

## DEMOGRAPHY, TERRESTRIAL BEHAVIOR, AND GROWTH OF SONORA MUD TURTLES (*KINOSTERNON SONORIENSE*) IN AN EXTREME HABITAT

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**ABSTRACT:** We studied the population biology of Sonora mud turtles (*Kinosternon sonoriense*) for 10 yr in an extremely hot and dry desert stream habitat in central Arizona. Adults made up 34.4% of the population. Modeling with Program MARK indicated that both age class (adult vs. juvenile-hatchling) and season contributed significantly to the probability of capture. The presence of exotic crayfish (*Orconectes virilis*) and age class were significant contributors to turtle survival, supporting the hypothesis that exotic crayfish are important predators on hatchlings. Population density estimates indicated low density over the range of water availability. Both adults and juveniles made long-distance movements along the dry stream bed between pools of water. Males and females were both likely to make long-distance movements and were sometimes absent from the study site for years at a time. In addition to terrestrial estivation in foresummer drought, turtles apparently hibernated on land in winter when standing water was available. Growth fit a von Bertalanffy model very well. We make the first report of growth rates for hatchling *K. sonoriense*. Growth rates estimated from shell annuli were consistent with similar estimates for older turtles in other studies. Measured growth rates, however, were much higher than annuli-based estimates. In contrast to other populations, we determined that hatchlings and juveniles in our study added 1–3 plastron annuli each year, making age estimation from annuli difficult. Understanding relationships between habitat use, invasive predators, and demographics is essential for effective management of low-density populations.

**Key words:** Crayfish; Demography; Growth rate; Kinosternidae; *Kinosternon sonoriense*; Movement; *Orconectes virilis*; Shell annuli; Sonoran Desert

THE DYNAMICS of small, low-density populations differ from those of larger more widely or contiguously distributed populations because they can be more influenced by stochastic events such as drought or floods rather than by density-dependent factors such as predation, competition, or disease (Brussard, 1991; Shaffer, 1981). Studying low-density populations and the behavior of individuals within them can be difficult because of low encounter rates. This difficulty can be exacerbated by cryptic behaviors such as nocturnality or long periods of dormancy. The very conditions that keep a population's density low may also cause behaviors to differ from higher-density populations that are more easily studied. For example, members of low-density populations may differ in mating behaviors because of low rates of encountering potential mates (Jirotkul, 1999; Kokko and Rankin, 2006) and in probability of

dispersal between habitat patches (Andreassen and Ims, 2001; Bowler and Benton, 2005). Detection of long-term population trends is difficult in low-density populations, and even more difficult for turtles because of late maturity and slow reproduction (van Loben Sels et al., 1997), requiring long-term study. The benefits of long-term ecological studies are well established (Cody, 1996; Strayer et al., 1986), particularly for understanding trends in population size and demographics (Olivier et al., 2010; Pechmann et al., 1991). Since 1996 we have been studying a low-density population of Sonora mud turtles (*Kinosternon sonoriense*), a small-to-medium kinosternid native to the southwestern United States and northwestern Mexico, including Arizona, New Mexico, Sonora, and Chihuahua (Ernst et al., 1994) and formerly California (Funk, 1974).

Animals that live in extreme or harsh habitats can be constrained to low population densities; for example, density-related compe-

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tition may be temperature dependent, affecting carrying capacity (Solomon, 1949). Our study population occupies a hot and dry, largely ephemeral, desert stream habitat. This harsh climate might be a significant cause of low population density (Solomon, 1949) and thermally challenging environments have been shown to influence habitat use in reptiles (Adolph, 1990; Blouin-Demers and Weatherhead, 2001; Jennings, 2007; Row and Blouin-Demers, 2006). Thus our study population provides an important opportunity for comparisons to populations from the full spectrum of habitats occupied by *K. sonoriense*.

The dry climate at our study site limits the available aquatic habitat for turtles. *Kinosternon sonoriense* was originally characterized as completely aquatic, dependent on permanent bodies of water (Emslie, 1982; Ernst et al., 1994; Hulse, 1974), including permanent, slow-flowing streams with shallow pools (Degenhardt et al., 1996; Hulse, 1982). This species is rarely encountered on land, but Degenhardt and Christiansen (1974) inferred that *K. sonoriense* must occasionally make long-distance overland movements to colonize isolated ponds. Subsequent studies, however, indicate far more terrestrial behavior than originally believed (Hall and Steidl, 2007; Ligon and Stone, 2003; Peterson and Stone, 2000; Stone, 2001). Although *K. sonoriense* has been the subject of several studies, its terrestrial ecology in the hottest and driest of its habitats (isolated ephemeral desert streams) is poorly known.

The main goals of our study were (1) to quantify basic demographics in a widespread yet understudied habitat, and (2) to assess the frequency and significance of terrestrial behavior in this species. These studies, however, were likely influenced by the presence of an aquatic predator, the invasive exotic crayfish *Orconectes virilis* in our study area. There are no native crayfish species in Arizona, and this species of crayfish is known to prey on *K. sonoriense* (Fernandez and Rosen, 1996; Schwendiman, 2001). Thus, our study also had a third goal, (3) to examine the impact of introduced crayfish on this population, and test the hypothesis that crayfish can seriously affect turtle recruitment (Fernandez and Rosen, 1996).

## MATERIALS AND METHODS

### Study Site

Our study site (Fig. 1) was at Cottonwood Creek (elevation 500–625 m), a tributary to Lake Pleasant, a large (30,000–40,000 ha) impoundment of the Agua Fria River in Yavapai and Maricopa Counties in central Arizona. The climate at the site is characterized by very low average rainfall and a highly variable temporal distribution of precipitation. Rainfall data from a weather station 9.1 km NNW of the study site at Castle Hot Springs (CHS) over 30 yr are shown in Fig. 2 (Western Regional Climate Center, 2001). Average annual rainfall from 1961 to 1990 was 388 mm. In typical years most rainfall occurs during summer monsoon and winter rainy seasons, which are separated by foresummer drought (Dimmitt, 2000). Rainfall is highly variable, and every calendar month has been free of rainfall at least once in the 30-yr span. Air temperatures at CHS (Fig. 2) cover a wide range and mean maximum temperature exceeds 35°C for June–September. The extremes of temperature were reflected in water temperatures as well; during the course of the study we recorded water temperatures ranging from 0.25°C to 40.0°C. Long-term temperature and rainfall data from CHS are corroborated by a less complete data set from a second weather station on an island in Lake Pleasant, 4.4 km east of the study site.

Cottonwood Creek is a small stream with both permanent, interrupted water and intermittent flow (Hall and Steidl, 2007; Levick et al., 2008). The relatively small basin drains 24.03 km<sup>2</sup> of the Hieroglyphic Mountains (United States Geological Survey, 2001) and has a stream gradient within the study site of ca. 14.1 m km<sup>-1</sup>. It is a “typical” Sonoran Desert stream, characterized by extensive drought punctuated by heavy, often violent, rainfall and flooding (Fisher et al., 1982; Minckley and Meffe, 1987). Surrounding terrestrial habitats are typical Arizona Upland Sonoran Desert (Turner and Brown, 1982) with riparian habitat being largely Sonoran Riparian Scrubland (Minckley and Brown, 1982). At the beginning of the study (1996) the most reliable pools supported populations of longfin dace (*Agosia chrysogaster*) and both temporary and permanent pools contained the

