

## Aspects of the Life History of the Texas Map Turtle (*Graptemys versa*)

PETER V. LINDEMAN<sup>1</sup>

*Department of Biology and Health Services, 150 Cooper Hall,  
Edinboro University of Pennsylvania, Edinboro 16444*

**ABSTRACT.**—The Texas map turtle (*Graptemys versa*) is endemic to the Colorado River drainage in southcentral Texas. A study of its life history was undertaken using data collected in 1998–2000 from a population in the South Llano River, southernmost tributary of the Colorado drainage, and data from museum specimens that had been collected from the South Llano River in 1949. Compared to congeners, *G. versa* is a small-bodied species. Its small body size is, predictably, linked to relatively small clutch size, small egg size, rapid growth toward asymptotic size and early maturation. As many as four clutches may be laid during an active season, although the effects of follicular atresia on clutch frequency are not known. Both clutch size and egg width were positively correlated with female body size, with the former relationship having a log-log slope significantly less than the expected value of 3, probably due to the latter relationship. Analyses were consistent with the hypothesis of an anatomical constraint on egg size, with at least smaller females laying eggs that are of less than optimal size. No differences were found in body size or clutch size between 1949 and 1998–2000 despite a large-scale change in diet associated with invasion of the river by Asian clams (*Corbicula* sp.). However, body size is substantially reduced in the South Llano River compared to other sections of the Colorado drainage, a finding mimicked by at least one other turtle species in the drainage, *Pseudemys texana*.

### INTRODUCTION

Map turtles (*Graptemys*) are medium-sized emydid turtles found primarily in eastern and central North American rivers. Twelve species are recognized (Ernst *et al.*, 1994). In a study of over 2200 museum specimens (Lindeman, 2000), maximum plastron lengths of females ranged from 152 mm in *G. oculifera* to 239 mm in *G. pseudogeographica* (erroneously reported as 229 mm for the latter in Lindeman, 2000). Males exceeded 102 mm in plastron length only in northern populations of *G. geographica*, *G. ouachitensis* and *G. pseudogeographica*. The largest female body sizes are achieved by members of the megacephalic clade (*G. barbouri*, *G. ernsti*, *G. gibbonsi* and *G. pulchra*) in the southeastern United States and by northern populations of *G. geographica*, *G. ouachitensis* and *G. pseudogeographica* (Lindeman, 2000). The large sexual difference in body size is driven primarily by extreme bimaturism, with males maturing at 2–5 y of age and females maturing perhaps as late as 14 y of age (Lindeman, 1999). Among all species of *Graptemys* that have been studied, average clutch size ranged from 4.7–14.1 eggs (Table 1). Average egg sizes ranged from 22.0–29.5 mm in width and from 34.0–39.4 mm in length (Table 1).

The Texas map turtle (*Graptemys versa*) is endemic to the Colorado River drainage of the Edwards Plateau in central Texas, between 30°N and 32°N (Vogt, 1981). In an exhaustive compendium of literature citations on the 56 species of turtles native to North America (Ernst *et al.*, 1994), *G. versa* has the distinction of having the shortest species account with the fewest citations of ecological studies. Such a lack of information on basic life history parameters and ecology is a serious impediment to management of a species. The paucity of

<sup>1</sup> Telephone: (814) 732-2447; FAX: (814) 732-2593; e-mail: plindeman@edinboro.edu

TABLE 1.—Reports of clutch size (minimum n = 8 clutches) and egg dimensions (minimum n = 15) for species of *Graptemys*

Species	State	Source	Mean clutch		Mean egg width		Mean egg length	
			size	n, range	(mm)	n, range	(mm)	n, range
<i>barbouri</i>	FL	Cagle, 1952			25.9	46, 22.2–29.3	37.1	46, 31.0–40.4
<i>barbouri</i>	GA	Ewert and Jackson, 1994	8.5	18, 4–14				
<i>barbouri</i>	GA	Wahlquist and Folkerts, 1973			29.5	17, 27.6–30.8	39.4	17, 38.3–41.6
<i>ernsti</i>	AL	Shealy, 1976	7.2	25, NR				
<i>flavimaculata</i>	MS	Horne et al., 2003	4.7	134, 3–9				
<i>geographica</i>	MO	White and Moll, 1991	10.1	14, 6–15				
<i>nigrinoda</i>	AL	Lahanas, 1982	5.5	9, 3–7	23.8	42, 20.9–26.0	37.0	42, 32.9–41.8
<i>ouachitensis</i>	WI	Vogt, 1980a	10.5	65, 6–16	22.0	345, NR	34.0	392, NR
<i>pseudogeographica</i>	WI	Vogt, 1980a	14.1	50, 8–19	25.1	240, NR	34.2	421, NR
<i>versa</i>	TX	Present study	5.6	14, 4–9	20.7	36, 18.4–22.2	35.1	36, 30.7–38.4

information on *G. versa* in the published literature, together with the availability of a large series of museum specimens collected five decades ago, provided the impetus for the present study of *G. versa* life history.

