeth Schwartz followed a population of *T. c. triunguis* in Missouri from 1965 to 1991 and 1998 to 1999 (Schwartz and Schwartz 1974, 1991; Schwartz et al. 1984; Kiester et al. 1991; Miller 2001; Schwartz 2001). C. Kenneth Dodd, Jr. began studying a Florida island population of *T. c. bauri* in 1991, and has continued to evaluate population structure over time (Langtimm et al. 1996; Dodd 1997b; Dodd et al. 2012).

The longest duration of these studies is approaching its 70th year, still less than two generations for an Eastern Box Turtle, and not long enough to understand the many effects on population processes. In addition, it is inevitable that over several decades there are changes in research methodologies, so we must interpret the results of these studies cautiously and recognize that natural and anthropogenic landscape change has occurred at each of these sites, all of which affect population processes. Still, these are the best records we have of long-term population trends for this species, and they are better than records available for most turtle species.

Of these five populations where long-term trends have been evaluated, only Dodd's *T. c. bauri* population has remained stable. At Patuxent, the population has been on a long downward trajectory, and in 1995 was just 23% of the 1955 population, though younger animals made up a larger portion of the population than in the past (Hall 1999). Williams' Indiana population declined from a density of 4.4–5.7 turtles/ha in the 1960s to 2.7 turtles/ha in 1983, and the Delaware population had declined from 91 (SE = 7.8) in 1968 to 22 (SE = 3.0) in 2002 (Nazdrowicz et al. 2008). The Schwartz's population of *T. c. triunguis* in central Missouri was assessed from 1966 to 1999 by Kiester et al. (1991) using the Jolly-Seber method (Seber 1973). Clearly after 1980, the population had declined. In addition to population declines, sex ratio was also observed to become increasingly male-biased at two of these sites (Stickel 1978; Niederriter and Roth 2004; Nazdrowicz et al. 2008).

Perhaps most discouraging is that the factors driving the observed declines are unknown and that these four study sites were relatively protected throughout the duration of the studies. In addition to these documented population declines, other study areas have been completely developed (e.g., Madden 1975), and their populations presumably lost altogether. In yet other areas, anthropogenically elevated sources of mortality in shorter-term studies suggest that other populations may be declining as well. Road mortality (Hester et al. 2008; Hagood 2009), mowing or haying (Rittenhouse et al. 2007; Hester et al. 2008; Nazdrowicz et al. 2008), and prescribed fire (Platt et al. 2010) may be influencing population dynamics and trajectories, even at protected sites.

Population and Metapopulation Processes. — On-site anthropogenic factors affecting recruitment and mortality that may have led to the observed population declines include the effect of pollutants and toxins, collecting, and habitat change. Stickel (1978) thought that a flood may have killed turtles either directly or by transporting pollutants onto the site. Williams and Parker (1987) suggested that collecting may have increased on their site between the years of their study. Unfortunately, none of the studies have any direct evidence of this activity. All four sites were left undisturbed during the course of the studies and underwent natural succession. Stickel (1978) noted that the habitat on her site had not changed much, and that the forest continued to have canopy openings because of ongoing natural tree falls, though Hall et al. (1999) later noted that the forest composition had markedly changed at the site, becoming beech dominated, but beavers continued to maintain canopy openings. Williams and Parker (1987) listed succession as a possible factor leading to population decline, though considered it less plausible than human disturbance or surrounding landuse change. Niederriter and Roth (2004) suggested that lack of suitable, open nesting habitat might have contributed to the decline at the Delaware site. Schwartz et al. (1984) recorded aerial photographs 16 years apart of their study area. Here, habitat succession was clearly shown, with both the forest canopy closing and the open areas becoming brush and small trees. In addition, Leuck and Carpenter (1981) noted that *T. c. triunguis* had disappeared from their study site as a result of succession, and Nazdrowicz et al. (2008) reported that populations may reach higher densities where early successional habitat is available.

