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Reproductive Ecology of the Concho Water Snake, *Nerodia harteri paucimaculata*

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The reproductive biology of the Concho water snake (*Nerodia harteri paucimaculata*) was studied from 1988 to 1992 in central Texas. Minimum snout–vent lengths (SVL) at maturity were 380 mm in males and 460 mm in females. Mating occurred primarily in late April and early May, although we observed some evidence of fall mating. Gestation was approximately three months. Parturition occurred predominantly in mid-August, ranging from 29 July to 22 September. Approximately 85% (range 79.5–88.8) of adult females were gravid each year with the proportion of reproductive females varying as a function of body size. Litter size averaged 11.1 (range 4–29) and varied both among and within study sites. Maternal SVL was correlated with litter size and mass but not offspring SVL or mass with litter size held constant. Litter size had no effect on offspring SVL or mass when female SVL was held constant. Relative clutch mass averaged 0.46 and was independent of female size. Mean offspring length and mass were 175 mm SVL and 3.8 g, respectively, showing no overall sexual differences. However, mean SVL was typically greater for females within litters.

L IFE-HISTORY theory attempts to characterize patterns of adaptive energy allocation to growth, maintenance, and reproduction (Emlen, 1984). Among squamate reptiles, reproductive characteristics are among the most important life-history variables (Tinkle et al., 1970; Dunham et al., 1988). Although reproduction is one of the best studied aspects of snake biology, attempts to summarize snake reproductive life-history patterns have revealed many gaps in the available data and indicated a need for documentation of life-history variation within and among populations (Dunham and Miles, 1985; Dunham et al., 1988; Seigel and Fitch, 1984). Multiyear studies targeting the effects of proximal factors on life-history variation (e.g. Brown, 1991; Seigel and Fitch, 1985; Seigel et al., 1995) are particularly needed.

The reproductive biology of some species in the genus *Nerodia* is relatively well known, including information on reproductive cycles (Aldridge, 1982; Mitchell and Zug, 1984; White et al., 1982), reproductive allocation (Semlitsch and Gibbons, 1978; Plummer, 1992), and endocrinology (Weil and Aldridge, 1981). However, reproductive data for *Nerodia harteri* are limited to litter size estimates from dissected females (McCallion, 1944; Williams, 1969; Rose, 1989) and two brief descriptions of litter characteristics from captive births (Conant, 1942; Carl, 1981). This paper provides baseline reproductive data for *N. h. paucimaculata*, evaluates variation in reproductive characteristics within and among captive-born litters, assesses reproductive investment among captive litters, and evaluates patterns of reproductive frequency in wild populations.

MATERIALS AND METHODS

We examined reproductive characteristics of snakes from 1988–1992 during a mark-recapture study in central Texas. Most data were gathered at Lake Ballinger, Lake Spence, and two locations on the Colorado River. The physical characteristics of these sites and the study region have been described previously (Greene et al., 1994). Because of the endangered status of the organism and the need to gather concurrent demographic data, all sampling was nondestructive. Snakes were captured by hand or with funnel traps. Snout–vent length (SVL), tail length, mass, and sex were recorded for all captured snakes. Female reproductive condition was assessed by palpation to determine the presence of enlarged follicles or embryos. Females were judged nonreproductive if captured during June or July with no discernible follicles or embryos; gravid females were never observed before mid-May. Litter size was estimated by counting palpated follicles. This method accurately depicts litter size in other species with similar body and clutch sizes (Seigel and Fitch, 1985; Farr and Gregory, 1991). Postparturient females were identified by their emaciated appearance (Fitch, 1987).