I used part of a large series of museum specimens captured on one day in 1949 and field work in 1998–2000 with a population from the same river to study body size, maturation, growth in body size and reproduction of *Graptemys versa*. Based on its southern distribution and lack of megacephaly, the species may be expected to be a relatively small-bodied, early-maturing species, life-history attributes which may be associated with relatively small clutch and/or egg size compared to other *Graptemys*. The specimens from 1949 were collected prior to a dramatic shift in diet in this species, from a varied diet in adult female *G. versa* that included moderately heavy reliance on native mollusks, to a substantially heavier reliance on the invasive exotic mollusk *Corbicula* sp. (Lindeman, 2005). I was, therefore, able to investigate whether the change in diet was associated with a change in the life-history parameters of body size and fecundity.

#### STUDY AREA

I studied a population of *Graptemys versa* inhabiting the South Llano River in Kimble County, Texas, in the vicinity of two bridges on State Highway 377. Additional captures were made in May 1999 on a site on East Johnson Fork, a tributary of the Llano River, 23 km east of the main study site. The main study site was immediately downstream (north) of the Paint Creek Ranch, where 42 specimens currently housed at the Strecker Museum, Baylor University, had been collected on 30 April 1949. The study area was a series of deep, slow-current pools alternating with shallow, fast-current riffle zones. Surrounding terrestrial areas were dominated by dry rocky soils and scrub vegetation.

## METHODS

I captured *Graptemys versa* using fykenets (Vogt, 1980b), floating basking traps (MacCulloch and Gordon, 1978) and occasional hand captures during May 1998, May 1999 and June 2000. I marked individuals by filing notches in marginal scutes of the carapace (Cagle, 1939) and released them at their sites of capture following data collection. Data collected from each individual included midline plastron length (PL) measured to the nearest 1 mm with a flexible plastic ruler, midline carapace length (CL) measured to the nearest 1 mm with bow calipers, sex as determined by relative size of the tail (Ernst *et al.*, 1994) and age, for younger specimens showing clear growth annuli on the pectoral scutes of the plastron. While the use of scute annuli for aging turtles is controversial (*e.g.*, Brooks *et al.*, 1997; Germano and Bury, 1998; Wilson *et al.*, 2003), the technique appears to be valid in many temperate-zone aquatic turtles—particularly among the Deirochelyinae (to which *G. versa* belongs)—if confined to young, rapidly-growing individuals (Germano and Bury, 1998; Wilson *et al.*, 2003). Unfortunately, none of a small number of recaptured turtles in the present study ( $n = 3$ ) had clear annuli and I was, thus, unable to verify the deposition of one annulus per year for this population.

I calculated sexual dimorphism index (Gibbons and Lovich, 1990, as modified by Lovich and Gibbons, 1992) using all males exhibiting a large tail base and all females as large as or larger than the smallest known mature female. I modeled growth of *Graptemys versa* using the von Bertalanffy growth model

$$PL_t = PL_A(1 - be^{-kt}),$$

where  $PL_A$  is asymptotic plastron length,  $k$  is rate of growth toward  $PL_A$ ,  $b$  is a parameter related to size at hatching,  $e$  is the base of the natural log and  $t$  is age (Richards, 1959). A growth curve was fit for females only, including data from unsexed juveniles, as no adult males with visible growth annuli were captured. Age of individuals exhibiting clear growth annuli was expressed as a continuous, rather than a discrete, variable (Lindeman, 1997). I used an active season of 1 February to 30 November and added 0.25 y to each age to denote the time between hatching and first hibernation, as done in previous growth modeling of *G. caglei* in an adjacent southcentral Texas drainage (Lindeman, 1999). Asymptotic PL was estimated using the mean of upper decile PLs for females (Germano, 1994; Lindeman, 1999) and the parameters  $k$  and  $b$  were estimated by nonlinear regression, with 95% support-plane confidence intervals (SPCI; Schoener and Schoener, 1978).

Clutch sizes of females captured in 1999 and 2000 were determined by radiography (Gibbons and Greene, 1979). I determined clutch size in half of the female specimens from 1949 by dissection and examination of oviducal eggs and enlarged follicles. Correlation of clutch size with PL was analyzed using both raw data and log-transformation of both variables (King, 2000). Egg width was measured from radiographs after correction for enlargement (Graham and Petokas, 1989). Oxytocin injection (Ewert and Legler, 1978) was used to induce egg laying in order to make direct measurements of egg length and egg width.

