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POPULATION ECOLOGY AND REPRODUCTION OF THE MEXICAN
MUD TURTLE (*KINOSTERNON INTEGRUM*) IN TONATICO,
ESTADO DE MÉXICO

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ABSTRACT.—Ecological data directly from the field are important in understanding the life history strategies of kinosternid species in the tropics. Herein we summarize the basic population ecology and life history of *Kinosternon integrum* in the municipality of Tonicato (southeastern Estado de México, México). From October 2003 to November 2004, we marked a total of 204 turtles and recaptured 118 of them. Mean population size using the Jolly-Seber model was 197 (95% CI 128–416) individuals, with a sex ratio of 1:1.7, biased to females. Males were larger than females in carapace length and plastron length. The reproductive season starts in late June and finishes in late October. The smallest female with oviductal eggs was 122 mm in carapace length. Mean clutch size was 4 eggs ($s = 1.77$, range 1–8) and was significantly and positively related to body size. Mean egg length was 30.43 mm ($s = 2.24$, range 23.92–35.96), mean width was 16.35 mm ($s = 1.01$, range 12.99–18.30), and mean weight was 5.14 g ($s = 0.60$, range 3.41–6.57). Mean egg length was significantly and inversely related to clutch size. Relative clutch mass (reproductive effort) was 0.043 ($s = 0.017$, range 0.017–0.071), which is the smallest value reported for the genus *Kinosternon*. Additionally, there was no evidence of a pelvic restriction on egg size in this population. This is the first study that documents basic population ecology and reproductive characteristics for a single population of the most widespread freshwater turtle in Mexico.

Key words: clutch size, *Kinosternon integrum*, population size, reproductive effort, sex ratio.

Kinosternids are a highly diverse group of turtles in México (Pritchard and Trebbau 1984) with 18 species distributed throughout the country (Liner and Casas-Andreu 2008). *Kinosternon integrum* has the most widespread distribution in the country, and its sister species, *K. scorpioides*, is widespread in northern and central South America (Iverson 1999). *Kinosternon integrum* is endemic to central and western México, where it inhabits diverse habitats over an altitudinal range between sea level and 2300 m (Iverson et al. 1998). The key to the success of this group in the Mexican tropics remains unknown, but special adaptations such as aestivation behavior, a “bet-hedging” life history strategy, and an omnivorous diet (Aguirre-León and Aquino-Cruz 2004, Macip-Ríos unpublished data) could be important factors.

Demographic and life history studies on *K. integrum* are limited. Life tables have been constructed for congeneric species such as *K. flavescens* (Iverson 1991a) and *K. subrubrum* (Frazer 1991), and some information is also

available on sex ratios (Carr and Mast 1988, Edmonds and Brooks 1996, Smith and Iverson 2002) and population sizes (Gibbons 1983, Moll 1990) of several North American species. For Mexican kinosternids, there are studies on the natural history of *K. chimalhuaca* (Berry et al. 1997), *K. oaxacae* (Iverson 1986), and *K. alamosae* (Iverson 1989), but the information on *K. integrum* is limited and anecdotal.

Iverson (1999) described the general reproductive pattern of *K. integrum* based on data from several localities within this species’ range, but no information is available on its demography or on basic trends in its population ecology. The aim of this paper is to describe basic trends in population ecology and life history (including possible pelvic restriction on egg size) for a natural population of *K. integrum* in Tonicato, Estado de México, in the upper Río Balsas basin, México. Our paper is the first to present such information on *K. integrum*, which is a representative species of the kinosternid turtle group in the Mexican dry tropic.

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METHODS

We conducted this study from October 2003 to November 2004 in the vicinity of Tonatico, Estado de México (18°48'N, 99°40'W). Tonatico is located in southeastern Estado de México, in the northern portion of the Río Balsas basin, at 1640 m above sea level. Vegetation is a mixture of tropical dry deciduous forest, agricultural (corn) fields, and cattle-breeding lands, combined with seasonal ponds that the turtles inhabit. The average monthly temperature is 20 °C and the average monthly rainfall is 150 mm, with a maximum monthly rainfall of 401.5 mm in the rainy season (June–October) and a maximum monthly rainfall of 30.3 mm in the dry season (November–May) (INEGI 2002).