During 1990 and 1991, we sampled cloacal fluids and examined them for sperm to evaluate

sexual maturity in males and recent mating in females. Samples were obtained by gently massaging the abdomen just anterior to the cloaca and collecting expelled fluid on a microscope slide. Each slide was then air-dried, lightly stained with methylene blue, and examined under 100× magnification for the presence of sperm. These or similar methods have been previously used to detect sperm in both sexes of various snake species (Fitch, 1987; Hailey and Davies, 1987). Because we could not examine oviducts, the minimum SVLs for females containing cloacal sperm and/or determined to be gravid were used as a conservative estimate of female reproductive maturity. Both measures indicate similar minimum SVL sizes at maturation (see Results).

Annual estimates of litter size and the proportion of reproductive females were used to evaluate variation in fecundity. We examined relationships between litter size and female SVL with separate linear regressions calculated for each study site, using data from all years, and for separate years within sites. Comparison of litter sizes among samples was evaluated using analysis of covariance (ANCOVA) with female SVL as the covariate when sample sizes were sufficient. Variation in the annual proportion of adult females that reproduced was analyzed using a chi-square test of independence (Sokal and Rohlf, 1981).

A total of 27 gravid females (two in 1988, 10 in 1990, and 15 in 1991) was collected and held for a maximum of 40 days prior to parturition. Captive females were individually housed in plastic terraria (61 × 32 × 32 cm) and offered minnows twice weekly. Within 24 h of parturition, we measured SVL to ± 1.0 mm and weighed (± 0.1g) females and their offspring and determined the sex of the neonates by manual eversion of the hemipenes of males. Dates of parturition also were recorded. We calculated total litter mass (TLM) as the sum of the masses of live and stillborn neonates. Litter size of captive females was recorded as the sum of live neonates, dead neonates, and undeveloped eggs. This method was used because it better relates captive litters to palpation estimates and provides the least variable estimate of litter size (Farr and Gregory, 1991; Gregory et al., 1992). Relative clutch mass (RCM) was calculated by dividing TLM by postpartum female mass (Shine, 1980). Means, standard deviations, coefficients of variation (CV), and ranges of neonate SVL and mass were calculated for each litter. Relationships of female size parameters on litter characteristics were evaluated with partial correlation and linear regression analyses using
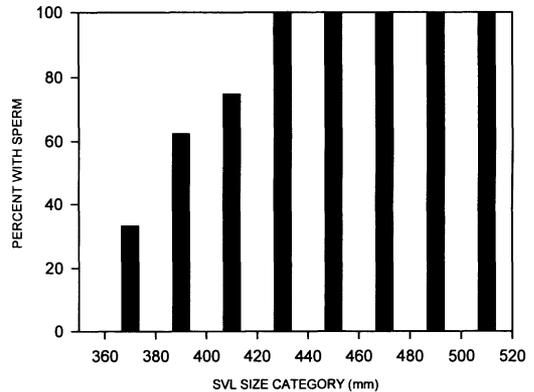

Fig. 1. Size at sexual maturity of male *Nerodia harteri paucimaculata*, sampled from April–November, as determined by the presence of cloacal sperm.

litter size and neonate size parameters as dependent variables.

Data were assessed for normality and heterogeneity of variance prior to testing. Reproductive variables were natural log-transformed where necessary to meet the assumptions of parametric statistics. Descriptive statistics for neonate size parameters were computed using STATISTIX software (Analytical Software, Saint Paul, MN, 1989, unpubl.). Inferential statistical procedures were performed using SAS (SAS Institute, Inc., Cary, NC, 1988, unpubl.).

RESULTS

Sexual maturity, mating, and parturition.—Of 132 males examined, motile sperm were present in cloacae at a minimum of 380 mm SVL, and all males above 420 mm SVL contained sperm (Fig. 1). Of 154 females examined, the minimum size containing cloacal sperm was 460 mm SVL.

The presence of sperm in the cloacal fluid of mature females (n = 126) indicated that reproductive activity occurred mostly during April and May and secondarily in October (Fig. 2). Only three females showed evidence of fall mating, and all were maturing individuals too small to breed the previous spring. No postparturient females showed evidence of fall mating.

