

# CONSERVATION BIOLOGY OF FRESHWATER TURTLES AND TORTOISES

A COMPILATION PROJECT OF THE  
IUCN/SSC TORTOISE AND FRESHWATER TURTLE SPECIALIST GROUP

EDITED BY

ANDERS G.J. RHODIN, JOHN B. IVERSON, PETER PAUL VAN DIJK,  
CRAIG B. STANFORD, ERIC V. GOODE, KURT A. BUHLMANN, AND RUSSELL A. MITTERMEIER



*Kinosternon flavescens* (Agassiz 1857) –  
Yellow Mud Turtle, Casquito Amarillo

JOHN B. IVERSON AND JAMES L. CHRISTIANSEN

CHELONIAN RESEARCH MONOGRAPHS  
Number 5 (Installment 17) 2023: Account 121



Published by  
Chelonian Research Foundation and Turtle Conservancy



in association with

IUCN/SSC Tortoise and Freshwater Turtle Specialist Group, Re:wild,  
Turtle Conservation Fund, and International Union for Conservation of Nature / Species Survival Commission



# CHELONIAN RESEARCH MONOGRAPHS

## Contributions in Turtle and Tortoise Research

---

### *Editorial Board*

**ANDERS G.J. RHODIN**

*Chelonian Research Foundation*

*Arlington, Vermont 05250 USA [RhodinCRF@aol.com]*

**PETER PAUL VAN DIJK**

*Re:wild and Turtle Conservancy*

*Herndon, Virginia 20170 USA [ppvandijk@rewild.org]*

**JOHN B. IVERSON**

*Earlham College*

*Richmond, Indiana 47374 USA [johni@earlham.edu]*

**CHELONIAN RESEARCH MONOGRAPHS (CRM)** (ISSN 1088-7105) is an international peer-reviewed scientific publication series for monograph-length manuscripts, collected proceedings of symposia, edited compilations, and other longer research documents focused on turtles and tortoises. The series accepts contributions dealing with any aspects of chelonian research, with a preference for conservation or biology of freshwater and terrestrial turtles and tortoises. Bibliographic and other reference materials are also of potential interest. Submit manuscripts directly to Anders Rhodin at the e-mail address above. The series is published on an occasional basis, from 1996–2016 by Chelonian Research Foundation, and from 2017 and on by Chelonian Research Foundation and Turtle Conservancy.

### **Published CRM Issues**

1. The Galápagos Tortoises: Nomenclatural and Survival Status. 1996. By PETER C.H. PRITCHARD. 85 pp.
2. Asian Turtle Trade: Proceedings of a Workshop on Conservation and Trade of Freshwater Turtles and Tortoises in Asia. 2000. Edited by PETER PAUL VAN DIJK, BRYAN L. STUART, AND ANDERS G.J. RHODIN. 164 pp.
3. Biology and Conservation of Florida Turtles. 2006. Edited by PETER A. MEYLAN. 376 pp.
4. Defining Turtle Diversity: Proceedings of a Workshop on Genetics, Ethics, and Taxonomy of Freshwater Turtles and Tortoises. 2007. Edited by H. BRADLEY SHAFFER, NANCY N. FITZSIMMONS, ARTHUR GEORGES, AND ANDERS G.J. RHODIN. 200 pp.
5. (Installments 1–17, 121 accounts to date). Conservation Biology of Freshwater Turtles and Tortoises: A Compilation Project of the IUCN/SSC Tortoise and Freshwater Turtle Specialist Group. 2008–2023. Edited variously by ANDERS G.J. RHODIN, JOHN B. IVERSON, PETER PAUL VAN DIJK, KURT A. BUHLMANN, PETER C.H. PRITCHARD, CRAIG B. STANFORD, ERIC V. GOODE, RAYMOND A. SAUMURE, AND RUSSELL A. MITTERMEIER. 2549 pp. to date.
6. Turtles on the Brink in Madagascar: Proceedings of Two Workshops on the Status, Conservation, and Biology of Malagasy Tortoises and Freshwater Turtles. 2013. Edited by CHRISTINA M. CASTELLANO, ANDERS G.J. RHODIN, MICHAEL OGLE, RUSSELL A. MITTERMEIER, HERILALA RANDRIAMHAZO, RICK HUDSON, AND RICHARD E. LEWIS. 184 pp.
5. (Installment 8). Turtles and Tortoises of the World During the Rise and Global Spread of Humanity: First Checklist and Review of Extinct Pleistocene and Holocene Chelonians. 2015. TEWG [TURTLE EXTINCTIONS WORKING GROUP: ANDERS G.J. RHODIN, SCOTT THOMSON, GEORGIOS L. GEORGALIS, HANS-VOLKER KARL, IGOR G. DANILOV, AKIO TAKAHASHI, MARCELO S. DE LA FUENTE, JASON R. BOURQUE, MASSIMO DELFINO, ROGER BOUR, JOHN B. IVERSON, H. BRADLEY SHAFFER, AND PETER PAUL VAN DIJK]. 66 pp.
7. Turtles of the World: Annotated Checklist and Atlas of Taxonomy, Synonymy, Distribution, and Conservation Status (8th Ed.). 2017. TTWG [TURTLE TAXONOMY WORKING GROUP: ANDERS G.J. RHODIN, JOHN B. IVERSON, ROGER BOUR, UWE FRITZ, ARTHUR GEORGES, H. BRADLEY SHAFFER, AND PETER PAUL VAN DIJK]. 292 pp.
8. Turtles of the World: Annotated Checklist and Atlas of Taxonomy, Synonymy, Distribution, and Conservation Status (9th Ed.). 2021. TTWG [TURTLE TAXONOMY WORKING GROUP: ANDERS G.J. RHODIN, JOHN B. IVERSON, ROGER BOUR, UWE FRITZ, ARTHUR GEORGES, H. BRADLEY SHAFFER, AND PETER PAUL VAN DIJK]. 472 pp.

---

**CHELONIAN RESEARCH MONOGRAPHS (CRM)** is variously available from Chelonian Research Foundation and Turtle Conservancy. No overall series subscription rate is available. Contact either Turtle Conservancy ([www.turtleconservancy.org](http://www.turtleconservancy.org)) or Chelonian Research Foundation ([www.chelonian.org/crm](http://www.chelonian.org/crm), 564 Chittenden Dr., Arlington, VT 05250 USA, 978-807-2902, RhodinCRF@aol.com) for prices, titles, and to place orders. Chelonian Research Foundation (founded in 1992) and Turtle Conservancy (founded in 2005 as Chelonian Conservation Center, renamed in 2010) are nonprofit tax-exempt organizations under section 501(c)(3) of the Internal Revenue Code.

## ***Kinosternon flavescens* (Agassiz 1857) – Yellow Mud Turtle, Casquito Amarillo**

**JOHN B. IVERSON<sup>1</sup> AND JAMES L. CHRISTIANSEN<sup>2</sup>**

<sup>1</sup>Department of Biology, Earlham College, Richmond, Indiana 47374 USA [johni@earlham.edu];

<sup>2</sup>Biodiversity Collections, Department of Integrative Biology,  
The University of Texas at Austin, Texas 78758 USA [jlchristiansen@drake.edu]

**SUMMARY.** – The Yellow Mud Turtle, *Kinosternon flavescens* (Family Kinosternidae) is a small (females to 13.5 cm straightline carapace length [SCL], males to 16.8 cm SCL), smooth-shelled, semi-aquatic turtle found in almost any lentic aquatic habitat within its range, but with a preference for ephemeral ponds and streams, especially with adjacent sandy terrain. It has one of the shortest activity periods of any North American turtle and spends most of the late summer, fall, and winter buried in soil upland from the pools where it feeds. It is omnivorous and may feed terrestrially as well as aquatically. Sexual maturity for females requires 9 to 15 yrs in Nebraska but only 6–7 in New Mexico. There is a tendency for turtles in the north and east to be smaller than those in the south and west. A single clutch of 1–10 eggs (usually 4–6) is produced in late May to early July each year in the north, although about 25% of mature females do not nest in a given year. Clutch size in females from Texas is 1–8 eggs (usually 3–5), deposited in late May to early July, and some females may produce two clutches per year. Clutch size tends to increase with body size, but egg size does not. Incubation lasts 87 to 128 days (averaging 103–105 days), and eggs hatch in the fall, but neonates in the north dig down below the frostline and do not emerge until the following spring. In the south, hatchlings may emerge in the fall if aquatic habitat is available. Warm incubation temperatures result in all female hatchlings, but colder temperatures result in mostly males. Primary threats to the species are habitat modifications, including drainage of wetlands, falling water tables, succession from open grassland to woody vegetation, agriculture in and around wetlands, increasing populations of mesopredators, and pollution. Peripheral populations in Illinois, Iowa, Missouri, and Arizona seem to be most vulnerable to local extirpation, and efforts should be made to maintain and expand ephemeral wetland habitats with a surrounding buffer zone.

**DISTRIBUTION.** – USA, Mexico. *Kinosternon flavescens* occurs from central Illinois to north-central Nebraska to southeast Arizona, Texas, and northern Chihuahua, Coahuila, Nuevo León, Tamaulipas, and northern Veracruz in northeast Mexico.

**SYNONYMY.** – *Platythyra flavescens* Agassiz 1857, *Cinosternon flavescens*, *Cinosternum flavescens*, *Kinosternum flavescens*, *Kinosternon flavescens*, *Kinosternon flavescens flavescens*, *Kinosternon flavescens spooneri* Smith 1951.

**SUBSPECIES.** – No subspecies are currently recognized.

**STATUS.** – IUCN 2022 Red List: Least Concern (LC, assessed 2011). CITES: Appendix II (2023). USA: Illinois: Endangered; Iowa: Endangered; Missouri: Endangered; Colorado: Species of Concern; Nebraska: Special Concern.

**Taxonomy.** – The Yellow Mud Turtle was originally described by Agassiz (1857) as *Platythyra flavescens*, but was quickly placed in the genus *Cinosternum* later in the same publication. Since then it has additionally been variously recorded as a species in *Kinosternum*, *Cinosternon*, and *Kinosternon*. Stone (1903) was the first author to publish the currently accepted binomen *Kinosternon flavescens*. The name *flavescens* is from the Latin *flavesco*, meaning “gold-colored” and referring to the general yellow color on the underside of the turtle.

The species was originally described from “Texas, near San Antonio; ... Camp Yuma ... Gila River” based

on six syntypes: MCZ 1918 (Barbour and Loveridge 1946; formerly USNM 61; Reynolds et al. 2007) and 1919 (Barbour and Loveridge 1946; formerly USNM 83; Reynolds et al. 2007); USNM 50, USNM 86 (now lost; Reynolds et al. 2007), 7892 (formerly USNM 68; possibly a misidentified *K. sonoriense*; Reynolds et al. 2007), and 131823 (formerly USNM 51, and later USNM 7867; Reynolds et al. 2007). USNM 50 was designated lectotype by Iverson (1978) who also restricted the type locality to “Rio Blanco, near San Antonio, Texas”. The confused history of the syntypes was detailed by Reynolds et al. (2007).





**Figure 1.** Adult male *Kinosternon flavescens* from south of Gate, Beaver County, Oklahoma. Photo by John B. Iverson.

Three subspecies of *Kinosternon flavescens* were subsequently described. Hartweg (1938) described *K. flavescens stejnegeri* from Arizona, which was synonymized with the Pliocene *K. arizonense* Gilmore 1923 by Iverson (1979a), but that synonymy was later reversed by McCord (2016), with both *stejnegeri* and *arizonense* retained as separate species. Smith (1951) described *K.f. spooneri* from Illinois, which has had a contentious history (see below) and is no longer recognized as distinct. Iverson (1979b) later described *K.f. durangoense* from Mexico, which has since been elevated to species status by Serb et al. (2001).

In a multivariate morphometric analysis of all four previously recognized subspecies of *K. flavescens*, Iverson (1979b) found strong support for the divergence of *stejnegeri* and *durangoense*, and lesser but identifiable support for the distinction of *spooneri*. However, in a separate study, Houseal et al. (1982) examined mensural and shell color characters in a multivariate analysis and also found support

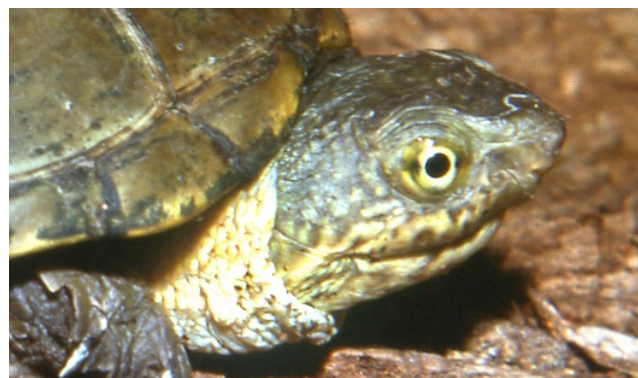
for *stejnegeri* and *durangoense*, but not for *spooneri*, and hence they recommended synonymization of *spooneri* with *flavescens*. In a third multivariate morphometric and color analysis of geographic variation in the *K. flavescens* complex, Berry and Berry (1984) also found strong support for the distinction of *stejnegeri* and *durangoense*, but not for *spooneri*, and agreed with Houseal et al. (1982) in their synonymization.

In a phylogenetic study of a mitochondrial locus, Serb et al. (2001) also found *spooneri* nested within *K. flavescens*, supporting their synonymy. That study also demonstrated that *flavescens*, *durangoense*, and *stejnegeri* (as *arizonense*) did not represent a monophyletic group, and argued for full species status for the latter two taxa. That recommended species-level taxonomy has not subsequently been questioned (e.g., Thomson et al. 2021).

Although based on only a single mitochondrial marker and relatively few samples, Serb et al. (2001) found two



**Figure 2.** Adult male *Kinosternon flavescens* from Gimlet Lake, Garden County, Nebraska. Note the extremely enlarged tail. Photo by John B. Iverson.



**Figure 3.** Adult male *Kinosternon flavescens* from south of Gate, Beaver County, Oklahoma. Photo by John B. Iverson.





**Figure 4.** Adult female *Kinosternon flavescens* from Gimlet Lake, Garden County, Nebraska. Note the dark shell and head color characteristic of northern populations. Photo by John B. Iverson.

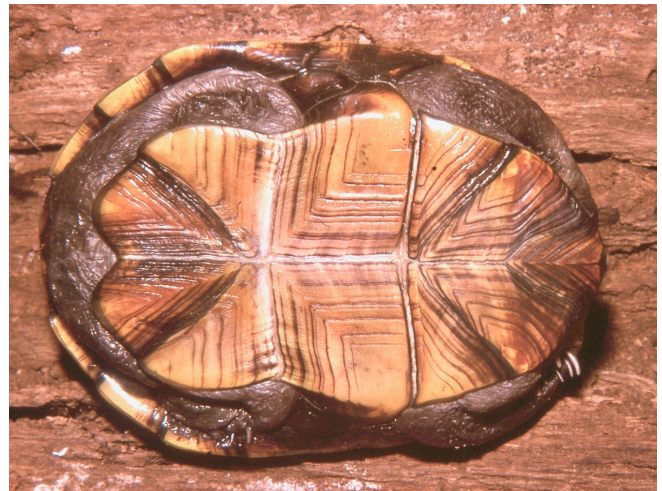
well-supported reciprocally monophyletic clades within *K. flavescens*. One (the northern clade) included specimens from the Canadian River basin in Oklahoma along with those from Illinois (“*spooneri*”), Iowa, Nebraska, and Kansas. The second clade included specimens from Texas and New Mexico. Interestingly, Berry and Berry (1984) also suggested that populations of *K. flavescens* from the Canadian River basin northward and those from the Red River basin southward might represent two distinct phenetic units, but made no taxonomic recommendations. An examination of variation in nuclear markers from across the range of the restricted *K. flavescens* (as currently recognized) is needed to clarify this possible geographic pattern. Should the northern populations be deemed taxonomically distinct, Smith’s (1951) epithet *K. f. spooneri* is available.

Based on an analysis of up to 14 nuclear loci, Spinks et al. (2014) identified three well-supported subclades within the genus *Kinosternon* (though they only discussed two of them): 1) a North American clade (Clade B) including *K. baurii* and *K. subrubrum* (and presumably *K. steindachneri*; Iverson et al. 2013), and the *flavescens* group,

including *K. flavescens*, *K. stejnegeri*, and *K. durangoense*, which could be recognized as the subgenus (or genus) *Thyrosternum* Agassiz 1857 (type species, *K. subrubrum*; Iverson et al. 2013); 2) a clade including *K. dunni* and *K. leucostomum* (and likely *K. angustipons*; Iverson et al. 2013), which could be recognized as the subgenus (or genus) *Cryptochelys* Iverson, Le, and Ingram 2013 (type species, *K. leucostomum*); and 3) a clade including the remaining Mexican, Central American and South America taxa which could be recognized as the genus *Kinosternon*, subgenus *Kinosternon*; type species, *K. scorpioides*. Based on a study of 15 nuclear loci, Thomson et al. (2021) identified the same three well-supported subclades within the genus *Kinosternon*. The latter two analyses also placed *K. flavescens* as sister to the clade comprising *K. stejnegeri* and *K. durangoense*, and hence its closest living relatives. *Kinosternon flavescens* is known to hybridize with *K. subrubrum* (Schipperijn 1987).

**Description.** — *Kinosternon flavescens* is a medium-sized kinosternid with a maximum straight-line carapace length (SCL) reaching 16.8 cm in males and 13.5 cm in females. The available data (Table 1; Iverson, unpubl. data) suggest that Yellow Mud Turtles in populations from the Canadian River basin north and eastward tend to be smaller than those to the south and west. Additional data are needed to test this preliminary observation, which is counter to Bergmann’s Rule (Ashton and Feldman 2003).

The species has a broad, smooth, unkeeled carapace that ranges from nearly black or very dark brown in northern populations (Iverson 1979b; Houseal et al. 1982; Berry and Berry 1984) to light olive or yellowish brown or tan in southern populations. The prominently double-hinged plastron does not protect the entire undersurface of the turtle, especially in males, and is yellowish with prominent growth rings (annulae). The skin is gray to black dorsally and cream to yellow ventrally. The toes are webbed. Beneath the protruding nose, the upper jaw is moderately hooked



**Figure 5.** Adult male *Kinosternon flavescens* (*spooneri* morphotype) from Beatty’s Pond, Louisa County, Iowa. Note dark coloration and massive forefeet. Photos by John B. Iverson.