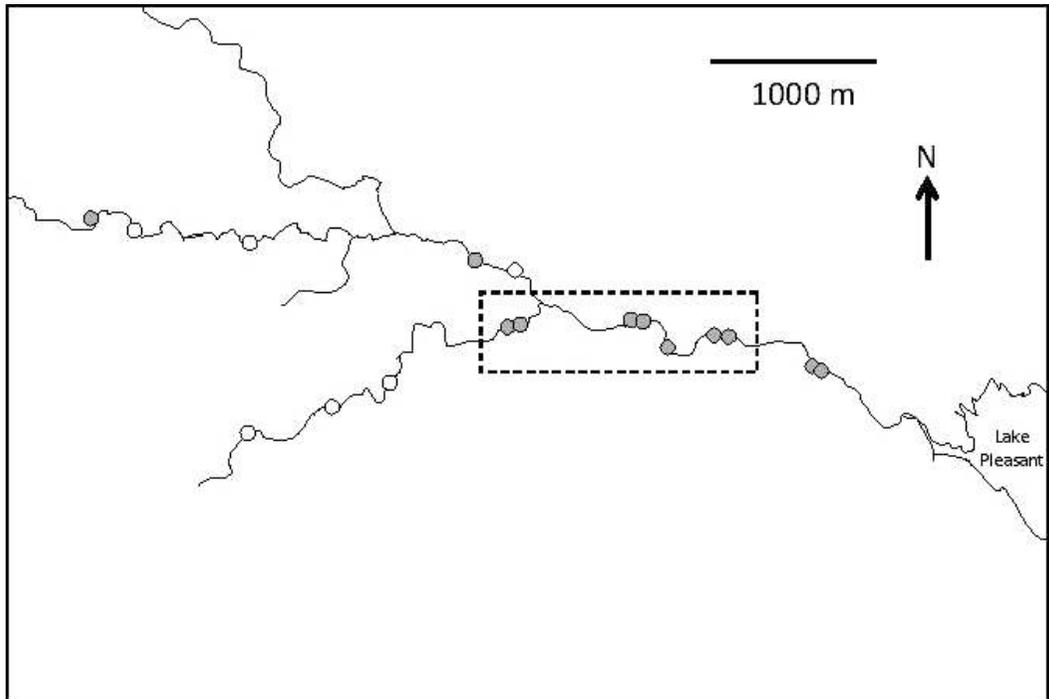


FIG. 1.—Map of Cottonwood Creek, Arizona, showing the distribution of pools after September 1999. The main study area is outlined by the dashed box and encompasses approximately 1600 m of stream bed. Circles represent locations of seasonal or perennial pools. Filled circles represent pools where *Kinosternon sonoriense* were encountered. Off-site pools were surveyed infrequently.

exotic crayfish *O. virilis*. From the early 1990s, and probably for years prior to that, crayfish were widespread and abundant throughout our study area. Crayfish of all size classes could be found in permanent and temporary pools, and large adults could be found dispersing during periods of flow (Jones and Hensley, unpublished data).

The study site was a ca. 1600-m-long stretch of creek bed and consisted of extensive reaches of seasonally dry gravel and bedrock, interrupted by relatively short reaches of semipermanent or permanent, bedrock-lined pools that generally had surface areas between 1 and 10 m<sup>2</sup>, except during brief periods when the creek was flowing. During winters of average or greater rainfall, and during summer monsoon, relative evapotranspiration decreased, groundwater levels rose, and there was continuous surface flow throughout the system. Surface flow sometimes persisted for periods of days or weeks, depending on local rainfall. There were four primary sets of pools

in our study area (Fig. 1). In years of average to above-average rainfall, sets of pools comprised nearly continuous reaches of water, and were separated from each other by long stretches (ca. 160–800 m) of dry wash. In dry years most pools dried completely, occasionally resulting in complete loss of standing water within one or more of the four primary sets of pools, thus extending the distance between adjacent water sources well beyond 300 m. In the entire 1600 m of habitat studied only two pools never dried, but both occasionally shrank to <0.5-m<sup>2</sup> surface area and to <10-cm maximum depth. These two tiny permanent pools were separated by >890 m of stream bed, and were each >1200 m from the nearest other permanent pools.

From 1996 to 2005 the study site underwent changes in stream morphology that reflected historical patterns. Flash flood events occurred in most years, either in summer monsoon, winter, or both. Most flood events removed some gravel and sediment

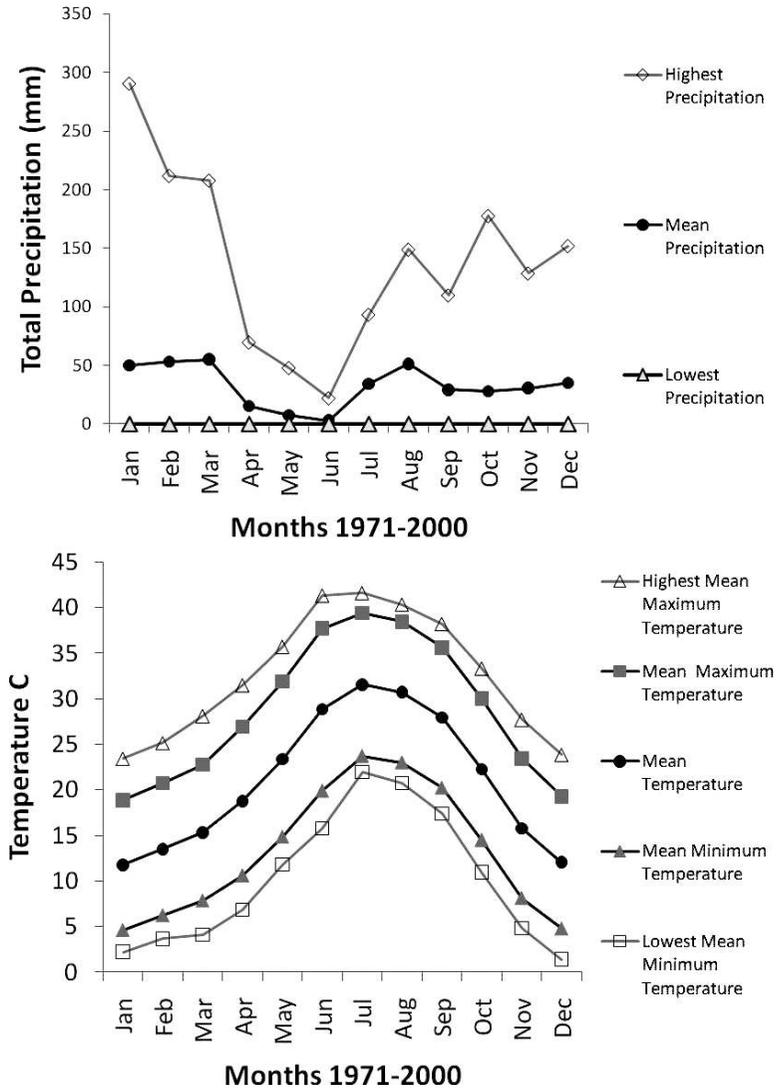


FIG. 2.—Monthly precipitation and temperature data from 1971 to 2000 at Castle Hot Springs, Arizona, 9.1 km NNW of Cottonwood Creek, elevation 606.5 m. Note the protracted season of high temperatures June–September.

and sometimes exposed bedrock depressions that then functioned as pools of various durations. Historic discharge data for this stream system, 1983–1993 (United States Geological Survey, 2001) suggest that most flash floods in this system are relatively small (<ca.  $2.83 \text{ m}^3 \text{ s}^{-1}$ ), although capable of moving considerable amounts of smaller sediments. These values are consistent with those reported for other Sonoran Desert streams (e.g., Martí et al., 2000). In those 10 yr of discharge data, four precipitation

events produced floods  $>25.5 \text{ m}^3 \text{ s}^{-1}$ , for which rainfall varied from 3.8 to 9.1 cm.

#### *Survey Methods and Data Collection*

We visited the study site opportunistically to search for turtles, making 402 visits between September 1996 and August 2005. We visited the site on average every 8.2 days (intervals between visits ranged from 1 to 86 days) and averaged 44.75 visits per calendar year (range = 18–68). We used minnow traps a few times early in our study

and made three captures in them. All other captures were by hand; we located turtles visually and by manually probing the vegetation along pool banks. Hulse (1982) also found hand capturing to be more efficient than trapping in shallow stream habitats. Visits varied in length of time, number, and experience of assistants, and time of day or night, but we generally spent from 2 to 3 hours at each visit and surveyed the entire site on approximately half of all visits. Approximately 15 times we also surveyed pools upstream or downstream of the main study site. The location of each turtle was recorded relative to mapped pools and landmarks. We calculated minimum movement distances from measured distances between pools, landmarks, and capture sites.

We individually marked all turtles by filing or cutting notches in unique patterns in the marginal scutes (Cagle, 1939). Turtles first encountered at off-site pools were also marked for future recognition if they immigrated. We measured medial (not maximum) carapace (CL) and medial plastron (PL) lengths in millimeters with the use of digital calipers or rulers. We determined sex for males by relative tail length, presence of a conical scale at the tip of the tail, and/or plastron concavity (Carr, 1952; Ernst et al., 1994). In Hulse (1974) and Hall and Steidl (2007), turtles were considered sexually mature at 76–80 mm CL, based on secondary sex characteristics, palpated eggs, or behaviors. Lacking other information, we categorized all turtles  $CL > 76$  mm as adults. We counted growth rings in the field on the plastrons of turtles with visible rings (Gibbons, 1983; Rosen, 1987; van Loben Sels et al., 1997). Except for three occasions, growth-ring counts were confirmed by at least one of two principal investigators (FRH or TRJ), whose counts were demonstrated to be consistent with each other. We released most turtles at the point of capture immediately after data collection; in a few cases turtles were returned to the laboratory for 1–2 days before release at the capture site.