Parturition dates of 27 captive-born litters ranged from 3 August to 22 September, with 92.5% of births occurring by 30 August. These dates correspond well with field observations; neonates appeared at most study sites by 10 August. The earliest evidence of parturition was a postpartum female observed on 27 July. The earliest neonates were observed in the field on 29 July. Assuming that mating approximates the
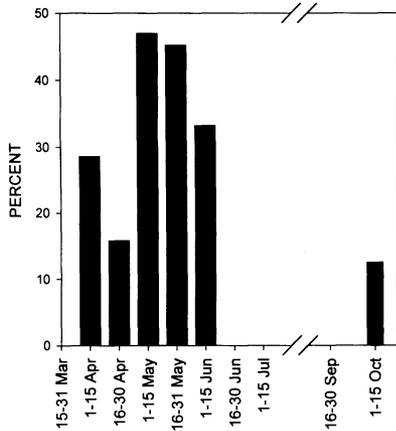
Fig. 2. Seasonal mating patterns as determined by the presence of active sperm in female cloacae based on 126 mature females sampled from mid March to mid-October during 1989–1990.
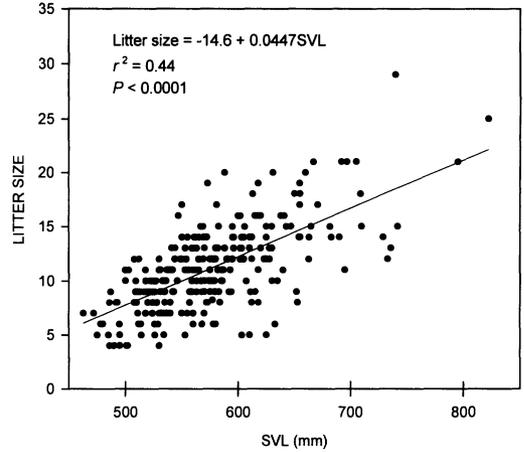

Fig. 3. Litter size as a function of SVL in 268 female *Nerofia harteri paucimaculata.*

timing of ovulation, as has been reported for other *Nerodia* (Aldridge, 1982; Bauman and Metter, 1977), the period between peak mating activity and mean of August parturition dates suggests a gestation period of 3–3.5 months.

Litter size and percent gravid.—Mean litter size in 268 females, determined by palpation (231 snakes), captive parturition (27 snakes), and dissection (10 snakes) during 1988–1992 was 11.1 ± 3.9, ranging from 4–29 young. A significant relationship exists between litter size and female SVL (F = 556.3, P < 0.0001, r^2 = 0.44; Fig. 3), increasing by one embryo for every 22 mm in SVL. Data on annual mean litter size estimates and female SVL for all sites combined are summarized in Table 1.

Data for female SVL and litter sizes at the four principle study sites are provided in Table 2. An among-site comparison demonstrated differences in female SVL/litter size relationships (ANCOVA homogeneity of slopes: F = 2.98, P = 0.034, df = 3, 119). Inspection of the individual regression equations showed the Lake Ballinger site to be the most deviant (Table 3). A

second ANCOVA excluding the Lake Ballinger site revealed no differences in slopes (F = 0.68, P = 0.508, df = 2, 100) or intercepts (F = 0.62, P = 0.538, df = 2, 100) among the remaining sites.

Evaluation of within-site female SVL/litter size relationships typically revealed annual variation. Female SVL/litter size regressions differed in slope between two successive years at Blair Ranch (ANCOVA F = 5.43, P = 0.025, df = 1, 45) and were marginally nonsignificant in slope (F = 3.60, P = 0.069, df = 1, 28) and intercepts (F = 4.14, P = 0.052) at the Freese Dam site. However, neither slopes (F = 0.27, P = 0.651, df = 1, 19) or intercepts (F = 0.30, P = 0.594) differed between two years at Lake Ballinger.