**Figure 6.** Hatchlings of *Kinosternon flavescens* from Gimlet Lake, Garden County, Nebraska captured as they emerged from brumation for their first activity season (hatchling on left with head to the right, hatchling on right with head down). Photo by John B. Iverson.

in males and very weakly hooked in females. Two pairs of barbels are present under the chin, and the anterodorsal head scale is furcate posteriorly. The tail is thick in males with a large distal spine and is at least half as long as the turtle is wide. Females have a much smaller tail and claw. Males also have a rough patch of scales (“clasping organ”) on the crus and thigh of each hind leg (Fig. 8). The male plastron is slightly concave, whereas that of females is flat.

Hatchlings in Nebraska ranged from 17.7 to 23.9 mm SCL (mean 22.0;  $n = 237$ ) and 2.0 to 3.7 g body mass (mean 2.88;  $n = 237$ ; Iverson, unpubl. data). Ten hatchlings from southeast Iowa measured by Christiansen et al. (1984) ranged from 22.4–24.0 mm SCL. They are brown at hatching, with black spots present at the posterior margin



**Figure 8.** Clasping organ (patch of rough scales) on the hind leg of male *Kinosternon flavescens* from Gimlet Lake, Garden County, Nebraska. Photo by John B. Iverson.



**Figure 7.** Head of female *Kinosternon flavescens* from Gimlet Lake, Garden County, Nebraska, illustrating the prominent chin barbels and massive forelegs. Photo by John B. Iverson.

of each of the large carapacial scutes (Christiansen et al. 1984). For 69 unsexed Texas turtles of all sizes (in mm and g),  $BM = 0.000422 * SCL^{2.825}$  (Long 1984). For 4137 males from western Nebraska,  $BM = 0.000304 * SCL^{2.908}$  and for 9525 females from western Nebraska,  $BM = 0.000180 * SCL^{3.045}$  (Iverson, unpubl. data).

There are 11 marginal scutes on the carapace, and each is yellow below and tan to nearly black above, usually with dark pigment along the ventral and lateral seams. The ninth and tenth marginals are distinctly higher than the other marginals. Axillary and inguinal scales on the short plastral bridge are usually in contact. The first of the five vertebrals is elongated posteriorly and the remainder are as broad or broader than long. The forelobe of the plastron is as long as the hindlobe. The hindlobe is shorter and notched more deeply in males than in females. The modal plastral formula is anal > abdominal > humeral > gular >> femoral > pectoral (after Ernst and Barbour 1989). The species has only eleven pairs of marginals, and the enlargement of both the ninth and tenth marginals easily distinguishes *K. flavescens* from other Recent mud turtles.

Like other kinosternines, *K. flavescens* has a pair each of axillary and inguinal musk glands, from which extremely pungent secretions are expressed when disturbed. It also has hypertrophied brachia and foreclaws relative to most other *Kinosternon* (Iverson, unpubl. data), an apparent adaptation to its fossorial activity (Figs. 5, 7).

As for all members of the *Thyrosternum* subclade, *K. flavescens* has a longitudinal groove along the posterior bridge (Fig. 5). The modal pattern for the neural bone series is the presence of six neurals in contact with the nuchal bone. Four posteriorly hexagonal neurals are followed distally by one quadrangular neural and a pentagonal one that does not contact the suprapygal (Iverson 1988). The species also has flexible plastral bone articulations, which may be an adaptation to trampling by Bison and other Great Plains



**Table 1.** Mean and maximum SCL (maximum straightline carapace length in mm) for male and female *Kinosternon flavescens* greater than 80 mm SCL, by major drainage basins. Unpublished data from museum and field specimens measured by Iverson.

Sample	Males			Females		
	Mean SCL	Max SCL	<i>n</i>	Mean SCL	Max SCL	<i>n</i>
Nebraska						
Sandhills	110.7	134.6	2339	98.6	117.7	3851
Republican						
River Basin	120.7	132.7	30	103.4	112.6	33
Arkansas to						
Canadian Basins	106.6	127.1	13	100.1	113.6	15
Basins south and west						
of the Red River	116.3	141.6	106	107.4	135.1	84

ungulates when buried in shallow soil or present in shallow water (see Habitat and Ecology section below). The bones of the shell are relatively light and thin in comparison to other kinosternids, resulting in among the lowest relative skeletal mass values for the genus (Iverson 1984).

As in other kinosternids, this species has 56 chromosomes, including 26 macrochromosomes and 30 microchromosomes (Killebrew 1975). Of those chromosomes, 16 are metacentric or submetacentric, 8 are subtelometric, and 32 are acrocentric or telometric (Stock 1972).

**Distribution.** — *Kinosternon flavescens* has the eighth largest distribution among the freshwater turtles of North America and the second most extensive for the genus (TTWG 2021). It ranges from western Illinois to northern Nebraska, eastern Colorado to southeastern Arizona, New Mexico to east Texas, and southward to Chihuahua and Veracruz, Mexico (Seidel 1978b; Iverson 1979b, 1992; Houseal et al. 1982; Berry and Berry 1984; TTWG 2021). Populations at the edge of the species' range tend to be isolated and relict (Iverson et al. 1983; Rosen et al. 1996; Rosen 2008; Christiansen et al. 2012). The distribution of *K. flavescens* overlaps that of the congeners *K. scorpioides cruentatum* (Seidel 1976), *K. subrubrum* (Strecker 1931; Olson 1959; Carter and Cox 1968), *K. herrerae*, *K. sonoriense*, and *K. hirtipes* (TTWG 2021). It is known to occur at elevations of up to 1500 m in New Mexico and southeastern Arizona (Degenhardt and Christiansen 1974).

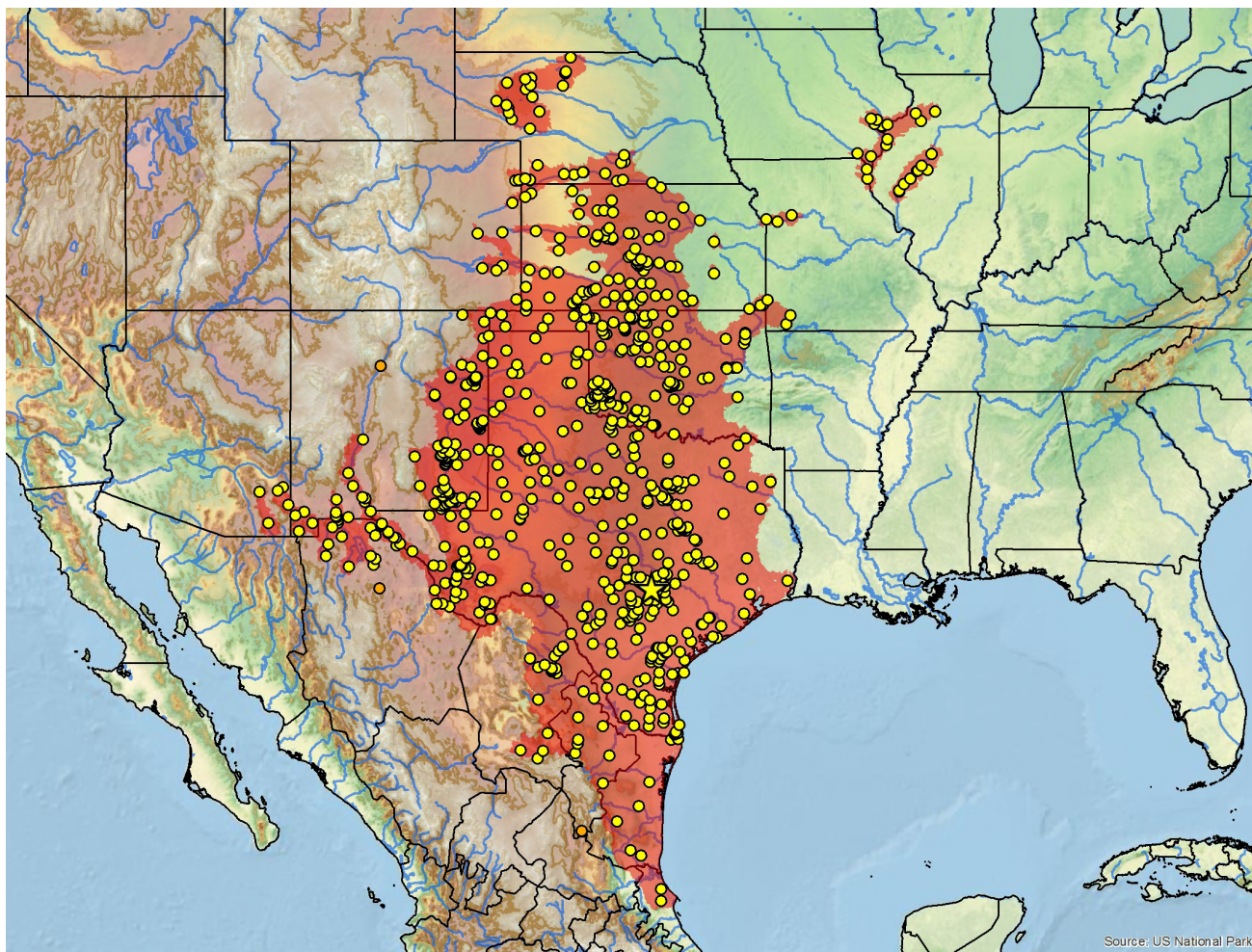
*Kinosternon flavescens* has an extensive fossil record dating back to at least the late Miocene (Parmley 1992). More recent Pleistocene fossils are known from Nebraska (Fichter 1969; Holman 1972), Kansas (Preston 1979; Holman 1986), Oklahoma (Preston 1979), and Texas (Preston 1979; Holman and Winkler 1987). Holocene archaeological specimens are known from Texas (Johnson 1974; Parmley 1990) and Illinois (Kuehn and VanDerwarker 2015). Medina-Casteñeda et al. (2022) identified Pleistocene fossils from southeast Puebla, Mexico, as *K. flavescens*, at a locality ca. 300 km beyond the Recent southern limit for the species; further study of these fossil elements is needed to confirm their identity.

**Habitat and Ecology.** — *Kinosternon flavescens* is supremely adapted to an existence in arid environments in North America where water is only available for short periods each year. The species evolved on the Great Plains (Fichter 1969; Iverson et al. 2013; Bourque 2015) and likely coevolved with the American Bison, in that the wallowing behavior of the buffalo created depressions (see Rainey 1933; Mahmoud 1969; Lardie 1983), many of which became seasonal wetlands that enhanced the diversity of at least plants, arthropods, and amphibians (e.g., Nickell et al. 2018). These aquatic habitats offered abundant food with few competitors, even if they were often ephemeral. The seasonal activity patterns and drought tolerance of Yellow Mud Turtles make them well-adapted to these engineered ecosystems. The flexible plastral bone articulations found in *K. flavescens* (and close relatives in its clade; Iverson, unpubl. data), and unreported in other kinosternids, may indeed be an adaptation against trampling by Bison and other Great Plains ungulates.

In addition, Long (1985, 1986b) demonstrated that Yellow Mud Turtles have the highest lipid stores of any reported turtle (particularly in hatchlings), and Seidel and Reynolds (1980) reported that they have a highly keratinized epidermis that retards water loss. The species is also physiologically adapted to long periods of dormancy. In addition to its ability to tolerate significant dehydration (see *Temperature and Hydric Relations* below), it is able to shift from ureotelism (urea as the nitrogenous end product) when in wetlands to uricotelism (uric acid) during dormancy (Chilian 1976; Ligon 2001; Ligon and Peterson 2002). Urea salts are then precipitated in the bladder to aid osmotic balance in the rest of the body (Chilian 1976). Both of these traits are presumably adaptations to their protracted annual terrestrial dormancy, and their extremely short annual activity season (Christiansen et al. 1985). In fact, Rose (1980) reported that Yellow Mud Turtles in Texas can estivate for up to two years in the absence of aquatic habitat.

Because of their ability to exploit almost any available aquatic habitat (even the most temporary), Yellow Mud Turtles can be found in nearly any flooded field, pond, shallow spring-fed creek, or slough (Mahmoud 1969), and seem to prefer shallow water with soft substrates (for burying), especially if vegetated (Mahmoud 1969; Webster 1986). Although ephemeral wetlands are their most common habitat, they can also be found in permanent, lentic wetlands, although they virtually never occur in lotic systems (except in backwaters of streams with little current; Iverson, pers. obs.). Yellow Mud Turtles are often very abundant in human-constructed aquatic systems, such as stock ponds, cattle tanks, windmill overflow ponds, and even roadside ditches (Mahmoud 1969). A living specimen found in a cave in Texas had apparently been washed inside (Reddell 1971).

At northern latitudes the species is faced with the risk of winterkill due to low temperatures. Hence, at the northern



**Figure 9.** Distribution of *Kinosternon flavescens* in USA and Mexico. Yellow dots = museum and literature occurrence records of native populations based on Iverson (1992), other more recent literature records (see TTWG 2017, 2021), and authors' additional data; orange dots = introduced or possibly historically relict populations or individual trade or translocated specimens; yellow star = restricted type locality. Distribution based on fine-scaled GIS-defined level 12 HUCs (hydrologic unit compartments) constructed around verified localities and then adding HUCs that connect known point localities in the same watershed or physiographic region, and similar habitats and elevations as verified HUCs based on Buhlmann et al. (2009), TTWG (2017, 2021), and data from authors and other sources.

and northeastern limits of the range extremely friable soils (e.g., sandhills) are essential in allowing these turtles to burrow below the frost line (Costanzo et al. 1995).

**Seasonal Activity.** — In general, Yellow Mud Turtles are mostly aquatic only in spring and early summer, but more terrestrial than other North American kinosternids (e.g., Mahmoud 1967). Northern populations in Iowa, Illinois, and Nebraska are closely associated with the ponds where they feed between mid-April and mid-July and are almost entirely terrestrial thereafter, estivating through most of the summer (Seidel 1978a), with only occasional activity by a small percentage of the population in August and September (Christiansen et al. 1985; Tuma 2006). The cessation of aquatic activity in mid-summer is consistent with the drying of ponds in much of the arid range of this species, but occurs even in northern populations inhabiting permanent wetlands. Turtles usually remain buried for

brumation through the winter. Terrestrial brumators have a selective advantage over aquatic brumators in that the latter may be eliminated when there are severe winterkills (Murphy and Corn 1977; Semmler 1979; Christiansen and Bickham 1989). *Kinosternon flavescens* is not at all freeze tolerant and even overwintering hatchlings must dig below the frost line for winter (Iverson 1991; Costanzo et al. 1995, 2001; Tuma 2006). In Illinois, Tuma (1993b, 2006) recorded three turtles at winter depths of 107–125 cm (mean, 117), and even in Texas, Ligon et al. (2011) reported that seven turtles immediately buried 11–80 cm below ground when they initially moved to brumate, but then burrowed progressively deeper as winter progressed.

Iverson and Greene (unpubl. data) quantified the brumation emergence dates and their correlates for 14,196 *K. flavescens* captured at drift fences over 12 yrs for a population in the Sandhills of western Nebraska. Average



spring emergence date over 9 yrs for 1691 males was 29 April and for 2546 females was 4 May. For both 6119 juveniles (<85 mm SCL) and 3840 hatchlings over 12 yrs, average emergence was 21 May. However, these means varied by about three weeks among years, and emergence seasons for each of these cohorts were typically about 40 days in length. When the drift fences were taken down in early July, movement to terrestrial habitats was decreasing but many turtles remained in the water (Iverson 1990). Hence, the estimated primary aquatic period for adults in Nebraska would be consistent with that found in Iowa (80–90 days; see below). However, given that the average brumation emergence date for females in Nebraska was 4 May and the median date that females departed the wetlands on nesting forays over 18 nesting seasons was 17 June (Iverson, unpubl. data; see below), and that females usually entered estivation directly after nesting (Iverson 1990), average aquatic activity season length would be only 45 days. Whether any of these turtles returned to the water in the late summer in Nebraska after estivation is unknown, but the aquatic activity season is remarkably short in any case.

Emergence is clearly not based primarily on narrow proximate climatic cues. Average emergence date for adult males and females was related to average spring temperatures in Nebraska, but climate cues for emergence of individual adults were not clear (Iverson and Greene, unpubl. data). Average dates for juveniles and hatchlings were not correlated with general patterns of spring weather; however, the combination of warm temperatures for several days and rainfall stimulated the most emergence by smaller turtles. The date of emergence from brumation was inversely related to body size in males, females and juveniles. Females that nested in the year of emergence had better body condition, but did not emerge earlier than those that did not. Although spring emergence is certainly influenced by temperature and moisture, precise timing varied by individuals.

In western Nebraska, Iverson (unpubl. data) recorded the interval between brumation emergence date and date of departure from the wetland for nesting forays. For 1487 females, the mean interval was only 44.6 days (range 14 to 76 days); however, many of these females returned to the wetland following nesting. Among those that did not return to the wetland by ca. 4 July (when drift fences were removed), many had intervals of only 20–30 days. For example, one female (106 mm SCL) emerged from brumation on 23 May and moved to nest (7 eggs) on 12 June (20 day interval); another (101 mm SCL) emerged from brumation on 20 May and moved to nest (6 eggs) on 10 June (21 days interval); another (86.6 mm SCL) emerged on 26 May and moved to nest (4 eggs) on 17 June (22 days interval); and another (96.5 mm SCL) emerged on 12 May and moved to nest (5 eggs) on 4 June (23 days interval). Many others had intervals less than 30 days. These intervals

are incredibly short for a female to fertilize and shell her eggs; however, we do not know if the females had stored sperm from the previous year or whether they returned to the wetland for longer periods later in the summer or fall after nesting.

In Iowa, adult and juvenile turtles emerged from their sand dune brumation areas from 21 April through 1 May, median 25–26 April (Cooper 1975; Christiansen et al. 1985; Christiansen, unpubl. data), and the median day for feeding to commence was 10 May. Hatchlings emerged from 29 April through 22 June (Christiansen and Gallaway 1984). Most turtles had left the water for nesting and/or estivation by 11–28 July (median 21 July), producing an activity period of about 80–90 days (with a median of 72 feeding days; Christiansen, unpubl. data). Very few turtles were captured in July. Adding 14 days of potential fall feeding for a few turtles would create a potential maximum aquatic activity season of 104 days.

In Illinois, nine adult radio-tagged turtles left their brumation sites 29 April–24 May and later began shallow terrestrial burrowing as early as 3 June (Tuma 2006), but remained active, continuing to move from burrow to burrow and within burrows, especially females that eventually nested. Seven hatchlings were captured as they emerged from brumation between 12 May and 30 June (Tuma 1993b). Three males and three females reentered ponds for a second aquatic feeding period from 8–27 July and one of these reentered the pond for a third feeding period from 10–25 September. The most aquatic of these individuals had a total of only 69 days of aquatic activity.

