CONSERVATION BIOLOGY OF FRESHWATER TURTLES AND TORTOISES

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Kinosternon sonoriense (LeConte 1854) –
Sonora Mud Turtle, Desert Mud Turtle, Sonoyta Mud Turtle, Casquito de Sonora

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Summary. – The Sonora Mud Turtle, *Kinosternon sonoriense* (Family Kinosternidae), is a medium-sized kinosternid (females to 175 mm SCL, males to 168 mm SCL) found in lentic and lotic aquatic habitats in desert and montane regions of the southwestern United States and northwestern Mexico. Two allopatric subspecies are currently recognized, *K. s. sonoriense* and *K. s. longifemorale*. Although primarily aquatic, individuals frequently move along aquatic corridors, make extensive overland movements, and estivate on land. *Kinosternon sonoriense* is omnivorous, matures in 5–9 yrs, and exhibits considerable geographic variation in growth and maturation. Average clutch size is usually related to female body size and ranges from 3 to 11 eggs. Eggs average 28–33 mm in length, 14–19 mm in width, and weigh 5–6 g. Females produce one to two clutches per year (potential maximum of four), and embryos exhibit temperature-dependent sex determination. The loss and degradation of natural aquatic habitats, including streams, spring runs, and ciénegas, is a primary threat to conservation of *K. sonoriense*, particularly to the very small, isolated populations of *K. s. longifemorale*. The loss of natural habitats has been partially mitigated by the widespread construction of impoundments; however, many impoundments are now experiencing dam failure and siltation, further contributing to habitat loss. In addition, the establishment of non-native predator species, particularly Virile Crayfish and American Bullfrogs, are known threats to juvenile *K. s. sonoriense*. The status and ecology of both subspecies have been studied in recent years, mainly in the United States, and conservation efforts have been focused primarily on the declining populations of *K. s. longifemorale*.

Distribution. – Mexico, USA. *Kinosternon sonoriense* occurs from southwestern New Mexico and western Chihuahua west through much of Arizona and Sonora. Historically known populations in the lower Colorado River basin of southwestern Arizona, southeastern California, and possibly northern Baja California and southern Nevada have apparently been extirpated.

Synonymy. – *Kinosternum sonoriense* LeConte 1854, *Cinosternum sonoriense*, *Cinosternon sonoriense*, *Thyrosternum sonoriense*, *Kinosternon sonoriense*, *Kinosternum henrici* LeConte 1859, *Cinosternum henrici*, *Cinosternon henrici*, *Swanka henricii*.

Subspecies. – Two currently recognized: *Kinosternon sonoriense sonoriense* LeConte 1854 (Desert Mud Turtle) and *Kinosternon sonoriense longifemorale* Iverson 1981 (Sonoyta Mud Turtle).

Status. – IUCN 2021 Red List: *K. sonoriense* [species]: Near Threatened (NT, assessed 2011), *K. s. longifemorale* [subspecies]: Critically Endangered (CR A3c, assessed 2017); CITES: not listed; US ESA: *K. s. longifemorale*: Endangered; Mexico: *K. s. longifemorale*: Endangered; Arizona: Species of Greatest Conservation Need (both subspecies); California: Species of Special Concern (*K. s. sonoriense*); New Mexico: Species of Greatest Conservation Need (*K. s. sonoriense*).

Taxonomy. — *Kinosternon sonoriense* was originally described as *Kinosternum sonoriense* by LeConte (1854) based on a single specimen "from Tucson in Sonora" (now = Tucson, Pima Co., Arizona, USA). That holotype has apparently been lost (Malnate 1971). Gray (1856) first assigned this species to *Kinosternon*, as currently spelled; it has also been included in other genera or various spellings of genera, including *Cinosternum*, *Thyrosternum*,

Figure 1. Adult *Kinosternon sonoriense sonoriense* from Blackwater Hole, Peloncillo Mountains, New Mexico. Photo by William M. Hammond.

Cinosternon, and *Swanka* (see synonymies in Smith and Smith 1980, Iverson 1981, Fritz and Havaš 2007, and TTWG 2017, 2021). LeConte (1859) also described *Kinosternum henrici* based on a specimen collected in "New Mexico" (data with holotype existing in the Academy of Natural Sciences in Philadelphia = "Gila River, New Mexico"), which was incorrectly restricted to "vicinity of Las Cruces [New Mexico, USA]" by Schmidt (1953); this taxon is considered a junior synonym of *K. sonoriense* (TTWG 2017, 2021). *Kinosternon sonoriense* is the sister taxon of *Kinosternon hirtipes* (Thomson et al. 2021) and the two comprise the *K. hirtipes* species group (*sensu* Iverson 1981 and Legler and Vogt 2013).

The relationship of this species group to its congeners, such as species of the *K. scorpioides* group, is not fully resolved (Iverson 1998; Iverson et al. 2013; Spinks et al. 2014; Thomson et al. 2021).

Iverson (1976, 1981) reviewed the literature for *K. sonoriense*, provided morphometric comparisons with its hypothesized sister taxon *K. hirtipes* (Iverson 1981; Iverson et al. 1991, 2013), included it in family-wide phylogenetic analyses (Iverson 1991; Iverson et al. 2013), and mapped its known distribution (Iverson 1992). Pritchard (1979), Smith and Smith (1980), Ernst et al. (1994), and Ernst and Lovich (2009) provided general reviews of *K. sonoriense*.

Figure 2. Subspecific variation in plastron shape. *Left*: *Kinosternon sonoriense sonoriense* from Chihuahua, Mexico. *Right*: *Kinosternon sonoriense longifemorale* from Quitobaquito Spring, Arizona. Photos by John B. Iverson.

Figure 3. Variation in head pattern in *Kinosternon sonoriense sonoriense*. *Left*: Male from Maverick Spring, Peloncillo Mountains, New Mexico. Photo by Paul A. Stone. *Middle*: Juvenile from East Fork of Gila River, New Mexico. Photo by Jonathan Duran. *Right*: Juvenile from Lower Bow Tank, Peloncillo Mountains, New Mexico. Photo by Brooke N. Massengill.

Iverson (1981) documented significant geographic variation in Sonora Mud Turtles and recognized two allopatric subspecies: *K. s. sonoriense,* which includes nearly all populations of the species throughout its range, and *K. s. longifemorale*, described from Sonoyta, Sonora, Mexico and endemic to the Río Sonoyta basin in Arizona and Sonora. Genetic evidence supports the recognition of *K. s. longifemorale* as a distinct form (Rosen et al. 2006). Additional unpublished morphometric analyses suggest additional diagnosable geographic variation in morphometry in Sonora, with populations in the Upper Yaqui basin diverging from other populations (Iverson, unpubl. data). Inclusion of additional samples from Sonora is sorely needed.

Standard English names are Sonora Mud Turtle for *K. sonoriense*, Desert Mud Turtle for *K. s. sonoriense*, and Sonoyta Mud Turtle for *K. s. longifemorale* (Iverson et al. 2017). In the literature, "Sonora" and "Sonoran" have been used interchangeably (e.g., Hall and Steidl 2007; Hensley et al. 2010). Standard Spanish names are *Casquito de Sonora* for the species, *Casquito Común de Sonora* for the nominal subspecies, and *Casquito de Sonoyta* for *K. s. longifemorale* (Liner and Casas-Andreu 2008).

Description. — *Kinosternon s. sonoriense* is a medium-sized kinosternid with a maximum recorded straight midline carapace length (SCL) of 175 mm for females (Rosen 1987) and 168 mm for males (van Loben Sels et al. 1997); maximum size for *K. s. longifemorale* is 148 mm SCL in females and 137 mm SCL in males (Rosen and Stone 2017). *Kinosternon sonoriense* is the only large *Kinosternon* that does not have strongly male-biased sexual size dimorphism (Ceballos et al. 2013). Females are typically larger than males, though the dimorphism is minimal (Gibbons and Lovich 1990; van Loben Sels et al. 1997; Stone 2001). There is considerable geographic variation in average body size, with mean female SCL varying from 112 to 145 mm among populations (Rosen 1987). Hatchlings may be as small as 22.3 mm SCL and 20.0 mm plastron length (Iverson 1991) and weigh 1–3 g (van Loben Sels et al. 1997).

The following description is adapted from Iverson (1976). The adult carapace is weakly tricarinate, with the medial keel most apparent. Some individuals possess three well-defined keels, whereas most have only the median keel present with hints of lateral keels, and still others have smooth shells, flat on top. Juveniles always have evidence of three keels. The first vertebral scute usually contacts the second marginal scutes, and the axillary scutes contact the eighth marginal scutes. The ninth marginal scutes are not elevated above preceding marginals, the tenth marginals are higher than the ninth, and the eleventh marginals may or may not be as high as tenth marginals. The nuchal bone very often contacts the first neural bone. The carapace is brown to olive, occasionally yellowish, with seams more darkly marked.