Clearly, Eastern Box Turtles live long enough to have their habitat successioned out from under them, but the effects on population dynamics are not clear. In unfragmented landscapes, metapopulation dynamics beyond the spatial extent of the study areas could be important in sustaining viable populations; habitat succession may simply force individuals to move greater distances to access early successional resources, and at several sites, Eastern Box Turtles have been observed to move further in more forested habitat (Kipp 2003; Iglay et al. 2007; Willey 2010). As roads divide and fragment habitat, such natural metapopulation dynamics may no longer function, forcing local extinctions without replacement from other source populations once disturbance renders the habitat suitable again.

Of the five long-term sites described above, only Dodd's population of *T. c. bauri* is an isolated (island) site. Both population and metapopulation processes must be examined for possible causes of decline. Factors on the periphery of the populations (e.g., increased development, road upgrades, and pollutants from the surrounding landscape) were suggested by the authors as potential factors in population decline in the other four non-isolated sites. In all these sites the surrounding areas of Eastern Box Turtle habitat were degraded either through habitat conversion or increased road density and traffic. We know that turtles enter and leave these populations and therefore any reduction in the amount of immigration will manifest itself as population declines. The associated effects of landscape change and reduced ecological integrity in the surrounding landscape (e.g., increased populations of subsidized predators, and increased rates of collection for the pet trade) may have played a role as well. Unfortunately, estimating these effects quantitatively is very difficult.

While the definitive and quantitative detection of population declines in a species that is widespread and has not clearly gone extinct is difficult (Connell and Sousa 1983; Blaustein et al. 1994), the weight of evidence on *T. carolina* shows that it is declining, as has been concluded by others reviewing the status of this species (Stevens 1994; Dodd 2001; van Dijk 2011). Certainly there is enough evidence to warrant concern and to design a better system for estimating the distribution and viability of this species in the United States, and examination of the subspecies in Mexico.

Mexican Subspecies. — In contrast to the U.S. subspecies, the Mexican subspecies are much less well known. The two subspecies have disjunct ranges from each other and from the U.S. subspecies. No quantitative studies of the distribution or density of either of these have been published, and their ecology is essentially unknown.

Terrapene c. mexicana is apparently not uncommon (Smith and Smith 1979; John Iverson, pers. comm.), being usually encountered crossing roads. Its general habitat seems relatively undisturbed, but nothing quantitative is known about its population status.

Terrapene c. yucatana, on the other hand, appears to be uncommon to rare. A series of recent surveys and interviews conducted throughout the Yucatán suggests that the subspecies is quite rare in the wild but is often kept as pets by local communities who collect animals from roads and on ranches and farms during and after rains or prescribed burns (Jones, Willey, Akre, Gonzalez, and Macip-Ríos, unpubl. data). The subspecies is used in a variety of preparations as a treatment for asthma (Carr 1991), sometimes eaten for food, and much of its habitat is heavily managed for agriculture of varying scales. Locals have indicated that because of its marketability, *T. c. yucatana* is now no longer found in the vicinity of human habitations, but can only be encountered in the *monte* or regions away from people (John Iverson, pers. comm.).

Threats to Survival. — The site-specific and broad-scale declines in abundance discussed above may be the result of several factors: habitat conversion and associated increase in road density and traffic, habitat succession and management, the pet trade, and disease. Additionally, the effects of climate change on habitat and survival are unknown, though models suggest *T. carolina* growth may be severely minimized given projected change in precipitation and temperature (McCallum et al. 2009), but over-wintering microhabitat may be less thermally affected (Savva et al. 2010). Climate change may also indirectly affect populations through increased susceptibility to the factors below, including disease or toxins.

Habitat Conversion. — Habitat degradation and conversion is a matter of degree, but much of the United States is being converted to habitats that cannot support Eastern Box Turtles. The rate of this conversion is not known specifically for Eastern Box Turtle habitat, but clearly conversion is widespread, continual, and substantial. Between 1973 and 2000, an estimated 3.7 million ha (or 4.1%) of eastern forests were lost or converted to other uses (Drummond and Loveland 2010). As observed in the four long-term studies with downward population trajectories, direct habitat loss is not the only way habitat conversion can lead to declines. This estimate of forest loss does not take into account the indirect effects on populations as a result of fragmentation, reduced metapopulation function, and increased mortality associated with roads, mowing, collection, and subsidized predators.

