

tion and thus the restoration of an endangered population. Additionally, considering the variability in sex ratios indicated by these studies, the adaptive significance of temperature-dependent sex determination (if any) may not be easily revealed. The effective evaluation of the adaptive significance of TSD may require long-term and comprehensive evaluations of sex ratios within specific populations as well as studies examining the affects of sex ratio on reproductive success.

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### Reproduction in the Mexican Mud Turtle *Kinosternon integrum*

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The Mexican Mud Turtle, *Kinosternon integrum* is one of the most widely distributed of all turtles in Mexico (Iverson, 1992), and may be the most commonly encountered turtle in the country (Iverson, 1982; pers. obs.). However, despite its abundance, natural history aspects of this species are lacking, and the only data on reproduction are anecdotal (Duellman, 1961; Scott, 1962; Hardy and McDiarmid, 1969; Flannery, 1972; Webb, 1984; Rudloff, 1986; Ewert, 1991). Reproductive data derived from the dissection of 52 females (>100 mm plastron length), collected during field work in the states of Guerrero, Jalisco,

TABLE 1. Reproductive characteristics of adult female *Kinosternon integrum*. Location is State in Mexico with river basin in parentheses. Samples are listed in chronological order by month.

Location	Date	N	Plastron length (mm)	Corpora lutea	Enlarged follicles	Egg length	Egg width	Egg mass
Michoacan (Balsas)	6 Apr	1	134.4	—	3	—	—	—
Michoacan (Artega)	6 Apr	6	143.2 (131–157)	—	4.83 (3–6)	—	—	—
Guerrero (Coyuca)	7–8 Apr	5	137.4 (132–146)	—	4.0 (3–6)	—	—	—
Puebla (Balsas)	3 May	7	139.6 (123–149)	4 (n = 1)	4.63 (2–7)	30.05 (n = 1)	17.30	5.45
Jalisco (Armeria)	9 May	2	139.1 (137–142)	4 (n = 1)	5.0 (3–7)	31.9 (n = 2) (31.7–32.1)	16.4 (16.2–16.4)	5.42 (5.24–5.60)
Jalisco (Chapala)	9 May	4	143.3 (141–145)	4 (n = 1)	6	30.93 (n = 3) (30.2–31.3)	16.83 (16.6–17.0)	—
Queretaro (Panuco)	22–23 June	2	156.3 (151–161)	5.5 (5–6)	5.5 (5–6)	30.36 (n = 7) (29.0–31.3)	17.53 (16.9–18.1)	—
Sonora (Matape)	18 Jul	2	153.8 (147–161)	5.5 (5–6)	6.5 (6–7)	34.40 (n = 5) (33.4–35.3)	18.60 (17.9–19.1)	7.23 (6.84–7.81)
Sonora (Yaqui)	19 Jul	1	159.8	6	8	33.14 (n = 6) (32.0–34.2)	17.43 (16.75–17.7)	6.04 (5.38–6.42)
Sonora (Yaqui/Mayo)	19 Jul	3	143.3 (138–149)	5.3 (5–6)	4.3 (4–5)	29.4 (n = 2) (29.0–29.8)	16.93 (16.8–17.1)	—
Morelos (Balsas)	3–9 Aug	3	147.9 (144–152)	9.7 (7–12)	8.0 (7–10)	27.78 (n = 29) (23.1–32.1)	16.31 (14.0–18.2)	—
Sonora (Yaqui/Mayo)	9 Aug	3	134.3 (125–144)	4.0 (3–5)	3.7 (3–4)	30.42 (n = 8) (27.1–35.4)	16.56 (16.3–16.9)	4.996 (4.41–6.04)

Michoacan, Puebla, Queretaro, Sonora, and Morelos between 1978 and 1985 (Table 1), form the basis of this report. The data from different localities are pooled for most analyses, since this is the first attempt to describe the female reproductive cycle of this species; however, traits that obviously vary geographically are discussed.

The average maximum (not mid-line) plastron length (PL) of 38 mature females examined in this study was 141.4 mm  $\pm$  9.8 (range 123 to 161), and the average carapace length (CL) was 146.9  $\pm$  8.7 (range 131 to 168). The largest two females of over 400 from museum and field collections were 168 mm CL (161 mm PL; from Queretaro) and 165 mm CL (161 mm

PL; from Sonora); however, Berry (1978) reported maximum female size among over 1060 specimens as 188 mm CL. The next largest female I observed (166 mm CL) was from Guanajuato, and it was my subjective impression that females reached larger sizes on the southern Mexican Plateau. The relationship between PL and body mass (BM in g) in 44 females was highly significant (BM = 0.0001263PL<sup>3.048</sup>;  $r = 0.99$ ;  $P < 0.0001$ ), and the ratio of PL to CL for 220 subadult and adult females in museum collections from throughout the species range averaged 0.954  $\pm$  0.027 (range 0.88–1.026; see also Mosimann, 1956: Fig. 8, who graphed the regressions of CL on PL for males and females based on 162 specimens from Michoacan).