Two well-developed plastral hinges border the abdominal scutes, and the plastron is emarginate posteriorly. The posterior width of the plastral forelobe averages 47% and 49% of SCL in males and females, respectively. The interpectoral seams are less than one-half the medial length of gular scutes and less than 8% (average 5% in males and 4% in females) of maximum plastron length. The axillary scutes almost always broadly contact the inguinal scutes. Plastron color varies from cream-yellow to reddish brown, often with dark brown seams. Bridge areas are dark brown. In hatchlings, the carapace is brown, with yellow or orange marks on the shell margin, the bridge is dark brown to black, and the plastron creamy yellow to orange with a brown to black, foliate, central figure applied to the seams.
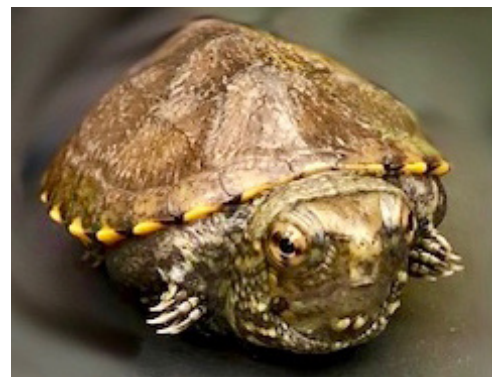

Figure 4. Hatchling *Kinosternon sonoriense longifemorale*, captive bred from Quitobaquito Spring assurance colony at the Arizona Sonoran Desert Museum. Photo by Howard G. Byrne.
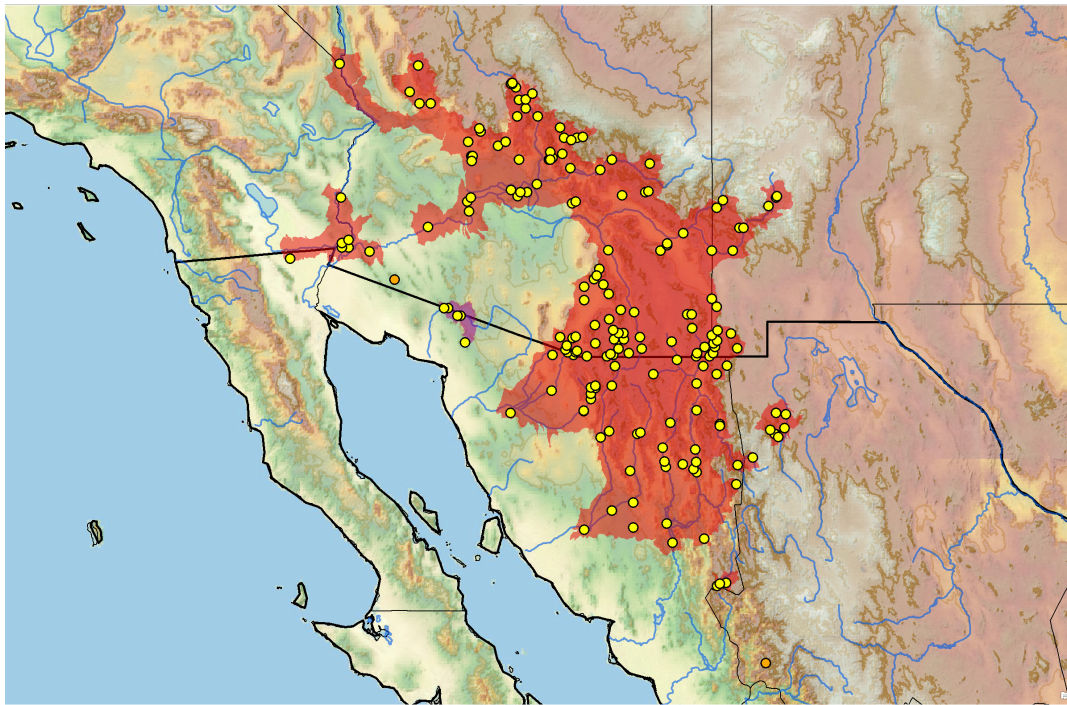
Figure 5. Presumed historical indigenous distribution of *Kinosternon sonoriense* in southwestern USA (Arizona, California, Nevada, and New Mexico) and northwestern Mexico (Chihuahua and Sonora). Yellow dots = museum and literature occurrence records of native populations based on Iverson (1992), Legler and Vogt (2013), other literature sources, and authors' data; orange dots = possibly misidentified or inaccurately reported specimens; red shading = *K. sonoriense sonoriense*, purple shading = *K. sonoriense longifemorale*. Distribution based on 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 (Buhlmann et al. 2009; TTWG 2021), and adjusted based on data from authors' and other sources.

At all ages the skin is dark gray. The head and neck bear cream colored mottlings that often form at least one pair of stripes on each side. From the orbit one stripe extends above the tympanum and the other passes below it, after intersecting the angle of the jaw. Head stripes are very distinctive and colored yellow in hatchlings. The degree of mottling varies among individuals and may fade with age (C. Drost, pers. comm.). A yellow or cream stripe also extends from the palmar surface of each foot to the base of the limb along its posterior surface in hatchlings and many adults. The nasal scale is large and triangular, rhomboidal, or bell-shaped (never furcate behind). The largest two pairs of chin barbels are very long; at least one pair is more than half the diameter of the orbit in length. Adult females have short, stubby tails, and males have long, thick tails. Both sexes have terminal tail spines, but they are larger in males. Only males have a patch of tuberculate scales (clasping organs) on the posterior surface of the crus and the thigh of each hind leg. Dimorphism in other characters is discussed by Hulse (1976b). *Kinosternon sonoriense longifemorale* differs from the nominate subspecies in its relatively long interfemoral seam, a relatively short interanal seam, a relatively narrow gular scute, and a relatively wide first vertebral scute (Iverson 1981).

Kinosternon sonoriense can be distinguished from all other mud turtles by the combination of size, basically tricarinate carapace, posteriorly notched plastron, wide first vertebral scute, long chin barbels, clasping organs, and bell-shaped nasal scale.

Distribution. — The presumed historical indigenous range of *K. sonoriense* is approximately 170,011 km^2 in the southwestern United States and northwestern Mexico (Buhlmann et al. 2009; TTWG 2021). Most of that geographic range encompasses the nominate subspecies (168,307 km^2), with *K. s. longifemorale* occupying a much smaller area (1,704 km^2) (TTWG 2021). In the United States, *K. s. sonoriense* has been recorded from hill areas below the Mogollon Rim (southern edge of the Colorado Plateau) in central Arizona and western New Mexico; Madrean Sky Island ranges in southeastern Arizona and southwestern New Mexico; and lower elevation tributaries of the Gila, Bill Williams, and Colorado rivers in Arizona, southern Nevada, and southeastern California (Iverson 1992; TTWG 2021). In Mexico, *K. s. sonoriense* occurs in the Magdalena, Sonora, upper Yaqui, and upper Fuerte basins of Sonora and southwestern Chihuahua, all of which drain into the Gulf of California (Iverson 1992; TTWG 2021). In addition, *K. s. sonoriense* occurs in montane headwaters of endorheic basins in western Chihuahua, as far north as the Sierra de San Luis (Lemos Espinal et al. 2015), and as far east as the Río Casas Grandes basin, where it crosses the Continental Divide (Legler

and Vogt 2013; TTWG 2021). *Kinosternon sonoriense longifemorale* is endemic to the Río Sonoyta basin on the border of Arizona, USA and Sonora, Mexico (Rosen and Stone 2017; TTWG 2021).

The eastern limits of distribution have been incorrectly portrayed in a number of older publications due to confusion with other species of mud turtles, particularly *K. hirtipes* and *K. flavescens*. Sonora Mud Turtles have been documented in the Gila River (Niles 1962; Degenhardt and Christiansen 1974) and Animas Mountains of western New Mexico (Degenhardt et al. 1996), and in the Río Casas Grandes drainage in western Chihuahua (Legler and Vogt 2013). However, Sonora Mud Turtles have not been documented in western Texas, northern New Mexico, central or eastern Chihuahua, Durango, or Coahuila despite range descriptions or maps in Strecker (1915), Stejneger and Barbour (1933), Brown (1950), Carr (1952), and Stebbins (1954, 1985, 2003), among others. Conant and Berry (1978) and Iverson (1978, 1981) reviewed and corrected many of the erroneous location records in the southwestern U.S. and northern Mexico; further discussion is in Smith and Smith (1980).

The southern range boundary in Sonora remains uncertain due to inadequate sampling. Legler and Vogt (2013) included most of the Río Sonora, Río Yaqui, Río Mayo, and Río Fuerte drainages on their range map, whereas TTWG (2021) included montane regions of the Río Sonora and upper Río Yaqui, with isolated records in the upper Río Mayo, and one questionable record in the upper Río Fuerte. The southern range boundary on the two maps differ by approximately 250 km (Legler and Vogt 2013; TTWG 2021).

Isolated locality records from the Colorado River and major tributaries below the Grand Canyon include the northern and western range boundaries of *K. s. sonoriense* (Iverson 1992). The northern range boundary is a lone record from southern Nevada (Iverson 1978), whereas the western range boundary includes five records from near the Mexican border (Iverson 1978; Lovich and Beaman 2008).

Fossils have been reported from Pleistocene deposits in Graham County, Arizona and Sonora (Moodie and Van Devender 1974; Van Devender et al. 1985); both sites are within the current range of the species.

Habitat and Ecology. — *Kinosternon sonoriense* inhabits a wide variety of aquatic habitats, including permanent (rarely or never dry), intermittent (dry annually or during drought), and ephemeral (temporary) (Rosen 1987; van Loben Sels et al. 1997; Stone 2001). Populations occur in both lotic and lentic habitats. Populations around the Mogollon Rim are mostly known from permanent aquatic habitats at relatively low elevations (range = 404–1219 m asl; Hulse 1974a; Emslie 1982; Rosen 1987), though individuals have been captured

at elevations up to 2042 m in the Gila River in western New Mexico (Niles 1962). Populations in the Madrean Sky Islands occur at intermediate elevations (range = 828-1762 m) and are usually centered on permanent or intermittent impoundments built by humans to water livestock (van Loben Sels et al. 1997; Stone et al. 2015), though undammed intermittent streams also harbor populations (Stitt and Swann 2000; Hall and Steidl 2007). In one Sky Island, the Peloncillo Mountains, intermittent impoundments connected to canyon reaches with ephemeral pools harbored the largest populations of *K. sonoriense* (Stanila 2009; Stone et al. 2015). Though fewer data are available, *K. s. sonoriense* has been captured at elevations up to 2100 m in Mexico and appears to be mostly montane in its southern range (Rosen and Melendez 2010; Legler and Vogt 2013). Populations of *K. s. longifemorale* occur at low elevations (300–425 m) in isolated wetlands (USFWS 2017b).