Ponds where turtles were collected were circular and shallow, ranging from 2 to 200 m in diameter and from 50 to 200 cm in water depth. We sampled 7 ponds of the following diameters: 200, 50, 20, 10, 8, 5, and 3 m. The larger ponds (200 and 50 m) were 4 km away from each other; the smaller ponds (20, 10, 8, 5, and 3 m) were approximately a 50 m away from each other, and this group of ponds was 200 m away from the 50-m-diameter pond. Turtles were also collected in a temporary stream near the 50-m pond. These ponds were very productive because cattle drink there and their fecal deposits cause eutrophication of the water. The typical faunal succession of seasonal lentic systems occurs in the ponds (Lampert and Sommer 1997), with invertebrates like dragonflies, beetles, and other insects being the most abundant prey for turtles. Other species common to this habitat include amphibians such as *Hypopachus variolosus*, *Lithobates forreri*, and *Hyla arenicolor* and reptiles such as semiaquatic snakes (*Drymarchon melanurus*).

We visited the study site monthly and caught turtles by seine and also by baited hoop traps. We seined 3 of the biggest ponds (200, 50, and 20 m) until no more turtles appeared in the net. On 2 nights, we set 10 traps (baited with fresh fish) in the other 4 ponds (4 traps in the 10-m-diameter pond and 2 in the 8-, 5-, and 3-m-diameter ponds). We performed the same capture effort on every visit to the study site for a total effort of 6 seine events per large pond and 10 traps per 2 nights each month on the small ponds. In the dry season, the larger ponds dry out; therefore, during this time, we

focused on the small ponds that remained filled due to dense vegetation cover.

Turtles were marked (by notching marginal scutes [Ferner 1979]), measured, weighed, and released. For each turtle, we measured carapace length (CL), plastron length (PL), carapace width (CW), plastron width (PW), carapace height (CH), and body mass (BM). Sex was determined by a single secondary sexual character—the conspicuous, long tail in adult males. Females that had a plastron length larger than 110 mm were brought to the laboratory and X-rayed to determine if they were gravid, and if so, clutch size was recorded (Gibbons and Greene 1979). Eggs were collected from gravid females by injecting an oxytocin dose at a concentration of 1.5 mL · kg⁻¹ (Ewert and Legler 1978). Turtles were then placed in 30 mm of water in a plastic box until the eggs were released. We measured egg length and width with a dial caliper (±0.02 mm) and egg mass with an analytical balance (±0.01 g). All measurements were conducted by the same person each time. To avoid measurement bias, we did not weigh eggs that remained more than 5 minutes in the water. On the X-ray plates, we measured the pelvic opening and the egg width of each turtle with eggs in the oviduct in order to determine whether there was a pelvic restriction on egg size (Congdon and Gibbons 1987; see statistical procedures below).

We conducted a multiple regression analysis to examine the influence of average monthly temperatures and average monthly rainfall on turtle abundance throughout the year. For this test, we used climate data provided by the Centro Meteorológico Nacional-México for Ixtapan de la Sal municipality, which is located near Tonatico (approximately 12 km away). We used the Jolly-Seber model (Krebs Ecological Methodology, version 0.94 [software]; Krebs 1996, Krebs and Brzustowski 1998) to estimate population size. To test the hypothesis of a 1:1 sex ratio (Wilson and Hardy 2002), we used a standard chi-square test (Krebs 1996).

A multivariate Hotelling's T^2 test was conducted on the morphological data (CL, CW, PL, PW, and CH as input variables) to explore for significant sexual dimorphism in body size measurements (Rancher 2002). We compared body mass between males and females with the nonparametric Wilcoxon's 2-sample test, as the body mass variable was not normally distributed. Reproductive effort was estimated by