## RESULTS

Eighty individual *Graptemys versa* were captured during 1998–2000, with three recaptures. Adult males ranged from 57–79 mm PL ( $\bar{x} = 66.1$  mm,  $n = 35$ ) and from 66–96 mm CL ( $\bar{x} = 79.4$  mm). Male specimens from 1949 ranged from 55–74 mm PL ( $\bar{x} = 67.1$  mm,  $n = 16$ ) and from 64–89 mm CL ( $\bar{x} = 81.1$  mm). Based on the presence or absence of oviducal eggs, or enlarged follicles in the case of dissected specimens, females reached maturity at a minimum body size of 115 mm PL and 128 mm CL. Among 13 dissected females from 1949, specimens

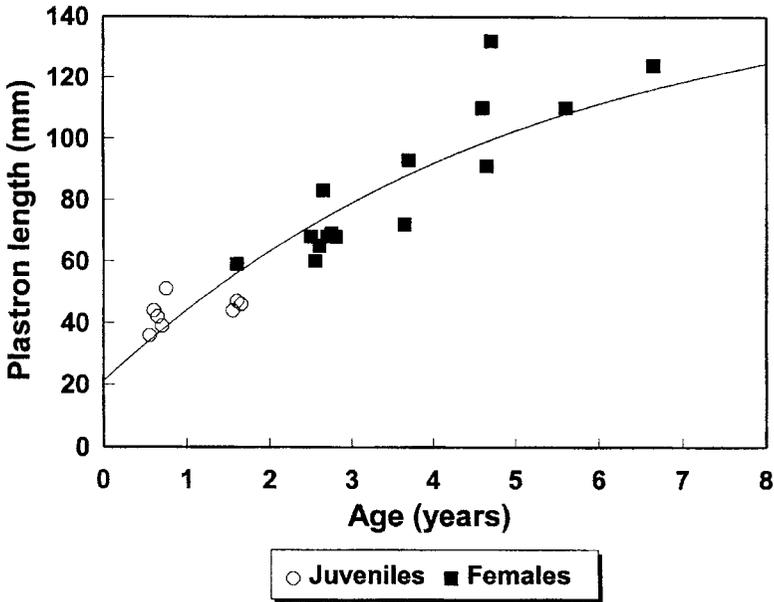


FIG. 1.—Size-at-age data and a von Bertalanffy growth curve for female *Graptemys versa* from the South Llano River

measuring 103, 124 and 130 mm PL had no eggs or enlarged follicles. A female measuring 110 mm PL had follicles that did not exceed 7 mm and may have been in the process of maturing. For all females 115 mm PL or larger in 1998–2000 ( $n = 20$ ), body size ranged from 115–163 mm PL ( $\bar{x} = 133.8$  mm) and from 128–183 mm CL ( $\bar{x} = 150.3$ ). Female specimens in the 1949 series that were  $>115$  mm PL ( $n = 22$ ) ranged to 148 mm PL ( $\bar{x} = 127.2$  mm) and from 128–166 mm CL ( $\bar{x} = 142.7$  mm).

Sexual dimorphism index was 1.02 using PL and 0.89 using CL for specimens captured in 1998–2000 and 0.90 using PL and 0.76 using CL for specimens of the 1949 series. Average size of males was not significantly different between time periods, with means for 1949 males being larger by  $<2$  mm in either measurement (for PL,  $t = 0.68$ ,  $P = 0.50$ ; for CL,  $t = 0.82$ ,  $P = 0.42$ ). Means for females from 1998–2000 were larger by  $>6$  mm for both measurements, but neither difference was significant (for PL,  $t = -1.93$ ,  $P = 0.061$ ; for CL,  $t = -1.96$ ,  $P = 0.057$  for CL).

For the von Bertalanffy growth curve for females (Fig. 1),  $PL_A$  was constrained at 152.5 mm based on the mean of the largest 4 of 36 females. The parameter  $b$  was estimated to be 0.862 (95% SPCI 0.622–1.102), which translates as an estimated PL at hatchling of 21.0 mm, and the growth rate parameter  $k$  was estimated to be 0.194 (95% SPCI 0.017–0.371). Although no adult males with readable growth lines were captured, maturation likely occurs during the second or third season of growth based on sizes of juveniles of known ages (Fig. 1). The growth curve for females reaches the minimum size of gravid females (115 mm PL) during the seventh season of growth.

Data on clutch size were based on numbers of oviducal eggs obtained from four of the 13 dissected females from 1949 as well as radiographs of five females captured on the main study area in 1999, one female from the main study area in 2000 and four females from East

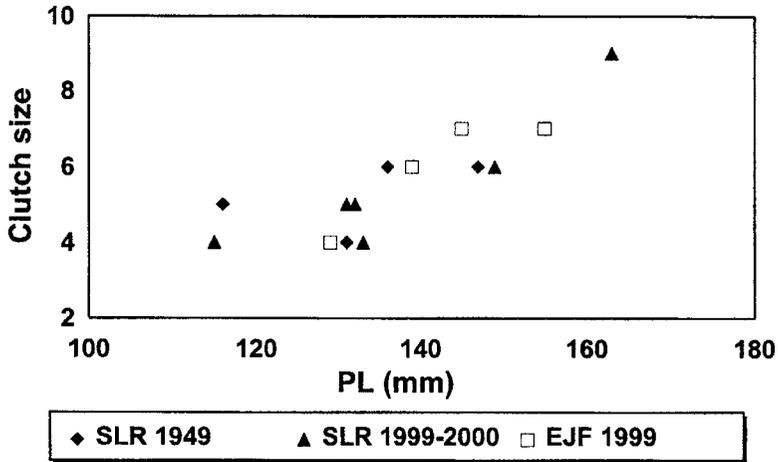


FIG. 2.—Correlation of clutch size with female plastral length (PL) in *Graptemys versa* for three samples of data from the Llano River drainage (SLR = South Llano River, EJF = East Johnson Fork)