Diel and Seasonal Activity. — Sonora Mud Turtles are primarily diurnal during cooler months (or at higher elevations) and crepuscular or nocturnal during warmer months (Hulse 1974a; Emslie 1982). However, at Sycamore Creek near Sunflower, Arizona, Rosen (1987 and unpubl. data) never found turtles active during the day, suggesting flexibility in activity times. Additionally, turtles will enter traps at midday even in mid-summer, and aerial basking is not unusual (Drost et al. 2021). Hulse (1974b) reported that turtles are active at water temperatures above 8°C, but feeding activity does not begin until temperatures reach 14 or 15°C. When inactive in aquatic habitats, *K. sonoriense* is often found in aquatic shelters such as root masses, rock crevices and overhangs, and undercuts in streambanks (Emslie 1982; Rosen 1987).

Winter activity varies, with turtles in some populations undergoing long periods of winter dormancy, either underwater or on land, whereas turtles in other populations remain active throughout the winter or enter short periods of dormancy. Winter activity appears to be influenced by elevation, aquatic habitat depth and permanence, and the potential for winter flooding. At Sycamore Creek, a permanent, high elevation site near the Mogollon Rim, turtles were active for 190 days, with hibernating turtles remaining in water, either buried in mud or under a rock or stump (Hulse 1974a). However, at Spring Creek, another permanent, high elevation site near the Mogollon Rim, Emslie (1982) hypothesized that turtles hibernated on land to avoid scouring floods caused by winter rains. At Tule Creek, a permanent low elevation site near the Mogollon Rim, turtles remained active year-round, with reduced activity and cessation of feeding in winter, but only short periods of dormancy (Hulse 1974a). At Cottonwood Creek, an intermittent low elevation site, one turtle followed with a thread tracking spool hibernated on land at the base of a

Figure 6. Impoundments with populations of *Kinosternon sonoriense* in Arizona and New Mexico (all *K. s. sonoriense* except as labeled). *Top Left*: Blackwater Hole, Peloncillo Mountains, New Mexico. Photo by Paul A. Stone. *Top Right*: Rucker Canyon Tank, Chiricahua Mountains, Arizona. Photo by Justin D. Congdon. *Bottom Left*: Montezuma Well, Arizona. Photo by Karl Ford. *Bottom Right*: Quitobaquito Springs, Organ Pipe Cactus National Monument, Arizona (*K. s. longifemorale*). Photo by John B. Iverson.

willow for 123 days (October to mid-February), even though shallow standing water was available throughout the winter (Hensley et al. 2010). Since Tule Creek and Cottonwood Creek are less than 15 km apart, differences between these sites might reflect the predation risk of occupying shallow aquatic habitats in winter. However, other observations suggest remaining in deeper water during winter is also risky. During a March hailstorm prior to a winter flood at Tule Creek, Rosen (1987) observed turtles leaving the creek and moving onto land, interpreted as avoidance of flood scour in a canyon-bound environment. Winter mortality of 14 turtles was observed in mid-March in the Peloncillo Mountains, probably due to a combination of a flood followed by a hard freeze (Massengill et al. 2014).

Movements and Terrestrial Activity. — In general, *K. sonoriense* in permanent habitats have low movement rates and little terrestrial activity other than nesting. During a two-year study, Emslie (1982) found little movement of turtles in Spring Creek, a shallow, permanent stream near the Mogollon Rim. Most recaptures were within 50 m of previous captures, either in the same riffle pool or one

pool up or downstream (Emslie 1982). Similarly, at low elevation lotic sites such as Quitobaquito and Montezuma Well, there was little evidence of terrestrial activity, and aquatic movements were limited to small, isolated wetlands (Rosen and Lowe 1996; Lovich et al. 2012). Desiccation experiments conducted in the laboratory indicated that Sonora Mud Turtles from a permanent spring in the Chiricahua Mountains were poor estivators (Ligon and Peterson 2002). Many individuals remained active during estivation trials, and as a result, water loss rates were high compared to *Kinosternon flavescens*, a competent estivator, and *K. sonoriense* from intermittent aquatic habitats (Ligon and Peterson 2002).

In contrast, *K. sonoriense* occupying intermittent aquatic habitats have higher movement rates, more extensive terrestrial activity, and are competent estivators compared to turtles occupying permanent aquatic habitats. Degenhardt and Christiansen (1974) reported finding Sonora Mud Turtles in intermittent impoundments as far as 8 km from permanent water and speculated that turtles must either migrate long distances or estivate underground. At higher elevations in

Figure 7. Canyon pool habitats of *Kinosternon s. sonoriense* in the Peloncillo Mountains, New Mexico. *Top Left*: Maverick Spring. Photo by Paul A. Stone. *Top Right*: pools below Buckhorn Tank. Photo by Brian D. Stanila. *Bottom Left*: Blackwater Canyon. Photo by Paul A. Stone. *Bottom Right*: Beehive Canyon, Clanton Draw. Photo by Marie E.B. Stone.

the Madrean Sky Islands, large populations are associated with intermittent impoundments (van Loben Sels et al. 1997; Stone 2001), and turtles are common in ephemeral canyon pools that are proximate to impoundments (Stone 2001; Stone et al. 2015). In the Peloncillo Mountains, *K. sonoriense* was more abundant in intermittent impoundments than in permanent impoundments, perhaps because predatory fish occurred in the latter (Stanila 2009). In intermittent aquatic habitats, Sonora Mud Turtles undergo terrestrial activity in a variety of contexts. During periods when aquatic habitat is absent, individuals estivate in terrestrial microhabitats (Stitt and Swann 2000; Ligon and Stone 2003a; Hall and Steidl 2007). Estivating turtles were found buried in shallow forms under vegetation, leaf litter, soil, or in boulder crevices (Ligon and Stone 2003a; Hall and Steidl 2007) within 70 m of a canyon bed (Ligon and Stone 2003a). All 10 radio-telemetered adults estivated during a drought in the Peloncillo Mountains for periods ranging from 11–34 days (Ligon and Stone 2003a). In the Rincon Mountains at Rincon Creek, four of six radio-telemetered adults died after terrestrial estivation bouts of approximately 305 days, suggesting an upper limit on desiccation tolerance in

Sonora Mud Turtles (Stitt and Swann 2000). Turtles from intermittent aquatic habitats were competent at estivation, rivaling *K. flavescens* in maintaining homeostasis during two laboratory desiccation experiments lasting 77 days (Peterson and Stone 2000) and 55 days (Ligon and Peterson 2002). In both studies, the majority of subjects remained inactive and buried in the substrate with their plastrons closed (Ligon and Peterson 2002), a condition which reduces desiccation rates (Wygoda and Chmura 1990).

Resources are both temporally and spatially clumped in intermittent aquatic habitats, which can increase interactions among individuals and risk of predation. Under conditions of diminishing aquatic habitat, some Sonora Mud Turtles remain active in aquatic habitats while others estivate on land (Stone 2001; Hensley et al. 2010; Stone et al. 2015). In the Peloncillo Mountains, population modelling based on repeated sampling of small aquatic habitats with little structure and few refugia revealed the probability of capturing a turtle known to be alive in the study area during a given sample (i.e. catchability) was 0.25 (Stone et al. 2015), implying that many individuals were estivating in terrestrial habitat

during a typical sample (Stone 2001; Stone et al. 2015). Similarly, during a drought in the Rincon Mountains at Chiminea Creek, 39% of locations of radio-telemetered turtles were on land even though dwindling aquatic habitat was available (Stitt and Swann 2000). In larger, more permanent pool complexes in the Santa Catalina Mountains, radio-telemetered turtles only estivated on land during June and July of drought years, when water availability was lowest (Hall and Steidl 2007).

In addition to moving between aquatic and terrestrial habitats, Sonora Mud Turtles also move among aquatic habitats. In the Peloncillo Mountains, about half of the adults in one population underwent seasonal migrations between an intermittent impoundment and ephemeral canyon pools (Stone 2001; Stone et al. 2015). During the dry season, individuals congregated in the intermittent impoundment, and during the monsoon season, individuals dispersed to ephemeral canyon pools (Stone et al. 2015). Seasonal migrations appeared to be timed so that turtles could exploit abundant resources in canyon pools during the monsoon season and avoid dehydration during the dry season (Stone et al. 2015).

Several studies have used mark-recapture data to quantify movements among intermittent or ephemeral canyon pools, with recapture intervals of weeks to years (Hall and Steidl 2007; Hensley et al. 2010; Stone et al. 2015). Though different studies have used different metrics to measure movement distances and are therefore difficult to compare, all show considerable linear movements along canyon bottoms, with sex differences within and among sites. In intermittent pools of an interrupted stream in the Santa Catalina Mountains, and in ephemeral pools proximate to an intermittent stock tank in the Peloncillo Mountains, male linear home ranges averaged 300 and 480 m, respectively, and were over twice as long as female home ranges (Hall and Steidl 2007; Stone et al. 2015). In contrast, in intermittent pools of an interrupted stream in the Hieroglyphic Mountains, female home ranges averaged 550 m, over twice as long as male home ranges (Hensley et al. 2010).