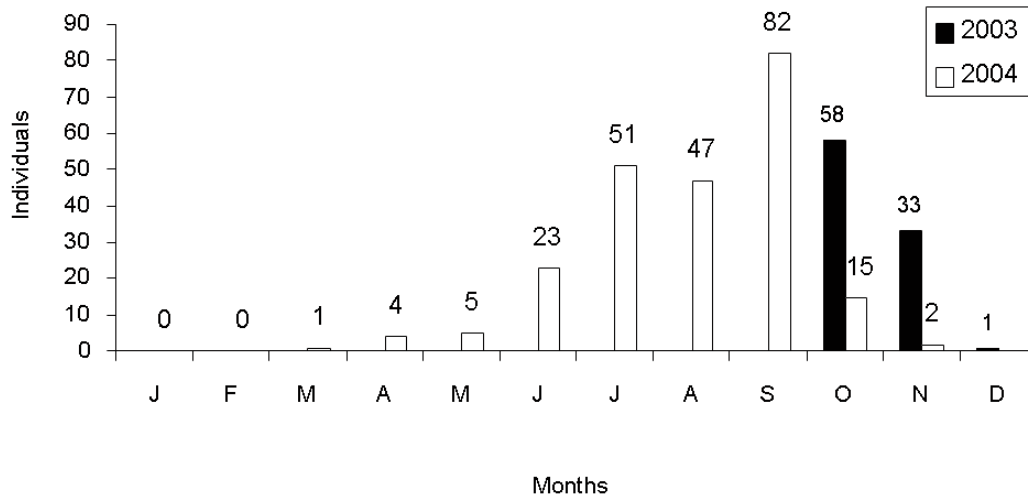


Fig. 1. Total abundance per month from October 2003 to November 2004 in the studied population of *Kinosternon integrum*. Solid bars indicate 2003 abundance. Open bars indicate 2004 abundance.

relative clutch mass (RCM) using Cuellar's (1984) formula:

$$\text{clutch weight} / [\text{female weight} - \text{clutch weight}].$$

We used typical linear regression analysis to test for significant relationships between body size and life history traits—such as clutch size, egg size, and reproductive effort—and between pelvic width and egg width. In order to test for a pelvic restriction on egg size, we also used an analysis of covariance (ANCOVA) to examine and compare 2 relationships: pelvic aperture regressed on body size and egg width regressed on body size (PL as covariate). Variation between slopes indicates no pelvic restriction, whereas parallel slopes indicate pelvic restriction (Congdon and Gibbons 1987, Zar 1999). Statistical analyses were performed using the statistical software JMP, version 5.0.1 (SAS Institute, Inc. 2002).

RESULTS

A total of 204 turtles were marked, and 118 individuals were recaptured (57.8% of the total). Of these 204 turtles, 89 were females, 50 were males, and 65 were too small to be sexed and considered immature. Most of the individuals (184 or 90%) were caught in the 50-m-diameter pond. Abundance per month was highest in September 2004, with 82 individuals captured, and lowest in January and February, with

no individuals captured (Fig. 1). The abundance per month was related positively and significantly to temperature and rainfall together (slope for temperature = -16.36 , $P = 0.01$; slope for rainfall = 5.64 , $P = 0.02$; $r^2 = 0.76$).

Estimated population size (adults and immatures) was 197 individuals (95% CI 128–416). To support this estimate, we also tested the equal-catchability assumption for the marked individuals (Krebs 1996), finding a random capture probability per individual ($\chi^2_{14} = 16.43$, $P = 0.10$). Population structure (Fig. 2) was 63% adults (>90 mm CL), 0.5% hatchlings (<3 mm CL), 35% immature individuals (30–90 mm CL), and 1% old adults (>17 mm CL). The sex ratio was skewed toward females, with 1 male (50) per 1.7 females (89). This result was significantly different from the 1:1 expected ratio ($\chi^2_2 = 10.94$, $P < 0.001$).

Sexual size dimorphism was evident; males were larger than females (T^2 , $F_{5,106} = 14.93$, $P < 0.0001$; Table 1). Variables with the largest effects in the model were CL ($CL_{\text{males}} = 156.3$ mm, $s = 35.1$; $CL_{\text{females}} = 142.7$ mm, $s = 23.8$) and PL ($PL_{\text{males}} = 126.4$ mm, $s = 26.0$; $PL_{\text{females}} = 119.5$ mm, $s = 20.6$). Body mass did not differ between males and females ($Z_{137} = 1.67$, $P = 0.09$).

The breeding season extended from early summer (July) to mid-fall (October). Apparently, females experience a single reproductive event per year. The smallest female with oviductal eggs was 122 mm CL, and the largest was 153