We tracked the exact movements of two adult turtles (1M, 1F) with the use of a modified thread trailing technique (Breder, 1927; Iglay et al., 2006) in which we placed a

cotton thread bobbin inside the severed bulb of a disposable pipette that we affixed to the rear margin of the carapace with electrical tape and then coated with epoxy. We limited thread trailing to these two individuals when it became apparent that as turtles moved around in small pools the accumulation of thread became an entanglement hazard for both the trailed turtle and any other turtle that entered the water.

Although we removed exotic crayfish whenever possible during the study, in 1999 we began an aggressive, albeit opportunistic attempt to eradicate crayfish from the study site. We captured crayfish by hand or used dip nets. The small size and isolation of pools made it possible to use dip nets to remove all macroscopic animals. When isolated pools dried, crayfish retreated under rocks, where they were easily captured by hand.

#### *Analyses*

We used Program MARK v5.1 (White and Burnham, 1999) to fit models to the data set and to determine which factors significantly affected the probability of survival and recapture. We modeled the effects of age class (adult vs. subadult), season, and the presence of crayfish on survival and capture probability. We used a time-dependent model with sampling trips pooled by season. Although the data adequately fit the assumptions of a fully time-dependent Cormack–Jolly–Seber model, we preferred the pooled model as more biologically meaningful. The fully time-dependent model was not parsimonious, because of the large number of time parameters estimated and the sparseness of our capture histories. Instead, we modeled time dependence of capture probability with five parameters representing the five seasons of the Sonoran Desert (winter, spring, foreshummer drought, monsoon, and autumn; Dimmitt, 2000) based on our observation that capture rates varied seasonally. We pooled data from 398 sampling trips, grouped according to season, resulting in 43 sampled seasons over a chronological span of 44 seasons. We accounted for the unsampled season in Program MARK by specifying sampling interval lengths. We predicted that the survival of juvenile turtles would be most

affected over time by the presence or absence of crayfish on the study site (Fernandez and Rosen, 1996; Schwendiman, 2001). We predicted that adult survival would differ from that of juveniles because adults should not be vulnerable to crayfish predation. Further, apparent survival was hypothesized to differ between adults and juveniles because age classes might have different probabilities of permanently emigrating from the site. Therefore, we modeled survival in terms of age class (adult vs. juvenile-hatchling) and crayfish presence. We used likelihood-ratio tests to compare the strength of factors in the more general model to nested submodels with fewer parameters.

We used the POPAN implementation of the Jolly-Seber model in Program MARK to obtain an estimate of population size for comparison to other studies. Sparse capture histories relative to the number of sampling trips required us to pool our capture data in the POPAN procedure, treating each calendar year as a single survey occasion (Cooch and White, 2007; Rosen and Lowe, 1996). Considering entire calendar years as sampling periods violates the model's assumption of zero mortality during sampling periods, but long sampling periods increase the probability of recapture and make estimation of model parameters possible when capture histories are sparse. Lengthy sampling periods bias the estimates of survival parameters because animals captured near the end of sampling periods have higher probability of survival than animals captured near the beginning of sampling periods (Williams et al., 2001). O'Brien et al. (2005) examined the implications of violating this assumption with the use of both simulations and data from ploughshare tortoise (*Geochelone yniphora*) recaptures. They found that extended sampling, contrary to expectations, actually provided the least biased and most reliable estimates of population size as long as recapture rates were  $>0.2$ . Our overall recapture rate was 0.61 and thus within the scope for extended sampling to provide more accurate population estimates.

We compared three methods of estimating growth rates for hatchlings and juveniles:

*Method 1.*—We calculated average linear growth rate (mm/yr) for each turtle from the

increase in carapace length measured for each recapture interval (Hulse, 1976).

*Method 2.*—We fitted our recapture growth data to a von Bertalanffy growth model, where growth declines exponentially from hatching size toward an asymptotic length. We followed the method of Fabens (1965) for modeling growth with the use of recapture intervals instead of known ages (Frazer et al., 1990; Spencer, 2002). The general equation for the model is

$$L = a(1 - be^{-kt}),$$

where  $L$  = length (mm),  $a$  = asymptotic length (mm),  $b$  = growth parameter calculated by setting  $t = 0$  and setting  $L$  = hatching size,  $e$  = base of the natural logarithm,  $t$  = recapture interval (days), and  $k$  is the growth constant. We used the size of our smallest turtle as an estimate of hatching size. We followed Fabens' (1965) method for estimating  $a$  and  $k$ , and then iterated from those estimates to find the model that minimized the squared residuals between observed and predicted carapace length. Spencer (2002) presented a formulation that allows estimation of age at any capture from measured size and known or estimated hatching size:

$$L_2 = a - (a - L_1)e^{-kdt},$$

where  $L_2$  is length at second capture and  $L_1$  is length at first capture and  $dt$  is the interval between captures.

*Method 3.*—We used plastron growth rings to estimate ages and examined the slope of carapace length vs. estimated age to estimate growth (Iverson, 1991; Rosen and Lowe, 1996; van Loben Sels et al., 1997; Wilson et al., 2003). Accuracy depends on annuli being produced in a consistent pattern that is strongly correlated with age (generally assumed to be one annulus per year, but see Discussion below).

## RESULTS

### *Demography*

We captured and marked 61 individual turtles on the study site and 6 turtles in pools upstream or downstream from the main site. We excluded from further analysis three off-

site turtles (2F, 1M) from upstream that were never recaptured. We included three turtles from downstream, however, when we determined that at least three turtles moved between the main study site and the downstream pools (Fig. 1). Of the 64 included turtles, we recaptured 39 marked individuals 158 times for a total of 222 captures. Among turtles included in the analysis we confidently identified 9 adult females and 12 adult males, and we captured two adults for which sex was not recorded. Based on size and season of first capture (see Discussion) we subdivided the 41 subadults into two groups: those with CL < 40 mm ( $n = 24$ ), which we refer to as hatchlings, and those with CL 40–76 mm ( $n = 17$ ), which we categorized as juveniles. The distribution of turtle captures by age class and season is shown in Fig. 3. Capture rates were highest during monsoon and lowest during winter. Only during monsoon seasons did capture rate average >1 turtle per site visit.

We found hatchlings from five annual cohorts; the first hatchlings appeared after 15 July in cohort years. The largest annual cohort of hatchlings during the study ( $n = 18$ ) coincided with a flash flood. On 11–12 September 1999, a single storm contributed ca. 3.6 cm of rain to the study area basin (averaged between two recording stations within 10 km of our site, Garfias Mountain Ranch and Lake Pleasant; Flood Control District of Maricopa County, 2007), resulting in a flood that we estimate was  $\gg 14.2 \text{ m}^3 \text{ s}^{-1}$ . Floods of this magnitude are capable of massive redistribution and deposition of gravel, cobble, and smaller sediments, resulting in biologically significant reorganization of basin morphology. This particular flood deposited up to 1 m of sediments, which completely filled several pool basins. Reliable aquatic habitat was reduced by 46.5% (measured linearly). Six hatchlings from the 1999 cohort were first captured prior to this flood (from 1–8 September), and two of those were recaptured afterwards. Eight other hatchlings were captured within 2 weeks postflood, five of those within a week. These eight hatchlings had a mean CL = 33.59 mm. This size is comparable to two hatchlings in the study with minimum ages of 51 days (CL = 34.37 mm) and 19 days (CL = 36.84 mm) and contrasts

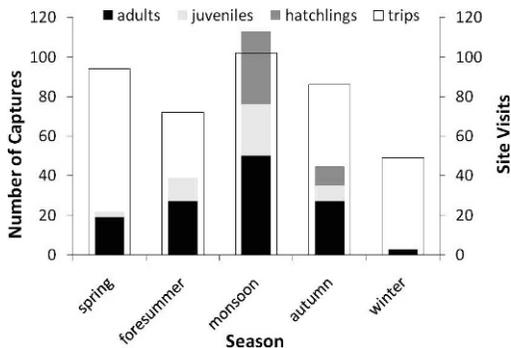


FIG. 3.—Distribution of visits (open rectangles) to Cottonwood Creek, Arizona, and captures (filled rectangles) of *Kinosternon sonoriense* by season.

with the five smallest hatchlings in the study, which had CL from 23.22 to 28.56 mm. Size, coupled with flatter carapace morphology than seen in the smallest hatchlings, suggests that the 8 quite likely hatched before the flood, and therefore at least 10 of 14 hatchlings in this cohort survived a catastrophic flood event.

