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Kinosternon subrubrum (Bonnaterre 1789) – Eastern Mud Turtle

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Summary. — The Eastern Mud Turtle, *Kinosternon subrubrum* (Family Kinosternidae), is a small (carapace length 85 to 120 mm) polytypic species of the eastern and central United States. All three historically recognized subspecies (*K. s. subrubrum, K. s. steindachneri*, and *K. s. hippocrepis*) are semi-aquatic turtles that inhabit much of the U.S. Atlantic and Gulf Coastal Plains. The Florida taxon (*K. s. steindachneri*) appears to represent a distinct species, but we continue to treat it as a subspecies for the purposes of this account. Nesting seasons are shorter and clutch sizes (range: 1–8, modal: 2–3 eggs) larger in northern populations of the species, with up to four clutches annually in the South. Populations vary greatly in size and may comprise only a small segment or major portion of an aquatic turtle assemblage. Population declines are well documented in the Northeast and Midwest (*K. s. subrubrum*). Major threats to this species come from the disruption or destruction of freshwater and surrounding terrestrial habitats as well as road mortality, but it is not considered globally threatened at this time.

Distribution. — USA. Distributed in the eastern coastal plain from New York in the northeast throughout the Gulf Coast Plain to Texas in the southwest, north in the Mississippi Valley to Illinois and Indiana, and south through peninsular Florida.

Synonymy. — *Testudo subrubra* Lacepède 1788 (*nomen suppressum*), *Testudo subrubra* Bonnaterre 1789, *Kinosternon subrubrum, Kinosternon subrubrum subrubrum*, *Testudo pensilvanica* Gmelin 1789, *Emydes pensilvanica, Kinosternon pensilvanicum, Cinosternum pensilvanicum*, *Emys pensylvanica* Schweigger 1812 (*nomen novum*), *Terrapene pensylvanica, Cistuda pensylvanica, Sternotherus pensylvanica, Kinosternum pensylvanicum, Cinosternon pensylvanicum, Clemmys (Cinosternon) pensylvanica, Kinosternon pensylvanicum, Cinosternum pensylvanicum*, *Kinosternon pennsylvanicum* Bell 1825 (*nomen novum*), *Emys (Kinosternon) pennsylvanica, Kinosternum pennsylvanicum, Cinosternon pennsylvanicum, Cinosternum pennsylvanicum, Cistudo pennsylvanica, Terrapene pennsylvanica, Thyrosternum pennsylvanicum*, *Kinosternon (Kinosternon) doubledayii* Gray 1844, *Kinosternon doubledayii, Kinosternum doubledayii, Cinosternum doubledayii, Cinosternon doubledayii*, *Kinosternon (Kinosternon) oblongum* Gray 1844, *Kinosternon oblongum, Cinosternum oblongum*, *Kinosternon punctatum* Gray 1856, *Cinosternum punctatum*, *Swanka fasciata* Gray 1869.

Subspecies. — Three have until recently been recognized: 1) *Kinosternon subrubrum subrubrum* (Eastern Mud Turtle) (distribution: eastern coastal plains from New York to northern Florida, west to the Mississippi River and north to Illinois and Indiana); 2) *K. s. hippocrepis* (Mississippi Mud Turtle) (distribution: generally west of the Mississippi River from eastern Texas to southern Illinois) (synonymy: *Kinosternon hippocrepis* Gray 1856, *Cinosternum hippocrepis, Cinosternon hippocrepis, Kinosternon subrubrum hippocrepis, Kinosternon louisianae* Baur 1893, *Cinosternum louisianae*); and 3) *K. s. steindachneri* (Florida Mud Turtle) (distribution: peninsular Florida) (synonymy: *Cinosternum steindachneri* Siebenrock 1906, *Kinosternon steindachneri, Kinosternon subrubrum steindachneri*).

Status. — IUCN 2017 Red List: Least Concern (LC, assessed 2011); CITES: Not Listed; ESA: Not Listed; FNAI: G5 (Demonstrably Secure).

Taxonomy. — *Kinosternon subrubrum* was first described as *Testudo subrubra* by Lacepède (1788), but that publication and name was suppressed by ICZN (2005), shifting the valid authorship of the same name to Bonnaterre (1789). Several other nominal taxa (and named *nomen novum* variants thereof) have been described that have been

Figure 1. *Kinosternon subrubrum subrubrum*, Apalachicola National Forest, Florida, USA. Photo by R.D. Bartlett.

synonymized with *K. subrubrum*: *Testudo pensilvanica* Gmelin (1789), *Kinosternon doubledayii* Gray (1844), *Kinosternon oblongum* Gray (1844), *Kinosternon punctatum* Gray (1856), and *Swanka fasciata* Gray (1869) (Iverson 1977a, TTWG 2014). Three subspecies of *K. subrubrum* have been recognized for a long time: *K. s. subrubrum*, *K. s. steindachneri* (Siebenrock 1906), and *K. s. hippocrepis* (Gray 1856).

Analysis of mitochondrial DNA of *K. subrubrum* has provided general conformity to the geographic distributions of the three subspecies (Walker et al. 1998), but further mtDNA analysis of the species by Iverson et al. (2013) indicated that *K. s. steindachneri* was more closely related to *K. baurii* than to *K. subrubrum*, suggesting that *steindachneri* deserves species status. However, Spinks et al. (2014) recommended retention of *steindachneri* as a subspecies of *subrubrum*.

Kinosternon s. steindachneri is different from both of the other subspecies in having a relatively reduced plastron and bridge (Meshaka and Gibbons 2006). Extensive morphological analysis of fossils and extant species by Bourque and Schubert (2015) and Bourque (2016) has led to the recommendation that *K. s. steindachneri* be considered a distinct species. This recommendation has been followed by Powell et al. (2016), and in their most recent checklist, TTWG (2017) also agreed, and listed *K. steindachneri* as a distinct species. However, we continue to treat *steindachneri* as a subspecies for the purposes of this account, pending further analysis and, hopefully, resolution of the issue.