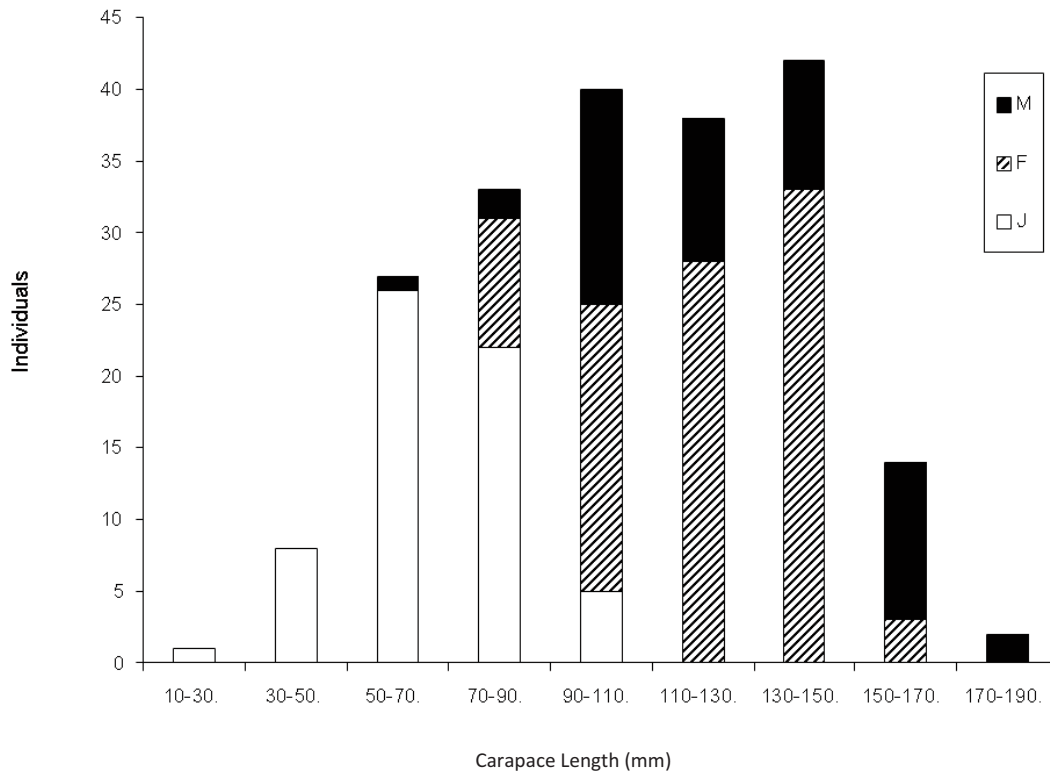


Fig. 2. Population structure by body size (carapace length) from October 2003 to November 2004 in the studied population of *Kinosternon integrum*. M represents males (solid bars), F represents females (dashed bars), and J represents immatures (open bars).

mm CL. Mean clutch size was 4 eggs ($s = 1.77$, range 1–8, $n = 20$). Of the 46 females collected during the breeding seasons (both 2003 and 2004), only 20 (43.47%) had eggs in their oviducts. Mean egg length was 30.43 mm ($s = 2.24$, range 23.92–35.96, $n = 78$), mean egg width was 16.35 mm ($s = 1.01$, range 12.99–18.30, $n = 75$), and mean egg mass was 5.14 g ($s = 0.60$, range 3.41–6.57, $n = 57$).

We found a positive relationship between clutch size (CS) and maternal body size using both CL and PL measurements (CS = $-10.38 + 0.90\text{CL}$, $r^2 = 0.58$, $P = 0.0003$; CS = $-13.64 + 1.32\text{PL}$, $r^2 = 0.63$, $P = 0.0001$; Fig. 3). Clutch size showed no relationship to egg width ($r^2 = 0.06$, $P = 0.29$) or egg mass ($r^2 = 0.11$, $P = 0.16$). However, there was a significant negative relationship between egg length and clutch size (egg length = $33.95 - 9.80\text{CS}$, $r^2 = 0.66$, $P = 0.0001$), suggesting a tendency for smaller eggs as clutch size increases (Fig. 4). Reproductive effort, measured as RCM,

was calculated only in the 16 females whose entire clutch was obtained. Average RCM was 0.043 ($s = 0.017$, range 0.017–0.071, $n = 16$); thus, females on average invested 4.43% of their body mass in the production of eggs. RCM was not related to body size measured either as CL ($r^2 = 0.005$, $P = 0.77$), PL ($r^2 = 0.001$, $P = 0.88$), or CS ($r^2 = 0.21$, $P = 0.07$).