In northeast Missouri the aquatic feeding period occurred when the water temperature was above 18°C, from 8 April through 10 July (94 days), the dates Yellow Mud Turtles were collected in baited traps (Kofron and Schreiber 1985). On 8 April the turtles all had thick algae growth indicating that they had probably been in the water a significant time before that, extending the primary aquatic period by at least 14 non-feeding days to a maximum of 107 days. They concluded that these turtles overwintered in water, but it appears from all other studies of the northern populations that they probably brumated on land. Aquatic trapping after that time failed to produce mud turtles, although one was found on land in September. Kangas et al. (1991) found mud turtles emerging from terrestrial habitats in the same county in Missouri as early as 1 April.

In Oklahoma, Mahmoud (1967, 1969) reported 140 days of mostly aquatic activity, beginning in early April, and that feeding began when water temperatures reached 16°C. Estivation commenced in mid-July, but turtles were sporadically active through August during rains.

In eastern New Mexico, Christiansen and Dunham (1972) estimated that activity lasted from mid-April to mid-October, a maximum of 183 days. However, they did not directly observe summer estivation, although they trapped very few turtles from August to November. If estivation



**Figure 10.** Permanent water habitat of *Kinosternon flavescens* on the Crescent Lake National Wildlife Refuge in the Nebraska Sandhills, Garden County, Nebraska. Gimlet Lake is in the background, and the Mallard Arm marsh complex of Gimlet Lake is in the foreground. Photo is at high water in spring; in dry years most of Mallard Arm lacks open water. Photo by John B. Iverson.



**Figure 11.** Mallard Arm of Gimlet Lake complex, Garden County, Nebraska. Gimlet Lake is off the image to the right. Photo by John B. Iverson.

did occur at their site (very likely even though their ponds were permanent), it would significantly reduce the actual activity season length. Semmler (1979) reported a maximum activity period of 172 days in eastern New Mexico, based on his observations of active individuals from 13 May to 2 November. Of course, the maximum season length did not account for nesting or estivation periods, which would significantly reduce that number. In Texas, Ligon et al. (2011) observed seven mud turtles enter brumation between 20 September and 4 October, and emerge from brumation between 5 March and 21 April.

Studies of southern populations show a much longer annual period of activity than northern ones, and in both areas it is likely that individual turtles have considerably

shorter annual activity periods than indicated by records of the earliest and latest activity seen in any one population in any one year.

In summary, the combined evidence suggests that extremely short periods of aquatic activity characterize northern populations. The Nebraska, Iowa, Illinois, and Missouri studies showed a range of 45–107 days of primary activity, with post-estivation rarely adding up to 14 additional days, for a total maximum activity for the populations of 59–121 days. In contrast, the Oklahoma and two New Mexico studies found total activity periods (emergence to the start of estivation plus post-estivation) of approximately 140–172 days for those populations, perhaps two months longer than for the northern turtles.



*Diel Activity.* — *Kinosternon flavescens* is a diurnal species (Mahmoud 1969; Semmler 1979; Webster 1986; Tuma 2006). For over 28,000 drift fence captures in Nebraska, Iverson (unpubl. data) never found evidence of nocturnal terrestrial activity (i.e., drift fence captures), and trapping studies failed to find evidence of nocturnal aquatic activity (e.g., Semmler 1979). We question the assertion that this species is active from midnight to 0740 hrs by Mahmoud (1969). In early spring, terrestrial activity may occur throughout the day if temperatures are warm enough. However, as temperatures increase in June and July, terrestrial activity (e.g., nesting forays) becomes decidedly bimodal (Mahmoud 1969; Semmler 1979; Iverson 1990), except on cool, overcast days (Semmler 1979).

Aspects of aquatic activity have not been well studied. This species is typically found in shallow water (see above), and can be found active in the water throughout the day (temperatures permitting), but whether aquatic activity varies across the day and season is unknown.

Yellow Mud Turtles bask aerially, especially in the first week or two after emergence from brumation (Smith 1950; Semmler 1979; Christiansen et al. 1985; Tuma 2006), sometimes on logs in woodland pools, but more commonly they bask in shallow water with just the dorsum of the shell exposed (Semmler 1979; Iverson, pers. obs.). The latter behavior simultaneously allows them to search for food while thermoregulating.

*Movements and Terrestrial Activity.* — Yellow Mud Turtles commonly make long-distance terrestrial movements, especially during and after rains (Mahmoud 1969; Iverson and Greene, unpubl. data). For example, in New Mexico, Degenhardt and Christiansen (1974) found them in a stock pond that was at least 8 km from the nearest ephemeral wetland depression (and 48 km from the nearest permanent water). In Iowa, Christiansen et al. (1985) reported that turtles estivated at distances up to 450 m from the nearest wetland, and in Illinois, Berger (2010) found that they moved overland in a season an average of 427.7 m (range, 39–2311 m) and estivated an average of 169.9 m (maximum, 530 m) from the nearest wetland. As a result of their often extensive movements, they are frequently found dead on roads that pass near wetlands (Brown and Moll 1979; Sparks et al. 1999; Gaston et al. 2001; Legler and Vogt 2013; Iverson, pers. obs.).

In Oklahoma, Mahmoud (1969) determined that the home range (by convex polygon including all aquatic and terrestrial locations) in males averaged about 0.11 ha and in females about 0.13 ha. Distance between successive locations averaged 199 m in males, 214 m in females, and 179 m in juveniles, but the respective data for aquatic vs. terrestrial activity were not reported. Iverson (in Steen et al. 2012) telemetered 39 females from the wetland to their nest sites on upland sandhills in Nebraska and calculated a straightline distance from the water of  $109.0 \pm 47.8$  m

(23–262 m). Tuma (1993b) reported the average distance between terrestrial relocations in Yellow Mud Turtles in Illinois as 36.5 m (range 1.5–225).

In Nebraska, Yellow Mud Turtles moved from brumation sites to the wetland, and back, including nesting forays, along individually consistent migration paths (Iverson 1990; Iverson et al. 2009). In addition, females returned to the same general areas on the sandhills to nest, year after year. This pattern of site fidelity was also observed in Illinois (Tuma 2006) and Iowa (Christiansen et al. 1985).

In order to explore the navigational basis of this migration path fidelity, Iverson et al. (2009) transported emerging hatchlings and second year turtles in the spring in Nebraska to upland circular arenas with no visual access to the wetland, and monitored their paths of migration relative to their original path to the water. Hatchlings oriented toward the wetland even though it was not directly visible, suggesting they were using visual or olfactory cues (perhaps including reflected light) to reach the wetland on their first emergence. However, second-year turtles maintained their original compass bearing (even if directed away from the wetland), suggesting that by their second emergence they had developed an internal compass (perhaps solar or magnetic) for orientation. After the second year, turtles at the Nebraska site followed the same migration path in and out of the wetland for the rest of their lives (Iverson et al. 2009), including at least one female that was captured 40 times as an adult on the same migration path between 1981 and 2015 (Iverson, pers. obs.).

Estivation sites are typically in upland habitats adjacent to wetlands (Mahmoud 1969; Christiansen et al. 1985; Tuma 1993b, 2006), although Mahmoud (1969) reported estivating turtles found 10–20 cm below the surface in the mud of a recently dried pond, and Burt (1935) reported finding six mud turtles buried together under a pile of drift at the edge of a dry pond in Kansas in August, with larger individuals on top. Upland estivation sites in northern locations are generally on east or south-facing slopes (or on hilltops), typically in sandhills (Tuma 1993b). In Illinois, Tuma (2006) reported estivation depths of 5–25 cm.

Estivation sites in more southern populations can be in any microsite with friable soil, such as in rodent burrows or under the roots of mesquite trees, yucca plants, chollas, or even in the banks of arroyos (Semmler 1979). Mahmoud (1969) found 20 estivating mud turtles in Oklahoma at soil depths of 13–51 cm.

Yellow Mud Turtles often relocate multiple times during the estivation season. Tuma (2006) found that three telemetered females used an average of 9.0 different burrows in one season, and five telemetered males used an average of 3.4 burrows. Semmler (1979) also reported that spool-threaded turtles often relocated multiple times during estivation. However, Iverson (unpubl. data) found that telemetered turtles in Nebraska often relocated if they

were disturbed even slightly during radio-location. It is not known whether some of the relocations reported by others were the result of disturbance. In any case, some estivation relocation events are stimulated by rainfall events (Christiansen et al. 1985; Tuma 2006; Iverson, unpubl. data).

*Temperature and Hydric Relations.* — *Kinosternon flavescens* is not freeze tolerant and typically avoids cold temperatures by burrowing below the frost line (Costanzo et al. 1995). Records of successful overwintering under water have not been reported, but winterkill in ponds has (Murphy and Corn 1977; Semmler 1979; Christiansen and Bickham 1989; Degenhardt et al. 1996). In captivity in Oklahoma, Mahmoud (1969) found that this species was active at temperatures of 18–32°C, and that field preferred body temperature was about 25°C. At 40°C they lost the ability to right themselves, and 43.3°C was their critical thermal maximum.

Yellow Mud Turtles are superbly adapted to water loss compared to other kinosternids (and other turtles; Chilian 1976; Seidel and Reynolds 1980; Ligon 2001; Ligon and Peterson 2002). For example, after 12 days in a laboratory desiccation chamber, they lost only 3.8% of their original body mass (compared to 10.1% in *K. hirtipes*; Seidel and Reynolds 1980). Seidel (1978a) found that the species was capable of surviving three months in 28°C soil (without access to water), though they lost 27% of their initial body mass, and after 55 days of desiccation, Ligon and Peterson (2002) recorded the loss of ca. 25% of body mass after which the turtles quickly fully hydrated when given access to water. Rose (1980) reported their ability to survive estivation of at least two years in the field if aquatic habitat was not accessible. These mud turtles minimize or tolerate water loss by adjusting their respiratory quotient (Seidel 1978a), increasing the keratinization of the integument, and maintaining the highest levels of body lipids of any known turtle (Seidel and Reynolds 1980; Long 1985, 1986a,b; Ligon 2001; Ligon and Peterson 2002; Costanzo et al. 2001).

*Social Behavior.* — Apart from observations on courtship and mating (see below) very little has been reported regarding social behavior in this species. Mahmoud (1967) observed aggressive behavior between males when one male mounted another, but whether this was a mistake in sexual recognition or intentional aggression was not discussed. Semmler (1979) also observed male-male aggression and some male-on-female aggression in captivity in New Mexico. Similarly, Lardie (1975a) reported a large captive male attacking and biting a smaller male after the former had mated with two females in the aquarium. In a more thorough study of aggression in this species, Lardie (1983) observed interactions among 30 female and 30 male turtles of various sizes. He did not report female aggression or aggression on females outside of courtship, but did observe male-male aggression 79 times, including 18 times when no females were present. He also observed males

attacking mirror images or mock images at least 20 times. He reported that he had seen male-male aggression in the field but provided no details. He interpreted this aggression as evidence of territorial behavior where aggressive males were defending areas that offered priority of access to food and/or females. He argued that this behavior would be adaptive in small ephemeral ponds and buffalo wallows that were much more common in the past than after the disappearance of the Bison. Whether this behavior is common in the field remains unknown.

*Diet and Foraging Behavior.* — *Kinosternon flavescens* is an opportunistic feeding generalist, consuming mostly animal matter. In southwestern Nebraska, Iverson (1975) listed snails, tadpoles, earthworms, and carrion in the diet. In the Nebraska Sandhills, Iverson (pers. obs.) found that snails were the predominant food item found in the feces. In northeast Missouri, Kofron and Schreiber (1985) examined 50 fecal samples and also found snails, insects (Odonata, Trichoptera, Coleoptera, Diptera, and Orthoptera), crayfish, and fish to be the most common items, along with some bivalves. They also found plant remains in 66% of the samples. In Illinois, Tuma (1993b) found plant material and snails (*Heliosoma*), insects, and anurans in their feces. He also observed turtles in the field eating tadpoles of *Lithobates clamitans*, and pursuing a Hydrophilid beetle.

In Iowa, drought and time of year impacted the diet (Christiansen et al. 1985). Fishes, crayfish, and microcrustaceans were the most abundant prey in stomachs during the May to July feeding period. When those items were not abundant due to previous drought, turtles fed primarily on snails, aquatic and some terrestrial beetles, and dipteran and odonate larvae. Early May feeding included Ephemeroptera, Hymenoptera, and Lepidoptera, but those items were rarely seen in the diet in later months (Christiansen et al. 1985). In those studies traps baited with fresh fish were more effective in catching Yellow Mud Turtles than those baited with sardines during the normal aquatic feeding period, but were ineffective during flood years when turtles were satiated with earthworms (Christiansen, pers. obs.). Duckweed was present in 61% of the stomachs, but like other plant material, may have been incidentally ingested.

In Oklahoma, Mahmoud (1968) reported that the diet of Yellow Mud Turtles was influenced by season, with carnivory dominating in the summer and herbivory in the colder months. Animal prey included primarily insects, crustaceans, mollusks, and amphibians, with some feeding on carrion and plant material.

In Texas, Minton (1959) observed Yellow Mud Turtles feeding on carrion, snails, belostomatids (giant water bugs), and larval odonates. Punzo (1974) examined the gut contents of 37 turtles collected in May and June in Texas and identified at least 33 families of invertebrates and four families of amphibians in the diet, and also found substantial plant



material in 94% of the turtles examined. Twelve or more animal prey species were found in 70% of those turtles. He stated that Yellow Mud Turtles foraged both aquatically and terrestrially, feeding aquatically during the day on flatworms, annelids, crustaceans, aquatic insect larvae, adult insects, snails, leeches, and larval amphibians. He also reported crepuscular terrestrial foraging on earthworms, millipedes, centipedes, spiders, and insects. Punzo (1974) also found nematodes in the guts, and included them in the diet, but they could have been parasites.

In southwest Texas, Bardwell (2006) examined 37 fecal samples taken in June and July. He found that the most frequently ingested organisms were unidentified plants (57%), giant water bugs (32%), beetles (30%), ants (24%), bivalves (22%), and backswimmers (19%), but also found mosquito larvae, snails, branchiopods, bees, damselflies, cattails, and tiger salamander larvae. However, the ingested prey with the greatest volumes were mosquito larvae (89%), tiger salamander larvae (70%), giant water bugs (61%), and clerid beetles (38%). He also found that the volume of bivalves increased with body size, whereas the diversity of food items decreased with body size.

Kaspar (2013) reported an adult male Yellow Mud Turtle feeding on the entrails of a road-killed Striped Skunk (*Mephitis mephitis*) in July in Texas. More study is needed to confirm the extent of terrestrial feeding in this species in other parts of its range, although Moll (1979) demonstrated subterranean feeding on earthworms in captivity in Illinois, and Punzo (1974) reported that crepuscular terrestrial feeding was common.

Strecker (1927) reported that captive Yellow Mud Turtles accepted meat but preferred insects and small mollusks, and even ate cut sections of a small Lined Snake (*Tropidoclonion lineatum*). Anderson (1965) found them to eat occasional bits of aquatic plants, along with pieces of tomato, lean beef, chopped fish, insects, and earthworms. Mahmoud (1968) observed that the prey choices in captivity were related to availability, and turtles ate nearly everything offered to them, including snails, tadpoles, adult frogs, garter snakes, June Bugs (Melolonthinae), and Dipterans. Thornton and Smith (1996) fed captives dead minnows, Tetra DoroMin, and chopped lettuce, and Britson (1994) fed captives unidentified tadpoles.

The aquatic feeding period of this species is much shorter in the northern part of the range than in the south, although terrestrial feeding (e.g., see Moll 1979) may extend the feeding season. Throughout the range, Yellow Mud Turtles are well-adapted to extreme, temporary aquatic environments, and are often the only turtle able to exist (and even thrive) in them. Their ability to exploit these ephemeral systems as the top predator no doubt contributes to their wide distribution and resistance to population declines (except in peripheral range populations).

**Reproductive Cycles.** — The male reproductive cycle of *K. flavescens* is typical of North American turtles with

maximum sperm production in August and September, and sperm storage in the epididymides until spring, when most mating presumably occurs (see below). Data from Mahmoud and Klicka (1972) from Texas and Oklahoma utilizing testicular mass and Christiansen and Dunham (1972) from New Mexico using testicular length were similar and correlated with the spermatogenic cycle in both studies. In January and February, testes were very small with no spermatogenesis, but sperm were present in testes and epididymides. In March and April, testes were the smallest as sperm had moved from the lumina of the testes and some from the epididymides to the vas deferens. From May through July, spermatogenesis began with increased numbers of spermatogonia and primary spermatocytes, and most of the previous year's sperm were expelled through mating. The interstitial cells of Leydig were most enlarged in May and PAS positive, indicating the presence of glycogen and presumably subsequent production of testosterone. In August and September spermatogonia declined with the final stages of spermatogenesis, sperm production was well underway, and sperm were attached to the Sertoli cells. Testes sizes were greatest in September. From October through December spermatogenesis was terminated and most sperm were present in greatly enlarged epididymides while many remained in the testes attached to Sertoli cells. All mature males examined had some sperm in the epididymides regardless of time of year.

Christiansen et al. (1984) provided the only detailed study of the testicular cycle in the northern part of the turtle's range, in Iowa. The only notable difference from southern populations was the termination of the spermatogenic cycle in August instead of September, with the largest testes present in August.

The ovarian cycle of *K. flavescens* differs from that of most other North American freshwater turtles in that it is continuous rather than cyclical (Kuchling 1999). In April and May, females already have a set of ovulatory sized follicles for that year's clutch, as well as a second set of enlarged follicles that represent the clutch destined to be ovulated in the following year (Christiansen and Dunham, 1972; Long 1986a; Iverson 1991). By nesting season in late May to early July, those follicles enlarged to 9.0 to 14.0 mm diameter (Long 1986a; Iverson, unpubl. data, Fig. 12), and continued to enlarge to ovulatory size by the following spring (Christiansen and Dunham, 1972; Mahmoud and Klicka 1972; Long 1986a; Iverson 1991). The presence of such large follicles in June might lead to the speculation of the production of a second clutch in the same season (e.g., see E.O. Moll 1979), but that was observed in northern populations, and given the short season there, that would be unlikely (Iverson 2022b). Thus, in Yellow Mud Turtles, vitellogenesis is much more protracted, requiring at least two years for follicles to be yolked to ovulatory size. *Clemmys guttata* is the only other North American turtle for which this continuous ovarian cycle has been proposed (Ernst



**Figure 12.** Ovaries and oviduct of a female *Kinosternon flavescens* from Rush Lake, Garden County, Nebraska, captured on 26 May 2018. Note the six shelled oviductal eggs, the five enlarged yolked follicles (9–12 mm diameter) representing the next year's clutch, and the most obvious of six corpora lutea in the upper left. Photo by John B. Iverson.

and Zug 1994). The unique ovarian cycle in these species seems to be another successful adaptation to unproductive or extreme environments (Kuchling 1999).