. **Description**. — *Kinosternon subrubrum* is a small, smooth-domed turtle. Adults of both sexes reach maturity at around 70–80 mm in carapace length (CL). Mean CL of adults is approximately 85 mm, with the largest individuals normally attaining lengths less than 120 mm, with no sexual size dimorphism (Gibbons and Lovich 1990). The color of the carapace of adults ranges from dark brown to black but is occasionally olive, and without lighter-colored carapacial stripes. *Kinosternon subrubrum* can be difficult to distinguish from the Striped Mud Turtle (*K. baurii*) in the panhandle of Florida, Georgia, the Carolinas, and Virginia because of the frequent absence of carapacial stripes in *K. baurii* in these areas (Duever 1972; Lamb 1983; Lamb and Lovich 1990; Ewert et al. 2004). However, *K. baurii* generally retains

Figure 2. *Kinosternon subrubrum subrubrum*, Apalachicola National Forest, Florida, USA. Photo by R.D. Bartlett.

Figure 3. *Kinosternon subrubrum steindachneri*, Monroe County, Florida, USA. Note the reduced plastron. Photo by J.B. Iverson.

distinct head stripes throughout its range, in contrast to *K. s. subrubrum* that lacks them. The carapace of hatchlings (21–26 mm CL) is black.

The carapace of *K. subrubrum* is oval in dorsal view, smooth, and rounded on the sides. It has 11 marginal scutes on each side, and the 10th marginal extends further dorsally than the others. The first vertebral scute is longer than wide and does not contact the 2nd marginal scute. The other vertebrals (2–5) are usually wider than long.

The plastron of adults is dark brown or a drab yellow. Because the plastron of subadult and adult *K. subrubrum* has a double hinge, complete closure of the shell is possible in some individuals. The anterior hinge is between the epiplastra and hyoplastra (the entoplastron is absent), and the posterior hinge is between the hypoplastra and xiphiplastra. The plastral formula is anal > abdominal > humeral > femoral >< gular > pectoral (Ernst and Barbour 1989); however, this formula is highly variable in species to which it has been applied (Lovich and Ernst 1989; Lovich et al. 1991; Ernst et al. 1997b).

The feet are webbed and the limbs are dark with no markings. The head is dark brown to black, but subspecific variation occurs in head markings. The Eastern Mud Turtle (*K. s. subrubrum*) and the Florida Mud Turtle (*K. s. steindachneri*) have plain heads or dull yellow mottling, whereas the Mississippi Mud Turtle (*K. s. hippocrepis*) has two yellow stripes on each side of the head. Differing from adults, hatchlings may have bright yellow, orange, or red plastrons with some dark markings. In this regard, the red color of the plastron among some juveniles gave rise to the specific name of *subrubrum*. Two faint light stripes are on the head and neck of *K. s. hippocrepis*, and a broad light postorbital stripe may be found on hatchlings of *K. s. steindachneri* (Ernst and Lovich 2009).

The upper jaw is mildly hooked with a slightly protruding snout. Sexual dimorphism is apparent in the head, tail, and hind limbs. Males have a larger head size, a keratinized claw-like tip at the end of the tail, and a longer tail length

Figure 6. *Kinosternon subrubrum subrubrum*, Apalachicola National Forest, Florida, USA. Photo by R.D. Bartlett.

Figure 4. *Kinosternon subrubrum hippocrepis*, Mississippi or Louisiana, USA. Photo by R.D. Bartlett.

Figure 7. *Kinosternon subrubrum hippocrepis*, Mississippi or Louisiana, USA. Photo by R.D. Bartlett.

Figure 5. *Kinosternon subrubrum steindachneri*, Monroe County, Florida, USA. Photo by J.B. Iverson.

Figure 8. *Kinosternon subrubrum steindachneri*, Levy County, Florida, USA. Photo by J.B. Iverson.

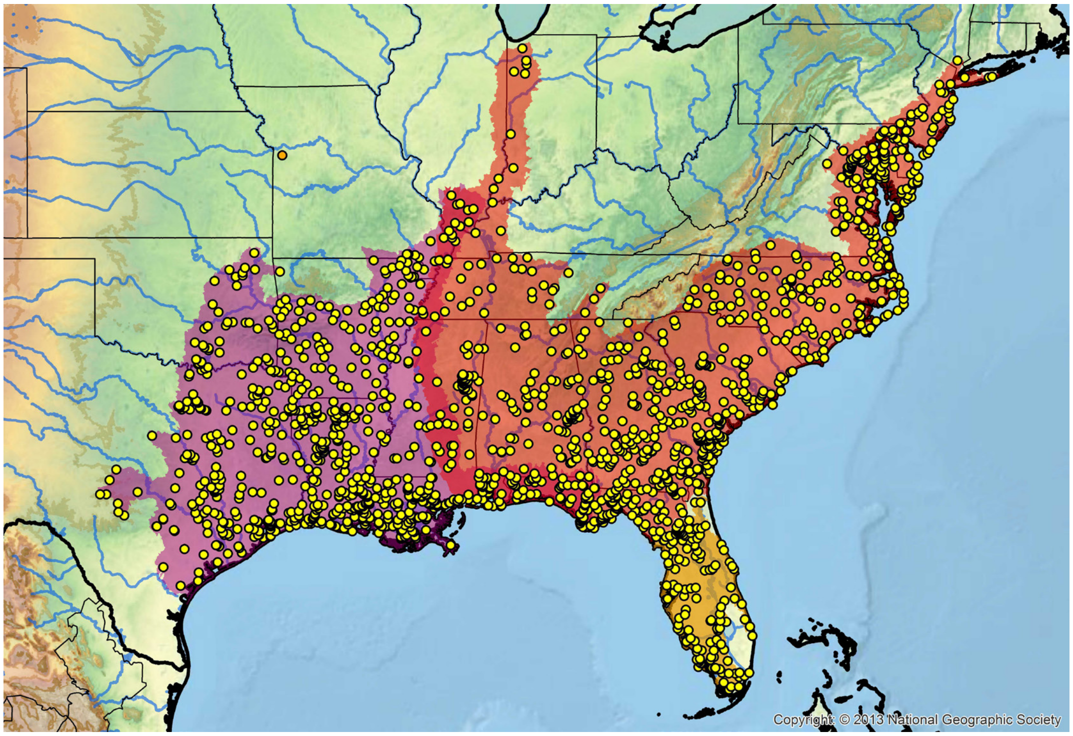

Figure 9. Historic distribution of *Kinosternon subrubrum* in eastern USA. Yellow dots = museum and literature occurrence records of native populations based on Iverson (1992), plus more recent and authors' data; orange dot = possibly introduced population; red shading = projected historic distribution of *K. s. subrubrum*; purple shading = *K. s. hippocrepis*; orange shading = *K. s. steindachneri*; overlap = intergrades. Distribution based on GIS-defined level 10 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 (Buhlmann et al. 2009; TTWG 2014), and adjusted based on authors' subsequent data.

than females. Two patches of enlarged scales are also present on the inner side of each hind limb of males, but absent in females.