Females of *K. integrum* in Tonatico did not show evidence of a pelvic constraint on egg size. The pelvic aperture (PA) was positively correlated with body size (PL) (PA = $-2.4 + 0.145\text{PL}$, $r^2 = 0.62$, $P < 0.0001$), in contrast to egg width, which was not correlated with body size (PL) ($r^2 = 0.13$, $P = 0.11$). Furthermore, the estimated variation in egg width was less ($s^2 = 0.85$) than the variation in pelvic aperture ($s^2 = 1.77$). Obviously then, the pelvic aperture was not related to egg width ($r^2 = 0.12$, $P = 0.12$). The ANCOVA showed that the 2 slopes, PA vs. PL and EW vs. PL (Fig. 5), were significantly different ($F_{1,38} = 156.03$, P

TABLE 1. Summary of morphological traits measured for males and females of *Kinosternon integrum* at Tonatico, Estado de México.

Trait	Males	Females
Carapace length (mm)		
Sample size	50	89
Mean	156.3	142.7
Standard deviation	35.1	23.8
Range	82.0–223.0	90.0–195.0
Carapace width (mm)		
Sample size	50	89
Mean	126.9	122.6
Standard deviation	29.0	22.7
Range	70.0–183.0	75.0–163.0
Plastron length (mm)		
Sample size	50	89
Mean	126.4	119.5
Standard deviation	26.0	20.6
Range	66.0–172.0	73.0–155.0
Plastron width (mm)		
Sample size	50	88
Mean	67.3	66.9
Standard deviation	13.3	12.1
Range	35.0–95.0	40.0–90.0
Carapace height (mm)		
Sample size	37	76
Mean	50.9	47.5
Standard deviation	11.1	9.8
Range	32.9–76.0	21.8–69.1
Body mass (g)		
Sample size	50	89
Mean	336.83	281.35
Standard deviation	190.42	143.60
Range	49.82–774.08	60.65–654.20

< 0.0001). According to Congdon and Gibbons (1987), this nonparallel pattern of slopes demonstrates a lack of pelvic constraint upon egg size.

DISCUSSION

The sex ratio was significantly biased to *K. integrum* females (1:1.7) and differed from the theoretical 1:1 expected (Seeger and Stubblefield 2002). We captured turtles systematically with a seine and consider this observed sex ratio to be representative of the studied population. Male-biased sex ratios have been found for *Sternotherus odoratus* (Edmonds and Brooks 1996, Smith and Iverson 2002) and female-biased sex ratios for *K. subrubrum* (Gibbons 1983), *K. herrerae* (Carr and Mast 1988), and *K. flavescens* (Iverson 1991a). Sex of turtles is determined by incubation temperature or by

sexual chromosomes (Ewert and Nelson 1991). In kinosternids, both patterns are present (Ernst et al. 1994, Pough et al. 2001); *Kinosternon*, *Sternotherus*, and *Claudius* species have specific temperatures for sex determination, whereas sex of *Staurotypus* species is determined by sexual chromosomes (Pough et al. 2001). Typically, when sex is determined by temperature, females are produced at extreme temperatures and males at intermediate ones. Therefore, female-biased sex ratios could be explained by the environmental temperature through time. However, Gibbons (1990) also mentioned that the main factors skewing sex ratios are local demographic processes, such as differential migration and immigration and differential ages of maturity between sexes. A combination of these factors could explain the biased sex ratio in *K. integrum* from Tonatico. Further research is needed on factors influencing observed sex ratio.

The population was composed primarily of immature and adult individuals; there were few old individuals and hatchlings were scarce. This pattern coincides with the survivorship curve reported for turtles by Iverson (1991b), in which immature organisms have the lowest probability of surviving and adults the highest. Nonetheless, Gibbs and Amato (2000) defined healthy (turtle) populations as structured mainly by young and prereproductive individuals and just a few adults. The population structure of *K. integrum* in Tonatico differed from this pattern. Abundance per month was highly correlated with temperature and rainfall, as is the case for other kinosternid species distributed in the northern hemisphere (Iverson 1986, 1989, 1991a, Frazer 1991). Morales-Verdeja and Vogt (1997) suggested that in the tropics, rainfall is the primary factor affecting turtle activity. Our findings agree with this suggestion, because in the Tonatico population turtles were more abundant during the rainy season (summer to mid-fall) and most of them estivate during the dry season.