It is not known whether the closest relatives of *K. flavescens* (*K. stejnegeri* and *K. durangoense*) share this continuous ovarian cycle (Iverson 1989; Iverson et al. 2018), but it is apparently not present in other members of the *flavescens* (*Thyrosternum*) clade (*K. baurii*, *K. steindachneri*, and *K. subrubrum*) (Iverson 1979c,d; Ernst and Lovich 2009).

At the northern margin of the range in Nebraska, ovulation occurs in mid-May to late June and a single clutch of eggs is produced in late May to early July (Iverson 1991, unpubl. data). In Iowa, ovulation was estimated to occur in late May or early June with oviposition possibly extending into July (Christiansen et al. 1984). In southern populations, the first ovulations occur in late April (Long 1986a) to mid-May (Christiansen and Dunham 1972). By July and August (post-oviposition) the enlarged follicles for next year's clutch have reached 11–15 mm diameter (Long 1986a). However, occasional follicular atresia is seen in these, especially in turtles with only a single enlarged follicle, possibly reflecting inadequate stored energy for the following year's clutch (Christiansen and Dunham 1972).

Once in the oviducts, shell formation begins with the formation of organic spheres or cores on the outer surface of the shell membrane that serve as deposition centers for the mineral components of the egg shell (Packard et al. 1984a,b). Those studies showed that the mineral deposition expands beyond the time when the shell deposition centers join, and during this time the egg shell elongates; they further concluded that shell rigidity was related to the amount of calcareous material deposited. Packard (1980) described the comparative details of this mechanism for the non-flexible shells of *Chelydra serpentina*.

**Courtship and Mating.** — Courtship and mating behavior were observed 66 times by Mahmoud (1967) in captive Oklahoma turtles in a 1.8 m x 0.6 m x 1.2 m high enclosure in 12.5 cm of water at 20–30°C. The initial tactile phase involved the male approaching the female from the rear and probing the tail region of the female with his nose. This was followed by probing the region of the plastral bridge, presumably investigating her musk gland odors, with the neck of the male extended, followed by probing or biting the head of the female. The entire tactile process lasted up to three minutes (up to five minutes according to Lardie 1975a). The tactile phase sometimes involved the female fleeing with the male chasing, and this behavior was concluded to be stimulatory.

The mounting phase occurred if the female was receptive, demonstrated by the female becoming immobile, and sometimes occurred without the initial courtship. Mounting occurred either from the posterior or the right or left side, and once in position with all four feet grasping the margins of the carapace, the turtles sank to the bottom. Using one hindleg the male then grasped the tail of the female between the patches of enlarged scales on the lower thigh and upper calf of the leg, with the male's tail holding the female's leg aside as the penis was inserted. This position was maintained through coitus, although both Taylor (1933) and Pope (1939) observed that the male detached the front claws and stood erect during coitus; this behavior was also noted by Lardie (1975a, 1978). Mahmoud (1967) reported that during coitus the male repeatedly rubbed, and often bit at the head or neck of the female. The mounting phase lasts from 30 sec to 5 min, and the copulatory phase lasts from 5 min to 2.5 hrs (Lardie 1975a). During ejaculation the legs stiffened spasmodically. Mahmoud (1967) observed similar courtship and mounting between males, although without the tactile phase. Berry and Shine (1980) suggested that male *K. flavescens* engaged in forced copulation with females, although it is difficult to discern the receptiveness of the female in cases when mating occurs without courtship.

Lardie (1975a), using smaller aquaria and shallower water, observed similar behavior in the tactile and mounting phases, photographing many of 226 partial and complete mating performances of 74 captive turtles. In the initial mounting, the enlarged third and fourth digits of the forefeet were approximately in contact with the first and second marginals of the female, and the large claws of the first three digits of the hind feet were in contact with the ninth and tenth marginals. At this point Lardie (1975a) observed that the tail of the female is not long enough to reach the enlarged scale patches of the male (as suggested by Mahmoud 1967); however, after observing over 1000 total copulations, Lardie (1978) later confirmed that the male does indeed secure the end of the female's tail between these scale patches. Lardie (1975a) also noted that the head



and neck rubbing and biting by the male did not occur until coitus was underway. The rear legs of the male were used to maintain balance and to guide the tail of the male under that of the female so that the cloacae were in contact. To put the male's tail in position to insert the penis, the male had to release its claws from the anterior marginals to the region of the second and third pleurals, putting the male in more of the standing position, as reported by Taylor (1933), Pope (1939), and Lardie (1978).

In line with the species' bet-hedging natural history, male *K. flavescens* are sexually opportunistic. Christiansen et al. (1985) observed copulation in Iowa as early as 6 May even though the water temperature was only 18°C, when most Yellow Mud Turtles had not begun feeding. Christiansen (unpubl. data) also observed mounting and occasional copulation in dry 19-liter buckets almost any time males were placed with females throughout May, June, and July, and occasionally observed males mounting other males. Copulatory behavior was observed in the field in Oklahoma on 5 July by Lardie (1975a) and in Texas on 25 June and 13 August (Davis et al. 2021). In captivity, copulation was observed on 29 October in Kansas (Taylor 1933) and on 5 August in Texas (Thornton and Smith 1996). Taylor (1933) also reported attempted courtship between a male *K. flavescens* and female *Chrysemys picta* on 28 October. These observations, coupled with the year-round presence of sperm in the epididymides, suggest that males are capable of mating at any time during the year, although most mating probably occurs in the spring coincident with emergence from brumation and the annual peak in rainfall on the Great Plains. Whether females can store viable sperm for a long time whenever they are inseminated is unknown.

**Nesting.** — In Nebraska, gravid females left wetlands in late May to early July (see below) and traveled 21–262 m (mean, 109 m) from the shoreline (Iverson 1990, 1991; Tuma 1993b; Steen et al. 2012) and buried at shallow depths (<10 cm) in the nearby sandhills. They then relocated up to several times on the hillside until they chose a final nest site. They then buried 10–20 cm, and while completely buried, oviposited their clutch at ca. 20 cm below the surface (range 17–23; Iverson 1990). They remained buried with their clutch for up to 38 days, though many returned to the wetland, and some of those re-emerged and moved to the sandhills to estivate by July. More females tended to remain with their clutches in years with low rainfall in June; more returned to the wetland in wet years (Iverson 1990). It is not known if a female remaining buried with her clutch increases egg survivorship.

Only an average of 75% of females nest in a given year in Nebraska. During hot and dry years, less than 50% of females may nest, but during warm, wet years up to 95% may nest. This pattern is an additional component of their bet-hedging life-history strategy. At the Nebraska site, 4 June was the average first date of gravid female

departures from the wetland for a nesting foray (range of first departure dates: 26 May to 10 June;  $n = 19$  years, 4984 gravid females), and the median date of all female departures for nesting forays per season over 18 seasons was 17 June (range of median departure dates per season: 9–27 June; Iverson, unpubl. data), and was inversely correlated with spring temperatures (Janzen et al. 2018; Iverson, unpubl. data). Although the exact dates of nesting could not always be documented, dates of departure from the wetland correlated closely with actual nesting, which occasionally extended into the first week of July in cooler years (Iverson, unpubl. data).

In Illinois, Tuma (1993b, 2006) observed females moving to nesting areas in June. Once there they relocated as many as six or more times. During the week before oviposition they relocated to distances of 1.5 to 29 m (mean, 12.8). He found six nest sites within 70 m of the nearest wetland. He also reported subterranean nesting from 22–26 June (four females), and located four nests 10–20 cm below ground (mean 12.6 cm). He also found two females that appeared to split their clutches between two nest sites (Tuma 1993a,b); however, given the high rates of nest depredation by hognose snakes at the site, it is possible that ovipositing females relocated due to disturbance by snakes.

In Iowa, Christiansen et al. (1984) found that nesting began on 16 June and continued to 8 July, and in Oklahoma Mahmoud and Klicka (1972) estimated the nesting season as late May to the first week in July, based on dissections. Similarly, Christiansen and Dunham (1972) estimated the nesting season in eastern and southern New Mexico to extend from 1 June to the first or second week in July. However, Zenor (2021) found gravid females from 11 May to 30 June in west Texas, suggesting that southern populations may begin nesting earlier than those farther north.

**Incubation.** — Eggs hatch in the fall. Laboratory incubations at 27–28°C lasted 89–125 days and averaged 103 days in four studies (Lardie 1975b, 1979; Christiansen et al. 1984; Thornton and Smith 1996); and at 30°C lasted 87–128 days, averaging 105 days (Ewert 1985; see also Ewert and Nelson 1991). Upon hatching, neonates in the north dig downward as much as 66 cm or more (i.e., well below the frost line; Costanzo et al. 1995) and brumate there until spring (see also Christiansen and Gallaway, 1984; Christiansen et al. 1985; Iverson 1990; Tuma 2006; Iverson and Greene, unpubl. data). In west Texas, Long (1986b) reported that hatching occurred in the fall, but that the hatchlings overwintered in the nest and emerged the following spring.

Sex of hatchlings is determined by temperature, with nests incubated at lower temperatures (e.g., 25°C) producing mostly males, those at intermediate temperatures (27–30°C) producing nearly all males, and those at high temperatures (>30°C) producing all females (Vogt et al. 1982; Etchberger 1991; Ewert and Nelson 1991; Janzen and Paukstis 1991; Ewert et al. 1994, 2004).

**Table 2.** Summary of mean reproductive data for *Kinosternon flavescens* across its range. Abbreviations are *n* (sample size), SCL (maximum straightline carapace length in mm), BM (body mass in g), CS (clutch size), EL (mean clutch egg length in mm), EW (mean clutch egg width in mm), EM (mean clutch egg mass in g), CM (clutch mass in g), and RCM (relative clutch mass, CM/BM in %).

Location	Latitude	<i>n</i>	SCL	BM	CS	EL	EW	EM	CM	RCM	Source
NW Nebraska	42.19	11	NA	NA	NA	25.87	15.40	3.57	NA	NA	Iverson 1991
W Nebraska	41.75	132	102.5	271.3	6.48	26.74	16.22	4.25	27.54	10.15	Iverson 1991
E Iowa	41.33	4	NA	NA	5.0	29.8	17.20	4.95 <sup>a</sup>	24.75	NA	Christiansen et al. 1984
Illinois	ca. 41	2	NA	NA	3.5 <sup>c</sup>	28.5	16.50	4.49 <sup>a</sup>	NA	NA	Smith 1961
SW Nebraska	40.12	11	104.5	247	5.67	26.96	16.17	4.17	23.04	9.12	Iverson 2022b
Oklahoma	36.44	3	101.3	260.7 <sup>b</sup>	1.8 <sup>c</sup>	30.75	17.39	4.84	8.71	3.34 <sup>c</sup>	Lardie 1979
ca. Oklahoma	ca. 36	21	NA	NA	ca. 5	27.5	17.50	4.79 <sup>a</sup>	ca. 24	NA	Mahmoud and Klicka 1972
N Texas	35.91	13	93.2	214.0	3.69	27.71	16.50	4.33	16.03	7.47	M. Ewert, unpubl. data
N Texas	ca. 35	NA	NA	NA	3.7	NA	NA	NA	NA	NA	Lange and Kazmaier 2009
New Mexico	ca. 34	8	NA	NA	4.1	NA	NA	NA	NA	NA	Christiansen and Dunham 1972
Texas	33.68	14	106.3	223.2	4.86	26.9	16.60	4.84	23.54	10.55	Long 1986a
New Mexico	33.20	6	104.0	244.0	5.0	28.82	16.82	4.88	24.42	10.02	Iverson, unpubl. data
Texas	32.45	3	116.1	315.3	4.75	27.34	16.60	4.33	20.57	6.52	J.F. Berry, unpubl. data
Texas	31.73	1	117.2	319.7	4	28.2	16.7	4.8	19.2	6.01 <sup>c</sup>	Thornton and Smith 1996

<sup>a</sup> EM estimated from equation:  $EM = 0.112EL + 0.431EW - 6.103$  (Iverson 1991)

<sup>b</sup> BM estimated from BM-CL equation in Iverson (1991)

<sup>c</sup> captive

**Reproductive Output.** — Average clutch size in *K. flavescens* varies across populations from about 4 to 6.5 eggs, with a maximum range of 1 to 10 eggs (Table 2; Iverson 1991, 2022b, unpubl. data). Clutch size generally increases with female body size (Long 1986a; Iverson 1991; Iverson et al. 2019; but see the abstract in Mahmoud and Klicka 1972), and there is a tendency for clutch size to increase with latitude (Iverson 2022b). Relative to body size, *K. flavescens* produces very large clutches in comparison to most other turtles, including other kinosternids, but not as large as pelomedusids (Iverson and Greene 2022).

The eggs of *K. flavescens* are small, elongate and brittle shelled (Iverson 1991), and average 27.0–31.0 mm in length, 16.0–17.5 mm in width, and 4–5 g in mass (Table 2). For 216 eggs from Nebraska and Texas (Iverson, unpubl. data), mean egg length (EL) was 27.1 mm (range, 23.5–31.4) and mean egg width (EW) was 16.2 mm (range, 14.2–19.3); mean egg mass (EM) was 4.25 g (range, 3.03–6.96). For those eggs,  $EM = 0.308*EL - 4.09$  ( $r = 0.80$ );  $EM = 0.680*EW - 6.77$  ( $r = 0.92$ ); and  $EM = 0.148*EL + 0.512*EW - 8.05$  ( $r = 0.97$ ). Smith (1950) reported egg size as 25.4 x 10 mm (1" x 3/8"; estimated EM from equation above = 0.83 g) and Anderson (1956) reported eggs as 24 x 13.5 mm (estimated EM = 2.41 g), but both of these reports are suspect since they deviate significantly from all other available data. There is no evidence of pelvic aperture constraint on egg size in this species (Long and Rose 1989; Iverson 1991).

Egg size in *K. flavescens* tends to increase with body size within a population (Long 1986a; Iverson 1991; Iverson et al. 2019), and there is little variation in egg size across the species' range (Iverson 2022b and Table 2). Relative to body size, *K. flavescens* produces relatively large eggs (as do most kinosternids) in comparison to other turtle families (Iverson and Greene 2022).

Although a maximum of a single clutch is laid per year in most populations (Christiansen et al. 1984; Iverson 1991; Tuma 2006), McVay (2017) and Zenor (2021) reported the possibility of a second annual clutch in three radiographed females from northwest Texas. In addition, Rose (in Long 1986a) also reported the possibility of a second clutch in northwest Texas, based on x-rays. The unique reproductive cycle of *K. flavescens* (see above), apparently allows for the ovulation of a second enlarged set of follicles in optimal years. Whether this diminishes reproductive output in the following year is unknown.

Relative clutch mass (clutch mass/gravid body mass) for four populations with samples for >10 females (Table 2) ranged from 7.5% to 10.55% (mean 9.32%), and exhibited no evidence of a latitudinal effect. In addition, these values are typical of most (but not all) turtles (Iverson and Greene 2022). Bronikowski et al. (2023) found no evidence of senescence in reproductive output in Yellow Mud Turtles in Nebraska.

The reproductive biology of *K. flavescens* is unusual among turtles, and evidently a response to the unpredictability of its arid environment. The species has evolved a complex suite of traits that serve as one of the best examples of a bet-hedging life history strategy among all turtles.

**Sex Ratios.** — In Nebraska, Iverson and Greene (unpubl. data) monitored the emergence from brumation of Yellow Mud Turtles over nine years (i.e., population-wide numbers that are unbiased by usual trapping methods) over a 36-year study. Sex ratios varied yearly from 1M:1.30F to 1M:1.98F (mean 1M:1.51F; total of samples for all years = 4237), and was positively correlated with year ( $r^2 = 0.71$ ;  $p = 0.005$ ), perhaps reflecting changes in climate over time.

In Illinois, Tuma (1993b) reported a wetland population with 8 males and 8 females (1:1). In Missouri, Kofron and Schreiber (1985) studied a population of 20 males and 12 females (1.67M:1F). In Kansas, Seim (2015) found



statistically significant male bias in five separate wetlands (range 1.4M:1F to 2.6M:1F; mean 2.1M:1F). However, in Oklahoma, Mahmoud (1969) recorded sex ratios in three ponds as 1M:1.52F (total  $n = 58$ ), 1M:1.38F ( $n = 152$ ), and 1.54M:1F ( $n = 33$ ). Likewise, in New Mexico, Semmler (1979) found female-biased populations in three ponds: 1M:4.14 ( $n = 36$ ), 1M:4.0F ( $n = 40$ ), and 1M:3.0F ( $n = 28$ ). In addition, in west Texas, LaDuc and Christiansen (2012) reported female-biased sex ratios (with no details) across four perennial (windmill supplemented) stock ponds. In Texas, Zenor (2021) studied mud turtles in six ponds and found sex ratios of 1.01M:1F (total  $n = 382$ ), 1M:1.20F ( $n = 240$ ), 1M:1.04F ( $n = 188$ ), 1M:1.20F ( $n = 266$ ), 1M:1.88F ( $n = 147$ ), and 1M:2.01F ( $n = 214$ ).

Only four of these samples included more males than females, but three of them were not significantly different from 1:1 by chi-square analysis. The populations in central Kansas are the only ones with a significant male bias. However, the general pattern for this species seems to be female biased, which may reflect the fact that males are only produced at low temperatures, but at least some females are produced at all temperatures (see above).



**Figure 13.** Subadult female *Kinosternon flavescens* from Gimlet Lake, Garden County, Nebraska known to be 11 winters old since first marked at 2 winters old. Note the variation in growth between sets of annuli and that the fourth and fifth annuli appear as one annulus, indicating no growth in the intervening activity season. The sand cemented to the plastral forelobe is typical of turtles as they emerge from brumation; that on the hindlobe was washed away when checking for identification marks. Photo by John B. Iverson.