Sonora Mud Turtles occasionally undertake long-distance movements, both within (Hall and Steidl 2007; Hensley et al. 2010; Stone et al. 2015) and among drainages (Hall and Steidl 2007; Stone et al. 2015). In the Peloncillo Mountains, 21 turtles (18 males) changed drainages, with average straight-line movement distances of 3094 ± 453 m (range = 1513–8876 m; Stone et al. 2015). In the Santa Catalina Mountains, two males changed drainages, moving an average straight-line distance of 2550 m (Hall and Steidl 2007). In the Hieroglyphic Mountains, 7 of 9 movements that exceeded 700 m were made by females, with one female having a cumulative movement distance of 7960 m (Hensley et al. 2010). In the Chiricahua Mountains during

Figure 8. *Kinosternon s. sonoriense* basking at Montezuma Well, Arizona. Photo by James N. Stuart.

1990–2008, 14 males and one juvenile moved from 1800–2400 m between two drainages (Congdon, unpubl. data).

Social System. — The social system of Sonora Mud Turtles is undescribed, though territoriality has been inferred from spacing patterns in two studies. Emslie (1982) never found more than one male in a pool at the same time and hypothesized that males were territorial. Hall and Steidl (2007) used spacing patterns to infer that males and large females were territorial. However, in both studies, there were large spatial overlaps across time (Emslie 1982; Hall and Steidl 2007), with 19 males occurring in one pool during two years of sampling in Emslie's (1982) study area. Moreover, in both studies the number of available canyon pools exceeded the number of turtles in respective sex classes (Emslie 1982; Hall and Steidl 2007), making low overlap of consexuals in canyon pools unsurprising. Field observation of hatchling *K. sonoriense* biting and chasing each other have been reported (Stone et al. 2010), but there are no published observations of interactions among consexual adults. An inference of territoriality seems premature without evidence demonstrating priority of access to resources by individuals.

Diet and Foraging Behavior. — The only quantitative study of diet of *K. sonoriense* involved 101 dissected turtles from four permanent creeks; stomach contents indicated the species is an active forager and opportunistic carnivore, feeding primarily on aquatic insects, snails, and crustaceans (Hulse 1974b). In habitats with reduced benthic faunas there was a shift to omnivory, with algae and aquatic angiosperms taking up as much as 31% of stomach and intestine contents volume (Hulse 1974b). Vertebrates were also encountered in dissections, with leopard frogs and fish present in 3% and 7%, respectively, of examined guts (Hulse 1974b).

Several studies have since observed vertebrates in the diet of Sonora Mud Turtles, including three species of passerine birds (Stone et al. 2005; Stanila et al. 2008; Andresen 2019), three squamate reptiles (Stone et al. 2005; Lovich et al. 2010), two anurans (Ligon and Stone

2003b; Zarlingo et al. 2020), and a young Collared Peccary (*Pecari* [= *Dicotyles*] *tajacu*; Andresen 2019). In most cases, it was unclear whether the observed feeding event was predation or scavenging; however, the observation involving the peccary was clearly scavenging, and in three cases, the feeding event was clearly predation (Stone et al. 2005; Andresen 2019; Zarlingo et al. 2020). First, a Black-necked Gartersnake (*Thamnophis cyrtopsis*) was killed and partially eaten by an adult *K. sonoriense* in a shallow pool in the Peloncillo Mountains (Stone et al. 2005). Second, a Sonora Mud Turtle was encountered while consuming a living Western Tanager (*Piranga ludovician*) at a wetland associated with the San Pedro River, Arizona (Andresen 2019). Third, a *K. sonoriense* was found consuming a juvenile Chiricahua Leopard Frog, (*Lithobates* [= *Rana*] *chiricahuensis*) at a small earthen stock tank in the Pajarito Mountains, Arizona, and behavioral observations suggested turtles at the tank edge were ambushing frogs in shallow water along the shore (Zarlingo et al. 2020).

Movement of turtles between intermittent impoundments and ephemeral canyon pools in the Peloncillo Mountains is consistent with exploitation of abundant seasonal resources in ephemeral pools with standing water (Stone et al. 2015). Feeding trials in the field indicate that tadpoles (*Anaxyrus punctatus* and *Hyla arenicolor*) are readily eaten by all size classes of Sonora Mud Turtles (M. Stone, unpubl. data).

Predation and Defensive Behavior. — A variety of aquatic species are potential predators of Sonora Mud Turtles. Otters (*Lontra* spp.) are common predators of turtles (Gasbarrini et al. 2021) and two species of otter (*L. canadensis* and *L. longicaudis*) occur within the geographic range of Sonora Mud Turtles; both are rare but could prey on Sonora Mud Turtles in larger lotic habitats. Giant Water Bugs (Belostomatidae) are known to prey on hatchlings of other turtle species (Ohba 2011) and are common in canyon pools where hatchling mud turtles are abundant. Two non-native aquatic predators, American Bullfrogs (*Lithobates* [= *Rana*] *catesbeianus*; Akins and Jones 2010) and Virile Crayfish (*Faxonius virilis*; Fernandez and Rosen 1996; Schwendiman 2001), are known to prey on hatchling and juvenile Sonora Mud Turtles, possibly limiting recruitment in some populations (Schwalbe and Rosen 1988; Fernandez and Rosen 1996; Hensley et al. 2010). Non-native centrarchid fish (Centrarchidae) are also suspected to prey on hatchling Sonora Mud Turtles (Rosen 2008a; Stanila 2009; but see Semlitsch and Gibbons 1989).

Kinosternids in general (Beissinger 1990; Iverson et al. 1991), including *K. sonoriense* (Stone 2001; Stone et al. 2011), are susceptible to terrestrial predators while on land or in shallow water. Sonora Mud Turtles were

Figure 9. Defensive behaviors of *Kinosternon s. sonoriense*. *Top*: Hatchling threatening to bite. Photo by Justin D. Congdon. *Bottom*: Adult retracted into shell. Photo by Marie E.B. Stone.

present in less than 1% of identifiable prey items in the diets of mountain lions (McCain 2008) and bald eagles (Grubb 1995). During a drought in 1987 at Tule Creek, 11 predator-killed turtles were found at drying pools in July (Rosen, unpubl. data). Such mortality suggests that exiting streams to find terrestrial concealment may reduce risks compared to staying in shallow pools. When disturbed by humans in aquatic habitats, Sonora Mud Turtles undergo terrestrial flight responses, leaving the water to enter a terrestrial refuge (Stone et al. 2011). Terrestrial flight responses did not occur in deep water habitats and movements from shallow habitats were interpreted to be a defensive behavior (Stone et al. 2011). Adults were more likely to undergo terrestrial flight responses (Stone et al. 2011), employ head retraction and shell closure (Peno et al. 2016), and less likely to bite (Peno et al. 2016) than juveniles, suggesting ontogenetic differences in defensive behavior. All size classes produce musk, which has long been regarded as a defensive behavior (Ehrenfeld and Ehrenfeld 1973).

Parasites and Epibionts. — Among the parasites known from Sonora Mud Turtles are protozoans in the bile ducts and gall bladder (Ernst and Barbour 1972), haemogegarines in the blood (Nordmeyer 2019), and external leeches of two genera (Hulse 1976a). Turtles also often have epibiotic algae (particularly of the genus *Arnoldiella*, [formerly *Basicladia*); Boedeker et al. 2012]) on the carapace (Dixon 1960; Hulse 1976a), and

sometimes they have unidentified, nonpathogenic fungi on the plastron (Hulse 1976a).

Bliss (2016) measured fecal parasite prevalence in 142 *K. sonoriense* from six Sky Island ranges in Arizona and New Mexico (103 samples from the Peloncillo Mountains, 28 from the Pajarito Mountains, and 11 samples total from four other Sky Island ranges). Trematode prevalence was 4.96%, significantly lower than prevalence in a Nebraska population of *K. flavescens* (70.46%, *n* = 44) or an Oklahoma population of *K. subrubrum* (16.13%, *n* = 31) measured using similar methods (Bliss 2016). Reduced white blood cell counts in *K. sonoriense* (12,320 cells/microliter median cell count) further supported the conclusion that *K. sonoriense* were more lightly parasitized than *K. flavescens* (18,400 cells/ microliter) or *K. subrubrum* (23,600 cells/microliter; Bliss 2016). Necropsies on 3 *K. sonoriense* revealed no evidence of parasites or pathology in organs or tissues, and examination of red blood cells revealed no evidence of haemogregarine parasites (Bliss 2016). Bliss (2016) hypothesized that parasites in general may have difficulty colonizing and successfully establishing in *K. sonoriense* due to unpredictable and low aquatic habitat availability.

Abnormal Morphology. — In a series of 164 *K. sonoriense* collected from several Arizona streams, 21.8% had scute abnormalities (mostly split or extra plastron scutes), 26.2% had pitting on the carapace, and 6.2% had obvious shell injuries (Hulse 1976b). In a population of 1064 *K. sonoriense* (excluding yearlings) in the Chiricahua Mountains, abnormal vertebrals, costals, or plastron scutes were recorded for 34 males, 16 females, and 17 juveniles (6.3%) and injuries to legs, head, tail, carapace, plastron, and bridge were recorded for 55 males, 30 females, and 15 juveniles (9.4%; Congdon, unpubl. data). We know of no records of kyphotic individuals; however, individuals in multiple populations develop a rugose carapace due to scute and bone remodeling, perhaps associated with algal infections (J. Christiansen, pers. comm.).