Although conversion to developed landuse types and its associated effects are negative, forest management may be beneficial for Eastern Box Turtle populations in some instances, but the size, location, and configuration of such management, as well as the seasonality and methodology, are important considerations.

Roads, Density, and Traffic. — Roads are a source of anthropogenic mortality and habitat fragmentation throughout the species' range, and several attempts have been made to quantify the magnitude of this problem using a variety of techniques (Dodd et al. 1989; Steen et al. 2006; Shepard et al. 2008; Hagood 2009; Marsack and Swanson 2009). Eastern Box Turtles may be more susceptible to road mortality than other turtle species due to their behavioral tendency to close when threatened and remain closed for longer than other species (Gooley 2010). Because they are primarily terrestrial, they may also be more likely than aquatic species to cross roads at locations without passage structures. Increased road traffic (without any further habitat alteration) and consequent increased probability of mortality may result in a threshold effect that breaks down the metapopulation structure and causes widespread local extinction. Roads may also disproportionately affect nest-searching females (Steen et al. 2006), possibly resulting in skewed sex ratios in some instances (Stickel 1978; Niederriter and Roth 2004; Nazdrowicz et al. 2008). Though fragmentation appears to be causing population loss, loss of genetic diversity does not yet appear to be an immediate threat in Eastern Box Turtle populations, likely due to the long generation time (Marsack and Swanson 2009).

Succession in Protected Areas. — As discussed above, there is a concern that in areas set aside for conservation, succession will tend to slowly erode *T. carolina* habitat. If this is indeed a problem, it could have important implications for the management of such areas, and raises the possibility of a conflict between managing for Eastern Box Turtles and managing for other biodiversity goals. In many ways, this issue is really a question of scale and suggests the necessity of protected areas that are large enough to retain a natural disturbance regime that maintains habitat in the various stages of succession required by Eastern Box Turtles.

Habitat Management. — One of the major difficulties that Dodd (2005) pointed out, is that when a species has been labeled "common", it makes it difficult to protect and prioritize on otherwise "protected" land. Consequently, such species may not be taken into account when developing habitat management plans, which can lead to inappropriate management (such as mowing, burning, and invasive species removal) that reduces survival rates and threatens populations, even on protected lands (Dodd 2006).

Fire can be a threat to Eastern Box Turtle populations and the fire ecology of the species has been examined at several areas within the species' range (Bigham et al. 1965; Ernst et al. 1995; Gibson and Kingsbury 2008; Platt et al. 2010; Woodley and Kingsbury 2011; Howey and Roosenburg 2013). Fire damage to the shells of living animals is also common (Rose 1986; Dodd et al. 1997), and the body condition of animals in recently burned areas may also be poorer (Howey and Roosenburg 2013). The disappearance of the Eastern Box Turtle from areas like the Albany Pine Bush in New York has, at times, been attributed to fires (Hunsinger 2001). From 10–21% of the population in a given area may be killed by fire during wet season fires in Florida (Platt et al. 2010), and seasonally adjusting the timing of prescribed burns could help minimize such losses. Mowing and haying are additional sources of anthropogenic mortality (Brisbin et al. 2008; Hester et al. 2008; Nazdrowicz et al. 2008) that should be considered in evaluating population dynamics.

Forestry and management practices that create forest gaps may be beneficial for Eastern Box Turtles in some instances. At a site in Alabama, juveniles were caught more frequently in recently cut stands than uncut stands (Felix et al. 2008), and as noted above, early successional habitat is preferred by some populations in some seasons, and its availability may increase population density and reduce movement. In developing management plans, care should be taken to ensure that all life stages are considered, that mortality is not elevated as a result of the management action, that the seasonality of the management action is appropriate and does not conflict with turtle activity, and that sufficient mature habitat remains available.