The largest immature females (no corpora lutea nor follicles  $>5$  mm) were 130, 129, and 128 mm PL (133, 136, and 134 mm CL; and 353, 339, and 345 g BM, respectively); all females under 120 mm PL were immature. The smallest mature females (with corpora lutea or follicles  $>8$  mm diameter) were 123, 125, and 126 mm PL (133, 132, and 136 mm CL; and 352, 323, and 270 g BM, respectively); all females over 130 mm PL were mature. These data suggest that maturity is attained at between 120 and 130 mm PL (ca. 130 and 140 mm CL, and 300 and 350 g BM). No evidence of significant geographic variation in size at maturity was detected.

Females bore ovulatory-sized follicles (15–17 mm) throughout the seasons sampled (April–August; Fig. 1). The ovaries of three females from the Rio Fuerte basin in Sonora collected by T. R. Van Devender in February of 1978 had smaller follicles (Fig. 1) and

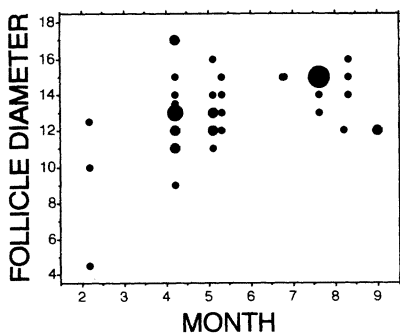


FIG. 1. Monthly variation in maximum follicle diameter (in mm) in female *Kinosternon integrum*. Point overlap is indicated by size of dot.

TABLE 2. Variation in nesting season among species of Mexican *Kinosternon*. Species are listed in approximate geographic order from northwest to southeast.

Species	Hypothesized nesting season	Annual clutch frequency	Source
<i>sonoriense</i>	June–Sept	2–4	Rosen, 1987; Van Loben Sels et al., 1997
<i>flavescens</i>	July–August	2 (–3?)	Iverson, 1989b
<i>alamosae</i>	July–Sept	1–2	Iverson, 1989a
<i>hirtipes</i>	May–Sept	3–4	Iverson et al., 1991
<i>integrum</i>	May–Sept	2–4?	This paper
<i>herrerai</i>	July–Aug	2–3	Carr and Mast, 1988
<i>chimalhuaca</i>	July–Aug	1	Berry et al., 1997
<i>oaxacae</i>	July–?	1–2	Iverson, 1986
<i>leucostomum</i>	late Aug–March	2+	Morales-Verdeja and Vogt, 1997
<i>scorpioides</i>	August–April	2–3+	Alvarez del Toro, 1983; Iverson, pers. observ.
<i>acutum</i>	Sept–March	2–4	Vogt, unpubl. (in Iverson and Vogt, 1998)
<i>creaseri</i>	August–?	2–3	Iverson, 1988

lacked corpora lutea. The earliest date for a female with oviducal eggs was 3 May, suggesting egg laying in early May; however, several females captured on 6 April had follicles as large as the mean egg diameter, suggesting that ovulation in some females may occur in April. The earliest date for a female with two distinct sets of corpora lutea was 19 July; however, only two females were available between 9 May and 18 July, and thus it is possible that July females with only one distinct set of corpora lutea may have produced an earlier clutch, but the corpora lutea from that clutch had fully regressed. Females in early August still bore one or two sets of enlarged ovarian follicles (>9 mm), suggesting that the nesting season may extend at least into September. Indeed, although based on a captive female, Webb (1984) reported egg-laying in early October.

The hypothesized nesting season of *K. integrum* (early May to September) is nearly identical to that of *K. hirtipes* (Iverson et al., 1991; Table 2), which co-occurs with *K. integrum* over much of the southern Mexican Plateau (Iverson, 1992). It apparently begins prior to the onset of the summer rainy season (June to early July, depending on location). However, in the driest

habitats, ponds may completely dry during the winter and not refill until the next rainy season (pers. observ.). Turtles in these habitats may estivate for part of the year (see also Slevin, 1926; and Zweifel, 1960) and presumably do not nest until the summer rains begin. For example, we found an estivating *K. integrum* in the dry season (7 May 1981) under a rock in an oak woodland at 2075 m elevation along Hwy 110 just west of the Michoacan-Jalisco border; no surface water was present in the area at that time.