Johnson Fork in 1999. In ANCOVA there was no interaction of PL and site ( $F_{2,8} = 1.18$ ,  $P = 0.36$ ) and no difference in clutch size was noted among the three samples when PL was used as a covariate ( $F_{2,8} = 0.05$ ,  $P = 0.95$ ). Overall clutch size based on oviducal eggs averaged 5.6 (range 4–9,  $n = 14$ ) and was significantly correlated with female PL (untransformed data,  $r^2 = 0.71$ ,  $P = 0.0001$ ; log-log regression,  $r^2 = 0.66$ ,  $P = 0.0004$ ; Fig. 2). The slope of the log-log relationship of clutch size and PL was 2.05 with 95% confidence limits 1.13–2.97. Additional estimates of clutch size in the South Llano population were obtained from dissected females from 1949 by grouping enlarged follicles into distinct size classes, with up to four sets per female (Table 2). Average clutch size was 5.0 (range 3–7,  $n = 10$ ) based on each female's largest set of follicles and 4.6 (range 2–7,  $n = 29$ ) based on all sets of follicles  $>3$  mm in

TABLE 2.—Results of dissection of female *Graptemys versa* for reproductive tracts, from specimens collected 30 April 1949. Enlarged follicles are grouped according to size ranges (in mm) in parentheses

Female PL (mm)	Oviducal eggs	Groups of enlarged follicles			
		1 N (range)	2 N (range)	3 N (range)	4 N (range)
103	0				
110	0	5 (6–7)	5 (4–5)	4 (3)	
116	5	3 (17–20)	2 (9–12)		
121	0	4 (16–17)	4 (9–11)	6 (5)	5 (3–4)
124	0				
127	0	4 (12–14)	5 (7–8)	2 (5–6)	
130	0				
131	4	5 (15–19)	2 (9–10)	6 (5–6)	
132	0	6 (17–18)	4 (6–12)		
134	0	4 (11–13)	4 (8–10)	4 (3–6)	
136	6	7 (15–19)	6 (11–13)	3 (6–8)	
147	6	5 (18–20)	7 (10–13)	5 (6–7)	
148	0	7 (17–22)	3 (10–12)	7 (4–6)	

diameter. No change in clutch size over time (first through fourth clutches) was revealed in ANCOVA with PL as the covariate ( $F_{1,29} = 0.76$ ,  $P = 0.39$ ).

Based on radiographs, mean egg width (EW) was 21.18 mm (range 17.9–24.0;  $n = 57$ ). The full complement of eggs was deposited by only 2 of 10 females injected with oxytocin. The numbers of eggs retained by females were 1 (of 4 eggs detected by radiograph, recorded for two females), 1 (of 5, two females), 1 (of 6), 2 (of 6), 7 (of 9) and 7 (of 7). Mean egg length (EL) of the 36 eggs that were oviposited was 35.09 mm (range 30.7–38.4 mm) and mean EW was 20.73 mm (range 18.4–22.2 mm). The log of mean EW within a clutch was positively correlated with the log of female PL both for measurements from radiographs (intercept 0.19, slope 0.53,  $n = 10$ ,  $r = 0.90$ ,  $P = 0.0004$ ) and for measurements of oviposited eggs (intercept 0.28, slope 0.48,  $n = 9$ ,  $r = 0.89$ ,  $P = 0.0013$ ), but the log of mean EL and the log of female PL were not correlated ( $n = 9$ ,  $r = 0.31$ ,  $P = 0.41$ ; Fig. 3).

#### DISCUSSION

Compared to other *Graptemys*, *Graptemys versa* in the South Llano River produced small clutches of small eggs (Table 1). Small body size of females undoubtedly influences the small size of their clutches and eggs. The species' record size of 180 mm midline PL (or 188 mm maximum PL; see below) is smaller than maximum female sizes recorded for 8 of the other 11 species of *Graptemys* in a survey of museum specimens (Lindeman, 2000). The smallest mature size I recorded, 115 mm PL (measured along the midline), is less than the smallest previous gravid female *Graptemys* recorded in the literature, a *G. oculifera* of 128 mm maximum PL (Cagle, 1953), even considering correction for differences in how measurements were taken. However, a female *G. ouachitensis sabinensis* measuring 116 mm maximum PL has been recorded as gravid and was hence almost certainly smaller than the smallest gravid *G. versa* of the present study (M.A. Ewert, pers. comm., 1999). Male *G. versa* are also small in body size compared to congeners, having the smallest known sizes at which males show tail elongation and being one of only three species of *Graptemys* in which males are not known to reach 100 mm midline PL (see Tables 5, 6 in Lindeman, 2000). Small body size is consistent with the north-south trend in body size exhibited among species of *Graptemys* with micro- or mesocephalic females (see Introduction).