Associated Turtle Species. – Sonora Mud Turtles are sympatric or parapatric, but rarely syntopic, with five other species of *Kinosternon*. Lemos-Espinal et al. (2015) stated that *K. sonoriense* is sympatric with *K. integrum* in northwestern Mexico, although only narrowly, as the latter is the characteristic mud turtle in perennial waters. In Arizona, *K. sonoriense* is almost never syntopic with *K. stejnegeri* or *K. flavescens* (Iverson 1992; Rosen et al. 1998), mud turtles that use summer rain pools and ponds at low elevation sites in the Madrean Sky Islands. A similar situation occurs in northern Sonora, where *K. alamosae* occupies non-perennial valley floor waters at low elevations, and *K. sonoriense* occurs at higher elevations (Rosen and Melendez 2010). Given that both *K. sonoriense* and *K. hirtipes* have crossed the Continental Divide – in

Figure 10. Development of rugose carapaces in *Kinosternon s. sonoriense*. *Top*: Shell with rugose carapace collected near Cucurpe, Sonora. Photo by John B. Iverson. *Bottom*: Individual with algal growth and rugose carapace from Parker Canyon Lake, Arizona. Photo by Jeremy K. Massengill.

opposite directions – in northwestern Chihuahua, these two sister species with similar habitat associations could occur in syntopy at sites deep within the Sierra Madre Occidental that have not been surveyed to date.

Sonora Mud Turtles co-occur naturally with the emydid slider turtle, *Trachemys yaquia*, in large rivers and ciénegas in northern Sonora (Rosen and Melendez 2010). In the Colorado, Gila, and Bill Williams drainages in Arizona and New Mexico, Sonora Mud Turtles have not been observed in syntopy with other native turtles (Degenhardt and Christiansen 1974; Moll and Moll 2004) but do co-occur with non-native softshells (*Apalone spinifera emoryi*) and sliders, *Trachemys scripta* (Lovich and Beaman 2008; Drost et al. 2021). Lovich and Beaman (2008) suggested non-native *Apalone spinifera* may have contributed to the demise of Sonora Mud Turtles in the lower Gila and Colorado Rivers, and Drost et al. (2021) argued that introduced *Trachemys scripta* adversely impacted the Sonora Mud Turtle population at Montezuma Well.

Courtship and Reproduction. — Courtship or mating of *K. sonoriense* has been observed in captivity and in the field from March through early May (Iverson 1981; Hulse 1982). In the Chiricahua Mountains, X-rays revealed only non-gravid females in May, and females with shelled eggs in oviducts occurred from June to mid-August (when field

work ceased; van Loben Sels et al. 1997; Hollett 2002). Gravid females were found from April 23 to early October in Montezuma Well, where water temperatures are high and seasonally stable (Lovich et al. 2012).

Follicle and Embryo Development. — Follicles of first clutches are ovulated in late May and the earliest shelled eggs detected by X-ray in the Chiricahua Mountains was 4 June (Cameron 2004; Congdon, unpubl. data). In both laboratory and natural settings in the Chiricahua Mountains, embryos in oviducts of female *K. sonoriense*: 1) arrest development at late gastrula, 2) remain in diapause (i.e., arrested development in an environment suitable for development; Ewert 1991) for an extended period after oviposition, and 3) initiate development after prolonged exposure to low nest temperatures followed by soil temperatures reaching approximately 15°C (Ewert 1991). Rosen (unpubl. data) incubated Sonora Mud Turtle eggs at relatively stable temperature in a closet and embryos remained in extended diapause for approximately 11 months and then developed and hatched. Embryonic diapause represents an economical way to minimize energy use by embryos while they overwinter in nests and to initiate emergence of hatchlings with the predictable monsoon rains (July through September) in the Sonoran Desert region (Cameron 2004).

Clutch Size and Frequency. — Among populations, average clutch size varies from 3.1–8.1 with an among-population range of 1–12 brittle shelled eggs (Hulse 1982; Rosen 1987; van Loben Sels et al. 1997; Hollett 2002; Lovich et al. 2012). Egg widths and lengths, respectively, averaged 15.8 x 28.8 mm, (Rosen 1987), 19 x 33 mm (Ewert 1979), 14.4 x 31.1 mm (Hulse 1982), and 16.8 x 28.9 mm (van Loben Sels et al. 1997). Egg wet mass averaged 5.0 g (range = 4.7–5.5 g) and yolk dry mass averaged 0.96 g (range = 0.73–1.25 g) in the Chiricahua Mountains (van Loben Sels et al. 1997). X-ray egg widths averaged 16.9 mm (range = 16.0–18.2 mm) in the Chiricahuas (van Loben Sels et al. 1997) and 19.4 mm (range =17.8–21.7 mm) at Montezuma Well (Lovich et al. 2012). Egg mass (EM; in g) can be estimated from egg length (EL; in mm) and egg width (EW; in mm) by the formula: $EM = 0.261EL + 0.620EW – 13.204$ (Iverson, unpubl. data). In populations of large bodied Sonora Mud Turtles, clutch size and X-ray egg widths both increased significantly with body size of females (van Loben Sels et al. 1997; Congdon, unpubl. data); whereas in some populations with small-bodied females, clutch size and egg size were weakly or not correlated with body size (Rosen 1987; Lovich et al. 2012). Relative clutch mass (clutch mass divided by gravid female mass) averaged 7.8% for 13 studied populations (Iverson, unpubl. data).

Repeated X-rays of individual females indicate annual clutch frequencies of 0–3 clutches/yr in multiple populations (van Loben Sels et al. 1997; Lovich et al. 2012). X-rays combined with dissections and counts of preovulatory follicles and ovulation scars suggest four clutches per year are possible in some populations (Rosen 1987). At Montezuma Well in 2007–2008, 36–54% of females produced clutches in a given year, some females did not produce clutches in consecutive years, and only one female produced two clutches in one year (Lovich et al. 2012). In the Chiricahua Mountains, females produce multiple clutches with a minimum interval of 20 days between clutches (van Loben Sels et al. 1997). At least 23% of all females produced two clutches in a single year (van Loben Sels et al. 1997), and one female produced three clutches (Hollet 2002).

Nesting Movements. — The relatively long nesting seasons (June–August) and relatively small populations of Sonora Mud Turtles result in low densities of nesting females on land at any one time. Females in the Chiricahua Mountains made long distance and long duration nesting movements prior to nesting, and to and from summer estivation sites. The maximum daily straight distance an adult female outfitted with a tracking spool traveled along a stream with intermittent aquatic habitat was 409 m, and the maximum daily straight distance traveled on land was 330 m (Hollet 2002). Females in the Chiricahua Mountains traveled between 8 and 440 m away from water before selecting a nest site and spent from 12 to 48 hrs before nesting (Hollet 2002). Some females did not return to water for at least five days after nesting (Hollet 2002; Congdon, unpubl. data). The duration of movements from a wetland to a nest site was sometimes greater than two days, and one female remained on land for 4 days before selecting a nest site (Hollet 2002). Construction of three nests (i.e., digging, egg laying, and covering) occurred during 1100–2000 hrs and took approximately 3 hrs to complete (Hollett 2002; Congdon, unpubl. data).

Sex Determination and Sex Ratios. — *Kinosternon sonoriense* exhibits temperature-dependent sex determination (TSD), with all females being produced from constant incubation temperatures of 30–32°C, and nearly all males being produced at or below 27°C (Ewert et al. 2004). In large samples of adult turtles, Rosen (1987) indicated male-biased sex ratios in three pond populations (San Bernardino National Wildlife Refuge, Quitobaquito, and Montezuma Well); whereas strongly female biased sex ratios were found in three stream populations (Tule Creek, Sycamore Creek, and Sharp Spring). In addition, approximately 1:1 adult sex ratios have been found in a number of populations (van Loben Sels et al. 1997; Hall and Steidl 2007; Hensley et al. 2010). Hulse (1982) suggested adult sex ratios were male-biased primarily because males mature at younger ages than females. At Blackwater Canyon, male-biased

sex ratios were associated with captures of highly vagile transient males; removing the transients reverted the sex ratio to unity (Stone et al. 2015).

Life-history Trait Values. – The entire set of co-evolved life history trait values of Sonora Mud Turtles have not been adequately documented, and nest survivorship data in particular will require extensive investment in time and personnel. Relatively high adult mortality has been found in some populations based on frequent presence of dead individuals and longevity estimates of less than 40 yrs. Data from two decades of study in the Chiricahua Mountains allowed a first order prediction that an annual fecundity of 5 female eggs would require high nest survivorship and an average juvenile survivorship from age 1 to maturity of approximately 0.60 to maintain a stable population (van Loben Sels et al. 1997; Congdon, unpubl. data).

Growth, Maturation, and Longevity. — Growth rates of Sonora Mud Turtles at Cottonwood Creek from hatching to age 3 yrs were 18.9 mm SCL/yr (Hensley et al. 2010), and in the Chiricahua Mountains, growth rates from hatching to age 6 were 17.5 mm SCL/yr (van Loben Sels et al. 1997). Adult growth rates of males and females at Tule Creek averaged 1.6 and 1.5 mm SCL/yr, respectively (Hulse 1976b). In the Chiricahua Mountains, growth rates of males and females averaged 1.4 ($n = 99$) and 1.3 mm ($n = 89$) SCL/ yr, respectively, and approximately 12% of adults with >10 yrs recapture intervals did not grow (Congdon et al. 2013).

