Life History and Ecology of the Sonoran Mud Turtle (*Kinosternon sonoriense*) in Southeastern Arizona: a Preliminary Report

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ABSTRACT. - From 1990 through 1994 we conducted a mark-recapture study of Kinosternon sonoriense in the West Turkey Creek area of the Chiricahua Mountains in southeastern Arizona. A total of 580 individuals was marked, and 913 recaptures were made. Approximately 90% of the individuals were initially captured in stock tanks, 5% in stream pools, and 5% on land. Sex ratio of adults was 1 male to 1.29 females. Of the 573 individuals captured alive, 18.5% were classified as juveniles, 35.8% as adult males, and 45.7% as adult females. Four hatchlings captured in early August averaged 3.0 g body mass and 22.2 mm carapace length (CL). Growth rates of juveniles from hatching to age 6 averaged 17.5 mm CL/yr. The youngest gravid female was 5 years old and the smallest had a CL of 106 mm. Maximum CL of adult males and females was 168 and 160 mm, respectively. There was no sexual size dimorphism between age classes 5 and 10 yr. Based on 39 females captured twice during the reproductive season, a minimum of 23% of the females in the population produced at least 2 clutches of eggs in a single year. Over all years clutch size averaged 6.7 eggs (range 2–11) and the sizes of first and second clutches were similar. Clutch means of actual egg widths from six females averaged 16.85 mm and were similar to mean egg widths taken from radiographs (XREW) of the same females (16.95 mm). Both clutch size and egg widths taken from radiographs were significantly and positively related to body size. No pelvic constraint on egg width was apparent since the slope of the relationship of CL to the pelvic aperture width determined with radiography (0.144) was significantly steeper than that of egg widths (0.041). The relationship between the residuals of clutch size with CL to XREW was negative. The average dry mass of egg yolks averaged 0.96 g (range 0.73-1.25 g), and comprised 28.75% non-polar lipids (range 26.47-29.87%). Egg shells averaged 32.75% of the total dry mass of the egg and were similar in proportion to eggs of other Kinosternon.

KEY WORDS. - Reptilia; Testudines; Kinosternidae; Kinosternon sonoriense; turtle; ecology; lifehistory; reproduction; morphometrics; eggs; Arizona; USA

Major differences are predicted between life history trait values of long- vs. short-lived organisms (Williams, 1966; Gadgil and Bossert, 1970; Tinkle et al., 1970; Wilbur, 1975; Wilbur and Morin, 1988; Congdon and Gibbons, 1990a). However, studies that adequately document the magnitude and causes of variation in life history trait values are by nature of long duration, labor intensive, time consuming, and expensive. Because the difficulties in conducting life history studies are magnified when study organisms are long-lived, the majority of quantitative life history data are from studies of short-lived organisms (Tinkle, 1979; Dunham et al., 1988; Tinkle et al., 1993). The paucity of life history data on long-lived organisms continues to hamper tests of life history theories and the formulation of conservation and management programs.

In comparison to most organisms, all turtles are longlived (Gibbons and Semlitsch, 1982; Brecke and Moriarty, 1989; Congdon et al., 1993) and many are excellent models for life history and demographic studies (Hammer, 1969; Wilbur, 1975; Gibbons, 1983; Obbard, 1983; Brooks et al., 1988; Mitchell, 1988; Zweifel, 1989; Frazer et al., 1991; Iverson, 1991; Congdon et al. 1993, 1994). The Sonoran mud turtle (*Kinosternon sonoriense*) occurs in northwestern Mexico and in the southwestern USA where it ranges from western New Mexico through central and southern Arizona. It is the only native freshwater turtle that occurs in the Chiricahua Mountains of southeastern Arizona. Although there have been two studies of the ecology of *K. sonoriense* (Hulse, 1982; Rosen, 1987), many aspects of the life history of the species remain essentially unknown (e.g., nesting ecology and almost all aspects of age-specific biology).