Pet Trade. — During the latter 20th century, *T. carolina* was thought to make a good pet, especially for children who suffered allergies to mammalian species. As a consequence, there was a substantial pet trade in this species. Stevens (1994) reported that the U.S. Fish and Wildlife Service informally estimated that over 35,000 Box Turtles (both *T. carolina* and *T. ornata*) were shipped to other countries from the U.S. each year. Information is not available on the number collected for U.S. sale, but it must have been at least as large. In response, *Terrapene* was listed in CITES Appendix II (CITES 1994), regulating their international trade. Still, they are often found in markets around the world, a trend that could have devastating effects on populations, particularly of the poorly known subspecies *T. c. yucatana*.

Perhaps less important than collection for the commercial trade are two related concerns: incidental collection from populations (suggested as a factor in the population decline at Allee Memorial Woods [Williams and Parker 1987]), and the release of pet Box Turtles into wild populations. Such releases may affect local populations through introduction of disease and non-locally adapted genes, and they confuse distributional questions, particularly at the edges of ranges. Though relative lack of shyness is often used as a factor to determine whether animals are native wild turtles or released pets, varied behavioral responses of Eastern Box Turtles to handling has been noted by several authors (Nichols 1939b; Dodd 1997b), and genetic evaluation appears to be the only reliable way to identify released or transported animals.

Turtle Races. — Eastern Box Turtles are a favorite species in turtle races that occur throughout the species' range. Races often occur in association with fairs, festivals, and Independence Day celebrations, and in some locations they are weekly events in the summer months (Lee 2012). Bars and restaurants across the country also host regular turtle races. Heeb (2007) found that over 520 turtle races occur each year in the U.S. and estimated that 26,000 box turtles are taken from the wild annually to participate in these races. A loss of adult box turtles of this magnitude could have serious detrimental effects on box turtle populations, and those that are returned to the wild are often returned to different locations, may have been exposed to disease, may have been dehydrated or malnourished, and may have been painted or otherwise decorated, making them susceptible to predation or further collection. Lee (2012) described the many risks of such events to both turtles and humans. The Center for Biological Diversity in Tucson, Arizona has begun a campaign to end turtle races, and some states and jurisdictions have outlawed the practice, but these events are still a major threat to box turtle populations.

Diseases and Toxins. — Though parasites have often been reported in Box Turtles (Packard 1882; True 1884; Leidy 1888; Wheeler 1890; Peters 1948; Rokosky 1948), there is no evidence that they are a widespread threat to their survival. Injuries were observed in 9.8% of a population in Virginia (Boucher and Ernst 2004) and 17.7% of turtles in a population in Florida had damage to marginal scutes, with smaller percentages of trauma to the carapace and plastron, exposed bone, or fire scars (Dodd et al. 1997), but again, there is no evidence that such injuries are threats to population persistence.

Evans (1983) found chronic bacterial pneumonia in free-ranging Eastern Box Turtles. This disease is common in captive turtles and this observation raises the possibility that diseased captives might, when released, infect wild populations. Such a process is implicated in some mortality of wild desert tortoises (*Gopherus agassizi*) (Desert Recovery Team 1993). *Mycoplasma* spp. has also been found in free-ranging Eastern Box Turtles in North Carolina and Virginia (Siefkas et al. 1998; Rossell et al. 2002; Feldman et al. 2006).

The presence of *Ranavirus* in captive and in wild Eastern Box Turtle populations is becoming a growing concern (De Voe et al. 2004; Johnson et al. 2008; Allender et al. 2011, 2013), and although prevalence seems to be generally low (Allender et al. 2011, 2013), several die-offs of unknown cause have occurred (Rossell et al. 2002), and incidents in New York, Pennsylvania, Georgia, and Florida may have been caused by *Ranavirus* (Johnson et al. 2008). Currylow et al. (2014) found sub-lethal prevalence in their study population in Indiana, suggesting that there may be widespread resistance and that large die-offs may be the result of altered strains. Additional work should investigate this growing concern and researchers should take precaution to avoid spreading disease when moving between sites and working with study animals.