We report the first population size estimate for *K. integrum*. Most individuals were found in a single small and shallow pond (50 m in diameter). This higher abundance may be related to the proximity of a running water system, in contrast with the other ponds surveyed (200, 20, 10, 8, and 5 m in diameter) that are isolated from streams or rivers. The high concentration of individuals in the 50-m

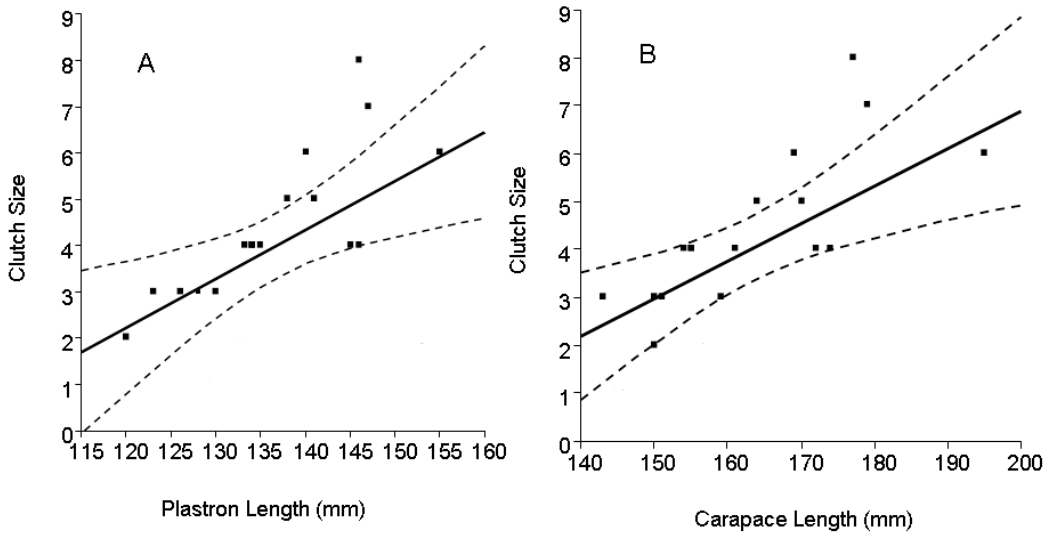


Fig. 3. Relationships between clutch size and maternal body size measured as (A) plastron length and (B) carapace length for the studied population of *Kinosternon integrum*. Dashed lines represent 95% confidence intervals.

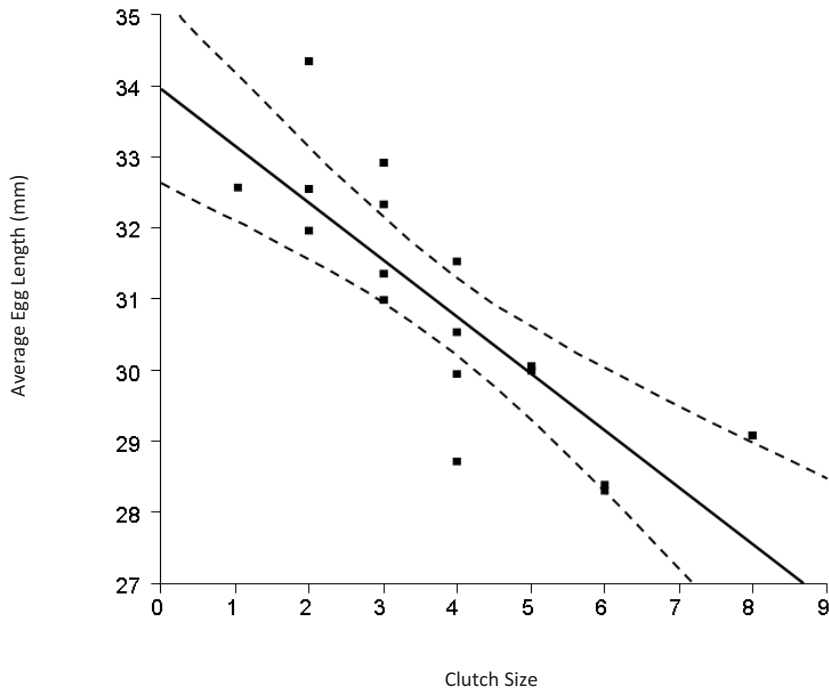


Fig. 4. Relationship between average egg length (mm) and clutch size in the studied population of *Kinosternon integrum*. Dashed lines represent 95% confidence intervals.