Two important biotic changes during the study that had the potential to affect turtle demographics included the local extinctions of native fish and invasive exotic crayfish. Long-finned dace (*A. chrysogaster*), a prey species for *K. sonoriense* (Jones and Hensley, unpublished data), had been widespread throughout the study area, but declined and disappeared in response to drought in 2002. Crayfish were initially abundant on the study site. During 1999–2000, small pool size, isolation by dry reaches, and pool reduction by drought contributed to our eradication effort. For example, on 19 May 2000 we removed 164 crayfish from a pool that had a surface area  $< 2 \text{ m}^2$ . No crayfish remained on the study site by September 2000, and they failed to recolonize the pools for at least 4 yr. The relationship between crayfish presence and hatchling turtles is shown in Fig. 4. When crayfish were abundant, hatchling turtles from the 1996 cohort ( $n = 7$ ) were never recaptured, and no hatchlings or juveniles were ever encountered that could be assigned to 1997 or 1998 cohorts. Once crayfish declined, we frequently recaptured hatchling turtles (cohorts of 1999–2002, Fig. 4). Eight hatchlings captured when the crayfish population

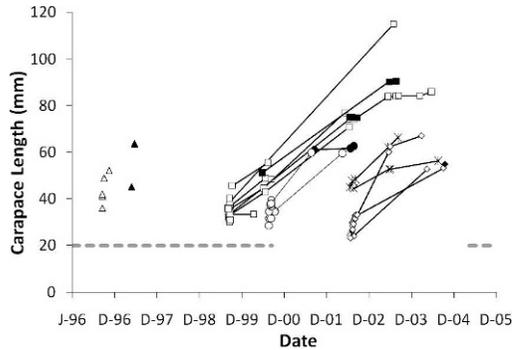


FIG. 4.—Presence of crayfish (horizontal dashed line) and recaptures of subadult *Kinosternon sonoriense* ( $n = 41$ ) plotted from January 1996 (J-96) to December 2005 (D-05), at Cottonwood Creek, Arizona. Active eradication of crayfish spanned 1999–September 2000. Recaptures of individuals are connected, showing individual growth. Plot symbols identify apparent turtle cohorts (triangle = 1996,  $n = 7$ ; square = 1999,  $n = 18$ ; circle = 2000,  $n = 5$ ; asterisk = 2001,  $n = 2$ ; diamond = 2002,  $n = 4$ ). Filled plot symbols or asterisks represent turtles that apparently hatched the previous summer but were not encountered until their second year ( $n = 6$ ). No hatchlings or juveniles were encountered that could be assigned to cohorts 1997–1998 or 2003–2005.

was actively being eliminated (1999–2000) survived and were recaptured. Crayfish recolonized the lowermost pool set on the study site in 2005 by moving upstream from Lake Pleasant when the creek was flowing, but they did not spread to the upper three sets of pools.

To examine demographics with Program MARK, we compared a general model,  $\phi_{(\text{age} * \text{crayfish})} P_{(\text{age} * \text{season})}$ , to a model in which age and season do not interact in affecting capture probability,  $\phi_{(\text{age} * \text{crayfish})} P_{(\text{age} + \text{season})}$ . A likelihood ratio test indicated that the two models were not significantly different ( $P = 0.3299$ ), so we preferred the more parsimonious additive model, because it had fewer parameters.

We examined simpler models nested within our additive model and used likelihood ratio tests to examine the importance of each component. Age class ( $P = 0.0028$ ) and season ( $P < 0.0001$ ) contributed significantly to the probability of capture, as compared to models that eliminated these factors. Likelihood ratio tests also showed that both the presence of crayfish ( $P = 0.026$ ) and age class (adult vs. juvenile–hatchling,  $P = 0.013$ ) were significant factors in survival probability over the

course of the study. The POPAN procedure yielded a population estimate of 77 subadults (95% confidence interval 57–96) and 27 adults (95% confidence interval 20–34).

#### Terrestrial Behavior

We calculated minimum movement distance for 153 recaptures and detected no pattern in movement direction upstream vs. downstream. Adult females moved an average of 172.6 m between captures ( $n = 58$  movements; range 0–1540 m, but see Discussion). Adult males moved an average of 75.6 m between captures ( $n = 40$  movements; range = 0–878 m). The difference in mean distance between males and females approached statistical significance (two-tailed Z test,  $Z = 1.889$ ,  $P = 0.059$ ). For turtles that were juveniles both before and after documented movements ( $n = 20$ ), the average distance moved between captures was 99 m (range 0–891 m). Twenty-two movements were documented for hatchling turtles, ranging from 0 to 90 m, with an average of 5.4 m. For hatchlings that grew to juvenile size between captures ( $n = 9$ ), the average distance moved was 98.5 m (range = 0–532 m). Thus, once animals grew beyond 40 mm CL, all movement distances were roughly similar.

Of 28 movements that exceeded 165 m (17.7% of recaptures), 27 required turtles to traverse more than 100 m of stream bed that was generally dry. Eight of these movements (>165 m) were between 500 and 1000 m in length, and two exceeded 1000 m (<1% of all recaptures). Long-distance movements were made by 5 of 11 adult males and by all 6 adult females that were ever recaptured. Long-distance movements were not made exclusively by adult animals; five were made by juveniles and two by hatchlings. We only encountered turtles moving in the stream bed, away from the four main pool areas, on two occasions. Both times the creek was flowing and the turtles were in water. Because of long between-capture intervals, it was not possible to determine if long-distance movements were generally associated with brief flow events. Turtles were encountered out of water only on two occasions, except for animals tracked by thread trailing. Long recapture intervals (>700 d) were not always associated with

long-distance movements; i.e., when turtles disappeared from the study site for long periods they often returned to their most recently occupied pool.

We found evidence of winter terrestrial hibernation even when temperatures were mild and water was readily available. We observed that turtle activity was lower during winter months when our manual searches of all available water only rarely resulted in encounters with turtles, even in holes under overhanging banks (Fig. 3). The adult female (No. 10-13) that we thread-trailed hibernated on land, more than 30 m from the nearest permanent water, but within the creek bed. She left the water on 9 October 2001 and returned to water after 12 February 2002. During her first 3 days on land she made two movements of 28 m and 38 m before settling into her hibernation site. During the next 123+ days that she was on land, she spent most of her time under dead vegetation at the base of a Gooding willow (*Salix goodingii*), but she made five movements from this hibernation site, ranging from 4.1 to 11.3 m. During the entire hibernation period there was standing water available in the nearest permanent pool, and for much of the time there was water available in temporary pools even closer to the hibernation site. Once the trailed turtle returned to water in March, she remained associated with the nearest permanent pool of water until the end of September, with the exception of a 1–3-week visit to another permanent pool 168 m away. Thus, during the spring and summer she was highly aquatic and rather sedentary.

#### Growth Rates

All turtles with CL < 30 mm ( $n = 5$ , 10 captures) were encountered between 16 July and 20 August, and we categorized them as hatchlings. Turtles with CL > 30 mm and < 40 mm (24 individuals including recaptures of the 5 just mentioned, 30 total captures), were only encountered between mid-August and mid-October. Thus, 19 additional turtles were also categorized as hatchlings. Ten of the 24 hatchlings in the study were recaptured after their first winter and eight of these animals were recaptured in subsequent years (Fig. 4). The average size (CL) of adult males in our

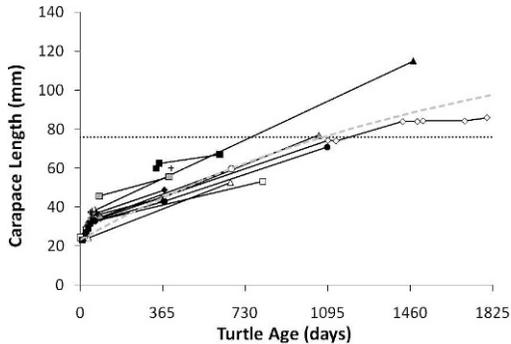


FIG. 5.—Growth of marked *Kinosternon sonoriense* hatchlings that were recaptured at least once ( $n = 14$ , each has a unique plot symbol) at Cottonwood Creek. Ages are estimated from July 15 of the year the hatchling was first encountered. Note more rapid growth rate of hatchlings < 40 mm. The gray dashed curve represents the best-fit von Bertalanffy model for the population, and the horizontal dotted line indicates the presumptive size at sexual maturity, 76 mm.

study was 121 mm ( $n = 12$ , range 97.7–142.5) and the average for females was 142 mm ( $n = 7$ , range 128.0–145.0). Sexual dimorphism in CL was significant ( $t = 3.39$ ,  $df = 16$ ,  $P < 0.01$ ).