Eastern Box Turtles, partly by virtue of their longevity, may concentrate toxic chemicals and isotopes in their tissues (Jackson et al. 1974; Holcomb and Parker 1979; Beresford et al. 1981). The effect, if any, on the behavior and population dynamics of Eastern Box Turtles of these chemicals is unknown, though environmental contaminants (particularly organochlorines) have been suggested as a potential cause for illness (Tangredi and Evans 1997) and abscesses in turtles due to its interference with metabolism of vitamin A (Holladay et al. 2001; Brown et al. 2003), but results are mixed (Sleeman et al. 2008). It would appear that Eastern Box Turtles could be excellent subjects for monitoring some forms of long-term environmental contamination (Meyers-Schöne and Watson 1994) and recent work with *T. ornata* suggests that carapacial growth rings may be ideal for such work (Murray and Wolf 2013).

Conservation Measures Taken. — *Terrapene carolina* has been assessed as having the following conservation ratings. The IUCN Red List assessed it as Vulnerable in 2011; the Committee on the Status of Endangered Wildlife in Canada (COSEWIC) lists it as Extirpated there; CITES includes it on Appendix II. In the USA it is listed as Special Concern in Connecticut, Indiana, Massachusetts, Michigan, New Hampshire, New Jersey, New York, and Ohio, Protected in Rhode Island, and Endangered in Maine. Many states have recently closed or limited commercial harvest, but 16 states allow personal collection (Nanjappa and Conrad 2011). In Mexico this species is protected by law from foreign commercial exploitation.

As a result of the indications of very high numbers of Box Turtles entering the pet trade, the absence of systematic data on both national and international trade, and the lack of consistency and coordination between state regulations, the New York Zoological Society (1991) proposed that all species of *Terrapene,* including *carolina,* be listed on CITES Appendix II. Such listing requires the collection of data on the numbers of Box Turtles captured for sale to the pet trade and allows a more reliable estimate of the impact of trade on the survival of this species. Initially the petition was turned down, but it was resubmitted and, with the support of the U.S. Fish and Wildlife Service, was eventually listed (CITES 1994).

Several states and the Province of Ontario have laws and regulations that apply to Eastern Box Turtles (New York Zoological Society 1991; Lee 2007), and 17 of the 29 states in which they occur, as well as the District of Columbia, list them as a Species of Greatest Conservation Need (Nanjappa and Conrad 2011), but there is no national consistency or coordination. Species that cannot be sold in one state may nonetheless be collected and sold in another (Stevens 1994). Throughout the species' range, various state agencies are beginning to look more closely at this species, its status, and ways to improve its conservation outlook (Todd 2000; Smith 2004; MNHESP 2011).

The U.S. Fish and Wildlife Service, International Wildlife Trade Program, hosted a meeting entitled Conservation and Trade Management of Freshwater and Terrestrial Turtles in the United States in September 2010 in St. Louis to discuss species of concern in the U.S., such as the Eastern Box Turtle. In addition, the North American Box Turtle Conservation Committee (www.boxturtleconservation.org) has hosted workshops to discuss Box Turtle conservation issues since 2004. *Terrapene carolina* is also a focal species of the USA Turtle Mapping Project sponsored by the Partners in Amphibians and Reptile Conservation (http://www.parcplace.org/news-a-events/year-of-the-turtle.html?id=203).

Eastern Box Turtles occur in many protected areas throughout the United States and in Mexico, and any area of sufficient size within the range of this species that is maintained in a natural state could theoretically function as a reserve for Eastern Box Turtles, though the caveats provided above should be noted. We do not know what the minimum size that an Eastern Box Turtle reserve should be, though the declines observed at long-term study populations and the results from genetic work (Kimble 2012) suggest that reserve areas should be larger than the scale at which we typically envision a population functioning. Seibert and Belzer (2013) suggested that a preserve area of at least 800 ha would be needed to contain the movements of their translocated population in Pennsylvania, but they noted that it would need to be much larger to contain movements of transients observed in other studies. Protected areas able to sustain a population should be large enough so that natural disturbance regimes and metapopulation dynamics can continue to persist, increased mortality rates from road mortality, collection, and subsidized depredation is minimal, and heavy-handed management is not necessary. No census of suitable protected areas exists at present, although the protected areas database assembled by the USGS GAP Analysis Program (USGS GAP 2012) could provide a starting point for such a census (Kiester and Olson 2011). Estimating the number and location of effective reserves that exist for this species and monitoring their populations should be a priority action.