Distribution. — *Kinosternon subrubrum* is a North American species of generally southern latitudes in the United States. Its geographic distribution is within the eastern and central United States (Powell et al. 2016) and the northern distributional limit overlaps the southern terminus of the Wisconsin glaciation (Craig et al. 1980). The species ranges southerly from southeastern New York (Craig et al. 1980; Iverson 1986; Klemens 1990, 1993) across the Atlantic Coastal states and Piedmont through peninsular Florida (Ernst and Lovich 2009). Its geographic range extends westward along the Gulf Coastal Plain to eastern Texas and Oklahoma, with a northward extension in the range following the Mississippi and Ohio River valleys to southwestern Indiana, southern Illinois, and southeastern Missouri (Ernst and Lovich 2009). Possibly disjunct records occur from northwestern Indiana (Grant 1935; Stille 1947; Minton 1972) and northwestern Missouri (Anderson 1965), although the latter was interpreted as an introduction (Johnson 1987).

Figure 10. *Kinosternon subrubrum subrubrum*, small juvenile in the wild, Wallops Island, Virginia, USA. Photo by P.R. Delis.

The nominate subspecies, *K. s. subrubrum*, occurs throughout the northeastern and southeastern coastal plain, south into northern Florida, west towards the Mississippi River, and north into the Midwest into Illinois and Indiana (Ernst and Lovich 2009).

Kinosternon s. hippocrepis is the westernmost form that occurs along the Mississippi Valley north to southeastern Missouri, western Kentucky, and southern Illinois, and westward to central Oklahoma and eastern Texas (Ernst and Lovich 2009). A broad zone of intergradation exists along its east extension where it contacts *K. s. subrubrum* from southern Illinois south to the coasts of Mississippi and Alabama (Powell et al. 2016), and along the Florida panhandle (Carr 1940; Powell et al. 2016).

The geographic range of the Florida endemic, *K. s. steindachneri*, includes only peninsular Florida south of the

Suwannee River drainage and Jacksonville to the southern tip of the state, but not the Florida Keys (Meshaka and Gibbons 2006). In northern Florida, *K. s. steindachneri* intergrades narrowly with *K. s. subrubrum* (Powell et al. 2016).

Habitat and Ecology. — *Kinosternon subrubrum* is a semi-aquatic turtle whose terrestrial habits vary in degree among the subspecies. Aquatic habitats of the species tend to be shallow and slow moving or lentic freshwater systems, but it also has been reported to inhabit brackish marshes (Ernst and Lovich 2009) and is a successful colonizer of barrier islands (Gibbons and Coker 1978). This turtle appears to avoid major rivers, streams, and spring runs (Gibbons 1983; Huestis and Meylan 2004). In Virginia, the aforementioned lentic habitats are occupied, and especially those with aquatic or emergent macrophytes and a soft substrate (Mitchell 1994). *Kinosternon s. subrubrum* was reported from coastal plain freshwater marshes in Maryland subject to tide cycles (Cordero and Swarth 2010). In North Carolina, the species has also been found in association with sandy-bottomed creeks, streams, farm ponds, vernal woodland pools, meadows and pastures, swamps, canals, and drainage ditches (Palmer and Braswell 1995). Ditches in managed forests in eastern North Carolina proved to be acceptable habitat for *K. subrubrum*, and their occupancy was unaffected by neither time since maintenance, which ranged 3–17 yrs, nor by landscape metrics of nearby forest and wetlands (Homyack et al. 2016). In some cases, golf course ponds could be more suitable for this species than farm ponds (Failey et al. 2007). In turn, farm ponds with high nitrite/nitrate concentrations in association with cattle were inhabited by individuals that were significantly smaller and produced narrower eggs than those that did not have cattle grazing (Lindsay and Dorcas 2001). In South Carolina, individuals were found in association with older beaver ponds (Russell et al. 1999). In Alabama, *K. subrubrum* was least likely to be found in free-flowing creeks and rivers (Mount 1965), and in Alabama farm ponds this species did not venture more than 5 m from shore and no deeper than 1 m (Scott 1976). An affinity for shallow, heavily-vegetated habitat, *K. subrubrum* in two southeastern Oklahoma rivers (Riedle et al. 2009) and an East Texas wetland (Riedle et al. 2015) were seldom captured with two *Sternotherus* species, which were associated with greater water depth and flow. In a lake in Louisiana, *K. subrubrum* was captured in abundance in the vicinity of *Lotus* beds at water depths ranging 0.9–1.2 m (Cagle and Chaney 1950). Individuals were also seen foraging in many shallow rivulets and streams in water that did not cover their carapaces (Cagle and Chaney 1950).

In Florida, *K. s. subrubrum* and *K. s. steindachneri* occur in small streams, drainage ditches, and ponds (Carr 1940); however, the Florida form also inhabits sloughs and marshes (Carr 1940) and canals (Duellman and Schwartz 1958). This subspecies can occupy aquatic habitats that fluctuate widely in pH on a daily basis (Ernst et al. 1972). In a central Florida lake, *K. s. steindachneri* was most commonly found in vegetated littoral zones with thin-stalked emergent vegetation (Bancroft et al. 1983). More than 95% of all individuals in the lake were found in water that was < 1.6 m in depth with a sandy substrate and thick vegetative cover, especially *Potamogeton illinoensis* (Bancroft et al. 1983). In west-central Florida, *K. s. steindachneri* was the only kinosternid turtle found in a shallow basin marsh-sandy upland association (Enge and Wood 2001), whereas

Figure 11. Habitat of *Kinosternon subrubrum*. *Top*: Wallops Island, Virginia. Photo by P.R. Delis. *Middle and Bottom*: Apalachicola National Forest, Florida, USA. Photos by R.D. Bartlett.

in the marsh and prairie of the Everglades, it was replaced in abundance by *K. baurii* (Duellman and Schwartz 1958; Meshaka et al. 2000).