Three hatchlings in our study grew beyond threshold adult size (CL > 76 mm; Fig. 5). One (No. 13-22, sex not determined) reached 115 mm at age 4 and interpolating a linear growth trajectory suggests that this turtle may have crossed the 76-mm threshold at age 2, but there are no data for this animal between hatchling and age 4. A second hatchling (No. 1-10, male) reached 74.2 mm at ca. 3 yr and growth plateaued between ages 4 and 5 (CL ca. 84–86 mm). A third hatchling (No. 3-15, sex not determined) reached 76.9 mm at age 3. A fourth hatchling (No. 2-13, sex not determined) reached 70.8 mm at age 3 (Fig. 5). Overall, it appears that turtles at our study site approach this minimum adult size by about age 3 and exceed it by age 4.

**Method 1.**—Average linear growth rate (mm/yr) was very high in hatchlings, sometimes exceeding 100 mm/yr, and declined as CL increased (Fig. 6). A summary of growth-rate measurements and estimates is in Table 1, along with comparisons to other studies.

**Method 2.**—For our data, the best von Bertalanffy model is

$$L = 137.5(1 - 0.831 e^{-0.000575t}),$$

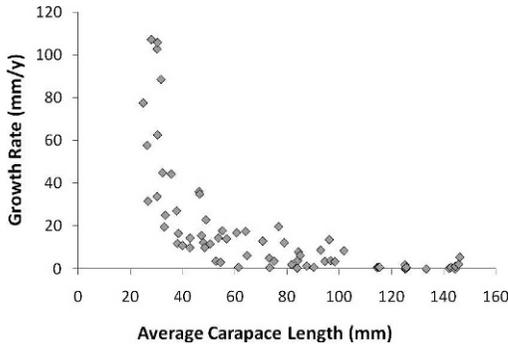


FIG. 6.—Growth rate (mm/yr) during a recapture interval vs. average size during that interval, at Cottonwood Creek. Note the extremely high growth rates of the smallest turtles, and the rapid decline in rate as size increases.

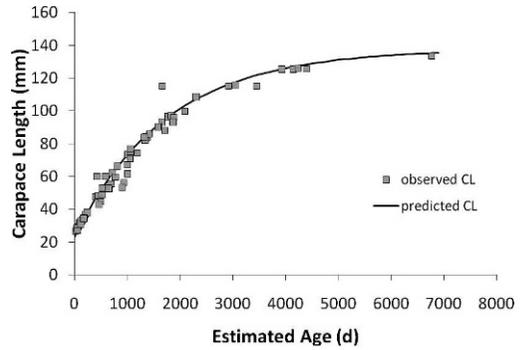


FIG. 7.—The fit of growth increments between captures to a von Bertalanffy model. The curve is the best fit model for the population. Individual points are observed carapace length at the end of a capture interval, assuming that age at first capture is as predicted by the model.

with an excellent fit between observed and predicted carapace lengths (linear regression,  $r^2 = 0.98$ ). We visualized the fit of observed growth increments to the predictions of Spencer’s (2002) formulation of the model (Fig. 7). The age estimate for CL = 76 mm, our criterion for classification as adult, is 2.95 yr (1077 days), which agrees with the four observations of individual growth presented above.

*Method 3.*—Because encounter dates and growth data indicate that all 24 turtles >30 mm and <40 mm CL had likely hatched in July or August of the year we first encountered them, we have reliable ages for these turtles, permitting us to test whether growth rings on the plastron were reliable indicators of actual age. We detected no differences among annuli that would support categorizing some as secondary or “weak, non-

TABLE 1.—Comparison of growth rate estimates and measurements for *Kinosternon sonoriense* in several studies.<sup>a</sup>

Population	Age/sex/size	Method	Growth rate	Source
<b>Method 1</b>				
Tule Creek	Adult males	Size vs. recapture interval	1.57 ± 0.32 mm CL/yr	Hulse (1976)
Tule Creek	Adult females	Size vs. recapture interval	1.50 ± 0.28 mm CL/yr	Hulse (1976)
Cottonwood Creek	Hatchlings CL < 40 mm	Size vs. recapture interval	51.09 mm CL/yr	This study
Cottonwood Creek	Juveniles CL = 40–76 mm	Size vs. recapture interval	12.96 mm CL/yr	This study
Cottonwood Creek	Adults >76 mm	Size vs. recapture interval	3.86 mm CL/yr	This study
<b>Method 3</b>				
Tule Creek	Juvenile to adult 40–120 mm	Size vs. annuli	4.5 mm PL <sup>a</sup> /yr <sup>-b</sup>	Hulse (1976)
Sycamore Creek	Juvenile to adult 40–120 mm	Size vs. annuli	9 mm PL <sup>a</sup> /yr <sup>-b</sup>	Hulse (1976)
West Turkey Creek	Hatchling to 6 yr	Size vs. annuli	17.5 mm/yr <sup>c</sup>	van Loben Sels et al. (1997)
Cottonwood Creek	Known age hatchlings/juveniles	Size vs. annuli	18.9 mm/yr <sup>d</sup>	This study

<sup>a</sup> CL = carapace length; PL = plastron length.  
<sup>b</sup> Assumed 1 annulus per yr.  
<sup>c</sup> Validated 1 annulus per yr.  
<sup>d</sup> 9.47 mm/annulus; most produce 2 annuli per yr.

annual rings" (Rosen and Lowe, 1996). We found that age was significantly correlated with the number of rings ( $r^2 = 0.748$ ,  $P < 0.001$ ; Fig. 8). Despite this positive correlation, growth rings were produced inconsistently (1–3 rings/yr) in small turtles. Wilson et al. (2003) pointed out that few studies have tested whether age is a better predictor of growth ring number than is body size. We tested this (Fig. 8) and found similar correlation coefficients, indicating that age is no better than size at predicting growth ring number. This reinforces the idea that age and size are highly correlated in this population, as suggested by the excellent fit of the von Bertalanffy model.

## DISCUSSION

### *Habitat*

The results of our study are best understood in the context of habitat variability. The population biology of *K. sonoriense* has been studied at several localities that vary in temperature, precipitation, size of bodies of water, and permanence of water. In all habitats, lotic sites are subject to unpredictable and often catastrophic flash flooding (e.g., Tule Creek, Collins et al., 1981; Hulse, 1974; Sharp Springs, Meffe, 1984; Rosen, 1987; this study). At higher elevations, streams may be permanent and/or associated with permanent, nutrient-rich stock tanks and impoundments (e.g., Hall and Steidl, 2007; van Loben Sels et al., 1997) or may be intermittent and subject to total drying (Stone, 2001). At lower elevations, such as Sonoran Desert habitats, streams are seasonally intermittent and characterized by extreme temperatures and persistent drought (Tule Creek, Hulse, 1976; this study) but permanent water may be available in isolated locations (Quitobaquito Springs, Rosen, 1987). Even within the Sonoran Desert, habitats might comprise large drainage basins with relatively reliable water sources (e.g., Sycamore Creek, Rosen, 1987) or intermittent habitats that rely on recharge by unpredictable rainfall (this study). Also, in smaller drainages, including habitats such as Cottonwood Creek (this study), flash floods can redistribute sediments such that pools might be unavailable on a decadal scale.

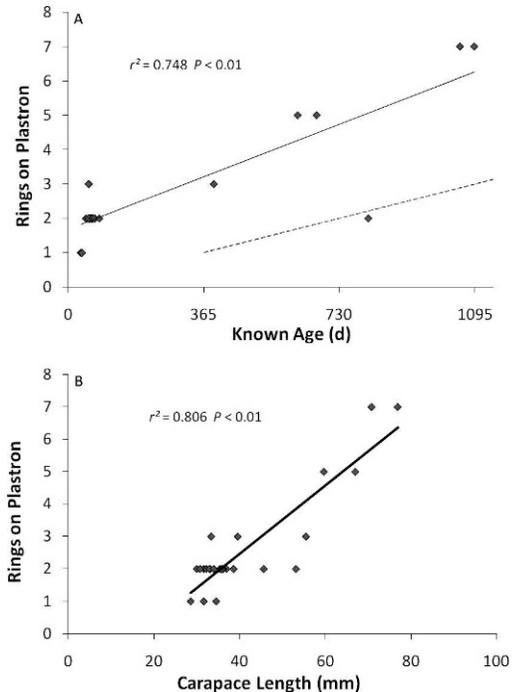


FIG. 8.—The relationship between number of annuli on the plastron and known age and size of *Kinosternon sonoriense* marked as hatchlings (26 observations of 22 individuals) at Cottonwood Creek. (A) Annuli vs. age. The solid line is the least-squares regression. The dotted line represents the hypothesis of 1 growth ring/yr. (B) Correlation between carapace length and number of growth rings on the plastron. The overall growth rate is 9.47 mm/annulus.