**Growth, Maturation, and Longevity.** — In the Sandhills of western Nebraska, Iverson (1991) found that females matured at 88 to 93 mm SCL at ages of 9–15 yrs (average 11.4 yrs, although the smallest gravid female in a subsequent sample of 4984 total gravid females captured between 1981 and 2018 was 85.1 mm SCL). In New Mexico, Christiansen and Dunham (1972) reported that the minimal size at maturity of both males and females was 90 mm SCL, at an age of 6–7 yrs. In Texas, Long (1986a) found the minimum size at maturity to be 90 mm SCL; however, in the same state, Zenor (2021) found a gravid female with a SCL of only 78 mm, and five more with a SCL of 80–90 mm, but all others were larger than 90 mm. A report by Mahmoud (1967) that female Yellow Mud Turtles matured as young as 4–5 yrs in Oklahoma is probably erroneous (see Mahmoud 1969).

Growth rates for juvenile Yellow Mud Turtles are available only for Nebraska, Oklahoma, and Texas. In western Nebraska, known-aged juvenile males ( $n = 1909$ ) between 2 and 10 winters old (1–9 activity seasons) increased in SCL according to the linear regression  $SCL \text{ (in mm)} = 6.87 * \text{age} + 22.29$  ( $r = 0.855$ ;  $p < 0.0001$ ; Iverson, unpubl. data) and females ( $n = 2896$ ) aged 2–10 winters increased according to  $SCL = 5.57 * \text{age} + 26.66$  ( $r = 0.866$ ;  $p < 0.0001$ ; Iverson, unpubl. data). In addition, Iverson (1991) provided a von Bertalanffy growth curve based on 319 captures of 92 females:  $SCL = 107.15 * (1 - 0.9326e^{-0.1588t})$ , where  $t$  = age in the number of winters post hatching.

In Dundy County in extreme southwestern Nebraska, Iverson (unpubl. data) measured intra-abdominal (IAB) scute lengths from growth annuli for 29 female *K. flavescens*. Assuming that the ratio of IAB to maximum plastron length (MPL) remains constant through life, MPL (and estimated SCL) for turtles 2–10 winters old were 31.4 (34.0), 40.5 (42.8), 49.1 (51.1), 55.5 (57.3), 62.5 (64.0), 70.9 (72.1), 78.9 (79.8), 83.6 (84.4), and 88.0 (88.6) mm. These data indicate a faster growth rate at this site than in the Nebraska Sandhills 200 km farther north, and the possibility of an earlier maturity at ca. 10 yrs.

In Oklahoma, Mahmoud (1969) found that two juveniles between 21 and 40 mm SCL grew 7.7 mm/year, seven between 41 and 60 mm SCL grew 7.9 mm/year, one between 61 and 80 mm SCL grew 3.1 mm/year, and one >81 mm SCL grew only 0.3 mm/year. He also provided a growth curve based on 761 turtles aged by plastral annuli, although he combined the sexes and offered no equation. His graph (Mahmoud 1969: Fig. 5) suggested that 4-yr-old turtles measured ca. 70 mm SCL and 7-yr-old turtles measured ca. 95 mm SCL. Not surprisingly, given the longer activity season, the rates in Oklahoma were faster than those in Nebraska. Mahmoud (1967) and Mahmoud and Klicka (1972) estimated maturity in males at 4–7 yrs and in females, 5–8 yrs, and estimated maturity to occur between 80 and 120 mm SCL.

Lardie (1975b) recorded a captive hatchling from an Oklahoma adult female that grew from 23 mm SCL on 31 August (when it hatched) to 39.5 mm SCL by the following 15 February. He also captured a 39 mm SCL juvenile (presumably at the end of its first growing season) that grew in captivity to 51.5 mm SCL by the following 15 February. These rates clearly exceed those found in nature, presumably because they were maintained at warm temperatures and were feeding during winter months. In Texas, Long (1986a) found the smallest mature female was 95 mm SCL, and based on his equation relating age (from annuli) to SCL ( $\log_e \text{SCL} = 0.331(\log_e \text{Age}) + 3.858$ ), he estimated age at maturity to be 8–15 yrs (mean, 11).

Interestingly, Wunder et al. (1962) and Dodge and Wunder (1962) found that under high gravity conditions, juvenile *K. flavescens* had greatly increased growth rates. First year turtles grew twice as fast at 5–6G as under normal gravity. This and other species of turtles were much more tolerant of high G conditions than mammals.

Latitudinal patterns in age and size at maturity are still uncertain, although there may be a trend for a larger size at maturity in southern populations. However, the available data suggest earlier age at maturity in the middle of the range in Oklahoma, which seems unlikely.

The captive longevity record for this species is only 10 years, four months and 25 days (Snider and Bowler 1992; Slavens and Slavens 1999). However, *K. flavescens* in western Nebraska frequently lives beyond 50 yrs and recapture data suggest that they may live beyond 60 yrs (Hedrick and Iverson 2017). Recapture data from that study were modeled by Bronikowski et al. (2023), and post-maturation maximum life span (i.e., when only 5% of individuals were estimated to still be alive) was estimated to be 42.4 yrs for females and 35.6 yrs for males. Given an assumption of 11 yrs to maturity, this model is supported by the actual long-term recapture data.

In Iowa, based on counts of plastral annuli, Christiansen et al. (1996) found rare individuals that he believed were beyond 25 yrs old (see also Williams 1996). Most studies that used annuli to estimate age have not been successful at accurately aging individuals beyond 12–20 yrs (e.g., Mahmoud 1969; Iverson 1991; McVay 2017; Zenor 2021).

Because Yellow Mud Turtles do not shed their scutes like many emydids, and since their season of inactivity is so long, scute annuli can be very distinctive on younger turtles. Hence, a number of studies have relied on counts of annuli to age turtles (e.g., Christiansen et al. 1985; among others); however, this technique needs to be used with great caution in this species. First, since some turtles become active in the fall after a typical long period of summer estivation, they may produce a second (secondary) annulus that year, potentially resulting in over-estimations of age. Second, in particularly harsh years (i.e., hot and dry), the activity season may be so short (or nonexistent) that the turtle does not grow substantially, and hence what appears



**Figure 14.** Plastron of adult female *Kinosternon flavescens* from Gimlet Lake, Garden County, Nebraska, first captured as an 102 mm SCL adult in 1981 (at an estimated > 20 years old), and still alive in 2018 (i.e., >58 years old). Marginal notch is evident anterior to left hind foot. Photo by John B. Iverson.

to be a single annulus may in fact represent multiple years without growth (Fig. 13, also illustrated in Iverson 2001). This may be a particular problem in the most arid parts of the species' range, where ephemeral wetlands may have water for several, very short periods in a given year. Only by tracking individuals using mark and recapture can annulus counts be substantiated. In addition, once turtles are about 15 or more years old, annulus counts are completely useless given the slow growth rates of adults.

**Demography.** — Only a few age-class distributions are available for *K. flavescens*, and most are hampered by methods that under-sample juveniles and rely on age estimates based on plastral annuli. In Iowa, Christiansen and Gallaway (1984) used drift fence trapping and reported that juveniles (<90 mm CL) comprised an average of 21.1% of the population prior to raccoon removal and 41.7% after their removal. Based on a full brumation emergence census of a population of Yellow Mud Turtles via drift-fencing in 2018 at the end of a 39-year mark-recapture study in western Nebraska, Iverson (2022a: Fig. 5) recorded 1472 turtles, of which 1021 (69.4%) were less than 11 winters old (the average age of maturity). The lower proportion of juveniles in Iowa than in Nebraska may have been an



early indication of the decline in the former population as was later verified by Christiansen et al. (2012).

In Oklahoma, Mahmoud (1969) used aquatic trapping and hand collecting and estimated that juveniles (sizes undefined) comprised 10.6 and 11.4% of his population over two years. In Texas, McVay (2017) and Zenor (2021) used several extensive passive and active capture techniques in order to reduce sampling bias, but still relied on scute annuli counts for aging. McVay (2017) found an average of only 3.1% (range, 0–6.2%) of the turtles in seven wetlands had over 10 annuli, and similarly Zenor (2021) found an average of only 4.7% (range, 2.2–5.9%) in six wetlands that had over 10 annuli. Between these two studies, the oldest turtle bore only 17 annuli. Given these two unusual age-class distributions, the reliance on scute anuli for aging may be problematic, and future demographic studies of this species should seek to base age estimates on recapture data rather than simply scute annuli, and also strive to sample small turtles more effectively. Aquatic trapping does not produce reliable size class representation.

Survival estimates for individual Yellow Mud Turtles are available only for populations in Nebraska, Missouri, and Texas, and those from the latter two states remain unpublished. In Nebraska, based on recapture rates in a heavily sampled population, Iverson (1991) found that survival from egg deposition to hatchling emergence from brumation the following spring was only 19.1%, primarily due to predation (especially by hognose snakes; Iverson 1990). Annual survival estimates for the next seven years of life were 40.4, 61.2, 76.8, 87.0, 92.7, 94.9 and 94.6%. Beyond that (at least for females) annual survival averaged 95%. However, age-specific mortality increased very slightly with age in both adult males and females, suggesting some actuarial senescence, and mortality in males was slightly higher than in females (Bronikowski et al. 2023).

These data support the conclusion by Iverson (1991) that *K. flavescens* exhibits a Type III survivorship curve, with high mortality of eggs and hatchlings and increasing survivorship with age. That study is the only one with sufficient data on age-specific reproduction and survival to produce a life table, and estimated a generation time of 28.2 years. In addition, it estimated a net reproductive rate ( $R_0$ ) of 1.06, suggesting a population slowly increasing by about 6% over 28 years.

In Missouri, Kangas (1986a,b) used age-frequency distributions to estimate annual survival in turtles older than four years, and reported 50%, 54%, and 55%. He also directly estimated annual survival of hatchlings at 17%. Although these rates seem to suggest a declining population, later confirmed by Christiansen et al. (2012), Kangas asserted that the populations seemed capable of maintaining themselves.

In west Texas, Zenor (2021) also used age-frequency distributions (excluding the youngest age classes and only up to ages 11 to 16 years based on counts of annuli)

to estimate annual survival in six populations. Estimates were 62.2%, 69.1%, 71.6%, 76.9%, 80.2%, and 85.3%. These values are not strikingly different from the juvenile/subadult values found in Nebraska.

For years in Nebraska when the emergence season was sampled completely, Iverson (unpubl. data) recorded 1147 Yellow Mud Turtles in 1990 (excluding hatchlings), 1141 in 1993, 1137 in 1994, 1117 in 1998, 1252 in 1999, 1476 in 2000, 1122 in 2007, and 1305 in 2018. These data suggest a stable population over at least three decades. However, the size of the hatchling cohort varied considerably by year. Over 12 years with thorough sampling of the hatchling emergence (April–June), Iverson (2022a) captured 0–712 hatchlings (mean, 376), with only three hatchlings emerging in the two years following the volcanic eruption of Mount Pinatubo, and the subsequent global cooling. The number of hatchlings in a given year was not related to the number of females that nested in the previous year, but instead was positively correlated with July–September temperatures during the previous year. The long incubation time for the species (see above) results in the failure of eggs hatching in colder years, suggesting that activity season temperatures limit the northern distribution of the species (Iverson 2022a).

Mud turtles can be extremely abundant in appropriate habitats, especially in southern populations. In 2007, Iverson (unpubl. data) captured 474 hatchlings and 1122 post-hatchling mud turtles in Gimlet Lake (permanent) in Nebraska (surface area = 24.5 ha; Befus et al. 2012). Assuming a mean hatchling mass of 2.88 g and the mean body mass of the other turtles captured that year (131.6 g; mean SCL = 78.33 mm), Gimlet Lake supported at least 46.8 turtles per ha and at least 149 kg of mud turtles, a standing crop biomass of 6.1 kg/ha of water surface.

In Kansas, Seim (2015) sampled mud turtles in five wetlands on the Quivera National Wildlife Refuge and estimated mud turtle densities of 0.2, 1.7, 6.7, 16.9, and 79.8 turtles/ha. Assuming a mean turtle mass of 131.6 g (see above), standing crop biomass for the densest of the five populations was estimated at 10.5 kg/ha.

In Iowa, Christiansen et al. (1990) estimated a population of 1049 mud turtles in Beatty's Pond in 1988, which we estimated to cover 26 ha from Google Earth. This suggests a density of 40.3 turtles per ha, and assuming a mean body mass of 131.6 g (from Nebraska; see above), a standing crop biomass of about 5.3 kg/ha. In Illinois, Tuma (1993b, 2006) estimated a population of 44.8 turtles inhabited a wetland estimated (from Figs. 3 and 5 in Tuma 2006) to be about 0.8 ha, suggesting a density of about 60 turtles/ha, and an estimated biomass (assuming a mean turtle mass of 131.6 g; see above) of 7.9 kg/ha.

In Oklahoma, Mahmoud (1969) found 33 mud turtles in a 0.40 ha pond (81.5 turtles/ha), 105 in a 3.72 ha pond (28.2 turtles/ha), and an incredible 34 in a 0.01 ha pond (3366 turtles/ha). If average body mass at these sites was the same as for Nebraska (131.6 g; see above), then

standing crop biomass would have been 10.7, 3.7, and 443 kg/ha, respectively. The last estimate was likely an unusual temporary congregation in the very small pond.

However, in New Mexico, Semmler (1979) estimated populations of 56, 56, and 70 Yellow Mud Turtles in three separate ponds, each ca. 0.1 ha in size, indicating densities of 560 to 700 turtles/ha (see also Iverson 1982). No body mass data were reported in that study, but if the mean turtle body mass were the same as in Nebraska (131.6 g; see above), then biomass estimates would be 76 to 92 kg/ha. In Trans-Pecos Texas, LaDuc and Christiansen (2007) estimated that 50–60 mud turtles inhabited a 0.1 ha pond, for a density of 500–600 turtles/ha. Assuming an average body mass of 131.6 g (see above), estimated standing crop biomass would be 65.8–79.0 kg/ha. These data suggest that northern populations of *Kinosternon flavescens* may generally be an order of magnitude less dense than those in the south, perhaps due to the colder environmental conditions.

**Predation and Defensive Behavior.** — Predators of Yellow Mud Turtles include fish (*Micropterus* sp.), Bullfrogs (*Lithobates catesbianus*), water snakes (*Nerodia*), Hognose Snakes (*Heterodon nasicus*), Snapping Turtles (*Chelydra serpentina*), large wading birds (*Ardea herodias*; *Botaurus lentiginosus*), Black Hawks (*Buteogallus anthracinus*), Roadrunners (*Geococcyx californianus*), Western Kingbirds (*Tyrannus tyrannus*), Loggerhead Shrikes (*Lanius ludovicianus*), Brown Thrashers (*Toxosoma rufum*), Coyotes (*Canis latrans*), Raccoons (*Procyon lotor*), Striped Skunks (*Mephitis mephitis*), shrews (Soricidae), and burrowing rodents (Platt 1969; Dodd 1983; Christiansen and Gallaway 1984; Iverson 1990; Degenhardt et al. 1996; Tuma 1993b, 2006; Ernst and Lovich 2009; Kazmaier et al. 2021; Iverson, pers. obs.). Eggs are eaten by hognose snakes and numerous mammals (Platt 1969; Christiansen and Gallaway 1984; Iverson 1990; Tuma 1993b, 2006; Ernst and Lovich 2009). Increased survival of hatchlings and juveniles was reported by Christiansen and Gallaway (1984) following predator removal.

**Parasites and Epibionts.** — Leeches were found on 65% of Yellow Mud Turtles collected in aquatic habitats in Missouri by Kofron and Schreiber (1985), and nearly all subadult and adults from western Nebraska (Iverson, pers. obs.), but were less commonly seen on Iowa mud turtles in spite of heavy density on pond bottoms (Christiansen et al. 1985). A new coccidian parasite, *Eimeria lutotestudinis*, was described from bile and intestinal contents of *K. flavescens* in Iowa by Wacha and Christiansen (1976) and later found in that species in Texas by McAllister and Upton (1988, 1989). A second species, *Eimeria graptemydos*, was found in *K. flavescens* from Texas by McAllister and Upton (1988, 1989), and a third, *E. mitraia*, was listed by McAllister et al. (1994).

The polystomatid trematode *Polystomatidella whartoni* was found in the urinary bladder of *K. flavescens* from Johnson County, Texas, by McAllister et al. (2008).



**Figure 15.** Adult female *Kinosternon flavescens* from Gimlet Lake, Garden County, Nebraska with extensive algal growth as she was migrating to nest. Photo by John B. Iverson.

The digenetic trematode *Telorchis corti* was found in the small intestine of *K. flavescens* in Nebraska by Brooks and Mayes (1976). Bliss (2016) found that unidentified trematode prevalence was greater in *K. flavescens* than in *K. sonoriense* or *K. subrubrum*. She also found numerous unidentified nematodes and a hemogregarine species in *K. flavescens*. Rose et al. (1989; see also Long 1993) found oxyurid nematodes of the genus *Aplectana*, as well as *Spiroxys contortus* and *Camallanus microcephalus* in the stomach of *K. flavescens* from sewage ponds in Lubbock, Texas.

Turtles also often have epibiotic algae, particularly of the genus *Arnoldiella* (formerly *Basicladia*; Boedeker et al. 2012), on the carapace (Maslin 1950; Proctor 1958; Dixon 1960; Hulse 1976), and sometimes have unidentified, nonpathogenic fungi on the plastron (Hulse 1976). Christiansen et al. (2020) described a shell disease involving invasion of natural pores by *Arnoldiella chelonum* and subsequent lateral invasion by the algae of progressively deeper epidermal lamellae, producing soft, raised lesions that may be lost, exposing the underlying bone. At least early stages of this disease were found throughout the species' range (e.g., in Coahuila, Mexico, by Williams 1961; and Texas by Davis et al. 2021). Christiansen et al. (2021) described a second shell disease in this species, of unknown cause, resulting in progressive pigment loss of the carapacial scutes, followed by loss of portions of the scute and exposure of the underlying bone. This disease appears to be limited to an industrial area south of Muscatine in eastern Iowa (Christiansen et al. 2021; Christiansen, unpubl. data).

**Blood and Immunity.** — Solitary melanin-producing macrophages were found in the liver, spleen, lung, and



kidney of *K. flavescens* by Christiansen et al. (1996) and were similar in structure to those known as melanomacrophages in fishes, amphibians, and in at least eight turtle families. Christiansen et al. (1996) determined that these cells aggregate throughout the life of Yellow Mud Turtles in the sinusoids and portal canals, making the liver progressively darker with age. The distribution throughout the body, and the phagocytic and hypothermic functions of these cells have been confirmed in chelydrid, emydid, and trionychid turtle species by Rund et al. (1998), Johnson et al. (1999), and Christiansen et al. (2005). Melanomacrophages are believed to be indicators of the accumulated humoral adaptive response in poikilotherms (Steinel and Bolnick 2017). Bliss (2016) found that white blood cell counts for *K. flavescens* were between those of *K. sonoriense* and *K. subrubrum* at 18,400 (range 10,560–38,720) cells/ml.