In 1990 we initiated a still ongoing long-term study of an isolated population of the Sonoran mud turtle in southeastern Arizona. The goals of the study are to obtain longterm data on life history trait values, to identify the sources of variation in trait values, and to document aspects of the natural history of Sonoran mud turtles. Such data will: 1) enhance our understanding of the ecology of Sonoran mud turtles in particular and long-lived organisms in general, 2) allow tests of existing life history theories that predict contrasts between long- and short-lived organisms, and 3) expand the life history and demographic data base to provide a basis for formulating conservation and management programs for long-lived organisms. Although this paper cannot report results that completely meet the long-term goals of the study, we present preliminary data on aspects of the life history of *K. sonoriense* based on the first five years of study.

MATERIALS AND METHODS

For 5 years (summers of 1990–94), we conducted a mark-recapture study of Sonoran mud turtles in the Chiricahua Mountains, Cochise County, southeastern Arizona. The primary study area was located at approximately 1675 m elevation on the El Coronado and Rock Creek Ranches. The area consists of a 3 km stretch of West Turkey Creek (WTC) and a series of stock tanks (farm ponds) associated with less permanent tributaries of WTC. In 1994 we added the Rock Creek site that is isolated from WTC by approximately 5 km. Exchange of turtles between WTC and Rock Creek almost certainly requires overland movements.

Some turtles were captured on land, by hand in shallow stream pools, or with dip nets, but most were captured using baited hoop traps (fitted with floats to prevent submergence during heavy rains). Turtles captured alive were marked with a unique sequence of notches filed in the marginal scutes of the carapace, and weighed (to 0.1 g on a Sartorius balance). The following straight-line measurements were taken (to 0.1 mm with dial calipers): 1) length of the anterior plastron (anterior edge to the hinge along the midline), 2) length of the posterior plastron (hinge to posterior edge along the midline), 3) carapace length (CL), and both 4) shell height and 5) shell width at the plastron hinge. Plastron length (PL) was recorded as the sum of the anterior and posterior plastron lengths. After processing and data collection, all turtles were released at their capture location. All unmarked turtles found dead were assigned an individual identification number and, when possible, CL was measured.

Because many of the juveniles (>75 mm CL) and small females could not be palpated to determine the presence of eggs, radiographs were taken of all individuals to establish the minimum size and age at sexual maturity. Radiographs were taken of all adult females captured after May of each year to determine the relationships among age, body size, egg widths, pelvic aperture widths (indexed as the shortest distance between the ilia; Congdon and Gibbons, 1987), clutch sizes (CS), and clutch frequencies (Gibbons and Greene, 1979; Hinton et al., 1997). Two females with clutches of one egg were omitted from analyses because turtles are known to occasionally retain one or more eggs after nesting. In addition, we compared actual egg widths to egg widths measured from radiographs (XREW). Minimum annual clutch frequency was determined from changes in CS in subsequent radiographs of an individual female. The clutch means of 21 eggs obtained from six females averaged 16.85 mm when measured directly and 16.95 mm when measured from radiographs; the measurements were not significantly different (paired t-test, t = -0.797, p > 0.469; Table 1).

Because survivorship within a nest is usually very different from other age classes of turtles, we kept this demographic period distinct by assigning the period betwen egg laying by females and hatchling emergence as age class 0 (Congdon et al., 1993, 1994). As such, we think that hatchling body metrics best represent the size of the individual at the end of age class 0 (growth during the embryonic stage). Age class 1 contains yearling turtles between leaving the nest and the end of their second winter. All subsequent age classes correspond to the turtles' year of life between the beginning of each active season to the beginning of the next active season. At first capture turtles with fewer than 9 obvious growth rings on one of the plastral scutes were assigned an age based on the assumption that these rings were laid down annually in juveniles and young adults. Recaptures of juveniles over all age classes during the past 4 yrs support this assumption. Some turtles younger than age class 8 with poor growth rings and a few turtles with more than 8 exceptionally clear plastral annuli were assigned age classes with a comment code indicating that the assigned age had a potential error ± 1 yr. Older individuals were not assigned ages. For comparison of adult males and females, we assumed that males mature at approximately age class 5. We based the assumption on substantial reductions in agespecific growth rates of males and females beginning at age 5 yr; a similar pattern was observed in K. sonoriense from Sharp Spring, Arizona (Rosen, 1987). Therefore, comparisons of size distributions of adults were restricted to individuals of both sexes that were equal to or greater than the minimum size of females found carrying eggs (CL > 105 mm). Restricting the analyses to adults greater than minimum size may bias the sample by excluding the smallest adult males and by including individuals of both sexes that were not yet mature, but were larger than 105 mm CL. However, substantial sexual size dimorphism in older juveniles and young adults was not apparent because CL of all male and female turtles between 5 and 10 yrs of age were not significantly different ($F_{1,201} = 0.88$, p = 0.35).