Our study site was characterized by low precipitation and protracted heat (Fig. 2), and mostly ephemeral water and a few small perennial pools, and a minimum distance of 1.3 km to a large body of permanent water. Populations studied at higher elevations (Emslie, 1982, 1050 m; Hall and Steidl, 2007, 874–2476 m; Stone, 2001, 1700 m; van Loben Sels et al., 1997, 1675 m) lack the prolonged high temperatures that occur at our site. Populations in permanent springs (Emslie, 1982; Hulse, 1974, 1982; Rosen and Lowe, 1996) or at locations with stock tanks (van Loben Sels et al., 1997) are less frequently exposed to the limitations of water availability that occur at Cottonwood Creek. An exception to this is the study site with a stock tank in the Peloncillo Mountains of New Mexico (Stone, 2001) which is the only study site to report complete drying of all water sources. Differences

TABLE 2.—Demographics of several populations of *Kinosternon sonoriense*.

Population	Elevation (m)	Density (turtles/ha)	Total no.	No. of adults	No. of subadults (juveniles + hatchlings)	No. of hatchlings	% adult	Source
Quitobaquito Springs, AZ	306	220	—	—	—	—	—	Rosen (1987)
Quitobaquito Springs, AZ	355	Low	378	236	142	19	62.4	Rosen and Lowe (1996)
Tule Creek, AZ	549	3624	—	—	—	—	—	Rosen (1987)
Cottonwood Creek	575	8.4–40.6 <sup>a</sup>	64	22	42	24	34.4	This study
Cottonwood Creek		270–406 <sup>b</sup>						This study
Tule Creek, AZ	610	750–825	190	119	71	—	62.6	Hulse (1974)
Palm Lake, AZ	732	188	—	—	—	—	—	Rosen (1987)
Cardogera, Montrose, and Sabino Canyons, AZ	810–2476	—	215	143	72	—	66.5	Hall and Steidl (2007)
Spring Creek, AZ	1050	—	124	98	26	—	79.0	Emslie (1982)
Montezuma's Well, AZ	1113	974	—	—	—	—	—	Rosen (1987)
Sycamore Creek, AZ	1219	1972	—	—	—	—	—	Rosen (1987)
Sharp Spring, AZ	1402	8829	—	—	—	—	—	Rosen (1987)
West Turkey Creek, AZ	1675	—	573	467	106	4	81.5	van Loben Sels et al. (1997)
Peloncillo Mountains, NM	1700	3000	274	182	92	26	66.4	Stone (2001)

<sup>a</sup> At maximum water level (see Discussion).

<sup>b</sup> At typical water level.

between our study site and cooler or more mesic or predictable habitats at other study sites might explain variation in use of terrestrial habitats including movements and estivation, variation in growth rates, variation in numbers of annuli produced each year, and variation in demography. The degree to which these vary has been partially documented for some populations, but thorough comparisons across the habitat continuum are not yet possible.

#### *Demographics, Population Size, and Density*

Our analysis suggests that our population is dominated by subadults. Adults comprise 34.4% of the population and hatchlings 37.5%. Other studied populations of *K. sonoriense* are 62–81% adult and less than 10% hatchlings (Table 2). There is a weak trend across these studies for percent adults in a population to be correlated with average elevation ( $r^2 = 0.23$ ,  $P < 0.10$ ).

Turtle densities are generally reported in terms of turtles per hectare of water surface. Rosen (1987) estimated densities for six populations of *K. sonoriense* in Arizona ranging from 188/ha (Palm Lake) to 8829/ha at Sharp Spring (Table 2). Stone (2001) and Hulse (1974) also reported densities within this range (Table 2). Population density is

weakly correlated with study-site elevation ( $r^2 = 0.29$ ,  $P < 0.10$ ) across studies in Table 2.

Morales-Verdeja and Vogt (1997) cautioned that an accurate estimate of freshwater turtle density would require a thorough understanding of movements and habitat use. In their study of *Kinosternon leucostomum* in México, turtles used only the margins of the lake, so including the entire surface or volume of the lake led to underestimates of density. Growing evidence shows that *K. sonoriense* can be highly terrestrial (Hall and Steidl, 2007; Ligon and Stone, 2003; Peterson and Stone, 2000; Stone, 2001). This evidence, our terrestrial hibernation data, and our ability to search scattered, small, aquatic pools thoroughly led us to estimate density on the basis of entire stream channel habitat area in addition to estimating based on water surface area.

Despite regular visits to habitats outside the creek bed, we never encountered turtles there and discount it as usable habitat for *K. sonoriense*. Thus, we estimated the effective habitat to be ca. 20 m wide by 1600 m, or 3.2 ha. At peak stream flows this entire area was under water and thus density at those times is expressed per hectare of water surface, as is usual. For much of the year, however, water surface was much less, so density per hectare of water surface was higher.

We used the POPAN population estimates to estimate density; POPAN's 95% confidence intervals ranged from 77 to 130 turtles, yielding a mean estimate of 32.5 turtles/ha and a high value of 40.6 turtles/ha of stream bed. These density estimates are 4.4% to 21.6% of the lowest published density for *K. sonoriense* (Table 2; Palm Lake, AZ; Rosen, 1987).

With the use of typical water surface area during 2000 (ca. 0.1 ha) rather than the entire stream bed, and the POPAN values above, the mean estimate was 325/ha and the high estimate was 406/ha. These estimates based on water surface area rather than the entire stream bed are more biologically realistic and are similar in magnitude to densities of other populations (Table 2), but are still quite low. Total water surface on the study site occasionally fell as low as 1 m<sup>2</sup>, yielding unrealistically high estimates of 27,000–40,600/ha of water surface. At average to low water levels, however, we were able to search aquatic habitat thoroughly and determine actual occupancy of aquatic habitat. Ligon and Stone (2003) reported that in New Mexico *K. sonoriense* do not congregate in water during drought. At the lowest water levels, we never found more than three turtles in the water, so the observed density was  $3 \times 10^{-4}$ /ha, extremely low rather than extremely high in comparison to other studies (Table 2).

Stone (2001) reported population estimates that fluctuated wildly as water levels fluctuated. In habitats where water availability fluctuates, the best estimates of density would come from both thorough sampling of turtles and continuous recording of water surface availability and habitat use. Unfortunately, we lack the frequent measurements of water surface area required to make these estimates. Based on the estimates we are able to make, we conclude that population density at Cottonwood Creek is best understood as quite low.

### *Crayfish*

Invasive exotic predators that eat young turtles, such as crayfish, are potentially serious threats to the persistence of turtle populations, because long-lived, late-maturing species require high juvenile survivorship (van

Loben Sels et al., 1997) for population stability. Fernandez and Rosen (1996) found no evidence of recruitment in a central Arizona population of *K. sonoriense* years after invasion by exotic crayfish (*O. virilis*). They hypothesized direct predation by crayfish on young (CL < 65 mm) turtles that lack adequate shell calcification, and confirmed that possibility in a laboratory experiment (Fernandez and Rosen, 1996). Schwendiman (2001) verified predation by *O. virilis* on a hatchling turtle (CL = 33 mm; mistakenly reported as a 2-yr-old animal) at our study site. Additional, indirect evidence for crayfish predation at our site include an observation of a large adult *O. virilis* repeatedly pushing a hatchling turtle, and another hatchling (CL = 33.2 mm) found dead 3 September 1997 with its head and right forelimb missing and crushing and puncture injuries consistent with a crayfish attack. Accordingly, we predict that recruitment of hatchlings and immigration of juveniles <65 mm will be reduced wherever crayfish are present.