The estimated von Bertalanffy growth curve parameters for female *Graptemys versa* are unsurprising given a comparison to estimated parameters for females of four congeners. The estimate of  $b$  (0.862) is nearly identical to estimates for three other species (range 0.854–0.866; Lindeman, 1999) and slightly higher than the estimate for *G. oculifera* (0.754; Jones and Hartfield, 1995); it yields a biologically realistic estimate of size at hatching in the late summer (21.0 mm PL, compared to the smallest size I recorded in May, 36 mm PL). The estimated characteristic rate of increase ( $k$ ; 0.194) is the highest reported for female *Graptemys* (Jones and Hartfield, 1995; Lindeman, 1999); however, a high value of  $k$  is expected, given the small asymptotic plastron length: there is a negative correlation between asymptotic size and  $k$  (which measures rate of approach of the asymptote) among emydid turtles (Lindeman, 1999), a phenomenon that has been explained on mathematical (Knight, 1968) and theoretical grounds (Stamps and Krishnan, 1997).

Male *Graptemys versa* matured between about 55 and 60 mm PL, most likely in their second or third active season, while females likely matured in about their seventh season, at 115 mm PL or more, based on the growth curve. It is difficult based on present data to compare the timing of maturation among species of *Graptemys*. Variation in age at maturity likely occurs within populations (e.g., as in *Emydoidea blandingii*, Congdon and van Loben Sels, 1993) and may be especially substantial among females of the larger later-maturing species. In addition, among dissected specimens of *G. versa*, two presumably immature females were substantially

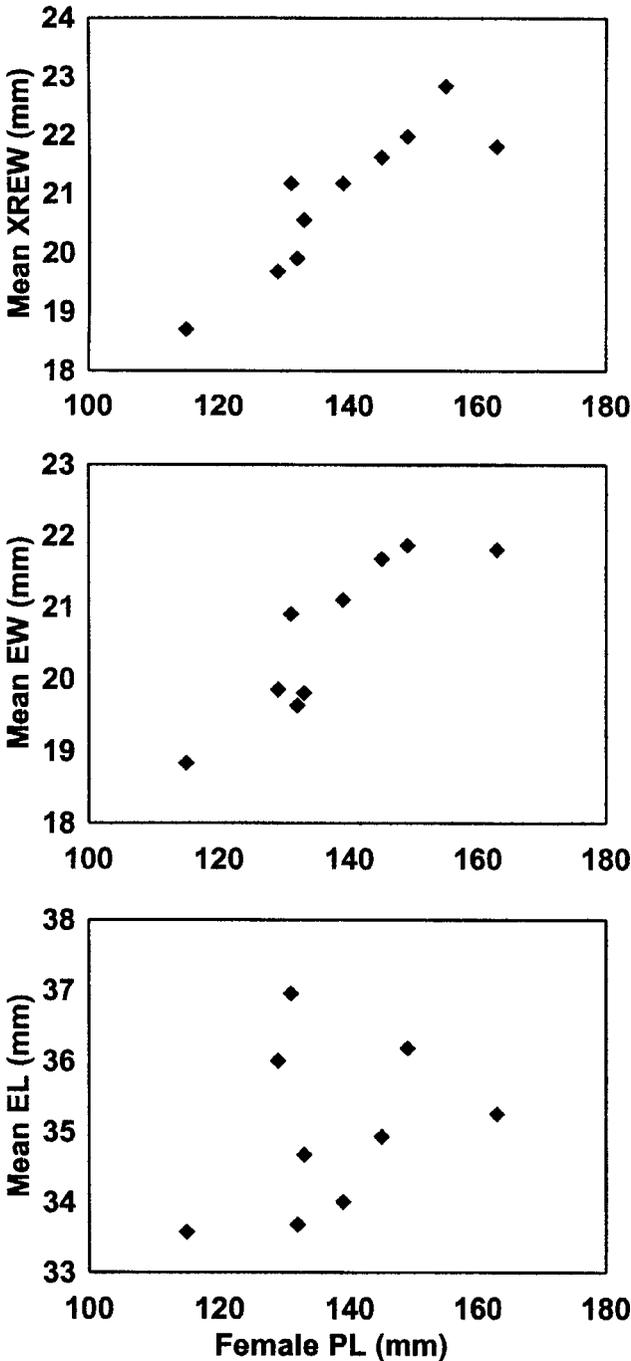


FIG. 3.—Correlation of means of egg size measurements (XREW = egg width from radiographs, EW = egg width from eggs oviposited after oxytocin administration, EL = egg length of oviposited eggs) with female plastral length (PL) in *Graptemys versa*

larger (124 and 130 mm PL) than the smallest mature females based on dissections or radiographs (115 mm PL). Finally, determination of age at maturity in *Graptemys* (particularly females) has been made by a variety of techniques involving growth analysis (*e.g.*, Shealy, 1976; Vogt, 1980a; Lahanas, 1982; Jones and Hartfield, 1995; Lindeman, 1999), rather than by direct observation of primiparity in females of known age. Nevertheless, overall it would seem that *G. versa* is an early-maturing species compared to congeners (Shealy, 1976; Vogt, 1980a; Lahanas, 1982; Jones and Hartfield, 1995; Lindeman, 1999), as would be expected based on its relatively small body size.