The activity season of *K. subrubrum* varies geographically. Seasonal activity is shortest in northern populations and longest in the South (Ernst and Lovich 2009): April–November in New York (Nichols 1947), January–November in North Carolina (Palmer and Braswell 1994), April–October in Oklahoma (Mahmoud 1969), and year-round in Alabama (Mount 1975) and Florida (Bancroft et al. 1983; Ernst and Lovich 2009). Seasonal activity of *K. s. steindachneri* in central Florida peaked in early summer and fall (Bancroft et al. 1983). Iverson (1979), having reported that only 2 of 62 *K. subrubrum* that he examined from north and central Florida were collected during 15 June–15 August, suggested the occurrence of a break in summer activity in that region.

Kinosternon subrubrum is active at night and during the day. In northern Virginia, most captures of *K. s. subrubrum* occurred during 0700–0830 hrs (Ernst et al. 1997a). In Alabama, *K. subrubrum* is active more often at night than during the day (Mount 1975), and in central Florida, *K. s. steindachneri* was captured by day and night with no apparent seasonal component to its diel activity pattern (Bancroft et al. 1983). In the summer, activity peaks during 0500–0800 hrs and 1900–2200 hrs for both *K. s. hippocrepis* in Oklahoma (Mahmoud 1969) and *K. s. steindachneri* in Florida (Ernst and Lovich 2009).

Aquatic movements are generally short, and home ranges are small in *K. subrubrum*. Average daily movements in New York were 5.6 m for males and 4.2 m for females during the aquatic activity season, and 5.3 and 4.0 m, respectively, during terrestrial searching for hibernation sites (Larese-Casanova 1999). First-last capture distances in less than 100 days averaged < 50 m for *K. s. hippocrepis* in Oklahoma (Mahmoud 1969). In central Florida, the average distance moved by *K. s. steindachneri* between captures was 32.8 m (Bancroft et al. 1983). In Oklahoma, the average home range of *K. s. hippocrepis* was 0.05 ha (Mahmoud 1969). Contrary to these patterns, aquatic movement data yielded maximum distance movements > 1000 m and mean home range sizes of 18.6 and 16.3 ha for two different years in a Maryland population of *K. s. subrubrum* (Cordero et al. 2012a). *Kinosternon subrubrum* can be highly terrestrial in its habits.

Terrestrial movements can be initiated by nesting (Burke et al. 1994) or drought (Gibbons 1983; Ernst and Lovich 2009). In South Carolina, individuals temporarily left a drying environment, burrowed solitarily up to 600 m away, and returned later; this was interpreted to be an adaptation to a fluctuating environment, whereby selection works against aggregation in the drying pond where a population could be devastated by a predator (Bennett et al. 1977). In other drought conditions, the number of emigrating individuals was within the mean reported for non-drought years (Gibbons et al. 1983). Terrestrially moving turtles can be at risk from fire; however, *K. subrubrum* will burrow into the substrate to avoid fire (Folk and Bales 1982).

Although some individuals will overwinter in underwater retreats, others will make overland movements to hibernate away from water (Larese-Casanova 1999; Buhlmann and Gibbons 2001; Harden and Dorcas 2008; Cordero et al. 2012b), and the overwintering sites can be far from aquatic habitat. For example, in Maryland, turtles overwintered 55–224 m from the edge of the wetland (Cordero et al. 2012b), and in South Carolina distances traveled ranged to 600 m (Bennett et al. 1970). In southwestern Georgia turtles overwintered at an average of 72 m from a wetland for an average of 107 days (Steen et al. 2007).

Winter burrow depth varies geographically. In Illinois, turtles burrowed 20–40 cm or more deep (Skorepa and Ozment 1968); in New York, depths averaged 25 cm (Larese-Casanova 1999). Burrow depths in Maryland ranging 7.0–25 cm (mean burrow depths for two years = 12.1 and 13.2 cm) were presumed to be in response to freezing temperatures (Cordero et al. 2012b). In Oklahoma, burrow depths were 10–15 cm (Mahmoud 1969). In South Carolina, individuals burrowed 2–11 cm below the surface, and movement from burrows did not commence until maximum air temperature exceeded 21 °C (Bennett 1972).

The length of hibernation is positively correlated with latitude. Hibernation lasted an average of 211 and 220 days over two winters in southeastern New York (Larese-Casanova 1999), although Nichols (1947) reported a hibernation period of 151 days on Long Island. Gibbons (1970) and Bennett (1972) reported a hibernation period of about 120 days in South Carolina, Mahmoud (1969) recorded 100 days in Oklahoma, and Scott (1976) observed 70 and 86 days in Alabama.

In southwestern Georgia, turtles preferred extensive leaf and pine litter and lesser canopy cover for overwintering sites than for other temporary refuges or random sites (Steen et al. 2007). Habitat quality was found, in turn, to depend on timing of prescribed fires that would best suppress oaks if conducted in the spring and summer (Steen et al. 2007). In a disturbed site in North Carolina, individuals likewise preferred physical components of leaf and pine litter, herbaceous vegetation, fallen woody debris and canopy cover associated with overwintering sites (Harden et al. 2009). Consequently, adults inhabiting an artificial pond avoided human-altered terrestrial habitat on their way to overwintering sites (Harden et al. 2009).

Nesting activity was associated with rain in South Carolina (Burke et al. 1994) as were terrestrial movements in Virginia (Mitchell 1994). In North Carolina, most terrestrial activity occurred during morning and late afternoon (Palmer and Braswell 1995). Overland distances could be long: up to 600 m by *K. s. subrubrum* in South Carolina, which were traversed a few meters at a time (Bennett et al. 1970). The number of days it takes to complete overland movements can likewise be long in duration, up to 142 days (Bennett et al. 1970) and 170 days (Buhlmann and Gibbons 2001) in South Carolina. Individuals remain under cover when they rest between movements (Richmond 1945; Skorepa and Ozment 1968; Gibbons 1970; Mount 1975). Dietz and Jackson (1979) and Elsey et al. (2013) documented their use of alligator nests for nest sites.

Although not exclusively aquatic, *K. s. steindachneri* is the least terrestrial of the three subspecies. In southern Florida, individuals have been collected on roads (Duellman and Schwartz 1958), even if rarely (Meshaka, Gibbons, pers. obs.); however, it is very aquatic in its habits (Carr 1940), having never been seen on land during a three-year study in central Florida (Bancroft et al. 1983). In this connection, the reduced plastron and reduced bridge, which are the primary differences between *K. s. steindachneri* and the other Florida subspecies, are suggestive of a more aquatic existence.