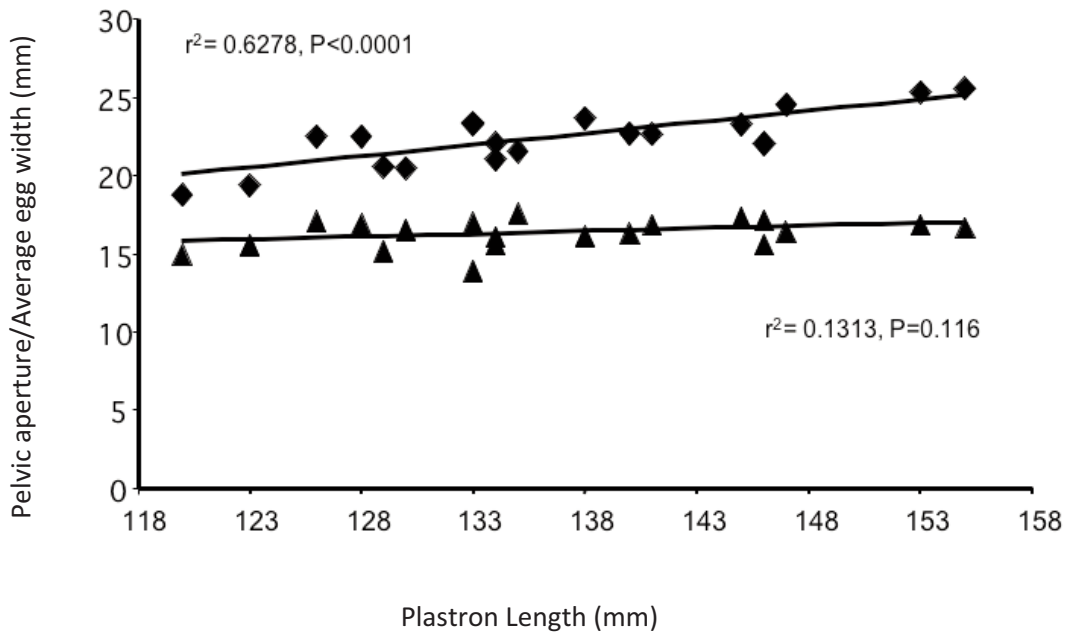


Fig. 5. Comparison of slopes for the relationships between plastron length and size of pelvic aperture (diamonds) and between plastron length and mean egg width (triangles) for the studied population of *Kinosternon integrum*. The r^2 coefficient and P value for each relationship are presented.

pond could also be explained by the high productivity of this pond via the constant input of organic matter from cattle. Seasonal aquatic habitats have been considered highly productive (Lampert and Sommer 1997). The presence of second- and third-year turtles (non-reproductive individuals) suggests that the habitat also contains suitable nesting sites. Morales-Verdeja and Vogt (1997) found in *K. leucostomum* a similar abundance and distribution pattern.

Kinosternon integrum is one of the largest species of the genus, and in fact, we recorded in Tonatico the largest male in terms of carapace length (223 mm) observed for the species (Macip-Ríos and Casas-Andreu 2006). Sexual size dimorphism is common in this group of turtles (Carr and Mast 1988, Iverson 1989, Iverson et al. 1991). Our results indicate that males are larger than females, and this pattern of sexual size dimorphism in kinosternids has been explained as a result of males' territorial behavior: the bigger the male, the better the phenotype for competing for territories and females (Wilbur and Morin 1988). Other kinosternids like *K. scorpioides* (Pritchard and Trebbau 1984), *K. oaxacae* (Iverson 1986), *K.*

herrerai (Carr and Mast 1988), *K. creaseri* (Iverson 1988), and *K. alamosae* (Iverson 1989) show similar sexual dimorphism patterns with larger males.

The reproductive season of *K. integrum* in Tonatico (July–October) was similar to that reported for other freshwater turtles in North America, like *Chrysemys picta* (Iverson and Smith 1993), *Apalone ferox* (Iverson and Moller 1997), and *Chelydra serpentina* (Iverson et al. 1997). The breeding season was also related to weather because these turtles need water for courtship and mating. Iverson (1999) reported a breeding season for *K. integrum* (data from several populations) from May to September; our findings extend that period by one month. The smallest female found with eggs in Tonatico was 122 mm in plastron length, almost the same size that Iverson (1999) reported previously (123 mm) in the upper Balsas River basin in Puebla. Average clutch size in the Tonatico population (4 eggs) was smaller than the average clutch size found by Iverson (1999; 5.8 eggs). However, we estimated clutch size by counting oviductal eggs on X-ray plates, which is more accurate than counting corpora lutea (Congdon and Gibbons 1990), as Iverson (1999) did.