Bronikowski et al. (2023) investigated immunosenescence in Yellow Mud Turtles in Nebraska and found that bactericidal competence, natural antibody-mediated hemagglutination, and complement-mediated hemolysis ability each declined with age, indicating immunosenescence. All three immune variables were higher in males than females.

**Abnormal Morphology.** — Porras and Beraducci (1980) hatched three eggs in captivity in Texas after only 39 days (which is atypical; see below) and one of the hatchlings was dicephalic. Iverson (unpubl. data) observed only a single juvenile Yellow Mud Turtle with kyphosis from among more than 24291 individuals captured in western Nebraska. Individual turtles with a rugose carapace have been found at numerous locations, presumably due to the shell disease described above (Christiansen et al. 2020). Other abnormalities have not been reported, although scute anomalies are known. For example, a few individuals have been found that lacked the distinctive elevation of the ninth marginal scutes (Iverson, unpubl. data).

**Associated Turtle Species.** — Because Yellow Mud Turtles favor ephemeral wetlands, they are frequently the only turtle species found in such habitats. However, in more permanent aquatic habitats, they can be found with Painted Turtles (*Chrysemys picta*), Blandings Turtles (*Emydoidea blandingii*), Ouachita Map Turtles (*Graptemys ouachitensis*), False Map Turtles (*Graptemys pseudogeographica*), Texas Map Turtles (*Graptemys versa*), River Cooters (*Pseudemys concinna*), Rio Grande Cooters (*Pseudemys gorzugi*), Rio Grande Sliders (*Trachemys gaigeae*), Red-eared Sliders (*Trachemys scripta*), Snapping Turtles (*Chelydra serpentina*), Smooth Softshell Turtles (*Apalone mutica*), and Spiny Softshell Turtles (*Apalone spinifera*) (Degenhardt and Christiansen 1974; Christiansen and Gallaway 1984; Christiansen et al. 1985; Christiansen and Bickham 1989; Kofron and Schreiber 1987; Tuma 1993b; Rose and Manning 1996; Stuart 2000; Kelly et al. 2004; Stone et al. 2005; Bernstein and Christiansen 2011; Bonner and Littrel 2016; Lindeman et al. 2016; Huijser et al. 2017; Iverson,

pers. obs.). *Kinosternon flavescens* has also been found sympatrically with *K. subrubrum* in east Texas (Strecker 1931; Olson 1959) and Oklahoma (Kelly et al. 2004), and in the same ponds in the Big Bend region with *K. hirtipes* (Miller 2003; S. Platt, pers. comm.), sometimes in the same trap (Scudday and Miller 1986). In addition, Carpenter (1957) found *K. flavescens* hibernating with *Terrapene ornata* in Oklahoma, and Iverson (pers. obs.) has observed *T. ornata* resting in shallow water near foraging adult *K. flavescens* in western Nebraska. The range of *K. flavescens* also overlaps that of *Sternotherus carinatus*; however, the latter usually occupies lotic environments and hence is not likely to occur in microsympatry with *K. flavescens*. Although their ranges overlap, Sutton and Christiansen (1999) reported that *K. flavescens* and *Sternotherus odoratus* were not microsympatric.

**Population Status.** — Yellow Mud Turtles are locally very abundant in the central portions of their range (Ernst and Lovich 2009) in New Mexico, Texas, Oklahoma, and Kansas, but populations around the periphery of its distribution in Colorado, Nebraska, Missouri, Illinois, Iowa, and Arizona are often isolated, uncommon, at low densities, and apparently at risk of local extirpation (see above). Nothing is known of the status of the species in Mexico. The abundance of Yellow Mud Turtles across the Great Plains has no doubt increased over the past 200 years as a result of the replacement of buffalo wallows with stock tanks, cattle ponds, and windmill overflow ponds. The species seems stable there, particularly in areas like the Llano Estacado in northwest Texas and eastern New Mexico with its ca. 12,000 natural, ephemeral playa lakes and ponds spread over 88,000 km<sup>2</sup> (Rose and Manning 1996). However, peripheral populations in at least Illinois, Iowa, and Missouri are in severe decline (Christiansen et al. 2012). From the late 1970s to 2009 five known Iowa populations had been reduced to two, 13 known Illinois populations had been reduced to two, and five known Missouri populations had been reduced to two. In addition, not one of these remnant populations was known to include more than ten individuals at that time (Christiansen et al. 2012), although a few more turtles have been found at the largest Iowa population since that time (Christiansen, unpubl. data).

**Threats to Survival.** — The primary threat to this species is habitat modification; i.e., the loss of ephemeral wetlands due to agriculture, droughts, draining, ditching, filling, and declines in water tables from groundwater pumping (e.g., Dodd 1983; Christiansen et al. 2012). In addition, because Yellow Mud Turtles require a large terrestrial buffer zone (at least 90 m; Tuma 2006) around those wetlands for brumation and estivation, modification of those areas by human activities or plant succession can also negatively impact their populations (Brown and Moll 1979). The result of these activities is the increasing fragmentation of populations, often isolating very small

populations with no likelihood of gene exchange or recolonization following local extirpation. Succession of buffer habitat from prairie to woodland (especially by Black Locust trees, *Robinia pseudoacacia*) is a particular problem for eastern populations in areas with higher rainfall (Brown and Moll 1979; Christiansen et al. 2012).

Yellow Mud Turtles are also known to be adversely affected by pollution (Flickinger and Mulhern 1980; Rose et al. 1989). The decline of mud turtles in the Illinois River in Illinois is believed to be the result of uncontrolled sewage effluent from the Chicago area as well as agricultural runoff (Moll 1977, 1980). Prairie fires can also occasionally result in mud turtle mortality (Christiansen et al. 2012).

Mesopredators like skunks and raccoons (and even wading birds, bullfrogs, and predatory fish) that have flourished after the removal of top predators (e.g., wolves, coyotes, bears, wolverines, and mountain lions) represent a major hazard for mud turtles. That impact was profoundly demonstrated in Iowa after raccoons were removed from the Big Sand Mound in early 1979 (Christiansen and Gallaway 1984). Only 14 hatchlings (all turtles species) were captured at their drift fences in 1978; however, between 77 and 80 were captured during each of the following three years. Unfortunately, raccoons began recolonizing the area in 1981 and by 1982 were once again abundant, and the number of captured hatchlings decreased to only 30 in 1982.

Because of their extensive overland movements, Yellow Mud Turtles are particularly vulnerable to road mortality (Brown and Moll 1979; Gaston et al. 2001; Christiansen et al. 2012; Legler and Vogt 2013; Iverson, pers. obs.). Fortunately, this turtle is not highly sought after for the animal trade (e.g., for pets or food).

**Climate Change.** — Butler et al. (2016) modeled climate change over the next 30 and 50 years on the suitable environmental conditions for this species, and estimated that suitable habitat might increase by 65 to 179%. They also estimated and predicted that the distribution centroid for the species would shift northward ca. 26 to 57 km per decade. However, Berriozabal-Islas et al. (2020) repeated the study and estimated that *K. flavescens* would lose ca. 1 to 18% of its currently suitable habitat. These results, though significantly different, provide some optimism for the future of the species, assuming other threats to its existence can be minimized. However, the potential impacts of climate change and global warming on temperature-dependent sex determination on future sex ratios have not been modeled.

**Conservation Measures Taken.** — *Kinosternon flavescens* has been assessed as Least Concern on the IUCN Red List (van Dijk 2011) and has been included on CITES Appendix II as of 2023. It is also included under various threat categories on several U.S. state lists: Colorado, Species of Concern (Colorado Parks and Wildlife); Illinois, Endangered (Illinois Department of Natural Resources); Iowa, Endangered (Iowa Department of Natural Resources); Missouri, Endangered (Missouri

Department of Conservation); and Nebraska, Special Concern (Nebraska Game and Parks).

In 1978, the then-recognized subspecies *K. f. spooneri* was proposed for listing as Endangered by the US Fish and Wildlife Service. This proved very controversial, especially since the largest remaining populations (and proposed Critical Habitat) occupied wetlands immediately adjacent to the largest agricultural Monsanto Chemical Plant in the USA in Muscatine, Iowa. The history of this controversy was recorded by Brown and Moll (1979), Dodd (1982), and Gallaway et al. (1985). The USFWS proposal was finally abandoned in the mid-1980s after *K. f. spooneri* was synonymized with *K. flavescens*.

Yellow Mud Turtle populations across most of the range are stable, and many are included in protected areas (see below). However, peripheral populations in Iowa, Illinois, and Missouri have been in steep decline, and many remain in only small, vulnerable sites, and appear unlikely to persist (Christiansen et al. 2012). Deepening of wetlands in Iowa (Watts and Christiansen 1989; Bernstein and Christiansen 2011) and construction of new wetlands in Missouri (Christiansen et al. 2012) have apparently had limited success.

Many populations of *K. flavescens* on the Great Plains occur on federally protected US Fish and Wildlife Refuges, including Crescent Lake NWR and Valentine NWR in Nebraska; Kirwin NWR and Quivara NWR in Kansas; Salt Plains NWR and Wichita Mountains WR in Oklahoma; Bitter Lakes NWR and Grulla NWR in New Mexico; and Buffalo Lake NWR, Muleshoe NWR, and Santa Ana NWR in Texas. In addition, the species is common in a number of State and Federal Fish Hatcheries (e.g., Rock Creek in Nebraska, Bitter Lakes in New Mexico), and many other local wildlife sanctuaries and wildlife management areas (e.g., the Lee County, Iowa, Conservation Board Preserve). Many populations exist on large tracts of private ranches where some degree of protection exists. The species is not yet known to occur in any protected area in Mexico.

**Conservation Measures Proposed.** — A range-wide phylogenetic analysis is sorely needed to clarify patterns of geographic and molecular variation in this species. Those results would provide a basis for protecting that variation. The construction of farm ponds, cattle tanks, and other impoundments without fish greatly benefits these turtles. Indeed, the removal of predatory fish from wetlands should improve turtle survival. In addition, as water tables recede, deepening existing ephemeral ponds can enhance *K. flavescens* populations (e.g., Wacha and Christiansen 1989; Christiansen et al. 1990, 2012). For all inhabited wetlands where grazing is allowed, it is important to restrict ungulates to small stretches of shoreline so as not to trample turtles. Retarding succession in terrestrial buffer zones around wetlands will enhance turtle populations (Christiansen et al. 2012). In situations where roads pass close to wetlands,



the construction of under-road wildlife corridors should be considered (e.g., Huijser et al. 2017). Managing populations of mesopredators can have immediate positive effects on Yellow Mud Turtle populations.

**Captive Husbandry.** — Adult Yellow Mud Turtles do well in captivity when fed a primarily carnivorous diet (e.g., fish, lean beef, commercial fish food, small snakes, tadpoles, frogs, snails, earthworms, aquatic insect, beetles, mosquito larvae, carrion, etc.) along with chopped lettuce and algae, and provided with appropriate light and heat (Strecker 1927; Mahmoud 1968; Lardie 1975a,b, 1979, 1983; Moll 1979; Drews 1981; Thornton and Smith 1996). Eggs are easily hatched and the young do well on a diet of mealworms, earthworms, and fish. They require water deep enough to completely cover the shell, a dry area large enough to allow basking, and diurnal variation in temperature.

**Current Research.** — The long-term studies in Iowa (21 years; Christiansen et al. 1990, 2012) and western Nebraska (40 years; Iverson 2022a) have been terminated, although data analyses from those long-term studies are ongoing. However, Neil Bernstein has recently initiated field work in eastern Iowa and R.T. Kazmaier and students at West Texas A&M University in Canyon have been involved in ongoing studies of at least eight Texas populations since 2006 (McVay 2017; Zenor 2021).

**Acknowledgments.** — Paul Stone, Steve Platt, Francis Rose, and Mike Seidel provided important input during the development of this review. Drake University and Iowa Department of Natural Resources supported much of the work of Christiansen and Earlham College supported Iverson.

### Literature Cited

- AGASSIZ, L. 1857. Contributions to the Natural History of the United States of America, First Monograph. Vol. 1 part 2, North American Testudinata. Boston: Little, Brown and Co.
- ANDERSON, P.K. 1965. The Reptiles of Missouri. Columbia: University Missouri Press, 330 pp.
- ASHTON, K.G. AND FELDMAN, C.R. 2003. Bergmann's Rule in nonavian reptiles: turtles follow it, lizards and snakes reverse it. *Evolution* 57:1151–1163.
- BARBOUR, T. AND LOVERIDGE, A. 1946. First supplement to typical reptiles and amphibians. Bulletin of the Museum of Comparative Zoology 96:59–214.
- BARDWELL, J.H. 2006. Dietary habits and prey selection among Yellow Mud Turtles (*Kinosternon flavescens flavescens*). Masters Thesis, Sul Ross State University, Alpine, Texas.
- BEFUS, K.M., CARDENAS, M.B., ONG, J.B., AND ZLOTNIK, V.A. 2012. Classification and delineation of groundwater-lake interactions in the Nebraska Sandhills (USA) using electrical resistivity patterns. *Hydrogeology Journal* 20:1483–1495.
- BERGER, A.J. 2010. Conservation and recovery of the Yellow Mud Turtle (*Kinosternon flavescens*) in Mason and Tazewell Counties, Illinois. Masters Thesis, Champaign-Urbana, University of Illinois.
- BERNSTEIN, N.P. AND CHRISTIANSEN, J.L. 2011. Response of a Yellow Mud Turtle (*Kinosternon flavescens* Agassiz) community to habitat change: management implications for a nature preserve. *Natural Areas Journal* 31:414–419.
- BERRIOZABEL-ISLAS, C., RAMÍREZ-BAUTISTA, A., TORRES-ÁNGELES, F., MOTA RODRIGUES, J.F., MACÍP-RÍOS, R., AND OCTAVIO-AGUILAR, P. 2020. Climate change effects on turtles of the genus *Kinosternon* (Testudines: Kinosternidae): an assessment of habitat suitability and climate niche conservatism. *Hydrobiologia* 847:4091–4110.
- BERRY, J.F. AND BERRY, C.M. 1984. A reanalysis of geographic variation and systematics in the Yellow Mud Turtle, *Kinosternon flavescens* (Agassiz). *Annals of the Carnegie Museum* 53:185–206.
- BERRY, J.F. AND SHINE, R. 1980. Sexual dimorphism and sexual selection in turtles (Order Testudines). *Oecologia* 44:185–191.
- BLISS, E.B. 2016. Variation in parasite prevalence of kinosternid turtles across multiple hydration regimes. Masters Thesis, University of Central Oklahoma, Edmund, Oklahoma.
- BOEDEKER, C., O'KELLY, C.J., STAR, W., AND LELIAERT, F. 2012. Molecular phylogeny and taxonomy of the *Aegagrophila* clade (Cladophorales, Ulvophyceae), including the description of *Aegagropilopsis* gen. nov. and *Pseudocladophora* gen. nov. *Journal of Phycology* 48:808–825.
- BONNER, T.H. AND LITTELL, B.M. 2016. Aquatic surveys of Delaware River of Texas. Final Report to Texas Comptroller, 15 pp.
- BOURQUE, J. 2015. New mud turtles (Kinosternidae, *Kinosternon*) from the middle to late Miocene of the United States. *Journal of Paleontology* 89:821–844.
- BRITSON, C.A. 1994. Preliminary observations on the feeding behavior of three species of hatchling freshwater turtles. *ASB Bulletin* 41:100–101.
- BRONIKOWSKI, A.M., HEDRICK, A.R., KUTZ, G.A., HOLDEN, K.G., REINKE, B., AND IVERSON, J.B. 2023. Sex-specific innate immunity and ageing in long-lived fresh water turtles (*Kinosternon flavescens*: Kinosternidae). *BMC Immunology and Ageing* 20:11, 12 pp.
- BROOKS, D.R. AND MAYES, M.A. 1976. *Telorchis gutturosi* sp. n. (Trematoda: Telorchidae) from *Gratemys pseudographica* Gray in Nebraska, with reports of additional species of trematodes from Nebraska turtles. *Journal of Parasitology* 62:901–905.
- BROWN, L.E. AND MOLL, D. 1979. The status of the nearly extinct Illinois Mud Turtle with recommendations for its conservation. Milwaukee Public Museum Special Publications in Biology and Geology 3:1–49.
- BUHLMANN, K.A., AKRE, T.S.B., IVERSON, J.B., KARAPATAKIS, D., MITTERMEIER, R.A., GEORGES, A., RHODIN, A.G.J., VAN DIJK, P.P., AND GIBBONS, J.W. 2009. A global analysis of tortoise and freshwater turtle distributions with identification of priority conservation areas. *Chelonian Conservation and Biology* 8:116–149.
- BURT, C.E. 1935. Further records of the ecology and distribution of amphibians and reptiles in the Middle West. *American Midland Naturalist* 16:311–336.
- BUTLER, C.J., STANILA, B.D., IVERSON, J.B., AND STONE, P.A. 2016. Projected changes in climatic suitability for *Kinosternon* turtles by 2050 and 2070. *Ecology and Evolution* 6:7690–7705.
- CARPENTER, C.C. 1957. Hibernation, hibernacula and associated behavior of the Three-toed Box Turtle (*Terrapene carolina triunguis*). *Copeia* 1957:278–282.
- CARTER, W.A. AND COX, R. 1968. Amphibians and reptiles known from Pontotoc County, Oklahoma. *Proceedings of the Oklahoma Academy of Science* 47:66–71.
- CHILIAN, W.M. 1976. Physiological strategies of dormancy of *Kinosternon flavescens*. Masters Thesis, Texas Tech University,