Growth rates and sexual maturity vary among populations of *K. subrubrum*. Both sexes of *K. s. subrubrum* mature in 4–6 yrs in South Carolina (Gibbons 1983) and 9 years in New York (Larese-Casanova 1999), whereas female *K. s. hippocrepis* in Arkansas are mature at 6–8 yrs (Iverson 1979). Sexual maturity in mixed subspecies from Florida was reached earlier in males (4–5 yrs) than in females (6–8 yrs) (Ernst et al. 1973). Sexual maturity is reached at 70–80 mm CL by both sexes of *K. s. subrubrum* in South Carolina (Gibbons 1983). Maturity in Arkansas females is at 80-85 mm CL (Iverson 1979). Ernst et al. (1973) reported maturity in Florida in males at 53–60 mm PL and in females at 66–75 mm PL (estimated CL from Iverson 1991, 67–76 mm and 76–87 mm, respectively)..

Body size dimorphism varies among the subspecies of *K. subrubrum*. Little body size dimorphism is apparent in *K. s. subrubrum* (Lovich and Lamb 1995). Carapace lengths of this subspecies are similar between the sexes in Virginia (Mitchell 1994), North Carolina (Palmer and Braswell 1995), and South Carolina (Gibbons and Lovich 1990); however, plastron lengths are smaller in males (Gibbons and Lovich 1990). Body size dimorphism is female-dominated in *K. s. hippocrepis* and is male-dominated in *K. s. steindachneri* (Lovich and Lamb 1995). In a central Florida population of *K. s. steindachneri,* mean adult body size of males (101.2 mm CL; n = 53) was significantly different than that of females (93.8 mm CL; n = 29; Bancroft et al. 1983). Among individuals examined from throughout Florida, the largest male (114.3 mm CL) was larger than the largest female (106 mm CL) (Iverson 1979), and the largest males averaged larger than the largest females in peninsular Florida (Ernst et al. 1973). The variability in body size dimorphism was considered to be a biologically meaningful difference among these three subspecies (Meshaka and Gibbons 2006).

The gonadal cycles of *K. subrubrum* are known only from a few areas. The testis of *K. s. hippocrepis* in the central United States is at its maximum size June–August and is smallest in size during September–December (Mahmoud and Klicka 1972). In Arkansas, follicular growth begins in late summer or early fall and increases rapidly the following spring (Iverson 1979).

Copulation has been described for *K. s. hippocrepis*. Mahmoud (1967) noted an initial approach by the male to the tail of the female, which was then followed by his movement alongside her. There, the male nudges the bridge area of her plastron, presumably to make contact with the musk glands. If the female continues to be receptive, the male then mounts from behind and above, and while *in copula*, bites her head and carapace.

Kinosternon subrubrum mates in the spring and early summer. Mating takes place during March–May, with southern populations breeding earliest (Ernst and Lovich 2009). Nesting seasons vary geographically and are shorter in northern populations (Iverson 1979): March–September in Virginia (Richmond 1945), March–June in Virginia (Mitchell 1994; Ernst et al. 2001), April–July in Arkansas (Iverson 1979), January–July in Louisiana (Dundee and Rossman 1989), and October–June in north Florida (Iverson 1977b). The frequency of nesting is highest in the summer throughout most of its geographic range (Gibbons 1983).

The eggs of *K. s. subrubrum* are brittle-shelled, with a granular appearance (Congdon and Gibbons 1985). Eggs average about 25–27 mm in length, 15–17 mm in width, and about 4 g (Carr 1940, Iverson 1979, Congdon and Gibbons 1985, Dundee and Rossman 1989, Mitchell 1994, Palmer and Braswell 1995, and Wilkinson and Gibbons 2005). There may be a weak pattern of smaller eggs at higher latitudes (Iverson 1979).

Clutch characteristics of *K. subrubrum* are variable. Clutch size in this species varies geographically, seasonally, and as a function of female size (Iverson 1979; Gibbons 1983). Throughout the geographic range of the species, clutch size varies from 1–8 eggs (Gibbons 1983) with larger clutches being more common in northern populations. Modal clutch size is 2–3 eggs (Gibbons 1983). Across its geographic range, *K. subrubrum* can lay up to four clutches annually (Iverson 1979; Gibbons 1983). In South Carolina, clutch frequency was shown to vary among individuals and among years (Frazer et al. 1991). In response to drought, the percentage of females that produced more than one clutch was lower than those of pre-drought conditions (Gibbons et al. 1983). Clutch characteristics among multiple clutches were shown to vary within annual reproductive cycles (Wilkinson and Gibbons 2005).

Table 1. Presence of *Kinosternon subrubrum* in major federally protected areas found within its natural distribution: National Parks (all), National Preserves (all), National Forests (> 30,000 ha), and National Wildlife Refuges (> 20,000 ha, except in smaller states such as Delaware). The distribution of *K. subrubrum* spans 21 states across the southeastern United States, including Alabama, Arkansas, Delaware, Florida, Georgia, Illinois, Indiana*, Kentucky**, Louisiana, Maryland, Mississippi, Missouri, New Jersey, New York*, North Carolina, Oklahoma, Pennsylvania*, South Carolina, Tennessee, Texas, and Virginia. Species presence or absence in a protected area was determined from federally protected area websites (US Forest Service, US Fish and Wildlife, National Park Service), primary literature sources, range map, published conservation plans, and various state field guides. * = State listed endangered species. ** = State listed species of greatest conservation need. X = presence confirmed from source(s); L = Presence determined to be highly likely based on source(s) and/or range map; P = Presence unknown, but determined to be probable based on source(s) and/or range map. ^ = Only National Recreation Area on this list. ^^ = Only National Wildlife Research Refuge on this list. ^^^ = Only National Reserve on this list.