Based on dissections, female *Graptemys versa* may lay as many as four clutches during an active season, with no evidence of a seasonal decline in clutch size. It is even more difficult to make intrageneric comparisons of clutch frequency or annual reproductive potential than it is for age at maturity, however, because all studies of *Graptemys* that have reported these parameters (*e.g.*, Cagle, 1952; Shealy, 1976; Vogt, 1980a; Lahanas, 1982; White and Moll, 1991) are based on dissections and enumeration of follicles of different size classes. It is not known to what extent smaller size classes of follicles may undergo late-season atresia or be retained for oviposition the following season (Moll and Legler, 1971; Vogt, 1980a; Kuchling, 1999). In addition, while I detected no decline from first through fourth clutch in *G. versa*, a seasonal decline in clutch size that might be detected through direct examination of clutches by radiography or observation of oviposition (*e.g.*, Iverson and Smith, 1993) could be masked in dissection studies, if the decline were to result from late-season partial follicular atresia. All estimates of clutch frequency and annual reproductive frequency based on dissections should therefore be regarded as maximum potentials, with verification possible only by intensive study of nesting females over the course of entire nesting seasons.

Egg width was correlated with female size although egg length was not. This finding is consistent with the hypothesis that female body size constrains egg size—egg width in particular (*see* Tucker *et al.*, 1978; Rowe, 1994)—via the size of the pelvic aperture (Congdon and Gibbons, 1987) or the gap between the carapace and plastron (Clark *et al.*, 2001), through both of which eggs must pass. Significant egg width-body size correlation also suggests that there is not an optimal egg size in the population, at least not one that smaller females are capable of attaining (Congdon and Gibbons, 1987).

The 95% confidence interval for the slope of the log-log relationship of clutch size and PL in *Graptemys versa* did not include the value of 3 that would be expected in a comparison of a linear measurement (PL) with a measurement (number of eggs) that might be expected to depend on female volume (*see* King, 2000). A log-log slope significantly <3 has also been reported for the trionychid turtle *Apalone ferox*, but, unfortunately, most reported regressions of clutch size on maternal body size in turtles are of untransformed data and their slopes cannot be compared among species (King, 2000). The possibility that females are not maximizing use of their abdominal cavities for clutch production seems implausible given the strong positive correlation of clutch size with female PL. Instead, the increase in egg width (and hence egg volume) with increasing female body size probably affects the log-log correlation of clutch size with female PL, in that egg enlargement partly constrains the ability of larger females to increase egg number. An interesting comparison would involve a species in which egg size is positively correlated with female body size with a species in which egg size is relatively constant over a range of female body sizes; perhaps only the latter species would show a log-log slope of ~3 for the correlation of clutch size with female body size.

Spatial or temporal dietary differences may influence the life-history parameters of emydid populations (*e.g.*, Gibbons, 1967; Gibbons and Tinkle, 1969; Moll, 1976; Lindeman, 1996). No differences were detected in clutch size or mean adult body size of *Graptemys versa* between 1949 and 1998–2000, in spite of a dramatic shift in the prey base of adult females,

from moderately heavy ingestion of native mollusks mixed with other prey to nearly exclusive ingestion of the super-abundant introduced clam *Corbicula* sp. (Lindeman, 2005). Maximum female body size during 1998–2000 sampling was 163 mm PL, or 15 mm (10%) larger than the largest female from 1949, but the second largest female in 1998–2000 sampling was only 2 mm larger, at 150 mm PL. Another potential impact of dietary conditions may be relatively accelerated growth and maturation (Gibbons, 1967; Moll, 1976; Lindeman, 1996). Unfortunately, due to a paucity of specimens with clearly readable growth annuli I was unable to examine growth rate or age at maturation of turtles in the South Llano population prior to invasion of their habitat by *Corbicula*, hence whether or not changes in these parameters have occurred could not be assessed.

McKinney (1987) reported similar body sizes (maximum 171 mm CL) for *Graptemys versa* of the South Llano River approximately 16 km downstream (north) of my study site. Data on body size from other portions of the Colorado River drainage indicate regional variation in the life history of the species, however, with larger individuals in other parts of the range. As part of a study of the evolution of trophic morphology in *Graptemys* I measured 213 specimens of *G. versa* (Lindeman, 2000). Of the 135 specimens from other portions of the Colorado drainage, nine males and four females exceeded the maximum values for PL recorded in the South Llano River. The largest specimens of each sex were from the San Saba River in Menard County (SMBU 17357, a male, 95 mm PL; TCWC 62676, a female, 180 mm PL) and exceeded the next largest specimens of their respective genders by 7 and 10 mm, respectively. (The female was previously reported as record size at 188 mm PL by Kizirian *et al.*, 1990, whose measurement was likely of maximum, rather than midline, PL.) The remaining larger specimens were from sites along or adjoining the mainstem Colorado River ranging from Concho County downstream to LaGrande County (eight males ranging in PL from 80–88 mm), the Concho River drainage in Concho and Tom Green counties (two females, 168 and 170 mm PL) and an unknown locality (one female, 165 mm PL). Texas river cooters (*Pseudemys texana*) in the South Llano River are similarly smaller than conspecifics from other localities in Texas (Lindeman, unpubl. data). Further research will be necessary to determine the ecological or evolutionary forces responsible for smaller body sizes in South Llano River turtle populations.