During 1988–1992, 85.3% of all adult females were gravid, varying from 79.5% to 88.8% (Table 4). The annual proportions of gravid and nongravid females were not significantly different (χ^2 = 3.68, P = 0.45, df = 4). Larger females were more likely to be gravid than smaller conspecifics (Table 5); the mean SVLs of gravid and nongravid females, 579.7 mm and 513.9

TABLE 1. COMPARISON OF ANNUAL LITTER SIZE AND FEMALE SIZE STATISTICS FOR ALL *Nerodia harteri paucimaculata* SAMPLED DURING 1988–1992. Means, standard deviations, and ranges (in parentheses) are given.

Year	Litter size	Female SVL	n
1988	10.76 ± 3.83 (6–21)	581.9 ± 45.20 (520–692)	29
1989	11.23 ± 3.72 (4–21)	595.9 ± 63.22 (486–742)	57
1990	9.96 ± 3.38 (4–21)	569.6 ± 61.97 (463–795)	54
1991	11.23 ± 4.38 (4–29)	570.9 ± 60.35 (472–822)	87
1992	11.82 ± 3.75 (4–21)	567.7 ± 51.11 (476–683)	45

TABLE 2. COMPARISON OF LITTER SIZE AND FEMALE SIZE STATISTICS FOR *Nerodia harteri paucimaculata* FROM FOUR SITES EXAMINED IN THIS STUDY. Data are listed as mean (top row), standard deviation and CV (middle row), and range (bottom row).

Location	Litter size	Female SVL (mm)	n
Freese Dam	12.17	569.7	29
	(2.82, 23.14)	(34.80, 6.11)	
	(7–17)	(509–625)	
Blair Ranch	10.09	565.5	53
	(3.41, 33.83)	(65.60, 11.60)	
	(4–21)	(463–795)	
Lake Ballinger	12.25	565.5	20
	(4.12, 33.70)	(47.67, 8.13)	
	(5–21)	(495–692)	
Lake Spence	10.32	557.6	25
	(4.10, 39.73)	(57.45, 10.30)	
	(4–21)	(472–695)	

mm, respectively, were significantly different ($t = 4.33$, df = 47, 269, $P < 0.0001$).

Neonate size, litter characteristics.—Reproductive data for 27 captive-born litters are summarized in Table 6. These litters produced 289 neonates, 27 stillborn embryos, and four infertile masses. Of 296 neonates and sexable stillborn embryos, 138 (46.6%) were male and 158 (53.4%) were female, providing a sex ratio not significantly different from 1:1 ($\chi^2 = 1.35$; $P > 0.10$).

Overall, neonates of each sex were similar in SVL (males: 173.5 ± 11.4, females: 174.9 ± 10.4, $t = 1.15$, df = 295, $P = 0.25$) and mass (males: 3.25 ± 0.56, females: 3.32 ± 0.55, $t = 1.03$, df = 295, $P = 0.30$). An ANCOVA assessing sexual differences in neonate length-weight relationships, using SVL as the covariate, showed no significant difference in slopes ($F = 0.01$, $P = 0.91$, df = 1, 293) or intercepts ($F = 0.05$, $P = 0.82$,

TABLE 4. ANNUAL NUMBERS AND PROPORTIONS OF ADULT FEMALE *Nerodia harteri paucimaculata* IN DIFFERENT REPRODUCTIVE CONDITIONS. Differences among years were not significant (Chi-square test of independence; $\chi^2 = 3.68$, $P = 0.45$, df = 4).

Year	n	Number of females	
		Gravid(%)	Nongravid(%)
1988	45	39(86.6)	6(13.4)
1989	79	66(83.5)	13(16.5)
1990	78	62(79.5)	16(20.5)
1991	116	103(88.8)	13(12.2)
1992	57	50(87.7)	7(12.3)
Total	375	320(85.3)	55(14.7)

df = 1, 293). However, neonate body size was sexually dimorphic within litters. Mean SVL was largest for females in a significant ($P = 0.003$, binomial test) proportion of litters and was significantly different from males (paired *t*-test, $t = 3.91$, $P = 0.0007$). Within-litter sexual differences in mean offspring mass were not significant (paired *t*-test, $t = 1.77$, $P = 0.09$).