Protected Area	Size (ha)	Presence	Source
Alabama			
Little River Canyon National Preserve	6,187	X	National Park Service
Talladega National Forest	158,866	X	US Forest Service
William B. Bankhead National Forest	73,300	X	US Forest Service
Conecuh National Forest	33,900	X	US Forest Service
Arkansas			
Hot Springs National Park	2,250	L	Robert and Irwin 2012; Trauth et al. 2004
Ouachita National Forest	722,100	X	Trauth et al. 2004
Ozark—St. Francis National Forest	469,400	X	Trauth et al. 2004
Dale Bumpers White River National Wildlife Refuge	64,335	X	US Fish and Wildlife
Cache River National Wildlife Refuge	26,776	L	Roberts and Irwin 2012; Trauth et al. 2004
Felsenthal National Wildlife Refuge	26,265	L	Roberts and Irwin 2012; Trauth et al. 2004
Delaware			
Bombay Hook National Wildlife Refuge	6,466	X	US Fish and Wildlife
Prime Hook National Wildlife Refuge	4,000	X	Coppola 2013
Florida			
Everglades National Park	610,484	X	Duellman and Schwartz 1958; Meshaka et al. 2000; Meshaka and Gibbons 2006; Meshaka and Layne 2015; Rice et al. 2004
Biscayne National Park	69,999	P	National Park Service (undetected, but *K. bauri* confirmed); Krysko et al. 2010 (unidentified *Kinosternon* spp.); Rice et al. 2007 (undetected)
Big Cypress National Preserve	291,603	X	National Park Service; Rice et al. 2005 (undetected)
Apalachicola National Forest	233,100	X	Krysko et al. 2011; Means 1976a
Ocala National Forest	174,196	X	Krysko et al. 2011; Means 1976b
Osceola National Forest	77,267	X	Krysko et al. 2011; Means 1976c
Key West National Wildlife Refuge	84,299	P	Morkill 2009 (undetected, but *K. bauri* confirmed)
Arthur R. Marshall Loxahatchee National Wildlife Refuge	58,256	X	Musaus 2000
Merritt Island National Wildlife Refuge	56,328	P	US Fish and Wildlife (undetected, but *K. bauri* confirmed)
Great White Heron National Wildlife Refuge	47,640	P	Morkill 2009 (undetected, but *K. bauri* confirmed)
National Key Deer Refuge	34,327	P	Morkill 2009 (undetected, but *K. bauri* confirmed)
Saint Marks National Wildlife Refuge	28,003	X	US Fish and Wildlife
Lower Suwannee National Wildlife Refuge	20,651	X	Gunzburger et al. 2005
Georgia			
Chattahoochee-Oconee National Forest	350,600	X	Jensen et al. 2008
Okefenokee National Wildlife Refuge	162,647	X	Constantino 2006
Illinois			
Shawnee National Forest	107,400	X	Smith 1961
Kentucky**			
Mammoth Cave National Park	21,380	X	Hibbard 1936
Land Between the Lakes National Recreation Area^	68,800	X	Kentucky's Comprehensive Wildlife Conservation Strategy 2013
Louisiana			
Kisatchie National Forest	244,000	L	Range map
Sabine National Wildlife Refuge	50,905	X	Valentine et al. 1972
Tensas River National Wildlife Refuge	29,611	X	Purkey 2009
Maryland			
Chesapeake Marshlands National Wildlife Refuge Complex	13,767	L	Range map
Patuxent National Wildlife Research Refuge^^	5,200	X	Knudsen 2013
Mississippi			
De Soto National Forest	209,900	X	Smith and List 1955
Homochitto National Forest	77,600	L	Range map
Bienville National Forest	72,200	L	Range map
Holly Springs National Forest	62,900	L	Range map
New Jersey			
Edwin B. Forsythe National Wildlife Refuge	16,200	P	Range map; Atzert 2004 (undetected)
New Jersey Pinelands National Reserve^^^	471,064	X	National Park Service; Pinelands Preservation Alliance
New York*			
Long Island National Wildlife Refuge Complex	2,606	X	Long 2006; Mann-Klager and Parris 1993
North Carolina			
Nantahala National Forest	215,000	L	Range map
Pisgah National Forest	207,500	X	Weeks 2008

Croatan National Forest	64,700	X	Graeter 2008
Alligator River National Wildlife Refuge	61,924	X	Gaul and Mitchell 2007
Pocosin Lakes National Wildlife Refuge	44,559	X	Phillips 2007
Mattamuskeet National Wildlife Refuge	20,305	X	Freske 2008
Pennsylvania*			
John Heinz National Wildlife Refuge at Tinicum	405	X	US Fish and Wildlife
South Carolina			
Congaree National Park	10,743	X	Congaree National Park
Sumter National Forest	150,000	L	Range map
Francis Marion National Forest	104,700	X	Beane et al. 2010; Francis Marion National Forest
Cape Romain National Wildlife Refuge	26,825	X	Nilius 2010
Tennessee			
Tennessee National Wildlife Refuge	20,784	X	Littrell 2010
Texas			
Aransas National Wildlife Refuge	46,412	X	Jones 2006
Big Thicket National Preserve	44,145	X	Parks et al. 1936, 1938
Sam Houston National Forest	65,900	X	Sam Houston National Forest
Sabine National Forest	65,100	L	Range map
Davy Crockett National Forest	65,000	L	Range map
Angelina National Forest	61,990	L	Range map
Virginia			
George Washington and Jefferson National Forests	724,764	L	Range map
Great Dismal Swamp National Wildlife Refuge	45,002	X	Bard 2006

The incubation period of *K. subrubrum* is variable, and hatching may be delayed depending on location. Incubation time lasts approximately 100 days and is thought to be negatively correlated with latitude (Iverson 1979; Gibbons 1983; Houseal and Carr 1983). The long incubation period in this species was thought to explain the high proportion of non-polar lipids in its eggs (Nagle et al. 1998). In South Carolina, *K. subrubrum* nests experienced a strong fluctuation in diel temperatures (Bodie et al. 1996). Their shallow (mean = 7.54 cm) nests placed in shaded areas provided protection from potential lethal temperatures > 40 °C (Bodie et al. 1996). On two occasions in extreme southern Louisiana, a single egg of *K. subrubrum* was found partially exposed under leaf litter (Anderson and Horne, 2009). Possible reasons for this phenomenon were reduced gas exchange in the clay soil substrate of the area, difficulty in digging in the compact clay soil, or anomalously by females that oviposited after earlier attempts at nest construction failed (Anderson and Horne 2009). Because the eggs were found on dikes were rarely subject to flooding, actively avoiding nest construction underground did not seem likely (Anderson and Horne 2009).