During 1994, 15 females captured at Rock Creek were injected with oxytocin (1.5 ml/kg body mass; Ewert and Legler, 1978) to induce egg laying. We attempted to incubate 7 eggs, and 14 eggs were frozen for lipid analysis at Savannah River Ecology Laboratory. The 14 eggs were

Table 1. The length, width, and wet mass of eggs of *Kinosternon sonoriense* from southeastern Arizona, and a comparison of clutch means of actual egg widths to those measured from radiographs (XREW) from the same six clutches (n = 21 eggs). In addition, the yolk dry masses and percent non-polar lipids are presented for 14 eggs from six clutches.

	Length (mm)	Width (mm)	XREW (mm)	Wet Mass (g)	Yolk Dry Mass (g)	Yolk % Non-Polar Lipids
Mean	28.93	16.85	16.94	5.03	0.96	28.75
Range	27.0 - 31.8	15.8 - 18.2	16.0 - 18.2	4.7 - 5.5	0.73 - 1.25	26.47 - 29.87
2 SE	0.518	0.185	0.172	0.32	0.12	0.16

separated into shells and contents (yolk and albumen) and both components were dried to a constant weight and ground with a mortar and pestle. Non-polar lipids were extracted from the egg yolks using a Soxtec apparatus with petroleum ether as a solvent (Fischer et al., 1991).

Parametric statistical tests were used when variables were continuous and the assumptions of the tests were met. Otherwise, non-parametric tests, such as Spearman's Rank Correlation (RHO; SAS, 1988) were used. Slopes of clutch size, XREW, and pelvic aperture width on CL were determined for females using simple linear regression, and differences between slopes were determined using an m-test (SAS, 1988). Unless otherwise stated, levels of significance were established at $\alpha = 0.05$. Measures of central tendency and dispersion are presented as the mean \pm two standard errors unless stated otherwise.

RESULTS

From 1990 through 1994, we marked and released 573 live individuals and made 913 recaptures of these individuals. In addition, we found 7 dead turtles that were not previously marked. Approximately 5% of the turtles were first captured in stream pools, 5% on land, and 90% in stock tanks. Of the 573 individuals captured, 18.5% were classified as juveniles, 35.8% and 45.7% were adult males and females, respectively. The sex ratio of adults (turtles larger than 105 mm CL) was 1 male to 1.29 females, which is significantly different from 1:1 ($\chi^2 = 6.93$, p < 0.01).



Figure 1. Mean body sizes $(\pm 2 \text{ SE})$ of *K. sonoriense* at ages from hatching to age 12 yr. Sample sizes for ages 1 to 13 are: 5, 5, 14, 37, 77, 85, 86, 49, 31, 11, 8, and 4, respectively. Dashed line indicates minimum age and size at maturity for females.

Growth rates from hatching to age 6 were essentially linear and averaged approximately 17.5 mm per year (Fig. 1). Adult females averaged 130 mm CL (maximum = 160 mm; Fig. 2a) and 340 g body mass (maximum = 610 g). Adult males averaged 128 mm CL (maximum = 168 mm; Fig. 2b) and 298 g body mass (maximum = 660 g). Minimum age class at sexual maturity of females was 5 yrs and the smallest turtle that produced a clutch of eggs was 106 mm CL and weighed 150 g.