Among populations, the minimum size at maturity of females has been reported as 90–125 mm SCL (Hulse 1974a, 1982; van Loben Sels et al., 1997; Lovich et al. 2012), and estimated ages of female maturity have varied from 5–9 yrs (Rosen 1987; Hulse 1974a). In populations with rapid juvenile growth rates, females matured at younger ages, whereas where juvenile growth rates were low, females matured at older ages (Rosen 1987). At lower elevations, immature males grow rapidly and matured at approximately 5–6 yrs and 76–82 mm SCL, whereas growth was slower at higher elevations and males matured at 7–8 yrs and 91–98 mm SCL (Hulse 1982). Within populations of other turtle species, rapidly growing juvenile *Chrysemys picta*, *Emydoidea blandingii*, *Chelydra serpentina*, and *Chelonia mydas* matured earlier and at larger body sizes than did slower growing juveniles (Ernst and McDonald 1989; Congdon and van Loben Sels 1993; Bjorndal et al. 2013; Congdon et al. 2018). Similar influences of juvenile growth rates probably occur within populations of Sonora Mud Turtles.

Sonora Mud Turtles in captivity survived at least 45 yrs at the Baltimore Zoo (Bowler 1977; Slavens and Slavens 2000; pondturtle.com). Based on adult survivorship estimates in Chiricahua Mountain populations, maximum longevities of adults of 40 yrs would probably be reached by a small number of individuals (Congdon, unpubl.

data). In Chiricahua Mountain populations, the oldest females ($n = 21$) were estimated to be 20–28 yrs with SCL ranging from 130–155 mm, whereas the oldest males ($n = 23$) were estimated to be 20–29 yrs with SCL ranging from 133–157 mm. In combination, the data from the oldest individuals do not indicate substantial sexual size dimorphism or differential longevities in the population (Congdon, unpubl. data). The years of tenure of adults in Blackwater Canyon in the Peloncillo Mountains averaged 7.8 yrs for males and 20.6 yrs for females, likely reflecting intersexual differences in emigration patterns (Stone et al. 2015). Ten individuals (6 females, 4 males) from Blackwater Canyon have recapture histories that span at least 20 yrs (P. Stone, M. Stone, unpubl. data). At Montezuma Well, 9 individuals (3 females, 6 males) have recapture histories spanning 27–33 yrs, with the oldest two individuals estimated to be 38 and 39 yrs old (C. Drost, pers. comm.). At Quitobaquito, based on long-term mark-recapture data with initial age estimation from growth line counts, six *K. s. longifemorale* (3 males, 3 females) were 35–41 yrs old (P. Holm, pers. comm.).

Demography. — The proportion of subadults in 6 well-sampled populations varied from 18.5% (van Loben Sels et al. 1997) to 64% (Hensley et al. 2010), averaging 38.9% (Hulse 1974a; Stone 2001; Hall and Steidl 2007; Riedle et al. 2012). The largest populations have fewer than 1000 adults (Hulse 1974a; Rosen 1987), typically occurring at high population densities. At Tule Creek, Sonora Mud Turtles reached population densities of 750–825 turtles/ ha (Hulse 1982), which translated to a biomass of about 100 kg/ha (Iverson 1982). These are among the highest reported values for freshwater turtle populations (Lovich et al. 2018). Subsequent studies have confirmed Sonora Mud Turtles often occur at high population densities (Stone 2001; Hall and Steidl 2007; Riedle et al. 2012). Indeed, at Sharp Spring, near Lochiel, Arizona, estimated population density was 8829 turtles/ha of pool habitat, and growth rates appeared to be constrained as a result (Rosen 1987). However, due to fluctuations in aquatic habitat availability, estimates of population density or biomass at intermittent sites are much more variable than estimates of population size (Stone 2001). For example, at Blackwater Canyon in the Peloncillo Mountains, Jolly-Seber population estimates during a five-year period ranged from 148–246 individuals, whereas population density estimates during the same period ranged from 389–3280 individuals/ha aquatic habitat (Stone 2001), and biomass estimates ranged from 47–390 kg/ha aquatic habitat (P. Stone, M. Stone, unpubl. data). Open population models from six other populations in the Peloncillo Mountains revealed population sizes ranging from 24–438 individuals and population densities (at average water levels) ranging from 59–1305 individuals/ha (Stanila 2009).

Population Status. — To assess population status, we divided the geographic range of *K. sonoriense* into five areas of geographic representation, based on geography, geology, genetics, and political boundaries: 1) populations of *K. s. longifemorale*; 2) populations of *K. s. sonoriense* in Mexico; 3) populations of *K. s. sonoriense* in the Colorado River basin; 4) populations of *K. s. sonoriense* near the Mogollon Rim, and 5) populations of *K. s. sonoriense* in the Madrean Sky Islands.

Populations of K. s. longifemorale. — Sonoyta Mud Turtles occur in the Río Sonoyta drainage on both sides of the border between the United States and Mexico. Five isolated populations are known, though there is much uncertainty about the status of populations in Mexico (Minckley et al. 2013; Rosen and Stone 2017; USFWS 2017a). These populations are confined to a 1704 km^2 region and occur in three impoundments totaling only about 7 ha of aquatic habitat and two canyon reaches totaling less than 6 km. *Kinosternon s. longifemorale* was recently assessed as Endangered on the U.S. Endangered Species List (USFWS 2017b) and Critically Endangered on the IUCN Red List (Rosen and Stone 2017).

Quitobaquito Oasis harbors the only population of *K. s. longifemorale* in the United States, at Organ Pipe Cactus National Monument, Arizona. Aquatic habitat at Quitobaquito Oasis currently includes a small impoundment (maximum area = 0.27 ha) and a 244 m long stream channel (USFWS 2017a). The population at Quitobaquito appears to have declined from several hundred in the late 1950s to about 100 in the early 1980s as a result of aquatic habitat loss (Riedle et al. 2012). Habitat improvements stabilized the population, but in 2006 aquatic habitat began to decline precipitously (Riedle et al. 2012; USFWS 2017a). Aquatic habitat loss became so concerning that during 2007–2009, 81 turtles were removed from the population and a captive breeding assurance colony was established at the Sonoran Desert Museum (see below; Riedle et al. 2012; USFWS 2017a). Following renovation, 24 individuals were returned to Quitobaquito Oasis in 2011. Intensive maintenance and renovation at Quitobaquito have stabilized water levels, and the population currently appears to be growing (USFWS 2017a).

In Mexico, the only large, reasonably secure population of *K. s. longifemorale* occurs at Papalote Reach, a spring-fed reach associated with the Río Sonoyta, within the Pinacate Biosphere Reserve. The reach was 1.5–3.0 km in length and perennial until the early 21st century, when prolonged drought and pumping of the aquifer rendered it intermittent (USFWS 2017a). However, despite reduced water levels, the population at Papalote Reach appears stable over the past 12 yrs with population estimates of 268–351 turtles (Grageda Garcia and Garcia Miranda 2018;

Grageda Garcia and Bogan 2019), making it the largest population of *K. s. longifemorale* known. Tolerance of habitat drying will be important for mid-term resistance to extirpation.

Two other populations of *K. s. longifemorale* were associated with the Río Sonoyta at the town of Sonoyta, near the Mexico/United States border (USFWS 2017a). One population at Xochimilco Reach persisted in a mix of permanent-water sewage effluent from a military base, non-permanent ponds associated with other sewage effluents, and small permanent rock pools below a large rock catchment dam at Presa Xochimilco; it has not been sampled since 2004. Another population was present in sewage lagoons formed by municipal effluent from the town of Sonoyta. Redevelopment of the water treatment system at Sonoyta during the last decade has resulted in the sewage lagoons being dry for long periods, which has resulted in mass mortality and potentially extirpation of the population (Grageda Garcia and Bogan 2019).

A fifth population of *K. s. longifemorale* occurred at Quitovac, an isolated spring-fed system about 40 km south of Sonoyta (Rosen et al. 2010), and is thought to have been introduced by the Tohono O'odham people. Maintenance of the Quitovac site involves periodic dredging that may kill turtles (USFWS 2017a). The current status of the population is unknown and the site was last sampled in 2002 (USFWS 2017a).

Populations of K. s. sonoriense in Mexico. — Outside the Río Sonoyta Drainage, *K. s. sonoriense* occurs across much of Sonora and western Chihuahua, Mexico (Legler and Vogt 2013). However, little is known about populations in this region. Rosen and Melendez (2010) documented *K. s. sonoriense* at 10 of 39 sites (26%) in Sonora and Chihuahua sampled in 2005. Population estimates could not be made since each site was only sampled once, and many sites were sampled without trapping (Rosen and Melendez 2010); however the survey suggests the presence of multiple populations of *K. s. sonoriense* in northwestern Mexico, though further sampling is needed.

Populations of K. s. sonoriense in the Colorado River Basin. — There are a limited number of widely spaced locality records, all more than 50 yrs old, for *K. sonoriense* in the Colorado River and its main stem drainages. One specimen was collected in southern Nevada (Iverson 1978), and a handful of specimens were collected from a few sites near the Mexican border, at elevations as low as 43 m (Jennings and Hayes 1994). In addition, there are records from the Bill Williams River drainage and the lower Gila River, two main tributaries of the Colorado River (Hulse 1974a; Iverson 1978). Because of aquatic habitat loss and exotic predators, *K. sonoriense* has probably been extirpated from the Gila River west of Phoenix and the Colorado River itself (Jennings and Hayes 1994; Brennan

and Holycross 2006; Lovich and Beaman 2008), with the last recorded observation in 1962 (Funk 1974). However, Hulse (1974a) collected *K. sonoriense* from four localities in the Bill Williams River drainage, an area with less anthropogenic change than the Colorado or lower Gila Rivers. Recent samples archived by the Arizona Game and Fish Department suggest the continued presence of *K. sonoriense* in the Bill Williams River drainage (Smith et al. 2019), but population status is unknown.