Crayfish coexisted with turtles at our site until 1999, when we initiated a concerted effort to remove crayfish, and all were eradicated by September 2000 (Fig. 4). In the MARK model crayfish presence had a significant effect on turtle survival, but we interpret the strength of the crayfish effect cautiously because of potential confounding effects. The complete lack of hatchlings in 2004–2005 may reflect the return of crayfish to the lower pools, an absence of nesting (only one adult female turtle was found on the site during 2004 and 2005), drought, and/or other factors including inadequate sampling. That our sampling for hatchlings and juveniles was not complete is demonstrated by the first capture of some turtles during their second summer (Fig. 4) rather than their first. Because we visited the site opportunistically, variation in sampling effort may contribute to apparent absence of hatchlings. From 1999–2004 our sampling effort during monsoon and autumn was approximately twice our effort in 1996–1998 (25.1 visits/yr vs. 11.0 visits/yr). The complete absence of two cohorts, however, seems unlikely to be entirely due to sampling error. In Arizona, where there are no native crayfish, *O. virilis* has become

widespread and abundant, resulting in dramatic changes in biotic community structure (Fernandez and Rosen, 1996), and our data suggest that recruitment and persistence of populations of *K. sonoriense* are jeopardized wherever crayfish become established.

#### *Terrestrial Habitat Use*

*Hibernation.*—Hulse (1974) found no evidence for terrestrial activity and concluded that *K. sonoriense* hibernates in water rather than on land like many other species of *Kinosternon* (Bennett, 1972; Bennett et al., 1970; Christiansen et al., 1985; Morales-Verdeja and Vogt, 1997); however Ligon and Stone (2003) used radiotelemetry to document terrestrial estivation of *K. sonoriense* during summer drying of aquatic habitat. They concluded that terrestrial estivation, rather than migration to water, was the dominant drought-survival strategy at their site in New Mexico (Ligon and Stone, 2003), a pattern confirmed by Hall and Steidl (2007) in Arizona. Stone (2001) also found that turtles would estivate on land during summer even when standing water was available. Thread trailing at our study site revealed that *K. sonoriense* will hibernate on land during winter, despite mild temperatures and available standing water. We conclude that factors other than water availability, such as food, predation risk, or temperature, must influence winter hibernation. A pattern of terrestrial hibernation in our population would explain both our observation that winter captures were extremely rare (Fig. 3) and the strength of the season effect in the Program MARK model.

*Movements.*—Where relatively large, permanent bodies of water are present, populations of *K. sonoriense* show highly aquatic behavior and relatively little terrestrial behavior or movement between water sources (Degenhardt et al., 1996; Emslie, 1982; Hulse, 1974; van Loben Sels, 1997). Recent work, however, has documented more extensive use of terrestrial habitats and terrestrial movements >1 km in more ephemeral habitats (Hall and Steidl, 2007; Ligon and Stone, 2003; Stone, 2001). Long-distance movements in aquatic turtles might be associated with various ecological factors (Gibbons, 1986)

including nesting, mate seeking, drought (Bennett et al., 1970; Gibbons et al., 1983; Yeomans, 1995), avoiding predators (Bennett et al., 1970; Teska, 1976), moving between aquatic foraging areas, or moving to estivation or hibernation sites. Stone (2001) found a seasonal trend for *K. sonoriense* to move downstream from a stock tank to stream bed pools when the pools filled, and then to return to the stock tank when pools dried. At our study site we detected no seasonal trends in movement direction.

Hall and Steidl (2007) found that large adult females were sedentary, but small females moved more. In their study adult males moved more frequently and for longer distances than females. In our study there was no statistically significant difference between average distance moved by adult males and females (though  $P = 0.059$ ), and juveniles moved similar distances as well. The direction of the trend, however, was the opposite of what Hall and Steidl observed; males on average moved about half the distance that females moved. Of nine movements that exceeded 700 m, seven were made by adult females, one by a juvenile, and one by an adult male. The longest movement in the study was made by adult female No. 10-15; she was found 1540 m downstream of her previous location and moving upstream during a period when the creek was flowing. We inferred, however, that she had traveled all the way to Lake Pleasant and back, a total distance of 4512 m, because she had a fish hook embedded in her cloaca. We removed the hook and released her, and she was recaptured four times over the next 18 months, adding an additional 2500 m of cumulative movements. Her three longest movements exceed the longest reported movement for an adult female (854 m; Hall and Steidl, 2007) and her total accumulated distance of 7.96 km exceeds the longest reported single movement for an adult male (7.2 km; Hall and Steidl, 2007).

For large adult females, Hall and Steidl (2007) described “home pools” within pool complexes and found considerable site fidelity. The extreme example of this was a female that occupied her home range continuously for 19 yr, with 97% of captures in her home

pool. In contrast, the longest individual movements and cumulative total movements in our study were made by adult females. Nine recapture intervals exceeded 700 days, but four turtles that were absent for these long intervals were subsequently recaptured <20 m from their former location, indicating some site fidelity. The two largest adult females for which we have the most extensive capture histories showed contrasting patterns of site occupancy. Female No. 10–13 was present on the study site for four intervals from 1997–2002, with absences of approximately 12, 17, and 18 months. In addition to the time period when she was tracked by thread trailing, 18 of her 20 captures were in the same set of pools, indicating strong site fidelity. In contrast, female No. 10–15 wandered extensively over the entire study site (and presumably well beyond), accumulating more than 4 km of distance on the study site itself. Her absences from the site were 5, 6, 7, 12, 15, and 38 months and four out of six reappearances after these absences were associated with long-distance movements. We found no association between the absences of these two females and drought or low water depths, such as reported by Hall and Steidl (2007).

The appearance of new adults on the study site also suggests that long-distance movements are a regular feature of our population (Fig. 9). At first capture, 22 turtles were already adults. Only five adults (CL > 76 mm) in our population were initially captured as hatchlings ( $n = 3$ ) or juveniles ( $n = 2$ ). Of the apparent immigrant adults, five were marked in the second year of the study, five in the fifth year, and three in the eighth year. We doubt that these turtles were study site residents that had simply not been detected previously. Additionally, four of these adult turtles were never recaptured, possibly because they left the study site. Appearance of apparent immigrants, and long capture intervals (or disappearance) of resident adults lend support to the conclusion that long-distance migration was common. A tendency for turtles to disappear from the study site for long periods of time, combined with terrestrial hibernation, contribute to the strength of the season effect ( $P < 0.0001$ ) in

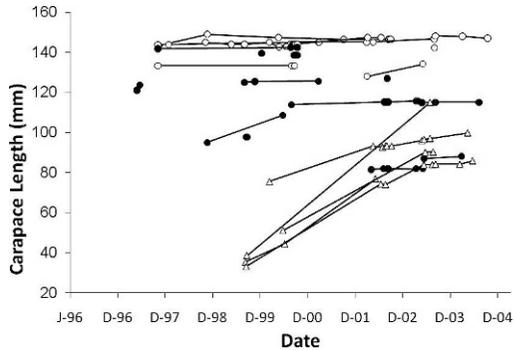


FIG. 9.—Presence and growth of adult *Kinosternon sonoriense* in Cottonwood Creek, Arizona, plotted from January 1996 (J-96) to December 2004 (D-04). Open circles represent adult females ( $n = 7$ ), filled circles represent males ( $n = 11$ ), and triangles represent hatchlings and juveniles that grew to adult size during the study ( $n = 5$ ). Adults first encountered after several years of study are likely immigrants. Note that turtles are occasionally absent for long periods.

the Program MARK model of capture probability.

When we began our study at Cottonwood Creek, our operative assumption was that turtles would be highly aquatic and therefore highly sedentary, given widely dispersed pools and the harsh terrestrial environment. Thus, we assumed that our study area was large enough to encompass most of the activities of turtles we encountered. The movements and patterns of long absence from the study site, however, clearly invalidated our initial assumptions.

#### Growth

Growth of *K. sonoriense* at Cottonwood Creek is described well by a von Bertalanffy model, showing high rates among hatchlings and exponential decline as turtles approach mature sizes. Many studies of turtle populations, including studies of *K. sonoriense*, rely on age estimates based on the assumption or evidence that growing turtles produce a single growth ring on each shell scute each year (Rosen and Lowe, 1996; Stone, 2001; van Loben Sels et al., 1997). Wilson et al. (2003) found that only a minority of 145 studies that used growth rings to estimate turtle age actually reported data that validated the technique. They examined just two studies of kinosternid turtles, both of which had valida-

tion (*Kinosternon flavescens*, Iverson, 1991; *K. sonoriense*, van Loben Sels et al., 1997). Rosen and Lowe (1996) cautioned that counting rings on *K. sonoriense* plastrons requires discrimination of annual rings from “weak, non-annual rings,” but they offered no criteria for making the discrimination. The critical question is whether growth rings are produced in a consistent pattern that is strongly correlated with age. Our observations of growing hatchlings support the use of annuli in our population only with caution, because ring production is sometimes inconsistent (Fig. 8). We found no evidence of weak or secondary rings in hatchlings, but the majority of hatchlings in our study produced two rings in the first 3–4 months after hatching, and usually 2 rings/yr afterward. Wilson et al. (2003) pointed out that location and environmental variation (hibernation, drought, heavy rainfall, etc.) can affect patterns of turtle growth and patterns of production of rings on scutes. Thus age estimates should not only be validated for each species, but for each study site and even for each year in highly variable environments.