- Lubbock.
- CHRISTIANSEN, J.L. AND BICKHAM, J.W. 1989. Possible historic effects of pond drying and winterkill on the behavior of *Kinosternon flavescens* and *Chrysemys picta*. *Journal of Herpetology* 23:91–94.
- CHRISTIANSEN, J.L. AND DUNHAM, A.E. 1972. Reproduction of the Yellow Mud Turtle, *Kinosternon flavescens flavescens* in New Mexico. *Herpetologica* 28:130–137.
- CHRISTIANSEN, J.L. AND GALLAWAY, B.J. 1984. Raccoon removal, nesting success, and hatchling emergence in Iowa turtles with special reference to *Kinosternon flavescens* (Kinosternidae). *Southwestern Naturalist* 29:343–348.
- CHRISTIANSEN, J.L., COOPER, J.A., AND BICKHAM, J.W. 1984. Reproduction of *Kinosternon flavescens* (Kinosternidae) in Iowa. *Southwestern Naturalist* 29:349–351.
- CHRISTIANSEN, J.L., COOPER, J.A., BICKHAM, J.W., AND SPRINGER, M.D. 1985. Aspects of the natural history of the Yellow Mud Turtle, *Kinosternon flavescens* (Kinosternidae) in Iowa: a proposed endangered species. *Southwestern Naturalist* 30:413–425.
- CHRISTIANSEN, J.L., GALLAWAY, B.J., AND BICKHAM, J.W. 1990. Population estimates and geographic distribution of the Yellow Mud Turtle (*Kinosternon flavescens*) in Iowa. *Journal of the Iowa Academy of Science* 97:105–108.
- CHRISTIANSEN, J.L., GRZYBOWSKI, J.M., AND KODAMA, R.A. 1996. Melanomacrophage aggregations and their age relationships in the Yellow Mud Turtle, *Kinosternon flavescens* (Kinosternidae). *Pigment Cell Research* 9:185–190.
- CHRISTIANSEN, J.L., SCHWESOW, C.T., AND JOHNSON, J.C. 2005. A refined method for culturing reptilian cells with comments on aggregations of melanomacrophages. *Herpetological Review* 36:279–281.
- CHRISTIANSEN, J.L., BERNSTEIN, N.P., PHILLIPS, C.A., BRIGGLER, J.T., AND KANGAS, D. 2012. Declining populations of Yellow Mud Turtles (*Kinosternon flavescens*) in Iowa, Illinois, and Missouri. *Southwestern Naturalist* 57:304–313.
- CHRISTIANSEN, J.L., DAVIS, D.R., JACOBSON, E.R., AND LADUC, T.J. 2020. Carapacial shell disease process revealed by a long-term field study of the Yellow Mud Turtle, *Kinosternon flavescens*, in Texas. *Journal of Herpetology* 54:1–8.
- CHRISTIANSEN, J.L., BERNSTEIN, N.P., AND JACOBSON, E.R. 2021. A shell disease in an Iowa, USA population of Yellow Mud Turtles, *Kinosternon flavescens*: evidence for an isolated local distribution. *Herpetological Review* 52:293–298.
- COOPER, J. 1975. Behavioral aspects of the life history of the Illinois Mud Turtle, *Kinosternon flavescens spooneri*. Masters Thesis, Drake University, Des Moines.
- COSTANZO, J.P., IVERSON, J.B., WRIGHT, M.F., AND LEE, R.E. 1995. Cold hardiness and overwintering strategies of hatchlings in an assemblage of northern turtles. *Ecology* 76:1772–1785.
- COSTANZO, J.P., LITZGUS, J.D., IVERSON, J.B., AND LEE, R.E. 2001. Cold hardiness and evaporative water loss in hatchling turtles. *Physiological and Biochemical Zoology* 74:510–519.
- DAVIS, D.R., ROBINSON, P.S., AND LADUC, T.J. 2021. *Kinosternon flavescens* (Yellow Mud Turtle). Reproduction. *Herpetological Review* 52:391–392.
- DEGENHARDT, W.G. AND CHRISTIANSEN, J.L. 1974. Distribution and habitats of turtles in New Mexico. *Southwestern Naturalist* 19:21–46.
- DEGENHARDT, W.G., PAINTER, C.W., AND PRICE, A.H. 1996. *Amphibians and Reptiles of New Mexico*. Albuquerque: University of New Mexico Press, 431 pp.
- DIXON, J.R. 1960. Epizotic algae on some turtles of Texas and Mexico. *Texas Journal of Science* 12:36–38.
- DODD, C.K., JR. 1982. A controversy surrounding an endangered species listing: the case of the Illinois Mud Turtle. *Smithsonian Herpetological Information Service* 55:1–22.
- DODD, C.K., JR. 1983. A review of the status of the Illinois mud turtle *Kinosternon flavescens spooneri* Smith. *Biological Conservation* 27:141–156.
- DODGE, C.H. AND WUNDER, C.C. 1962. Growth of turtles during continual centrifugation. *Proceedings of the Iowa Academy of Science* 69(90):594–599.
- DREWS, J.C. 1981. Pflege und Nachzucht einer wenig gehaltenen Kinosterniden-Art *Kinosternon flavescens flavescens*. *Schildkröte* 4:31–34.
- ERNST, C.H. AND BARBOUR, R.W. 1989. *Turtles of the World*. Washington DC: Smithsonian Institution Press, 313 pp.
- ERNST, C.H. AND LOVICH, J.E. 2009. *Turtles of the United States and Canada*. Baltimore: Johns Hopkins University Press, 827 pp.
- ERNST, C.H. AND ZUG, G.R. 1994. Observations on the reproductive biology of the Spotted Turtle, *Clemmys guttata*, in southeastern Pennsylvania. *Journal of Herpetology* 28:99–102.
- ETCHBERGER, C.R. 1991. Mechanistic and evolutionary considerations of temperature-dependent sex determination in turtles. Ph.D. Thesis, Indiana University, Bloomington.
- EWERT, M.A. 1985. Embryology of turtles. In: Gans, C., Billett, F., and Maderson, P.F.A. (Eds.). *Biology of the Reptilia*, Vol. 14, Development A. New York: John Wiley and Sons, pp. 75–267.
- EWERT, M.A. AND NELSON, C.E. 1991. Sex determination in turtles: diverse patterns and some possible adaptive values. *Copeia* 1991:50–69.
- EWERT, M.A., JACKSON, D.R., AND NELSON, C.E. 1994. Patterns of temperature-dependent sex determination in turtles. *Journal of Experimental Zoology* 270:3–15.
- EWERT M.A., ETCHBERGER, C.R., AND NELSON, C.E. 2004. Turtle sex-determining modes and TSD patterns, and some TSD pattern correlates. In: Valenzuela, N. and Lance, V.A. (Eds.). *Temperature-Dependent Sex Determination in Vertebrates*. Washington, DC: Smithsonian Books, pp. 21–32.
- FICHTER, L.S. 1969. Geographical distribution and osteological variation in fossil and Recent specimens of two species of *Kinosternon* (Testudines). *Journal of Herpetology* 3:113–119.
- FLICKINGER, E.L. AND MULHERN, B.M. 1980. Aldrin persists in Yellow Mud Turtle. *Herpetological Review* 11:29–30.
- GALLAWAY, B.J., BICKHAM, J.W., AND SPRINGER, M.D. 1985. A controversy surrounding an endangered species listing: the case of the Illinois Mud Turtle, another perspective. *Smithsonian Herpetological Information Service* 64:1–17.
- GASTON, M., GASTON, E., DIXON, J.R., SHERROD, L., AND FORSTNER, M.R.J. 2001. Geographic distribution: *Kinosternon flavescens* (Yellow Mud Turtle). *Herpetological Review* 32:192.
- GILMORE, C.W. 1923. A new fossil turtle, *Kinosternon arizonense*, from Arizona. *Proceedings of the U.S. National Museum* 62:1–8.
- HARTWEG, N. 1938. *Kinosternon flavescens stejnegeri*, a new turtle from northern Mexico. *Occasional Papers, Museum of Zoology, University of Michigan* 371:1–5.
- HEDRICK, A. AND IVERSON, J.B. 2017. *Kinosternon flavescens* (Yellow Mud Turtle). Female growth and longevity. *Herpetological Review* 48:178–179.
- HOLMAN, J.A. 1972. Amphibians and reptiles. In: Skinner, M.F. and Hibbard, C. *Early Pleistocene preglacial and glacial rocks and faunas of north-central Nebraska*. Bulletin of the American Museum of Natural History 148, pp. 55–71.
- HOLMAN, J.A. 1986. Butler Spring herpetofauna of Kansas (Pleistocene: Illinoian) and its climatic significance. *Journal of Herpetology* 20:568–570.



- HOLMAN, J.A. AND WINKLER, A.J. 1987. Amid-Pleistocene (Irvington) herpetofauna from a cave in southcentral Texas. *Pearce-Sellards Series, Texas Memorial Museum* 44:1–17.
- HOUSEAL, T.W., BICKHAM, J.W., AND SPRINGER, M.D. 1982. Geographic variation in the Yellow Mud Turtle, *Kinosternon flavescens*. *Copeia* 1982:567–580.
- HUISER, M.P., GINSON, K.E., AND FAIRBANK, E.R. 2017. Effectiveness of chain link turtle fence and culverts in reducing turtle mortality and providing connectivity along U.S. Hwy 83, Valentine National Wildlife Refuge, Nebraska, USA. Final report to Nebraska Department of Transportation Research Reports 201, 40 pp.
- HULSE, A.C. 1976. Carapacial and plastral flora and fauna of the Sonora Mud Turtle, *Kinosternon sonoriense* Le Conte (Reptilia, Testudines, Kinosternidae). *Journal of Herpetology* 10:45–48.
- IVERSON, J.B. 1975. Notes on Nebraska Reptiles. *Transactions of the Kansas Academy of Science* 78(1/2):51–62.
- IVERSON, J.B. 1978. Distributional problems of the genus *Kinosternon* in the American southwest. *Copeia* 1978:476–479.
- IVERSON, J.B. 1979a. On the validity of *Kinosternon arizonense* Gilmore. *Copeia* 1979:175–177.
- IVERSON, J. B. 1979b. A taxonomic reappraisal of the Yellow Mud Turtles, *Kinosternon flavescens* (Testudines: Kinosternidae). *Copeia* 1979:212–225.
- IVERSON, J.B. 1979c. The female reproductive cycle in north Florida *Kinosternon baurii* (Testudines: Kinosternidae). *Brimleyana* 1:37–46.
- IVERSON, J.B. 1979d. Reproduction and growth of the mud turtle, *Kinosternon subrubrum*, in Arkansas. *Journal of Herpetology* 13:105–111.
- IVERSON, J.B. 1982. Biomass in turtle populations: a neglected subject. *Oecologia* 55:69–76.
- IVERSON, J.B. 1984. Proportional skeletal mass in turtles. *Florida Scientist* 47(1):1–11.
- IVERSON, J.B. 1988. Neural bone patterns and the phylogeny of the turtles of the subfamily Kinosterninae. *Milwaukee Public Museum Contributions in Biology and Geology* 75:1–12.
- IVERSON, J.B. 1989. The Arizona mud turtle *Kinosternon flavescens arizonense* (Kinosternidae) in Arizona and Sonora. *Southwestern Naturalist* 34:356–368.
- IVERSON, J.B. 1990. Nesting and parental care in the turtle, *Kinosternon flavescens*. *Canadian Journal of Zoology* 68:230–233.
- IVERSON, J.B. 1991. Life history and demography of the Yellow Mud Turtle, *Kinosternon flavescens*. *Herpetologica* 47:373–395.
- IVERSON, J.B. 1992. A Revised Checklist with Distribution Maps of the Turtles of the World. Richmond, IN: Privately Printed, 363 pp.
- IVERSON, J.B. 2001. Aging Yellow Mud Turtles. In: Farrar, J. *Yellow Mud Turtles – Living on the Edge*. Nebraska 79(4):33.
- IVERSON, J.B. 2022a. Climate-mediated recruitment failure in a turtle population and its bearing on northern limits of distribution. *Chelonian Conservation and Biology* 21:181–186.
- IVERSON, J.B. 2022b. *Kinosternon flavescens* (Yellow Mud Turtle). Reproductive output. *Herpetological Review* 53:669–670.
- IVERSON, J.B. AND GREENE, D.U. 2022. Elevated reproductive output in pelomedusid turtles. *Herpetological Review* 53:400–404.
- IVERSON, J.B., BERRY, J.F., AND CHRISTIANSEN, J.L. 1983. Taxonomic status and distribution of *Kinosternon flavescens* in the northern part of its range. Final Report, USFWS Contract #14-16-0003-81-077.
- IVERSON, J.B., PROSSER, R., AND DALTON, E. 2009. Orientation in juveniles of a semiterrestrial turtle, *Kinosternon flavescens*. *Herpetologica* 65:237–245.
- IVERSON, J.B., LE, M., AND INGRAM, C.M. 2013. Molecular phylogenetics of the mud turtles of the family Kinosternidae. *Molecular Phylogenetics and Evolution* 69:929–939.
- IVERSON, J.B., LEMOS-ESPINAL, J., AND SMITH, G.R. 2018. *Kinosternon durangoense* (Durango Mud Turtle). Life history. *Herpetological Review* 49:109.
- IVERSON, J. B., LINDEMAN, P.V., AND LOVICH, J.E. 2019. Understanding reproductive allometry in turtles: a slippery slope. *Ecology and Evolution* 9:11891–11903.
- JANZEN, F.J. AND PAUKSTIS, G.L. 1991. Environmental sex determination in reptiles: ecology, evolution, and experimental design. *Quarterly Review of Biology* 66:149–179.
- JANZEN, F.J., HOFSTRA, L.A., BROOKS, R.J., CARROLL, D.M., GIBBONS, J.W., GREENE, J.L., IVERSON, J.B., LITZGUS, J.D., PARREN, S.G., ROOSENBURG, W.M., STRAIN, G.F., TUCKER, J.K., AND ULTSCH, G.R. 2018. Altered phenology of North American freshwater turtles and the importance of representative populations. *Ecology and Evolution* 8:5815–5827.
- JOHNSON, E. 1974. Zooarchaeology and the Lubbock Lake Site. In: Black, C.C. (Ed.). *History and Prehistory of the Lubbock Lake Site*. West Texas Museum Association, The Museum Journal 15, pp. 107–122.
- JOHNSON, J.C., SCHWIESOW, T., ECKWALL, A.K., AND CHRISTIANSEN, J.L. 1999. Reptilian melanomacrophages function under conditions of hypothermia: observations on phagocytic behavior. *Pigment Cell Research* 12:376–382.
- KANGAS, D.A. 1986a. Population size and some statistical predictors of abundance of *Kinosternon flavescens* in north Missouri. *Transactions of the Missouri Academy of Sciences* 20:98.
- KANGAS, D.A. 1986b. Survivorship and life table calculations for *Kinosternon flavescens*. *Transactions of the Missouri Academy of Sciences* 20:99.
- KANGAS, D.A., PALMER, K., MOLL, D., AND WALKER, R. 1991. Observations on the ecology and distribution of the Yellow Mud Turtle *Kinosternon flavescens* in northeastern Missouri. Report to the Missouri Department of Conservation.
- KASPAR, S. 2013. *Kinosternon flavescens flavescens* (Yellow Mud Turtle). Road-carrion feeding. *Herpetological Review* 44:305.
- KAZMAIER, R.T., GANN, W.J., RUTHVEN, D.C. III, AND SYNATSKA, D.R. 2021. Variation in the diet of Greater Roadrunners (*Geococcyx californianus*) in a mesquite-thornscrub ecosystem. *Southwestern Naturalist* 66:136–149.
- KELLY, J., STRONG, J., BAHM, J., AND COOPER, A.L. 2004. Mammal, bird and herpetological inventory of Chicksaw National Recreation Area NPS. Final Report to Oklahoma Natural Heritage Inventory, 6 pp.
- KILLEBREW, F.C. 1975. Mitotic chromosomes of turtles. III. The Kinosternidae. *Herpetologica* 31:398–403.
- KOFRON, C.P. AND SCHREIBER, A.A. 1985. Ecology of two endangered aquatic turtles in Missouri: *Kinosternon flavescens* and *Emydoidea blandingi*. *Journal of Herpetology* 19:27–40.
- KOFRON, C.P. AND SCHREIBER, A.A. 1987. Observations on aquatic turtles in a northeastern Missouri marsh. *Southwestern Naturalist* 32:517–521.
- KUCHLING, G.R. 1999. *The Reproductive Biology of the Chelonia*. Berlin: Springer, Zoophysiology 38, 223 pp.
- KUEHN, S.R. AND VANDERWARKER, A.M. 2015. Lamb site zooarchaeological analysis: early Mississippian faunal exploitation in the central Illinois River valley. *Illinois Archaeology* 27: 236–253.
- LADUC, T. AND CHRISTIANSEN, J.L. 2007. Preliminary demographics of *Kinosternon flavescens* in the Trans-Pecos. Abstract, ASIH/HL/SSAR Annual Meetings, St. Louis.
- LADUC, T. AND CHRISTIANSEN, J.L. 2012. Should I stay or should I