Populations of K. s. sonoriense near the Mogollon Rim. – Multiple populations of Sonora Mud Turtles have been documented in the Mogollon Rim region. Two theses and a dissertation produced during 1974–1987 focused on demography in several populations (Hulse 1974a; Emslie 1982; Rosen 1987), and the population at Montezuma Well has been intermittently monitored in recent years (Lovich et al. 2012). In addition, Hensley et al. (2010) monitored the population at Cottonwood Creek in the Hieroglyphic Mountains from 1996–2005. Aside from Montezuma Well and Cottonwood Creek, other known populations have not been sampled in over 30 years. Individuals have been observed in the Gila River drainage of western New Mexico, both historically (Niles 1962; Degenhardt and Christiansen 1974) and recently (J. Duran and T. Giermakowski [2018], pers. comm.; S. Drukker [2021], pers. comm.).

Populations of K. s. sonoriense in the Madrean Sky Islands. — Sonora Mud Turtle populations are also well represented in the Madrean Sky Islands. Several populations have been subjects of intensive (Stitt and Swann 2000) and long-term studies (van Loben Sels et al. 1997; Hall and Steidl 2007; Stone et al. 2015), with data spanning from the early 1990s to the present. In the Peloncillo Mountains, a large, stable population in Blackwater Canyon has been sampled twice annually since 1994 (Stone 2001; Stone et al. 2015). At least four other drainages in the Peloncillo Mountains have large populations at multiple sites within the drainage (Stanila 2009; Stone et al. 2015). Sites within drainages are connected to one another by frequent turtle movements (Stone et al. 2015), and drainages are connected to one another by less frequent, longer distance movements (Stone et al. 2015). A similar pattern of multiple known populations within a range has been found in the Chiricahua (van Loben Sels et al. 1997), Pajarito (Bliss 2016), Santa Catalina (Hall and Steidl 2007), Rincon (Stitt and Swann 2000), Huachuca and Galiuro mountains (P. Stone, unpubl. data). Individuals have also been observed in other Sky Island ranges, including the Animas (Degenhardt et al. 1996), Pinaleno and Whetstone (P. Stone, unpubl. data), and Santa Rita mountains (Congdon, unpubl. data).

Threats to Survival. — Sonora Mud Turtles are rarely the target of specific threats; they are not coveted by the pet trade nor widely consumed by humans (van Dijk 2011; Lovich et al. 2014; but see Schneider and Everson 1989 concerning consumption by early Native Americans). However, Sonora Mud Turtles are generally threatened by habitat loss, habitat fragmentation, exotic species, and climate change, including desertification. Water diversion and groundwater pumping has especially impacted populations of *K. s. longifemorale* and populations of *K. s. sonoriense* in the Colorado and Gila Rivers. The construction of large dams in the Colorado and Gila drainage has de-watered large sections of former river channels while turning other sections into large reservoirs that are generally unsuitable for mud turtles. Meanwhile, siltation and dam failures at small dams have also negatively impacted populations of both subspecies. Exotic crayfish, bullfrogs, and predatory fishes have all been implicated in negative impacts on *K. sonoriense* populations. All the above threats to turtle populations are exacerbated by climate change. Despite accelerating threats, there has been little assessment of impacts at most known localities of the nominate subspecies, and the full geographic extent and intensity of threats are unknown. Therefore, the status of the species as a whole is unclear.

Habitat Loss and Fragmentation. – Groundwater pumping leading to aquifer depletion has nearly eliminated once-abundant (Ruthven 1907) populations of *K. sonoriense* in the Santa Cruz River at Tucson (Rosen and Mauz 2001; Rosen 2005, 2008b), although small populations survive in downstream effluent, and one small population remains in a non-perennial reach in South Tucson (Rosen, unpubl. data). Similarly, *K. sonoriense* was not found at the historic locality of Caborca, Sonora, Mexico, where diversion and pumping have eliminated the city's desert river (Rosen and Melendez 2010), a likely fate of populations near numerous other desert towns and cities, and the major threat to *K. s. longifemorale*. The combination of climate warming, increased drought and flood severity, and aquifer depletion is likely to threaten many populations of *K. sonoriense*. Furthermore, because perennial streams at lower elevations maintain connectivity among montane canyons, habitat loss at lower elevations creates habitat fragmentation and isolation of populations at higher elevations (Hall and Steidl 2007).

At high elevation sites, most known populations of *K. sonoriense* occur in anthropogenic aquatic habitats. Many natural springs were capped and converted into troughs or drinkers for livestock, reducing aquatic habitat for wildlife. Restoration of springs is problematic because the modified structures are part of active grazing leases and because success depends on dwindling ground water availability. Spring loss was partially mitigated by the construction of impoundments in canyons, creating new intermittent and permanent aquatic habitat. However, impoundment

maintenance has been generally poor, and silt accumulation and dam failure are common, particularly in the Madrean Sky Islands (Stone et al. 2014). For example, in a 250 km² region of the Peloncillo Mountains, all 9 natural springs have been modified for livestock use, with only 2 retaining enough integrity to support mud turtle populations, and 15 of 21 impoundments have structural or siltation problems, including 9 that do not hold water (Stone et al. 2015 and unpubl. data). When an impoundment fails, not only does it directly impact the local population, it also fragments the habitat and decreases range-wide connectivity, likely decreasing gene flow and isolating populations. Thus, restoring impoundments is a primary tool for Sonora Mud Turtle conservation (Stone et al. 2014).

Exotic Species. — The non-native Virile Crayfish (*Faxonius virilis*) has become established in many water bodies and may threaten recruitment of Sonora Mud Turtles due to predation (Fernandez and Rosen 1996). In the laboratory, *F. virilis* was observed killing and partially eating a hatchling Sonora Mud Turtle (Fernandez and Rosen 1996), and in the field, attempted predation has been observed on a juvenile (33 mm SCL; Schwendiman 2001). One well-studied population of Sonora Mud Turtles had a marked decline in recruitment coincident with the establishment of *F. virilis* (Fernandez and Rosen 1996). Another population recovered from a decline in recruitment after removal of *F. virilis* (Hensley et al. 2010).

American Bullfrogs (*Lithobates* [=*Rana*] *catesbeianus*) have invaded perennial aquatic habitats in much of the range of *K. sonoriense* (USFWS 2007). Akins and Jones (2010) recovered four juvenile *K. sonoriense* from twelve bullfrog stomachs in three impoundments in the Atascosa/ Pajarito Mountains, Santa Cruz Co., Arizona. Turtles as large as 59 mm SCL were taken, indicating both hatchlings and second year individuals were susceptible to bullfrog predation (Akins and Jones 2010). In areas with high bullfrog densities, multiple researchers have reported Sonora Mud Turtle populations skewed toward larger, older individuals, suggesting bullfrog predation limits juvenile recruitment (Schwalbe and Rosen 1988; Akins and Jones 2010).

Centrarchid fish have been intentionally introduced as sports fish into many habitats that support mud turtles and implicated in the declines of native frogs and fish (Rosen and Melendez 2010; Rosen et al. 1994). Large-mouth Bass (*Micropterus salmoides*) and Green Sunfish (*Lepomis cyanellus*) introductions were correlated with low-density mud turtle populations with poor recruitment at three sites in the Peloncillo Mountains (Stanila 2009). However, direct observations of predation by centrarchid fish on Sonora Mud Turtles have not been reported, and in predation experiments Large-mouth Bass were averse to eating larger, more robust emydid hatchlings (Britson

1988; Semlitsch and Gibbons 1989). It is unclear if this aversion would translate to smaller, softer, and more compact Sonora Mud Turtle hatchlings, and predation experiments involving centrarchid fish and Sonora Mud Turtles hatchlings are warranted.

Trachemys scripta has become invasive in many parts of the world with negative consequences on native turtle assemblages (Cadi and Joly 2003). *Trachemys scripta* has not been widely introduced into the range of Sonora Mud Turtles, but where it has become established negative consequences were evident. Drost et al. (2021) documented the long-term decline in the population of Sonora Mud Turtles at Montezuma Well following the introduction of *T. scripta*, and subsequent recovery following removal of *T. scripta*. Drost et al. (2021) hypothesized that competition for basking sites was the mechanism for the decline in Sonora Mud Turtles.

Climate Change. — Climate change is expected to cause dramatic shifts in chelonian habitat worldwide (Ihlow et al. 2012). Within the geographic range of *K. sonoriense*, climate change is projected to increase temperatures (Garfin et al. 2013; IPCC 2021) and increase the frequency and severity of wildfires, drought, and floods (Seager et al. 2013; Seager and Hoerling 2014; Sankey et al. 2017). Recent analyses combining climate-based species distribution models with climate change projections had conflicting results about the future distribution of *K. sonoriense*. Butler et al. (2016) concluded that climate change would have little effect on *K. sonoriense* range size or range position, whereas Berriozabel-Islas et al. (2020) suggested significant declines in suitable habitat in the future. The studies differed in how points were selected. Using data from the EmySystem (Kiester and Bock 2007), constrained to include only one point per 25 km², Butler et al. (2016) identified 147 unique points of occurrence of *Kinosternon sonoriense*. Berriozabal-Islas et al. (2020) used a similar approach but further constrained the model to exclude points that were not proximate to a known body of water, resulting in a smaller dataset (98 records) with presumably more reliable records. It is unclear which approach best approximates the future distribution of *K. sonoriense*. Neither model considered reduced surface flows due to increased anthropogenic demands (Garfin et al. 2013), loss of aquatic habitat due to dam failures at impoundments (Stone et al. 2014), or loss of aquatic habitat due to siltation associated with increased wildfire frequency (Sankey et al. 2017). Climate change will exacerbate these threats, resulting in habitat loss, habitat fragmentation, and decreased hydroperiod and productivity of wetlands.