Clutch size (greater than 1 egg) over all locations and years averaged 6.7 eggs (range 2–11; 2 SE = 0.254; n = 231; Fig. 3a) and was significantly and positively related to body size of females (Spearman's RHO = 0.62, p < 0.05; Fig. 3b). Data from radiographs of gravid females captured between June and August provided direct evidence that from 1991 to 1994, 9 of 39 (23%) females captured at least twice during the reproductive season produced a minimum of two clutches of eggs. However, the actual proportions of adult females that produce more than one clutch annually, or skip reproduction in a given year, have yet to be determined. The minimum interval between clutches, determined by a change in clutch size between radiographs, was 20 days.

There was a significant positive relationship between XREW and CS (slope = 0.13; $F_{1.171} = 17.30$, $r^2 = 0.09$; p < 0.001). Analysis of covariance, with CL as a covariate, increased the amount of variation explained ($r^2 = 0.48$, $F_{2.170} = 38.62$; p < 0.0001). Mean XREW per clutch and pelvic aperture width were significantly and positively related to CL of females (Fig. 4). The slope of pelvic aperture width on CL was 3.5 times steeper (Wilks' Lambda = 0.7822, $F_{1.171} = 69.88$; p = 0.0001) than was the relationship of egg width on CL (Fig. 4). There was a negative relationship between XREW and the residuals of the linear relationship between Lutch size and carapace length (Spearman's RHO = -0.2104; p = 0.0008).

The ratio of egg length to egg width averaged 1.72 (2 SE = 0.92; n = 6 clutches, 21 eggs) and egg shells averaged 32.75% (2 SE = 1.3; n = 6 clutches, 14 eggs) of the total dry mass of the egg. Egg yolks averaged 60.2% (2 SE = 3.2; n = 6 clutches, 14 eggs) water by mass and 28.75% non-polar lipids by dry mass (Table 1).

Hatchlings (n = 4) with egg teeth captured in a nesting area on 5 August 1993 and 9 August 1994 averaged 3.0 g body mass and 22.2 mm CL.

DISCUSSION

Twenty-four thousand years ago a large portion of Sulphur Springs Valley, which is on the west side of the Chiricahua Mountains, was part of Lake Cochise (Cameron and Lundin, 1977). It is probable that as Lake Cochise dried about 10,000 yr ago (Long, 1966), populations of *K. sonoriense* became isolated in the most permanent streams (e.g., WTC) originating in the Chiricahua Mountains. That the majority of turtles presently occupy stock tanks rather than the stream bed of WTC suggests that they prefer the



Figure 2. Frequency histogram of body sizes of adult (a) female and (b) male *K. sonoriense*.



Figure 3. (a) Frequency histogram of clutch sizes, and (b) the slope (= solid line), and 95% confidence intervals (= dashed lines) of the linear relationship between clutch size and body size of adult *K. sonoriense* females (CS = -0.846 + 0.112 CL; $r^2 = 0.42$; n = 231 clutches).

more lentic habitats that are presumably more similar to those of Lake Cochise.

The proportion of juveniles in the WTC population is approximately half that reported for a population at Tule Creek in central Arizona in the early 1970s (Hulse, 1974). The minimum age class at maturity for WTC females (5 yr) is similar to that reported for most other populations of Sonoran mud turtles in Arizona (Rosen, 1987) and to that of K. hirtipes females (6 yr) from northwestern Mexico (Iverson et al., 1991). However, the differences between the estimates of minimum ages at maturity for the population of K. sonoriense at Sycamore Creek (9 yr, Hulse, 1974; 5 yr, Rosen, 1987) and at Tule Creek (8 yr, Hulse 1974; 6 yr, Rosen, 1987) demonstrate the problems of accurately determining even the minimum age at maturity without long-term mark recapture data. Data from Hulse (1974) and Rosen (1987) combine to suggest that substantial variation in minimum age at maturity may occur within populations of K. sonoriense.