Within-litter variation in SVL and mass of individual neonates was assessed using ranges and coefficients of variation. Neonate SVLs ranged from 141–201 mm with a mean of 174.0 and a mean CV of 2.8% (Fig. 4A). Neonate mass ranged from 1.5–4.1 g (mean = 3.8 g), with consistently greater variation than SVL (mean CV = 7.7%, Fig. 4B). Ranges and CVs of within-litter neonate SVL were not correlated to litter size or total litter mass.

Regression analyses evaluating the relationships between female size and litter characteristics indicated that larger females had larger ($P < 0.0001$) and heavier ($P < 0.0001$) litters. The mean litter mass for 27 captive females was 40.9 ± 15.6 ranging from 10.0–80.3. RCM values ranged from 0.31–0.663 with a mean of 0.46 ± 0.11. Variation in RCM was positively correlated

TABLE 3. SUMMARY OF REGRESSION ANALYSES OF SITE-SPECIFIC FEMALE SVL-LITTER SIZE RELATIONSHIPS.

Site	Year	y-intercept	Slope	r^2	P	n
Freese Dam	1991	27.9	−0.02	0.05	0.463	12
	1992	−10.7	0.038	0.30	0.018	18
	1991–1992	−11.5	0.042	0.26	0.004	30
Blair Ranch	1990	−13.4	0.04	0.83	<0.0001	20
	1991	−21.4	0.057	0.81	<0.0001	27
	1990–1992	−13.0	0.04	0.62	<0.0001	54
Lake Ballinger	1990	−34.7	0.097	0.74	<0.0001	10
	1992	−25.4	0.064	0.46	0.083	6
	1988–1992	−32.5	0.07	0.78	<0.0001	20
Lake Spence	1991–1992	−18.9	0.05	0.54	<0.0001	25

TABLE 5. PERCENTAGE OF ADULT FEMALE *Nerodia harteri paucimaculata* GRAVID BY SIZE CLASS, ALL YEARS COMBINED.

SVL size class (mm)	% Gravid	n
460–500	46.5	43
500–540	86.1	75
540–580	92.3	91
580–620	97.0	66
620–660	94.6	37
660–820	91.4	33

TABLE 6. SUMMARY OF REPRODUCTIVE DATA FOR 27 CAPTIVE FEMALE *Nerodia harteri paucimaculata*. Means, standard deviations, and ranges are given.

	Mean ± SD	Range	n
Female SVL	596.1 ± 73.7	509–822	27
Female mass	88.7 ± 43.5	44–258	26
Litter size	12.2 ± 4.5	7–25	27
Neonate SVL	174.3 ± 10.7	141–195	27
Neonate mass	3.8 ± 0.54	1.5–4.8	27
TLM	10.9 ± 15.6	18.8–80.3	27
RCM	0.47 ± 0.11	0.31–0.66	26

to litter mass ($r^2 = 42.3$, $P < 0.0001$) but not female SVL ($r^2 = 0.08$, $P = 0.151$) or female mass ($r^2 = 0.0$, $P > 1.0$). However, neonate SVL and mass were generally unrelated to female SVL and mass, although the influence of female SVL on neonate SVL approached significance ($P = 0.062$).

Because linear regression does not account for the effects of confounding variables, we reanalyzed the relationships between neonate size, female size, and litter size using partial correlation. This analysis indicated that litter size was affected by female SVL ($r = 0.56$, $P < 0.009$). Neither female SVL or litter size influenced neonate SVL or mass when other variables were held constant. However, the relationship between female postpartum mass and neonate SVL approached significance ($P < 0.065$).