*Acknowledgments.*—I thank the staff of the Texas Tech Center at Junction for their generous hospitality. For assistance in the field I thank T. Allen, L. Arkwright, D. Edwards, J. Lovell and L. Lovell. Radiographs were kindly provided by C. Skaggs and the Kimble County Hospital. Access to the East Johnson Fork site was courtesy of L. Densmore and the Froneberger family. I also thank D. Lynch and B. Brown for access to museum specimens and W. Gibbons and J. Greene for the loan of a cast saw to assist in dissections. The manuscript was reviewed prior to submission by D. Moll. Research was partly financed by a Chelonian Research Foundation Linnaeus Fund Turtle Research Award.

#### LITERATURE CITED

- BROOKS, R. J., M. A. KRAWCHUK, C. STEVENS AND N. KOPER. 1997. Testing the precision and accuracy of age estimation using lines in scutes of *Chelydra serpentina* and *Chrysemys picta*. *J. Herpetol.*, **31**:521–529.
- CAGLE, F. R. 1939. A system of marking turtles for future identification. *Copeia*, **1939**:170–173.
- . 1952. The status of the turtles *Graptemys pulchra* Baur and *Graptemys barbouri* Carr and Marchand, with notes on their natural history. *Copeia*, **1952**:223–234.
- . 1953. The status of the turtle *Graptemys oculifera* (Baur). *Zoologica*, **38**:137–144.
- CLARK, P. J., M. A. EWERT AND C. E. NELSON. 2001. Physical apertures as constraints on egg size and shape in the common musk turtle, *Sternotherus odoratus*. *Funct. Ecol.*, **15**:70–77.
- CONGDON, J. D. AND J. W. GIBBONS. 1987. Morphological constraint on egg size: a challenge to optimal egg size theory? *Proc. Natl. Acad. Sci. USA*, **84**:4145–4147.

- AND R. C. VAN LOBEN SELS. 1993. Relationships of reproductive traits and body size with attainment of sexual maturity and age in Blanding's turtles (*Emydoidea blandingi*). *Journal of Evolutionary Biology*, **6**:547–557.
- ERNST, C. H., J. E. LOVICH AND R. W. BARBOUR. 1994. Turtles of the United States and Canada. Smithsonian Institution Press, Washington, D.C. 578 p.
- EWERT, M. A. AND D. R. JACKSON. 1994. Nesting ecology of the alligator snapping turtle (*Macrochelys temminckii*) along the lower Apalachicola River, Florida. Unpubl. report to the Nongame Wildlife Program, Florida Game and Fresh Water Fish Commission.
- AND J. M. LEGLER. 1978. Hormonal induction of oviposition in turtles. *Herpetologica*, **34**:314–318.
- GERMANO, D. J. 1994. Growth and age at maturity of North American tortoises in relation to regional climates. *Can. J. Zool.*, **72**:918–931.
- AND R. B. BURY. 1998. Age determination in turtles: evidence of annual deposition of scute rings. *Chelonian Conserv. Biol.*, **3**:123–132.
- GIBBONS, J. W. 1967. Variation in growth rates in three populations of the painted turtle, *Chrysemys picta*. *Herpetologica*, **23**:296–303.
- AND D. W. TINKLE. 1969. Reproductive variation between turtle populations in a single geographic region. *Ecology*, **50**:340–341.
- AND J. L. GREENE. 1979. X-ray photography: a technique to determine reproductive patterns of freshwater turtles. *Herpetologica*, **35**:86–89.
- AND J. E. LOVICH. 1990. Sexual dimorphism in turtles with emphasis on the slider turtle (*Trachemys scripta*). *Herpetol. Monogr.*, **4**:1–29.
- GRAHAM, T. E. AND P. J. PETOKAS. 1989. Correcting for magnification when taking measurements directly from radiographs. *Herpetol. Rev.*, **20**:46–47.
- HORNE, B. D., R. J. BRAUMAN, M. J. C. MOORE AND R. A. SEIGEL. 2003. Reproductive and nesting ecology of the yellow-blotched map turtle, *Graptemys flavimaculata*: implications for conservation and management. *Copeia*, **2003**:729–738.
- IVERSON, J. G. AND G. R. SMITH. 1993. Reproductive ecology of the painted turtle (*Chrysemys picta*) in the Nebraska sandhills and across its range. *Copeia*, **1993**:1–21.
- JONES, R. L. AND P. D. HARTFIELD. 1995. Population size and growth in the turtle *Graptemys oculifera*. *J. Herpetol.*, **29**:426–436.
- KING, R. B. 2000. Analyzing the relationship between clutch size and female body size in reptiles. *J. Herpetol.*, **34**:148–150.
- KIZIRIAN, D. A., W. K. KING AND J. R. DIXON. 1990. *Graptemys versa* (Texas map turtle). Size maximum and diet. *Herpetol. Rev.*, **21**:60.
- KNIGHT, W. 1968. Asymptotic growth: an example of nonsense disguised as mathematics. *J. Fish. Res. Bd. Canada*, **25**:1303–1307.
- KUCHLING, G. 1999. The reproductive biology of the Chelonia. Springer-Verlag, Berlin. 223 p.
- LAHANAS, P. N. 1982. Aspects of the life history of the southern black-knobbed sawback, *Graptemys nigrinoda delticola* Folkerts and Mount. Unpubl. M.S. Thesis, Auburn Univ., Auburn, Alabama.
- LINDEMAN, P. V. 1996. Comparative life history of painted turtles (*Chrysemys picta*) in two habitats in the inland Pacific Northwest. *Copeia*, **1996**:114–130.
- . 1997. Contributions toward improvement of model fit in nonlinear regression modelling of turtle growth. *Herpetologica*, **53**:179–191.
- . 1999. Growth curves for *Graptemys*, with a comparison to other emydid turtles. *Am. Midl. Nat.*, **142**:141–151.
- . 2000. Evolution of the head and alveolar surfaces in map turtles (Testudines: Emydidae: *Graptemys*). *Biol. J. Linn. Soc.*, **69**:549–576.
- . 2005. Diet of the Texas map turtle (*Graptemys versa*): relationship to sexually-dimorphic trophic morphology and changes over five decades as influenced by an invasive mollusk. *Chelonian Conserv. Biol.*, **4**: In press.
- LOVICH, J. E. AND J. W. GIBBONS. 1992. A review of techniques for quantifying sexual size dimorphism. *Growth Devel. Aging*, **56**:269–281.
- MACCULLOCH, R. D. AND D. M. GORDON. 1978. A simple trap for basking turtles. *Herpetol. Rev.*, **9**:133.