From a life history and demographic perspective, minimum age at maturity is not a quantitatively adequate descriptor of maturation because variation within some populations of turtles may be substantial. For example, females within a single population mature at ages from 9-15 yrs (Kinosternon flavescens; Iverson, 1991), 14-21 yrs (Emydoidea blandingii; Congdon and van Loben Sels, 1993), and 11-16 yrs (Chelydra serpentina; Congdon et al., 1994). Within population variation in age at maturity can have less impact on population dynamics than other variables such as juvenile and adult survival (Iverson, 1991; Congdon et al., 1993, 1994). However, variation in age at sexual maturity should not be ignored or discounted, because it can have substantial impact on life table calculations and the dynamics of populations (Congdon et al., 1993, 1994). For example, approximately 23% of total variation in age specific fecundity in female K. flavescens is attributable to variation in ages at maturity (Iverson, 1991).

The turtles from WTC are among the largest in maximum body sizes of males and females among the populations of K. sonoriense studied in Arizona (Hulse, 1974, 1982; Rosen, 1987). Growth rates of K. sonoriense between hatching and age 6 averaged approximately 17.5 mm/yr in the WTC population (minimum age class at maturity = 5 yr; see Fig. 1). In comparison, juvenile K. sonoriense from Sharp Spring, Arizona, grew approximately 10 mm/yr (estimated from Rosen, 1987, Fig. 1) and K. hirtipes from northwestern Mexico grew at an average of 14.0 mm/yr (estimated from Iverson et al., 1991). Minimum CL at maturity for K. sonoriense from Sharp Spring and K. hirtipes females were both approximately 90 mm CL (Rosen, 1987; Iverson, et al., 1991), which is smaller than for K. sonoriense in WTC (105-110 mm CL). A minimum of 23% of the adult female K. sonoriense in WTC produced 2 clutches of eggs in one year. Females in some populations have been reported to produce up to 4 clutches per year (Rosen, 1987); however, studies of the same populations have provided conflicting estimates of clutch frequency. Clutch frequency in the Tule Creek and



Figure 4. The linear relationships of pelvic aperture width (squares) and egg widths (circles) taken from radiographs to body sizes of gravid female *K. sonoriense* (predicted line = solid line, and 95% confidence intervals = dashed line). Pelvic aperture width = 0.14 CL + 2.82; $r^2 = 0.40$; n = 175 females; mean XREW = 0.041 CL - 8.19; $r^2 = 0.41$; n = 175 clutches.

Sycamore Creek, Arizona, populations have been reported at 2 and 1 clutches, respectively (Hulse, 1974) and 4 and 3 clutches, respectively (Rosen, 1987). These conflicting estimates demonstrate the difficulty in accurately estimating clutch frequency within a population without long-term data. Our estimate of clutch frequency is a minimum value, and until further data are available, all estimates of clutch frequency for *K. sonoriense* should be viewed as tentative.

Body size explains approximately 42% of the variation in clutch size in the WTC population and an average increase of 5 eggs is associated with the 75 mm range of body sizes found in adult females. Average clutch size for the WTC population is higher than those reported for five populations of *K. sonoriense* (Beaver Creek, Indian Canal, Montezuma Well, Tule Creek, and Sharp Spring) and slightly smaller than those in three populations (Palm Lake, Granite Reef, and Sycamore Creek) reported by Hulse (1982) and Rosen (1987).

In many species of turtles, egg size has been shown to be related to hatchling size and hatchling size has been implicated as an important component of hatchling survival in some species (Brooks et al., 1991). The average dimensions of eggs from the WTC population (Table 1) are similar to those from other populations of *K. sonoriense* (31.1 mm long, 14.4 mm wide; Hulse, 1974). Egg widths determined from radiographs have been shown to be a good predictor of egg mass (Congdon and Gibbons 1985, 1987; Iverson, 1991), and X-ray egg widths of *K. sonoriense* were significantly and positively related to body size of adult females (i.e., average X-ray egg widths increased by 3 mm over the 75 mm range of CL among adult females). As a result, larger females should produce larger eggs and thus larger hatchlings. We do not think that the relationship between X-ray egg widths and body size is due to an enlarged image of the egg caused by the radiography, because actual egg widths and those measured from radiographs were similar in this study (see Table 1).