Hardy and McDiarmid (1969) reported finding hatchlings in Sinaloa in late July, August, and early September, and Scott (1962) found one in Sinaloa on 16 August. I collected one in central Oaxaca (with a brilliant red-orange plastron) on 17 June 1979. However, given that the species apparently exhibits embryonic diapause (Ewert, 1991), these turtles must have hatched from eggs laid the previous summer. Duellman (1961) recorded the only observation of copulation in the field on 26 August.

No female had three identifiable sets of corpora lutea. However, because at least some females had produced two clutches by mid-July to early August and still had two additional sets of enlarged follicles (>9 mm) that might have been ovulated that season, an annual clutch frequency of four may be possible. To estimate clutch frequency conservatively across all samples, I added the number of sets of enlarged follicles (>9 mm diameter) to the number of sets of distinctly identifiable corpora lutea. By this method average clutch frequency was estimated to be 2.26 (range 1–4;  $N = 38$ ), and was positively correlated with plastron length (Fig. 2). No other data on annual clutch frequency have been reported for this species.

Clutch size based on counts of corpora lutea averaged  $5.8 \pm 2.3$  (range 3 to 12;  $N = 19$ , including two distinct sets for each of two females) and was not significantly correlated with PL ( $P = 0.15$ ;  $N = 18$ ). However, three females from Morelos were clearly outliers (Fig. 3); excluding those three females revealed a significant positive relationship between clutch size and body size. Clutch size based on counts of near-ovulatory-sized follicles averaged  $5.00 \pm 1.69$  (range 2 to 10;  $N = 38$ ), and was highly correlated with plastron length ( $r = 0.60$ ;  $N = 38$ ;  $P < 0.0001$ ). Rudloff (1986) reported a clutch of three eggs from a captive female

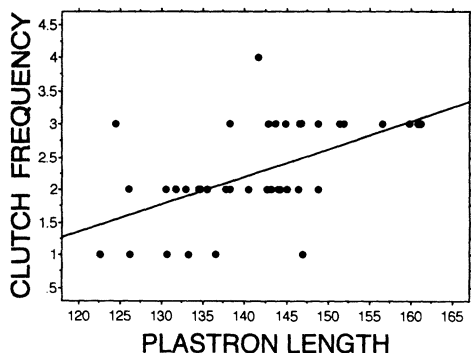


FIG. 2. Relationship between body size (plastron length in mm) and estimated annual clutch frequency. Method of estimation of clutch frequency in text. Regression line is highly significant ( $r = 0.55$ ;  $P = 0.0004$ ).

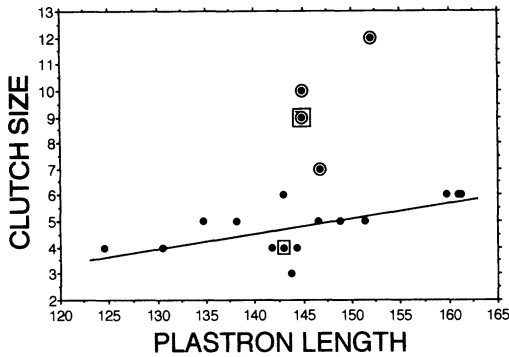


FIG. 3. Relationship between body size (plastron length in mm) and clutch size (based on counts of corpora lutea) in *Kinosternon integrum*. Regression line ( $y = 0.055x - 3.177$ ;  $r = 0.56$ ;  $P = 0.013$ ;  $N = 11$ ) excluded three outliers from Morelos (circled). Second (older) sets of corpora lutea are within squares. Circle in square represents older clutch of female with same plastron length.

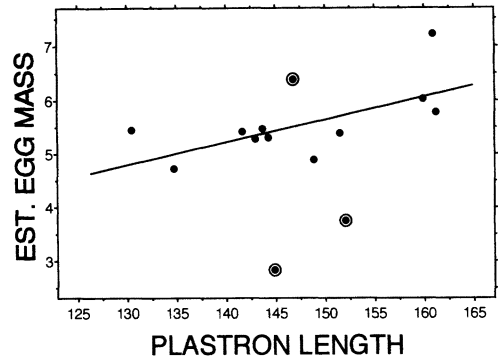


FIG. 4. Relationship between body size (plastron length in mm) and estimated egg mass (in g) in *Kinosternon integrum*. Regression line ( $y = 0.043x - 0.757$ ;  $r = 0.66$ ;  $P = 0.026$ ;  $N = 11$ ) excluded three outliers from Morelos (circled).

from Colima, and Webb (1984) recorded a clutch of nine eggs from a captive female from Sinaloa. Flannery (1972) observed a 135 mm CL (estimated PL = 129 mm) gravid female "with 11 eggs"; however, given its small size, and the smaller clutch sizes and follicle counts for other small females, I suspect that the author was referring to enlarged ovarian follicles rather than shelled eggs.