Conservation Measures Proposed. — Seigel and Close (1991) and Dodd and Franz (1993) have emphasized the need for more status information on common species of turtles. Dodd and Franz (1993) studied the status of information about *T. c. bauri* in Florida and found that most locality records were greater than two decades old. Because Florida has undergone large-scale change as a result of anthropogenic effects, they argue that we have little current information about the status of this widespread species. They point out that a "dilemma of common species" is that they are not the subject of regulations to the degree of threatened or endangered species, so there is less motivation to keep track of them. Yet, by not addressing conservation concerns with apparently common species, we run the risk of having a new threatened species created. For example, there is now evidence that several formerly common species of anurans have become rare in the last two decades (Blaustein and Wake 1990; Blaustein 1994; Blaustein et al. 1994).

Given its widespread range, the number of studies undertaken for this species, and its conservation concern, it would be well-suited to the type of coordinated, standardized monitoring strategy and conservation planning efforts already undertaken for other widespread species of concern, such as the Desert Tortoise, *Gopherus agassizii* (USFWS 2011, 2012), the Gopher Tortoise, *G. polyphemus* (FFWCC 2007), the Bog Turtle, *Glyptemys muhlenbergii* (USFWS 2006), the Wood Turtle, *G. insculpta* (Jones and Willey 2014), and the Blanding's Turtle, *Emydoidea blandingii* (NHFG 2011). Such efforts promote standardized monitoring, centralized reporting, and coordinated efforts to assess species status and prioritize conservation actions.

Captive Husbandry. — With the long-term popularity of Box Turtles as pets, much work has been devoted to their husbandry and to the treatment of diseases associated with captivity (e.g., Rosskopf and Woerpel 1983; Boyer 1992a,b). In general, their husbandry is similar to that of most reptiles (Frye 1991). Although captive breeding efforts do not seem to be prevalent among those who keep Box Turtles, it does occur, and there is no reason to think that it could not become common if people were interested. Should this happen, the opportunity would arise to investigate the genetics of color patterns which is of some real evolutionary interest (Milstead 1969).

Current Research. — Eastern Box Turtles continue to be popular subjects for a wide variety of research. Here we suggest six priority research programs that are needed to improve our knowledge of the conservation biology of this species.

1. Establish baseline information on Mexican populations. This is clearly the first priority for these two subspecies. Distribution, ecology, and population status information should be collected, as well as additional molecular work to evaluate the degree of distinctiveness of these taxa.

2. Implement CITES monitoring. This information is critical to estimating viability of populations. Mexican subspecies are openly traded in Asia; this should be examined.

3. Continue long-term monitoring of known populations. Long-term studies are obviously invaluable for this and all turtle species. At least five populations have been followed for several decades (see Population Status), and monitoring should continue on these wherever possible. Newer studies (e.g., Table 1) should be continued as well. Within the U.S., these studies have focused on every subspecies but *T. c. major*, which appears never to have been the subject of a population study. Given that *T. c. major* has the smallest range of any of the U.S. subspecies, this deficiency should be corrected as soon as possible. As suggested above, *T. carolina* would be well suited for a standardized monitoring program with centralized reporting and a coordinated conservation planning process.

4. Estimate the size, number, and status of all protected populations. The protected areas database (USGS GAP 2012) in conjunction with the research and coordinated monitoring suggested above should provide data necessary for a complete national estimate and an ability to make recommendations for their long-term conservation.

5. Understand thresholds in metapopulation dynamics. As road traffic increases there may be a point at which the metapopulation dynamics no longer function. That is, there may be a tipping point above which a small increase in traffic causes a big effect on the metapopulation. This possibility needs to be investigated both theoretically and empirically for Eastern Box Turtles.

6. Understand the role of succession and intermediate disturbance. The possibility exists that in protected areas, which are otherwise good Eastern Box Turtle reserves, succession may limit the numbers that can occur in a small area. This question needs to be addressed as one of the major aspects of Eastern Box Turtle reserve design.

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