DISCUSSION

Reproduction in *N. h. paucimaculata* is typical of temperate *Nerodia* with a spring mating period followed by summer parturition (Fitch, 1970). Our observations concur with studies of other temperate *Nerodia* that demonstrate spring vitellogenesis with ovulation closely following the mating period (Betz, 1963; Bauman and Metter, 1977; White et al., 1982). Males reached sexual maturity the summer following their birth. Although the spermatogenic cycle is unknown, this pattern fits an aestival spermatogenic cycle (Saint Girons, 1982) described in other *Nerodia* (Bauman and Metter, 1977; Mitchell and Zug, 1984). The observation that some mating activity occurs in the fall, to our knowledge, has not been previously described in this genus (Fitch, 1970; Wright and Wright, 1957).

The mean litter size of 11 reported here is less than estimates of 14.5 (Rose, 1989) and 18.6 (Williams, 1969) obtained by follicle counts from dissected snakes. However, actual clutch size is usually less than the total number of vitellogenic follicles available for ovulation (Betz, 1963; Shine, 1977). Ford and Karges (1987) re

ported a mean reduction of five follicles following ovulation in *Thamnophis marcianus*, a species similar in size to *N. h. paucimaculata*.

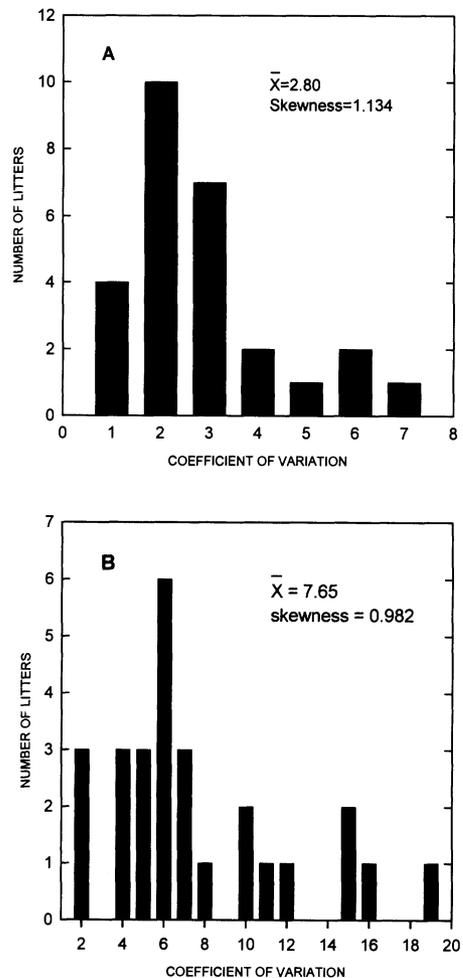The regression of litter size on female SVL was significant despite variation in part due to

Fig. 4. Within-litter variation in neonate SVL (A) and mass (B) of 27 captive-born litters.

site-specific differences in female size-litter size relationships. Female SVL was typically a stronger predictor of litter size within individual sites. Gregory and Larson (1993) observed that high intrapopulational relationships between female SVL and litter size in *Thamnophis sirtalis* were obscured when the data were pooled. We also found annual differences in female SVL-litter size relationships within sites. Although female SVL explained over 80% of the variance in litter size in each of two successive years at Blair Ranch, annual relationships between these variables were different, reducing explained variation in litter size when the data were combined (Table 3). As noted by Gregory and Larson (1993), future descriptions of snake reproductive characteristics should consider intersite variation.

A potential basis for site-specific differences in reproductive characteristics in *N. h. paucimaculata* was differences in food resources among lake and river systems (Greene, 1993; Greene et al, 1994). Ford and Seigel (1989) showed that litter size increases with food consumption in *Thamnophis marcianus* supporting various field studies that have tied prey availability to changes in litter size (Andren, 1982; Andren and Nilson, 1983; Seigel and Fitch, 1985).