TABLE 2. Relative clutch mass and body size of several kinosternids of North America. RCM = relative clutch mass; CL = carapace length.

Species	Locality	RCM	CL (mm)	Source
<i>Kinosternon alamosae</i>	Alamos, Sonora	0.112	106.3	Iverson 1989
<i>Kinosternon flavescens</i>	Gimlet Lake, Nebraska	0.109	102.5	Iverson 1991
<i>Kinosternon subrubrum subrubrum</i>	Ellenton Bay, South Carolina	0.106	86.3	Iverson et al. 1991, Gibbons 1983
<i>Kinosternon subrubrum hippocrepsis</i>	Hot Springs, Arkansas	0.079	96.3	Iverson 1979
<i>Sternotherus odoratus</i>	Richmond, Virginia	0.104	74.9	Mitchell 1985, Mitchell 1988
<i>Sternotherus minor</i>	Oviedo and Seminole Counties, Florida	0.092	100.1	Etchberger and Ehrhart 1987
<i>Kinosternon baurii</i>	Alachua, Levy, and Marion counties, Florida	0.090	91.6	Iverson et al. 1991
<i>Sternotherus carinatus</i>	Broken Bow, Oklahoma	0.081	102.0	Iverson 2002
<i>Kinosternon hirtipes</i>	Galeana, Chihuahua	0.710	110.6	Iverson et al. 1991
<i>Kinosternon sonoriense</i>	Sycamore Creek, Arizona	0.068	135.0	Hulse 1982
<i>Kinosternon flavescens arizonense</i>	Pima County, Arizona	0.065	145.1	Iverson 1989
<i>Kinosternon creaseri</i>	Coba, Quintana Roo	0.045	116.0	Iverson 1988
<i>Kinosternon integrum</i>	Several states in México	0.060	146.9	Iverson 1999
<i>Kinosternon integrum</i>	Tonatico, State of México	0.043	142.7	This study

As in other species of freshwater turtles, a significant positive relationship between body size and clutch size was observed in *K. integrum* at Tonatico (Congdon and Gibbons 1983, Iverson and Smith 1993, Iverson et al. 1997, Boot 1998). This pattern is more or less generalized in turtles (Congdon and Gibbons 1983, Iverson and Smith 1993, Iverson et al. 1997), as well as in other ectotherms such as lizards (Ballinger 1983) and snakes (Bronikowski and Arnold 1999). In addition, our results agree with a basic life history pattern, that suggests a trade-off between egg size and clutch size (Roff 2002). This pattern has been reported in other freshwater turtles (Congdon and Gibbons 1983, Iverson and Smith 1993, Iverson et al. 1997), in Iverson's (1999) combined data for *K. integrum*, as well as in other vertebrates like lizards (Sorci and Clobert 1999, Warne and Charnov 2008), snakes (Bronikowski and Arnold 1999), and mammals (Charnov and Ernest 2006).

We found that only 43.47% of females had oviductal eggs. These findings are consistent with findings for other species like *K. subrubrum* (Frazer 1991) and *K. flavescens* (Iverson 1991), which had an average of 50% gravid females per population. This trend is also common in organisms considered "bet hedgers" (Cunnington and Brooks 1996, Roff 2002, Fox and Rauter 2003) and grants them breeding opportunity every 2 or 3 seasons (Frazer 1991, Iverson 1991a), giving them the advantage of investing more energy in survival and growth than in reproduction. Mean reproductive effort is the lowest recorded for kinosternids (Table 2), but further intra- and interspecific comparisons of this trait and its relationships with body size and with other life history variables are needed in order to understand this result.

The lack of a pelvic constraint on egg size in the Tonatico population allows the smallest reproductive individuals to produce eggs of the same width as those of larger individuals. If there were a selective pressure for increasing egg size, this could be attained by increases in egg length, which according to our results shows a higher variation. In contrast, there is evidence of a pelvic constraint on egg size in other freshwater turtles (Congdon and Gibbons 1987). According to theoretical predictions (Congdon and Gibbons 1987), larger turtle species should not show a pelvic constraint, whereas smaller species should. Further

research is needed to clarify what kinosternids (considered small species) can tell us about this issue.

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