Measuring growth directly is preferred over age estimates if adequate recaptures are available. Previous workers have been unable to study recruitment and growth of juvenile *K. sonoriense* (Hulse, 1974; Rosen and Lowe, 1996; van Loben Sels et al., 1997), because of low sample sizes and recapture rates. The high number of hatchlings and juveniles in our study population allows us to report the first data set for recaptures and growth measurements of multiple hatchlings from multiple cohorts.

Hulse (1974, 1976) used recapture-interval data to measure growth of adult *K. sonoriense*, and found that adult males at Tule Creek, AZ (elevation 610 m) grew  $1.57 \pm 0.32$  mm CL/yr, and adult females grew  $1.50 \pm 0.28$  mm CL/yr. Hulse used growth ring estimates to plot growth of juvenile *K. sonoriense* from two populations for visual comparison but did not report rates (Hulse, 1976: Figs. 2 and 3). At Sycamore Creek, AZ (elevation 1200 m) Hulse’s plots are essentially linear with a slope of 9 mm PL/yr from ages 1 to 10 yr and sizes from ca. 40 to 120 mm PL (ca. 47 to 141 mm CL). At Tule Creek Hulse (1976) found

growth was similar to the Sycamore Creek population in both sexes through age 4, but was less rapid after that point. The overall slope at Tule Creek was 4.5 mm PL/yr. Hulse did not report growth rates for turtles less than 1 yr of age (<40 mm PL).

Overall, turtles at our study site averaged 1.46 annuli/yr (Fig. 8). This average, however, reflects a general pattern of producing two annuli during their first three months of life ( $n = 15$ , mean age of turtles with two annuli = 62 days, excluding one outlier aged 808 days). Turtles typically produced 2 annuli/yr thereafter. We hypothesize that this reflects 2 growth spurts/yr in most cases, possibly associated with the bimodal rainy seasons typical of the Arizona Upland subdivision of the Sonoran Desert (Ingram, 2000). Turtles are inactive during winter rainy season (Fig. 3), but might grow during spring, cease during foreshummer drought, and then grow again during monsoon. This hypothesis could be tested at other low-elevation desert sites.

Our estimate of hatchling and juvenile growth rates from annuli (9.47 mm CL/annulus, Fig. 8) is similar to Hulse’s (4.5 mm PL/y at Tule Creek, 9 mm PL/yr at Sycamore Creek; Hulse, 1974), but our direct measurements (hatchlings 57.25–65.7 mm CL/yr, juveniles 23.3 mm CL/yr; Table 1) are much higher. One difference is that Hulse used plastron length rather than carapace length, and thus his rates would be expected to be slightly lower by the ratio of plastron to carapace length for juvenile Sonora Mud Turtles (0.83 for males and 0.95 for females, calculated from Hulse, 1976: Fig. 6). The majority of the difference between Hulse’s rates and ours might be expected if Hulse were overestimating ages by a factor of 2—that is, if his turtles were also averaging two annuli per year. Although Hulse’s study sites differ in elevation from ours, all share the two rainy seasons typical of the Sonoran Desert. Depending on the timing of the arrival of summer monsoon rains, hatchlings should experience their first rainy season (monsoon) immediately, followed months later by winter rains, and at the age of 1 yr turtles should be in their third rainy season (second monsoon). The timing of monsoon rains or the effects of El Niño/La Niña Southern Oscillations on

TABLE 3.—Age and size at maturity for *Kinosternon sonoriense* from various populations.<sup>a</sup>

Population	Elevation (m)	Mean adult CL (mm)		Minimum adult CL (mm)		Minimum age for maturity (y)		Source
		M	F	M	F	M	F	
Quitobaquito Springs	355	87 <sup>b</sup>	—	84	100	4.8	6	Rosen and Lowe (1996)
Tule Creek	549	—	112	—	—	—	5	Rosen (1987)
Cottonwood Creek	575	121	142	—	—	—	—	This study
Tule Creek	610	94 <sup>c</sup>	103 <sup>c</sup>	76	93	5	8	Hulse (1976)
Santa Catalina Mts.	810–2476	—	—	80	100	—	5–6	Hall and Steidl (2007)
Sycamore Creek	1219	—	134	—	—	—	5	Rosen (1987)
Sycamore Creek	1219	123 <sup>c</sup>	137 <sup>c</sup>	91	130	8	11	Hulse (1976)
Sharp Spring	1402	—	115	—	85	—	8	Rosen (1987)
West Turkey Creek	1675	128	130	—	106	—	5	van Loben Sels et al. (1997)

<sup>a</sup> CL = carapace length.

<sup>b</sup> “Young adult” males.

<sup>c</sup> Estimated from Hulse (1974: Fig. 6).

winter rainfall could explain why hatchlings would vary in numbers of annuli produced in their first year, and why they might produce “weak, non-annual rings” (Rosen and Lowe, 1996).

In addition to variations in growth rates, age and size at maturity and adult body size also vary among *K. sonoriense* populations (Table 3). Hulse (1974) suggested that low-elevation populations mature at smaller sizes than high-elevation populations. The average CL of adult males in our study was 121 mm, and females averaged 142. These are both relatively large in comparison to other populations (Table 3) and do not fit the pattern of elevation suggested by Hulse (1974), but our low sample sizes require a cautious interpretation. We did not have an adequate sample size to determine minimum size at maturity for use in other analyses, so we relied on published estimates (Table 3) to establish a minimum. These published values used annuli to establish ages. Tule Creek, like our study site, is a low-elevation tributary of Lake Pleasant just 10.3 km from Cottonwood Creek, and has the lowest published minimum sizes for maturity (76 mm for males, determined by dissection; Hulse, 1974). Further, using this minimum size increases the number of turtles we classified as adults, minimizing the demographic contrast between our study site and others (Table 2). Turtles in our study approached this minimum size by age 3–4, suggesting younger maturity than generally reported. This growth rate is, however, within

the range of growth rates reported by Rosen (1987) for several populations, including those that appear to mature much later, at larger sizes. Thus, despite the rapid growth that we observed, we cannot conclude that turtles in our population mature any earlier than in other populations.

#### Implications

There is a natural continuum of habitats used by *K. sonoriense*, varying in elevation, temperature, and hydrology, which seems to influence both demographics and habitat use. A lack of understanding of habitat use can result in inadequate protection of essential resources for turtles, such as nesting sites (Burke and Gibbons, 1995).

Intermittent streams such as Cottonwood Creek are common throughout the Sonoran Desert, and historically, these habitats were interconnected, at least during periods of sustained flow, through perennial rivers such as the upper Agua Fria. Now, at varying spatial and temporal scales, most of these habitats are being isolated from one another by large impoundments or dewatering of major river corridors. Additionally, climate change may alter precipitation in ways that will affect habitat connectivity. Climate-change predictions for the southwestern United States (Levick et al., 2008) include increased warming and drying, more variability in precipitation, and more frequent or intense drought and flooding. Such change is likely to lead to loss of aquatic habitat and

increased habitat fragmentation for *K. sonoriense*.

Impoundment is not a solution, because permanent water often favors the establishment of exotic predators like bullfrogs and crayfish (Rosen et al., 1995), whose negative effects are strongest on hatchlings or juveniles (e.g., Akins and Jones, 2010; Fernandez and Rosen, 1996; Schwendiman, 2001; this study). It is possible that low recruitment may doom even high-density populations, but because turtles are long-lived, it might take many years for this to happen, and even longer for it to be recognized. Our data indicate that juvenile turtles are vulnerable to exotic predators, but under the right conditions they can grow extremely rapidly and reach mature sizes within 3–4 yr. The ability of juveniles to disperse long distances may be high, but low survivorship of juvenile turtles would limit ability of populations to recover from declines. High-density populations should be more resilient, if adequate habitat is present. Low-density populations from marginal or extreme habitats may be more vulnerable, and only careful management can ensure their long-term persistence.

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