- MCKINNEY, J. M. 1987. *Graptemys versa* (Texas map turtle). Maximum size. *Herpetol. Rev.*, **18**:17.
- MOLL, D. 1976. Environmental influence on growth rate in the Ouachita map turtle, *Graptemys pseudogeographica ouachitensis*. *Herpetologica*, **32**:439–443.
- MOLL, E. O. AND J. M. LEGLER. 1971. The life history of a Neotropical slider turtle, *Pseudemys scripta* (Schoepff), in Panama. *Bull. Los Angeles Co. Mus. Nat. Hist., Sci.*, **11**:1–102.
- RICHARDS, F. J. 1959. A flexible growth function for empirical use. *J. Exp. Bot.*, **10**:290–300.
- ROWE, J. W. 1994. Egg size and shape variation within and among Nebraskan painted turtle (*Chrysemys picta bellii*) populations: relationships to clutch and maternal body size. *Copeia*, **1994**:1034–1040.
- SCHOENER, T. W. AND A. SCHOENER. 1978. Estimating and interpreting body-size growth in some *Anolis* lizards. *Copeia*, **1978**:390–405.
- SHEALY, R. M. 1976. The natural history of the Alabama map turtle, *Graptemys pulchra* Baur, in Alabama. *Bull. Florida St. Mus., Biol. Sci.*, **21**:47–111.
- STAMPS, J. AND V. V. KRISHNAN. 1997. Sexual bimaturism and sexual size dimorphism in animals with asymptotic growth after maturity. *Evolutionary Ecology*, **11**:21–39.
- TUCKER, J. K., R. S. FUNK, AND G. L. PAUKSTIS. 1978. The adaptive significance of egg morphology in two turtles (*Chrysemys picta* and *Terrapene carolina*). *Bull. Maryland Herpetol. Soc.*, **14**:10–22.
- VOGT, R. C. 1980a. Natural history of the map turtles *Graptemys pseudogeographica* and *G. ouachitensis* in Wisconsin. *Tulane Stud. Zool. Bot.*, **22**:17–48.
- . 1980b. New methods for trapping aquatic turtles. *Copeia*, **1980**:368–371.
- . 1981. *Graptemys versa*. *Cat. Amer. Amph. Rept.*, **280**:1–2.
- WAHLQUIST, H. AND G. W. FOLKERTS. 1973. Eggs and hatchlings of Barbour's map turtle, *Graptemys barbouri* (Carr and Marchand). *Herpetologica*, **29**:236–237.
- WHITE, D., JR. AND D. MOLL. 1991. Clutch size and annual reproductive potential of the turtle *Graptemys geographica* in a Missouri stream. *J. Herpetol.*, **25**:493–494.
- WILSON, D. S., C. R. TRACY AND C. R. TRACY. 2003. Estimating age of turtles from growth rings: a critical evaluation of the technique. *Herpetologica.*, **59**:178–194.