In South Carolina, hatchlings overwinter in the nest and emerge the following spring (Gibbons and Nelson 1978), but it is unknown, though suspected, that this phenomenon occurs in Florida. Hatching is generally thought to occur during August–September (Ernst et al. 1994); however, in Florida, where the nesting season is long, recently hatched individuals have been found during December–February (Iverson 1977). Hatchlings in Arkansas averaged 22.0 mm CL and 18.4 mm PL (Iverson 1979). In a mixed sample of *K. s. subrubrum* and *K. s. steindachneri* from Florida, female hatchlings averaged 18.2 mm PL, and male hatchlings averaged 17.6 mm PL (Ernst et al. 1973). A single hatchling *K. s. steindacheri* from Orlando, Florida, measured 22 mm CL and 18 mm PL (Lardie 1975).

Population Status. — Population sizes vary widely in this species depending on the habitat: 8.2 turtles/ha in a farm pond in South Carolina (Congdon et al. 1986), 22–56 turtles/ha in a Carolina Bay in South Carolina (Gibbons 1983), 64 and 104 turtles/ha in a creek in Oklahoma (Mahmoud 1969), 58–160 turtles/ha in Alabama farm ponds (Scott 1976), 470 turtles/ha in a fertilized farm pond in Alabama (Stone et al. 1993), and 33–92 turtles/ha in ponds in southeastern New York (Larese-Casanova 1999). Biomass of *K. subrubrum* was estimated to be 0.7 kg/ha in a pond and 3.7 kg/ha in a Carolina Bay in South Carolina (Congdon et al. 1986), 2.1–11.1 kg/ha in ponds in New York (Larese-Casanova 1999), and, as calculated by Iverson (1982) from Mahmoud's (1969) study, 25.9 kg/ha in a creek in Oklahoma. These findings corroborated the suggestion that trophic position has less of an effect on biomass of a species than the habitat quality and the body size and population structure of the species (Congdon et al. 1986). Ernst et al. (1994) suggested that permanent streams support more *K. subrubrum* than do temporary aquatic systems, but this has not been documented to be a rangewide phenomenon and does not appear to be true on the Savannah River Site in the Upper Coastal Plain of South Carolina (Gibbons, pers. obs.). Changes in population sizes and physical condition of *K. subrubrum* in two Alabama farm ponds were thought to have been related in part to both superior colonization ability in initially finding the ponds and subsequently to land use conditions associated with them (Stone et al. 1993).

Sex ratios of *K. subrubrum* tend towards unity in large samples, with adults often dominating captures in field studies. In South Carolina, the sex ratio of *K. s. subrubrum* was found to be 1:1 (Gibbons 1983; Tuberville et al. 1996), as it was in New York (Larese-Casanova 1999). In three Oklahoma populations of *K. s. hippocrepis*, females outnumbered males (1:1.5, 1:1.5, 1:1.8) (Mahmoud 1969);

however, the small sample sizes of the latter study led Ernst et al. (1994) to question the applicability of the estimated sex ratios to the whole population. The apparent scarcity of juveniles at many sites across the range of this species has raised the question of sampling bias as a possible reason for this observed phenomenon (Ernst et al. 1994).

Variability in reproductive output can affect the dynamics of *K. subrubrum* populations. In South Carolina, annual fecundity was subject to variation in the number of clutches produced and the number of females laying eggs each year but not clutch size (Gibbons 1983).

Kinosternon subrubrum can live for several decades, thereby contributing reproductively for potentially 25 yrs or more. Maximum longevity in the wild is thought to exceed 30 yrs (Gibbons 1983; Parker 1996), and in a life table constructed for *K. s. subrubrum* in South Carolina annual survival for both sexes approached 90%, with some turtles projected to live to nearly 40 yrs of age (Frazer et al. 1991). However, the captive longevity record is 18.3 yrs, based on a turtle acquired as an adult (Slavens and Slavens 2000).

Kinosternon subrubrum can range from uncommon to rare relative to other kinosternid turtles and aquatic turtles generally. In North Carolina, Failey et al. (2007) found that it comprised 10.4% and 3.5% of all turtles (six species) and 100% and 67% of all kinosternids in golf course ponds and farm ponds, respectively. It totaled 4.4% of all turtle captures (and 26.3% of all kinosternid captures) in Texas (Riedle et al. 2015). It totalled 10.9% of kinosternid turtles and 1.1% of all aquatic turtles traversing or attempting to traverse a road that bisected a lake in northwestern Florida (Aresco 2005) and 12.7% of the three kinosternid turtles and 8.0% of all turtles found as roadkills on a road bisecting a prairie in north-central Florida (Smith and Dodd 2003). In a central Florida lake, it was the fourth most abundant species but accounted for less than 2% of all captured turtles (Bancroft et al. 1983). As measured by collection records and natural history observation cards in Everglades Regional Collection Center of Everglades National Park, *K. s. steindachneri*, like the Common Musk Turtle (*Sternotherus odoratus*), is scarce compared to *K. baurii* in the southern Everglades.

Kinosternon subrubrum is an omnivore with primarily carnivorous tendencies, and its diet is similar in widely separated populations. Insects, crustaceans, and mollusks dominated the diet of this species in Oklahoma (Mahmoud 1968), North Carolina (Brown 1992), New York (Larese-Casanova 1999) and central Florida (Bancroft et al. 1983). Crayfish and seeds have been found in stomachs of Virginia *K. s. subrubrum* (Mitchell 1994) and in *K. subrubrum* from Alabama (Graham and Sorrell 2008). Individuals from Alabama have been seen feeding on frogs (Mount 1975), an adult was seen scavenging a dead Southern Leopard Frog (*Lithobates sphenocephalus*) in Arkansas (Meshaka, pers. obs.), and snails were found in the stomach of an individual in Louisiana (Dundee and Rossman 1989). Schmidt and Inger (1957) reported dead fish in the diet of this species, and Pope (1939) included earthworms. A female from Tennessee was found to have ingested portions of a shed skin of a snake presumed to have been *Nerodia sipedon* (Steen et al. 2012). Food is eaten at body temperatures (BT) of 13–38°C (Mahmoud 1969) with higher energy demands reported at higher BTs (Litzgus and Hopkins 2003).