In some small-bodied turtles, egg size may be influenced by constraints imposed by the size of the pelvic aperture through which the egg must pass (Tucker et al., 1978; Congdon and Gibbons, 1987; Long and Rose, 1989). Similar slopes of the linear relationships between pelvic aperture width and XREW with CL for *Chrysemys picta marginata* (0.105 and 0.107, respectively) and *Deirochelys reticularia* in South Carolina (0.12 and 0.12, respectively) suggest that pelvic aperture size constrains egg size (Congdon and Gibbons, 1987). However, the respective slopes in *K. sonoriense* (Fig. 4) and in smaller-bodied *K. flavescens* in Nebraska (Iverson, 1991) are different and do not indicate pelvic constraint on egg size.

In addition to egg size, the proportional allocation to egg components such as shell, water, protein, and lipids also may be important aspects of hatchling quality (Congdon and Gibbons, 1985, 1990b). The proportion of total dry mass of eggs represented by egg shells of K. sonoriense (32.75%) was more similar to five species of turtles having brittle shelled eggs (40.70%) than to seven species having parchment shelled eggs (19.25%; Congdon and Gibbons, 1985). The proportion of lipids in eggs of WTC females is lower than that found in K. flavescens (Long, 1986) and similar to levels found in K. subrubrum eggs in South Carolina (Congdon and Gibbons, 1985; Long, 1986). In general, females of turtle species with hatchlings that delay emergence from the nest, including K. subrubrum, allocate proportionately more non-polar lipids to eggs than do females of turtle species that have hatchlings that do not delay emergence (Congdon and Gibbons, 1985). The pattern of egg incubation and hatchling emergence of K. sonoriense is poorly known; however, the high proportion of non-polar egg lipids compared to other species of turtles that have hatchlings that delay emergence from the nest, combined with our captures of hatchlings in a nesting area in August, suggests that either embryos (within eggs) or hatchlings overwinter in the nest.

The period of time that female *K. sonoriense* are found with eggs extends at least from June to September (Rosen, 1987); however, the majority of nesting may be restricted to the period of monsoon rains (July and August). Based on the duration of the reproductive season, our observations of gravid females on land, and hatchlings captured in August in a nesting area, we propose the following scenario for egg incubation and embryonic development. Ovulation and shelling of eggs begins in June, and eggs remain in the oviducts until the monsoon rains occur (July through August). Eggs are then deposited in terrestrial nests some distance from water. Embryonic diapause postpones development through fall and winter (Ewert, 1991) and then development commences as eggs warm during the following spring. Development takes about 80 days (Ewert, 1991), and hatchling emergence and dispersal from the nest coincides with the onset of summer rains. Because both nesting and hatchling emergence apparently coincide with summer rains, the total time from egg laying to hatchling emergence may exceed 11 months. If the scenario presented is accurate, *K. sonoriense* embryos within eggs (rather than hatchlings) overwinter in nests — a pattern that is similar to that of *Kinosternon baurii* (Ewert and Wilson, 1996) and *Deirochelys reticularia* (K. Buhlmann; *pers. comm.*). In contrast, hatchling *Chrysemys picta* may overwinter in the nest in northern areas with severe winters (Hartweg, 1946; Woolverton, 1963; Gibbons and Nelson, 1978; Breitenbach et al. 1984; DePari,1996) or in some populations may emerge in the fall following egg laying (Ernst, 1971).

In summary, our results document that K. sonoriense from WTC grow more rapidly and attain larger body sizes than do many other populations in Arizona. Both clutch size and egg size are positively correlated with body size of females within the population. Juveniles represent about 18.5% of the 573 marked individuals in the WTC population. Bullfrogs were introduced into the WTC drainage about 1983 (JTA, pers. obs.; Rosen et al., 1994), and at present their population numbers are high enough to potentially reduce survivorship of the earliest age classes because they are a predator of turtle hatchlings (Schwalbe and Rosen, 1988). Because high average annual juvenile survivorship (age 1 to sexual maturity) is required for populations of longlived organisms to maintain population stability (Congdon et al., 1993, 1994), bullfrogs may reduce recruitment into K. sonoriense population at WTC enough to cause the population to decline.

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