Egg size ranged from 23.1 to 35.4 mm length (EL; mean  $29.5 \pm 3.1$ ;  $N = 66$ ), from 13.9 to 19.1 mm width (EW; mean  $16.7 \pm 1.2$ ;  $N = 66$ ), and from 4.41 to 7.81 g (EM; mean  $5.80 \pm 0.97$ ;  $N = 23$ ). Egg mass was related to EL and EW by the multiple regression  $EM = 0.185EL + 0.761EW - 13.225$  ( $r = 0.98$ ;  $N = 23$ ;  $P < 0.0001$ ). Mean estimated egg mass for all 66 eggs (i.e., with EM estimated from the regression for 43 of the eggs) was  $4.93 \pm 1.42$  g (range 1.70 to 7.81). Rudloff (1986) reported three eggs from a captive female from Colima that averaged  $31 \times 16$  mm and weighed an average of 5 g each, and Webb (1984) recorded nine eggs from a captive female from Sinaloa that averaged 25.6 mm EL (range 25.0–27.1), 16.3 mm EW (15.4–16.8), and 4.2 g EM (3.74–5.30). Each of those captive eggs fell well within the range of variation in egg size noted here.

Neither EL, EW nor EM were significantly related to plastron length for thirteen females with eggs ( $P > 0.27$ ); however, three females from Morelos were outliers to this relationship. When those three females were excluded from the analysis, the relationship between EM and PL was significant (Fig. 4). Estimated relative egg mass (REM = mean egg mass/[BM-CM]) was determined for 14 females with oviducal eggs from actual ( $N = 4$ ) or estimated data on egg mass ( $N = 10$ ; from the regression of EL and EW on EM); REM averaged  $0.011 \pm 0.002$  (range 0.006 to 0.014), the smallest value recorded for any kinosternine turtle (Iverson et al. 1991).

Relative clutch mass (RCM = clutch mass/[BM-CM]; estimated by the same method as REM) averaged  $0.060 \pm 0.017$  (range 0.036 to 0.097;  $N = 14$ ).

This value is similar to those for other northern Mexican *Kinosternon* reviewed by Iverson et al. (1991; e.g., *K. hirtipes* at 0.071 and *K. flavescens arizonense* at 0.065), and agrees with the hypothesized positive relationship between latitude and RCM among kinosternine species in North America (Iverson et al., 1991). However, *K. integrum* differs reproductively from *K. hirtipes*, with which it coexists on the southern Mexican Plateau, in its larger average female body size (147 vs. 111 mm CL), larger clutch size (5.8 vs. 3.0), and relatively smaller eggs (REM 0.011 vs. 0.024). Nevertheless, the two exhibit very similar nesting seasons, annual clutch frequencies, egg sizes, and RCM's (Table 2; review in Iverson et al., 1991).

Despite its extensive distribution across almost 13 degrees of latitude and from sea level to 2500 m (pers. observ.), *Kinosternon integrum* apparently exhibits very little geographic variation in life history traits. The only divergent sample (with larger clutches of smaller eggs) was from a slow-moving, garbage-filled, human feces-lined stream passing through a very poor suburb east of Cuernavaca, Morelos. None of my other samples came from such a nutrient enriched environment, which might explain their distinctive reproductive traits. With its relatively large, multiple annual clutches of relatively tiny eggs, its ability to estivate when water is absent, and its generalized diet (Flannery, 1972; pers. observ.) *Kinosternon integrum* is well adapted to exploit both temporary and permanent aquatic systems in Mexico, which may explain its abundance and wide distribution.

Recent molecular and morphological work (Iverson, 1998) suggests that *K. integrum* is most closely related to *K. scorpioides*, with which it is parapatric (Iverson, 1992); however, preliminary reproductive data for the latter (Table 2) suggests that the timing of its reproductive cycle is completely asynchronous with that of *K. integrum*. Clearly, further research on the reproductive cycles of both of these species is needed in order to understand the evolution of reproductive strategies in this diverse genus.

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