Kinosternon subrubrum faces a wide range of predators throughout its potentially long life. Vertebrates, such as kingsnakes (*Lampropeltis*), opossums (*Didelphis*), raccoons (*Procyon*), crows (*Corvus*), gar (*Lepisosteus*), and blue crabs (*Callinectes*) are known predators of the species (Ernst and Lovich 2009). Kellogg (1929), Giles and Childs (1949) and Nifong (2014) reported *K. subrubrum* in the diet of the American Alligator (*Alligator mississippiensis*). Zimorski et al. (2013) reported attempted predation on an adult by several Whooping Cranes (*Grus americana*). In one instance, a live hatchling was removed from the stomach of a racer (*Coluber constrictor*; Brown 1979).

The shape and color of its carapace and its preference for vegetation cover could provide *K. subrubrum* with crypsis as an effective primary defense mechanism. Its production of musk is not as pronounced as that of *S. odoratus*; however, a provoked individual can defend itself with its sharp beak, strong jaws, and lengthy neck. Associated with terrestrial-predator deterrence, musk secretion under water might serve other functions in *K. s. subrubrum* (Cordero 2011). Its ability to partially or entirely close its shell and the presence of a thick shell were thought to have been helpful in preventing a successful predation attempt by a nesting Bald Eagle (Mitchell et al. 2006).

Egg survivorship of *K. subrubrum* nests in American Alligator nests may be at risk if nest opening activities by the Alligator precede hatching of *K. subrubrum* eggs (Deitz and Jackson 1979). A high three-year mean nest predation rate of 84.2% in South Carolina was not associated with density of nests (Burke et al. 1998).

Threats to Survival. — Habitat loss and road mortality are two well-documented threats to *K. subrubrum*. Mass mortality events can be profound following rain-related movements (Crawford and Doyle 2010). Cumulative mortality can result in local extirpations. For example, in New York, *K. s. subrubrum*, once known from at least 20 freshwater and estuarine sites (Latham 1969; Craig et al. 1980; A. Breisch, pers. comm.), presently exists only in five populations on Long Island, and possibly one additional population on Staten Island (A. Breisch, pers. comm.). This represents a loss of 75% of New York mud turtle populations since the 1930s, the declines attributed to the effect of habitat alteration and degradation resulting from sprawling development on Staten Island and along Long

Island's southern shore, road mortality, and by altered salinity regimes resulting from the permanent breaching of barrier beaches by catastrophic hurricanes (A. Breisch, unpubl. data). The negative effects of weather events aggravated by climate change and sea level rise place insular populations of *K. subrubrum* particularly at risk on Atlantic Coast barrier islands, where this species was found to be successful (Gibbons and Coker 1978). Surprisingly, Gibbons et al. (1983) could detect no impact of drought cycles on reproduction or terrestrial migration in this species. *Kinosternon subrubrum* was one of five North American mud turtle species whose geographic ranges were examined in relation to projected future climate change (Butler et al. 2016). For this species, suitable habitat was expected to increase, accompanied by a shift northward in distribution, evident by the mid- to late 2000s (Butler et al. 2016).

The loss of *K. s. steindachneri* in a central Florida lake was associated with shoreline alterations for a housing development (Bancroft et al. 1983). Roads bisecting aquatic habitat have had profound negative effects on aquatic turtles, including *K. subrubrum* (Smith and Dodd 2003; Aresco 2005), and populations in urbanized areas were associated with lower survivorship (Eskew et al. 2010).

Meshaka and Gibbons (2006) noted a near absence of population studies of *K. s. steindachneri* in Florida, thereby precluding an evaluation of its status anywhere in the state. In Florida, where habitat loss and road construction associated with the rapid development of the state adversely affect this regionally-distinct endemic subspecies, the inability to evaluate its status was thought to warrant its treatment at least as a separate conservation priority, if not a separate species (Meshaka and Gibbons 2006). Winzeler et al. (2015) reported systemic ranaviral infection in a *K. subrubrum* from a site in South Carolina where ranaviruses were present in several amphibian populations.

Conservation Measures Taken. — The species is considered State endangered in Indiana, New York, and Pennsylvania, and a species of greatest conservation need in Kentucky. It occurs in many protected areas—Table 1 lists the National Parks, National Preserves, National Forests, and National Wildlife Refuges where it has been recorded or projected to occur. It is not listed on the CITES Appendices, and the IUCN Red List assessed it as Least Concern in 2011 (van Dijk 2011).

Conservation Measures Proposed. — Several studies have provided the kinds of useful data necessary to make effective management decisions on the conservation of *K. subrubrum*. Undeveloped upland habitat zones of 1500 ft (457.2 m) from the edge of wetlands inhabited by *K. s. subrubrum* were recommended for populations in an increasingly suburbanized area of Long Island (Cavanaugh and Loop 1988). The upland habitat zone would be effective if cleared of physical obstructions to the overland movements of the species. Cavanaugh and Loop (1988) also noted the danger to *K. s. subrubrum* by roads and human commensal species associated with increased development of the area. Undeveloped upland habitat zones of 73 m could protect 90% of nesting sites and those of 275 m could protect 100% of nesting sites of *K. s. subrubrum* in South Carolina (Burke and Gibbons 1995). A range of 127–289 m from the edge of an aquatic site was considered core terrestrial habitat for reptiles, including *K. subrubrum* (Semlitsch and Bodie 2003). At a lake in northwestern Florida, a temporary drift fence connected to existing culverts reduced turtle mortality, including that of *K. subrubrum*, from 11.9 turtles/km/day to 0.09 turtles/km/day (Aresco 2005). The effectiveness of the fence was profound: a probability model predicted that at least 98% of the turtles diverted by the fence would otherwise have been killed (Aresco 2005).

As with most species of the world's turtles, broad conservation and management decisions cannot be made for *K. subrubrum* throughout most of its geographic range without further ecological information on population dynamics of the species and its responses to environmental variability.

Captive Husbandry. — Reptiles Magazine has provided an online care sheet for *K. subrubrum*. Hofer (2002) discussed the care and breeding of *K. s. steindachneri*.

Current Research. — Wallops Island, Virginia, is the site of an ongoing demographic study of *K. s. subrubrum* that inhabits shallow ditches of fluctuating water depth and salinity (Pablo R. Delis and Meshaka, unpubl. data). Ongoing M.S. thesis work by Safiya Ladidi Abubakar of Shippensburg University examines several life history traits of the Wallops Island population.

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