Conservation Measures Taken. — *Kinosternon s. longifemorale* has been assessed as Endangered in Mexico (SEMARNAT 2010) and as Critically Endangered on the

IUCN Red List (Rosen and Stone 2017). In 1997, the U.S. Fish and Wildlife Service designated *K. s. longifemorale* a candidate for protection under the U.S. Endangered Species Act (USFWS 1997). In 2016, a preliminary species status assessment report was prepared and *K. s. longifemorale* was formally proposed for listing as Endangered (USFWS 2016). A revised status assessment report was prepared (USFWS 2017a) and the subspecies was formally listed as Endangered in 2017 (USFWS 2017b). Critical habitat for the population in Quitobaquito Spring and Pond was proposed in 2018 and designated in 2020 (USFWS 2020). These federal actions in the U.S. will likely result in increased management actions at Quitobaquito Pond to ensure persistence of that population and collaboration with Mexico to address habitat loss in the Río Sonoyta in Sonora. *Kinosternon s. longifemorale* is protected from collection by its presence within Organ Pipe Cactus National Monument and its current status as a federal Endangered species.

The species as a whole has been assessed as Near Threatened on the IUCN Red List (van Dijk 2011). The nominate subspecies is unlisted by federal governments in both the United States and Mexico, but a Species of Greatest Conservation Need under both the Arizona and New Mexico state wildlife action plans (Arizona Game and Fish Department 2012; New Mexico Department of Game and Fish 2016), and a Species of Special Concern in California (Thomson et al. 2016). These designations indicate that the nominate subspecies also warrants attention and management resources but do not afford adequate protection of the subspecies or its habitat. A hunting license is required in Arizona to collect mud turtles. Commercial collection of *K. s. sonoriense* in New Mexico is limited by regulations under state statute 17-2-4.2 which designates most herpetofauna as protected nongame animals for commercial taking purposes. Further protections from collection of *K. s. sonoriense* in both states is afforded on some federal and state lands where removal of wildlife is restricted. Turtles in general are protected from exploitation under Mexican law; however, implementation of protections are uneven (van Dijk 2011), and data on conservation status are lacking for many species and subspecific taxa, including *K. s. sonoriense* (Macip-Ríos et al. 2015).

Though rarely targeted for specific conservation measures (except for *K. s. longifemorale*), Sonora Mud Turtles occur in a number of protected areas covering much of the geographic range. The two most secure populations of *K. s. longifemorale* occur in protected areas in the United States (Organ Pipe Cactus National Monument) and Mexico (Pinacate Biosphere Reserve). Most of the known populations of *K. s. sonoriense* in the United States occur in protected areas, including: Coronado National Forest, Coconino National Forest, Gila National Forest, Tonto National Forest, San Bernardino National Wildlife Refuge, Leslie Canyon National Wildlife Refuge, Bill Williams River National Wildlife Refuge, Montezuma Well National Monument, Saguaro National Park, Aravaipa Canyon Preserve, and Muleshoe Ranch Cooperative Management Area. Populations of *K. s. sonoriense* are also likely to occur in protected areas in Mexico, such as the Reserva de la Biósfera de Janos.

Aquatic Habitat Restoration. — Management actions already underway to address habitat needs of several other federal Endangered or Threatened species, such as Chiricahua Leopard Frog (*Lithobates* [= *Rana*] *chiricahuensis*), Mexican Gartersnake (*Thamnophis eques*), Narrow-headed Gartersnake (*T. rufipunctatus*), and Loach Minnow (*Rhinichthys cobitis*), are expected to benefit *K. s. sonoriense* due to its co-occurrence in springs and stream systems occupied by these species, which are also affected by many of the same non-native species that threaten *K. sonoriense*. Management actions specifically targeting Sonora Mud Turtle populations were applied at three Sky Island impoundments, where silt was removed (Stone et al. 2014). Two impoundments silted in again within one year, but the third, Blackwater Hole in the Peloncillo Mountains, remains relatively silt free. A leaky dam plate at Blackwater Hole was also replaced (Stone et al. 2014), and the mud turtle population has experienced increased juvenile recruitment in recent years (P. Stone, M. Stone, unpubl. data). At another impoundment in the Peloncillo Mountains, Buckhorn Tank, a similar pattern of siltation and dam plate failure was remediated by the rancher who holds the grazing lease (M. Gault, pers. comm.), with a subsequent increase in juvenile recruitment of mud turtles (P. Stone, M. Stone, unpubl. data).

Control of Exotic Species. — Eradication of bullfrogs is an important component of the Recovery Plan for the federally threatened Chiricahua Leopard Frog (USFWS 2007). Efforts at bullfrog eradication also promote Sonora Mud Turtle protection. Using a combination of seining tadpoles and shooting frogs, determined efforts have successfully eradicated bullfrogs from isolated impoundments and small watersheds (Kahrs 2006; T. Jones and A. Owens, pers. comm.). Similarly, on a small scale, crayfish eradication by physical removal has been successful, with measurable benefits to mud turtles (Hensley et al. 2010). However, eradication of crayfish from large watersheds using current methods is not feasible.

Conservation Measures Proposed. — Agreements among local, regional, and national authorities are in place to provide habitat and treated effluent water for *K. s. longifemorale,* as well as the endemic and endangered pupfish (*Cyprinodon eremus*), and the isolated Río Sonoyta population of longfin dace (*Agosia chrysogaster*)

(Rosen and Stone 2017; USFWS 2017a). However, implementation of these measures has not been completed.

Thus far, few conservation measures have been proposed specifically for populations of *K. s. sonoriense*. However, habitat restoration and removal of exotic species targeted at recovery of endangered aquatic species should indirectly benefit *K. s. sonoriense* populations. Improved water management that restores or augments surface flow is needed to provide adequate aquatic habitat and maintain connectivity among populations (Hall and Steidl 2007; Stone et al. 2015). Stone et al. (2014) emphasized the need to maintain interconnections among subpopulations and proposed two measures: restoring intermittent impoundments by dam repair and silt removal to increase the number of populations; and building small trencheras (i.e., loose rock dams) in canyon beds to increase hydroperiod in canyons that connect populations (Norman et al. 2016). In addition, the construction of additional small impoundments in mountain canyons may be one of the most cost-effective means of ensuring population persistence.

Captive Husbandry. — Since 2007, the Arizona Game and Fish Department, National Park Service, and the Arizona-Sonora Desert Museum (ASDM) have worked together to maintain an assurance colony of Sonoyta Mud Turtles (Riedle et al. 2012; USFWS 2017a). During 2007–2009, 81 turtles were removed from Quitobaquito Pond when the pond was losing water due to a leak. Some turtles were temporarily housed at the Phoenix Zoo, but all were transported to the ASDM by 2009 (Riedle et al. 2012; USFWS 2017a). Of these, 24 were repatriated after habitat restoration in 2011 (USFWS 2017a), 13 are currently housed at the ASDM, and the rest (44) died in captivity. Captive turtles died for various reasons, including predation by racoons, mostly during the early years of the assurance colony. In recent years, successful breeding has occurred, and there are currently 15 captive-bred Sonoyta Mud Turtles at the ASDM, three 2017 hatchlings, nine 2020 hatchlings, and three 2021 hatchlings (H. Byrne, pers. comm.). Currently, the assurance colony at ASDM totals 28 turtles, including 9 males, 4 females, and 15 juveniles (H. Byrne, pers. comm.). The long-term plan is to maintain an assurance colony of 12 turtles at the ASDM, with eventual release of the remaining turtles to Quitobaquito (USFWS 2017a).

Most turtles at ASDM are housed individually in indoor enclosures at relatively constant water temperatures (13–24°C). Three juveniles hatched in 2017 are housed together. Enclosures for larger turtles are 0.60–0.65 m² in area with water depths of 13–15 cm and access to soil or a dry basking/hiding area. Hatchlings are housed in smaller enclosures (0.09–0.37 m², 4–11 cm water depth). Four individuals (1 male: 3 females) are held together in an outdoor pond (3.1 m² aquatic surface area, maximum water depth 38–46 cm) with access to 2.2 m² of land. Water temperatures in the outdoor pond range from 0–24°C. All turtles are maintained on a varied diet that includes mealworms, crickets, cockroaches, krill, and pinky mice; they are fed 5–6 days per week during warmer months and 0–2 times per week during winter, when most turtles fast (C. Christie and H. Bryne, pers. comm.).

Current Research. — Several of our long-term studies of Sonora Mud Turtles are still active: P. Stone, M. Stone, and Congdon are sampling in the Peloncillo Mountains and several Sky Islands ranges in Arizona. David Hall is collecting data in Ciénega Creek at Empire Ranch. Jeff Lovich and Charles Drost periodically monitor the population at Montezuma Well. Peter Holm and Danny Martin (National Park Service) continue to sample the population of Sonoyta Mud Turtles at Quitobaquito in Arizona, and Miguel Grageda Garcia and Michael Bogan (University of Arizona) are monitoring populations in Sonora. Jim Christiansen is investigating shell abnormalities in museum collections. The Arizona Game and Fish Department (AGFD) and other state and federal agencies opportunistically collect data on Sonora Mud Turtles throughout Arizona. The AGFD provided funding to Greer Dolby and Kenro Kusumi (Arizona State University) to map distribution of mud turtles, and non-native invasive bullfrogs and crayfish, and develop risk assessments to guide invasive species control efforts.

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