- go? Temporal persistence and activity of *Kinosternon flavescens* (Yellow Mud Turtle) in permanent tanks in the Chihuahuan Desert. Abstract, World Congress of Herpetology, Vancouver, Canada.
- LANGE, M.J. AND KAZMAIER, R.T. 2009. Demography of the Yellow Mud Turtle in the Texas Panhandle II: sex ratio, reproduction and growth. Abstract, Turtle Survival Alliance 7th Annual Meeting.
- LARDIE, R.L. 1975a. Courtship and mating behavior in the Yellow Mud Turtle, *Kinosternon flavescens*. *Journal of Herpetology* 9:223–227.
- LARDIE, R.L. 1975b. Observations of reproduction in *Kinosternon*. *Journal of Herpetology* 9:260–264.
- LARDIE, R.L. 1978. Additional observations on courtship and mating in the Plains Yellow Mud Turtle, *Kinosternon flavescens flavescens*. *Bulletin of the Oklahoma Herpetological Society* 3(4):70–72.
- LARDIE, R.L. 1979. Eggs and young of the Plains Yellow Mud Turtle. *Bulletin of the Oklahoma Herpetological Society* 4(2/3):24–32.
- LARDIE, R.L. 1983. Aggressive interactions and territoriality in the Yellow Mud Turtle, *Kinosternon flavescens flavescens* (Agassiz). *Bulletin of the Oklahoma Herpetological Society* 8:68–81.
- LEGLER, J.L. AND VOGT, R.C. 2013. *The Turtles of Mexico: Land and Freshwater Forms*. Berkeley: University of California Press, 416 pp.
- LIGON, D.B. 2001. Coadaptation of physiology and behavior: variation in estivation among mud turtles (*Kinosternon* spp.). Masters Thesis, Oklahoma State University, Stillwater.
- LIGON, D.B. AND PETERSON, C.C. 2002. Physiological and behavioral variation in estivation among mud turtles (*Kinosternon* spp.). *Physiological and Biochemical Zoology* 75:283–293.
- LIGON, D.B., SANDERS, T., AND KAZMAIER, R. 2011. What do turtles do when they ain't doing nothing? Winter ecology of the Yellow Mud Turtle (*Kinosternon flavescens*). Abstract, Turtle Survival Alliance 9th Annual Conference.
- LINDEMAN, P.V., STUART, J.N., AND KILLEBREW, F.C. 2016. *Graptemys versa* Stejneger 1925 – Texas Map Turtle. In: Rhodin, A.G.J., Iverson, J.B., van Dijk, P.P., Stanford, C.B., Goode, E.V., Buhlmann, K.A., and Mittermeier, R.A. (Eds.). *Conservation Biology of Freshwater Turtles and Tortoises: A Compilation Project of the IUCN/SSC Tortoise and Freshwater Turtle Specialist Group*. *Chelonian Research Monographs* 5(9a):093.1–10.
- LONG, D.R. 1984. Inter-specific comparisons of growth relationships in chelonians. *British Journal of Herpetology* 6:405–407.
- LONG, D.R. 1985. Lipid utilization during reproduction in female *Kinosternon flavescens*. *Herpetologica* 41:58–65.
- LONG, D.R. 1986a. Clutch formation in the turtle, *Kinosternon flavescens* (Testudines: Kinosternidae). *Southwestern Naturalist* 31:1–8.
- LONG, D.R. 1986b. Lipid content and delayed emergence of hatchling Yellow Mud Turtles. *Southwestern Naturalist* 31:244–246.
- LONG, D.R. 1993. Yellow mud turtles. *Reptile and Amphibian Magazine* 1993(Mar/Apr), pp. 22–26.
- LONG, D.R. AND ROSE, F.L. 1989. Pelvic girdle size relationships in three turtle species. *Journal of Herpetology* 23:315–318.
- MAHMOUD, I.Y. 1967. Courtship behavior and sexual maturity in four species of kinosternid turtles. *Copeia* 1967:314–319.
- MAHMOUD, I.Y. 1968. Feeding behavior in kinosternid turtles. *Herpetologica* 24:300–305.
- MAHMOUD, I.Y. 1969. Comparative ecology of the kinosternid turtles of Oklahoma. *Southwestern Naturalist* 14:31–66.
- MAHMOUD, I.Y. AND KLICKA, J. 1972. Seasonal gonadal changes in kinosternid turtles. *Journal of Herpetology* 6:183–189.
- MASLIN, P.T. 1950. Herpetological notes and records from Colorado. *Herpetologica* 6:89–95.
- MCALLISTER, C.T. AND UPTON, S.J. 1988. *Eimeria trachemydis* (Acicomplexa: Eimeridae) and other eimerians from the Red-eared Slider, *Trachemys scripta elegans* (Reptilia: Testudines), in northcentral Texas. *Journal of Parasitology* 74:1014–1017.
- MCALLISTER, C.T. AND UPTON, S.J. 1989. The coccidia (Apicomplexa: Eimeridae) of Testudines, with descriptions of three new species. *Canadian Journal of Zoology* 67:2459–2467.
- MCALLISTER, C.T., UPTON, S.J., AND TRAUTH, S.E. 1994. New host and geographic records for coccidia (Apicomplexa: Eimeridae) from North American turtles. *Journal of Parasitology* 80:1045–1049.
- MCALLISTER, C.T., BURSEY, C.R., AND TRAUTH, S.E. 2008. New host and geographic records for some endoparasites (Myxosporidia, Trematoda, Cestoda, Nematoda) of amphibians and reptiles from Arkansas and Texas. *Comparative Parasitology* 75:241–254.
- MCCORD, R.D. 2016. What is *Kinosternon arizonense*? *Historical Biology* 28:310–315.
- MCVAY, T.J. 2017. Variation in demography of turtles in a semi-arid landscape, with emphasis on the annual survival of Yellow Mud Turtle populations. Masters Thesis, West Texas A&M University, Canyon.
- MEDINA-CASTAÑEDA, C.I., BRAVO-CUEVAS, V.M., AND CRUZ, J.A. 2022. Turtles from the Late Pleistocene of Hidalgo and Puebla and their paleobiographic and paleoclimatic significance. *Quaternary International* 634:111–123.
- MILLER, D. 2003. Tracking Big Bend Mud Turtles in Texas. *Reptiles Magazine* 11(12):32–41.
- MINTON, S.A. 1959. Observations on amphibians and reptiles of the Big Bend region of Texas. *Southwestern Naturalist* 3:28–54.
- MOLL, D. 1977. Ecological investigations of turtles in a polluted ecosystem: the central Illinois River and adjacent flood plain lakes. Ph.D. Thesis, Illinois State University.
- MOLL, D. 1979. Subterranean feeding by the Illinois mud turtle, *Kinosternon flavescens spooneri* (Reptilia, Testudines, Kinosternidae). *Journal of Herpetology* 13:371–373.
- MOLL, D. 1980. Dirty river turtles. *Natural History* 89(5):43–49.
- MOLL, E.O. 1979. Reproductive cycles and adaptations. In: Harless, M. and Morlock, H. (Eds.). *Turtles: Perspectives and Research*. New York: Wiley and Sons, pp. 305–331.
- MURPHY, J.C. AND CORN, M.J. 1977. A turtle vanishes (letter). *Natural History* 86(7):8.
- NICKELL, Z., VARRIANO, S., PLEMMONS, E., AND MORAN, M.D. 2018. Ecosystem engineering by Bison (*Bison bison*) wallowing increases arthropod community heterogeneity in space and time. *Ecosphere* 9:1–13.
- OLSON, R.E. 1959. Notes on some Texas herptiles. *Herpetologica* 15:48.
- PACKARD, M.J. 1980. Ultrastructural morphology of the shell and shell membrane of eggs of Common Snapping Turtles (*Chelydra serpentina*). *Journal of Morphology* 165:187–204.
- PACKARD, M.J., HIRSCH, K.F., AND IVERSON, J.B. 1984a. Structure of shells from eggs of kinosternid turtles. *Journal of Morphology* 181:9–20.
- PACKARD, M.J., PACKARD, G.C., AND IVERSON, J.B. 1984b. Morphology of shell formation in eggs of the turtle *Kinosternon flavescens*. *Journal of Morphology* 181:21–28.
- PARMLEY, D. 1990. A Late Holocene herpetofauna from Montague County, Texas. *Texas Journal of Science* 42:412–415.
- PARMLEY, D. 1992. Turtles from the Late Hemphillian (Latest Miocene) of Knox County, Nebraska. *Texas Journal of Science* 44:339–348.
- PLATT, D.R. 1969. Natural history of the Hognose Snakes *Heterodon platyrhinos* and *Heterodon nasicus*. University of Kansas Publications, Museum of Natural History 18:253–420.



- POPE, C.H. 1939. Turtles of the United States, Canada, and Baja California. Ithaca, New York: Cornell University Press, 542 pp.
- PORRAS, L. AND BERADUCCI, J. 1980. Dicephalic *Kinosternon*. Herpetological Review 11:35.
- PRESTON, R.E. 1979. Late Pleistocene cold-blooded vertebrate faunas from the mid-continental United States. I. Reptilia: Testudines, Crocodilia. University of Michigan Papers in Paleontology 19:1–53.
- PROCTOR, V.M. 1958. The growth of *Basicladia* on turtles. Ecology 39:634–645.
- PUNZO, F. 1974. A qualitative and quantitative study of the food items of the Yellow Mud Turtle, *Kinosternon flavescens* (Agassiz). Journal of Herpetology 8:269–271.
- RAINEY, G. 1933. The Cherokee Strip. Guthrie, Oklahoma: Cooperation Publishing, 410 pp.
- REDDELL, J.R. 1971. Checklist of cave fauna of Texas VI. Additional records of vertebrata. Texas Journal of Science 22:139–158.
- REYNOLDS, R.P., GOTTE, S.W., AND ERNST, C.H. 2007. Catalog of type specimens of Recent Crocodilia and Testudines in the National Museum of Natural History, Smithsonian Institution. Smithsonian Contributions to Zoology 626:1–56.
- ROSE, F.L. 1980. Turtles in arid and semi-arid regions. Bulletin of the Ecological Society of America 61(2):89.
- ROSE, F.L. AND MANNING, R. 1996. Comments on the biology of the Slider, *Trachemys scripta* (Reptilia: Emydidae), inhabiting man-made ponds in west Texas. Texas Journal of Science 48:191–206.
- ROSE, F.L., LONG, D.R., PENCE, D.B., AND WAID, D.D. 1989. Gastric oxyuriasis and its consequences in Yellow Mud Turtles (*Kinosternon flavescens*) associated with sewage effluent. Herpetopathologia 1(2):53–64.
- ROSEN, P.C. 2008. Aridlands turtles II: conservation status. Sonoran Herpetologist 21:130–135.
- ROSEN, P.C., SARTORIUS, S.S., SCHWALBE, C.R., HOLM, P.A., AND LOWE, C.H. 1996. Draft annotated checklist of the amphibians and reptiles of the Sulfur Springs Valley, Cochise County, Arizona. In: Tellman, B., Finch, D.M., Edminster, C., and Hamre, R. (Eds.). The Future of Arid Grasslands: Identifying Issues, Seeking Solutions. Fort Collins, Colorado: USDA Forest Service Conference Proceedings RMRS-P-3, pp. 65–80.
- RUND, C.R., CHRISTIANSEN, J.L., AND JOHNSON, J.C. 1998. In vitro culture of melanomacrophages from the spleen and liver of turtles: comments on melanomacrophage morphology. Pigment Cell Research 11:114–119.
- SCHIPPERIJN, A.J.M. 1987. A cross between *Kinosternon subrubrum* and *K. flavescens*. Lacerta 45(4):62–64.
- SCUDDAY, J.F. AND MILLER, D.J. 1986. The status of the Chihuahuan Mud Turtle, *Kinosternon hirtipes murrayi*. U.S. Fish and Wildlife Service Report, Contract 14-16-002-85-903, 40 pp.
- SEIDEL, M.E. 1976. *Kinosternon flavescens flavescens* (Yellow Mud Turtle). Herpetological Review 7:122.
- SEIDEL, M.E. 1978a. Terrestrial dormancy in the turtle *Kinosternon flavescens*: respiratory metabolism and dehydration. Comparative Biochemistry and Physiology 61A:1–4.
- SEIDEL, M.E. 1978b. *Kinosternon flavescens*. Catalogue of American Amphibians and Reptiles 216:1–4.
- SEIDEL, M.E. AND REYNOLDS, S.L. 1980. Aspects of evaporative water loss in the mud turtles *Kinosternon hirtipes* and *Kinosternon flavescens*. Comparative Biochemistry and Physiology 67A:593–598.
- SEIM, J.T. 2015. Population structure and habitat association of aquatic Testudines in Quivira National Wildlife Refuge. Masters Thesis, Fort Hays State University, Kansas.
- SEMMLER, R.C. 1979. Spatial and temporal activities of the Yellow Mud Turtle, *Kinosternon flavescens*, in eastern New Mexico. Masters Thesis, University of New Mexico, Albuquerque.
- SERB, J.M., PHILLIPS, C.A., AND IVERSON, J.B. 2001. Molecular phylogeny and biogeography of *Kinosternon flavescens* based on complete mitochondrial control region sequences. Molecular Phylogenetics and Evolution 18:149–162.
- SLAVENS, F.L. AND SLAVENS, K. 1999. Reptiles and amphibians in captivity. Breeding – longevity and inventory, current January 1, 1999. Seattle, Washington: Slavewave, 400 pp.
- SMITH, H.M. 1950. Handbook of Amphibians and Reptiles of Kansas. Miscellaneous Publications of the University of Kansas Museum of Natural History No. 2, 336 pp.
- SMITH, P.W. 1951. A new frog and a new turtle from the western Illinois sand prairies. Bulletin of the Chicago Academy of Science 9:189–199.
- SMITH, P.W. 1961. The amphibians and reptiles of Illinois. Illinois Natural History Survey Bulletin 28:1–298.
- SNIDER, A.T. AND BOWLER, J.K. 1992. Longevity of reptiles and amphibians in North American collections. Second Edition. Society for the Study of Amphibians and Reptiles, Herpetological Circular 21:1–40.
- SPARKS, D.W., BURR, A.G., BASS, M.N., AND LIGGETT, G.A. 1999. New county distribution records of amphibians and reptiles from southwestern Kansas. Herpetological Review 30:120–121.
- SPINKS, P.Q., THOMSON, R.C., GIDIS, M., AND SHAFFER, H.D. 2014. Multilocus phylogeny of the New-World mud turtles (Kinosternidae) supports the traditional classification of the group. Molecular Phylogenetics and Evolution 76:254–260.
- STEEN, D.A., GIBBS, J.P., BUHLMANN, K.A., CARR, J.L., COMPTON, B.W., CONGDON, J.D., DOODY, J.S., GODWIN, J.C., HOLCOMB, K.L., JACKSON, D.R., JANZEN, F.J., JOHNSON, G., JONES, M.Y., LAMER, J.T., LANGEN, T.A., PLUMMER, M.V., ROWE, J.W., SAUMURE, R.A., TUCKER, J.K., AND WILSON, D.S. 2012. Terrestrial habitat requirements of nesting freshwater turtles. Biological Conservation 150:121–128.
- STEINEL, N.C. AND BOLNICK, D.I. 2017. Melanomacrophage centers as a histological indicator of immune function in fish and other poikilotherms. Frontiers of Immunology 8(827):1–8.
- STOCK, A.D. 1972. Karyological relationships in turtles (Reptilia: Chelonia). Canadian Journal of Genetics and Cytology 14:859–868.
- STONE, P.A., POWERS, S.M., AND BABB, M.E. 2005. Freshwater turtle assemblages in central Oklahoma farm ponds. Southwestern Naturalist 50:166–171.
- STONE, W. 1903. A collection of reptiles and batrachians from Arkansas, Indian Territory, and western Texas. Proceedings of the Academy of Natural Sciences, Philadelphia 55:538–542.
- STRECKER, J.K. 1927. Observations on the food habits of Texas amphibians and reptiles. Copeia 162:6–9.
- STRECKER, J.K. 1931. A catalogue of the amphibians and reptiles of Travis County, Texas. Contributions of the Baylor University Museum 23:1–16.
- STUART, J.N. 2000. Additional notes on native and non-native turtles of the Rio Grande Drainage Basin, New Mexico. Bulletin of the Chicago Herpetological Society 35(10):229–235.
- SUTTON, K.L. AND CHRISTIANSEN, J.L. 1999. The habitat and distribution of the Stinkpot, *Sternotherus odoratus*, in Iowa. Proceeding of the Iowa Academy of Science 106:63–65.
- TAYLOR, E.H. 1933. Observations on the courtship of turtles. University of Kansas Science Bulletin 21:269–271.
- THOMSON, R.C., SPINKS, P.Q., AND SHAFFER, H.B. 2021. A global phylogeny of turtles reveals a burst of climate-associated diversification on continental margins. Proceedings of the National Academy of Sciences 118:7, e2012215118, 10 pp.

- THORNTON, O.W., JR. AND SMITH, J.R. 1996. Notes on the incubation of eggs of the Yellow Mud Turtle *Kinosternon flavescens flavescens*. Bulletin of the Chicago Herpetological Society 31:204–205.
- TTWG [TURTLE TAXONOMY WORKING GROUP: RHODIN, A.G.J., IVERSON, J.B., BOUR, R., FRITZ, U., GEORGES, A., SHAFFER, H.B., AND VAN DIJK, P.P.]. 2017. Turtles of the World: Annotated Checklist and Atlas of Taxonomy, Synonymy, Distribution, and Conservation Status (8th Ed.). Chelonian Research Monographs 7:1–292.
- TTWG [TURTLE TAXONOMY WORKING GROUP: RHODIN, A.G.J., IVERSON, J.B., BOUR, R., FRITZ, U., GEORGES, A., SHAFFER, H.B., AND VAN DIJK, P.P.]. 2021. Turtles of the World: Annotated Checklist and Atlas of Taxonomy, Synonymy, Distribution, and Conservation Status (9th Ed.). Chelonian Research Monographs 8:1–472.
- TUMA, M.W. 1993a. Life history notes. *Kinosternon flavescens* (Yellow Mud Turtle). Multiple nesting. Herpetological Review 24:31.
- TUMA, M.W. 1993b. Ecology of the state endangered Yellow Mud Turtle, *Kinosternon flavescens* in Henry Co., Illinois. Masters Thesis, Eastern Illinois University, Charleston.
- TUMA, M.W. 2006. Range, habitat use, and seasonal activity of the Yellow Mud Turtle (*Kinosternon flavescens*) in northwestern Illinois: implications for site-specific conservation and management. Chelonian Conservation and Biology 5:108–120.
- VAN DIJK, P.P. 2011. *Kinosternon flavescens*. The IUCN Red List of Threatened Species 2011:e.T163421A97380845.
- VOGT, R.C., BULL, J.J., MCCOY, C.J., AND HOUSEAL, T.W. 1982. Incubation temperature influences sex determination in kinosternid turtles. Copeia 1982:480–482.
- WACHA, R.S. AND CHRISTIANSEN, J.L. 1976. Coccidian parasites from Iowa turtles: systematics and prevalence. Journal of Protozoology 23:57–63.
- WATTS, M.R., AND CHRISTIANSEN, J.L. 1989. Turtle use and succession in a pool created in the bottom of a dry lake. Journal of the Iowa Academy of Sciences 96(1):A37.
- WEBSTER, C. 1986. Substrate preference and activity in the turtle, *Kinosternon flavescens flavescens*. Journal of Herpetology 20:477–482.
- WILLIAMS, K.L. 1961. Aberrant mud turtles, *Kinosternon flavescens*, from Coahuila, Mexico. Herpetologica 17:72.
- WILLIAMS, T.M. 1996. Senescent changes in the kidney of the yellow mud turtle *Kinosternon flavescens*. Ph.D. Thesis, Drake University, Des Moines, Iowa.
- WUNDER, C.C., DODGE, C.H., AND DUTTWEILER, C.G. 1962. Growth of juvenile turtles during continual exposure to high gravity. American Zoologist 2:569.
- ZENOR, J.A. 2021. Exploring demographic patterns in Yellow Mud Turtles: trade-offs between survival and reproduction. Masters Thesis, West Texas A&M University, Canyon.

#### Citation Format for this Account:

IVERSON, J.B. AND CHRISTIANSEN, J.L. 2023. *Kinosternon flavescens* (Agassiz 1857) – Yellow Mud Turtle, Casquito Amarillo. In: Rhodin, A.G.J., Iverson, J.B., van Dijk, P.P., Stanford, C.B., Goode, E.V., Buhlmann, K.A., and Mittermeier, R.A. (Eds.). Conservation Biology of Freshwater Turtles and Tortoises: A Compilation Project of the IUCN/SSC Tortoise and Freshwater Turtle Specialist Group. Chelonian Research Monographs 5(17):121.1–26. doi: 10.3854/crm.5.121.flavescens.v1.2023; www.iucn-tftsg.org/cbftt/.