The timing of parturition in *N. h. paucimaculata* may influence neonate foraging success. Scott et al. (1989) reported that young *N. harteri* occupied riffle habitats which provided substantial foraging opportunities. Juvenile *N. h. paucimaculata* consume riffle-dwelling minnows, particularly the red shiner (*Notropis lutrensis*) and bullhead minnow (*Pimephales vigilax*; Greene et al., 1994), which achieve peak population levels when water levels are lowest in late summer (Parker, 1964; Farringer et al., 1979). The simultaneous occurrence of low water levels, maximal prey numbers, high ambient temperatures, and parturition should enhance the foraging success and survival of neonates. In fact, neonates born early in August may nearly double in body size prior to hibernation (Greene, 1993). The timing of parturition in relation to prey availability may hold substantial adaptive value given the importance of neonate foraging success on first year survival in snakes (Parker and Plummer, 1987; Volkl, 1989). Early parturition may also be selectively advantageous to adult females by increasing postpartum foraging time to allow greater body mass recovery prior to hibernation.

Frequency of reproduction, as measured by the annual proportion of breeding females, is high in *N. h. paucimaculata* (85%) as has been reported in other *Nerodia* (Seigel and Ford, 1987). Reproductive frequency also varied among size categories of adult females with smaller individuals exhibiting a lower probability of reproduction. Some of this variation may undoubtedly be explained by individual variation in size at sexual maturity among females. However, Blem (1982) reported a similar phenomenon in *Agkistrodon piscivorus* and suggested that reproductive frequency may vary according to the size or age structure of a given population. Although total energy allocation to reproduction in female snakes is usually positively correlated to body size (Fitch, 1970; Shine, 1980), patterns of reproductive investment per offspring often vary among species. We found that large female *N. h. paucimaculata* produced significantly larger and heavier litters. However, neonate SVL was not correlated to female SVL or mass, even with litter size held constant. These results indicate that larger females allocated additional energy into more, rather than larger, offspring, supporting the predictions of optimal offspring size models (Smith and Fretwell, 1974; Stewart, 1979). Our data are consistent with reproductive investment patterns reported for *Storeria occipitomaculata* (Brodie and Ducey, 1989) and *Thamnophis butleri* (Ford and Killebrew, 1983) but in contrast to *T. marcianus* (Ford and Karges, 1987) and *N. rhombifer* (Plummer, 1992), where maternal size and neonate size were significantly correlated. We also observed no trade-off between offspring size and litter size in *N. h. paucimaculata*, affirming the results of Plummer (1992) for *N. rhombifer* but contrasting with Ford and Seigel (1989) who reported a negative effect of litter size on offspring size in three species of oviparous snakes.

We observed significant within-litter sexual size dimorphism in neonates with females exceeding males in SVL. Similarly, neonate *Thamnophis sirtalis* exhibit sexual dimorphism in head size due to inhibitory effects on growth by androgens in males (Shine and Crews, 1988). In contrast, Seigel (1992) reported males to be longer than female siblings in *Regina grahami*. These and other recent studies (e.g., Charland, 1988) suggest that sexual size differences in neonate snakes may be more common than previously thought.

We observed a higher mean RCM (0.466) than has been previously reported in *Nerodia*. Barron (1997) reported means for multiple years and study sites ranging from 0.28 to 0.43 (estimated from figure) in *N. sipedon*. We also recalculated RCM using both female mass and litter mass in the denominator for comparison

with other studies, yielding a mean value of 0.314. This estimate exceeded all mean values (range 0.112–0.289) for *Nerodia* reported in a literature review of snake RCM (Seigel and Fitch, 1984) and a subsequent report of 0.300 by Plummer (1992) for *N. rhombifer*. The RCM value of 0.164, reported by Seigel and Fitch (1984) for *N. harteri*, was calculated from a single large female with a very small litter (Conant, 1942) and does not seem to reflect typical female reproductive effort in this species. Our data indicated RCM to be independent of maternal SVL, which is typical of snakes in general (Seigel et al., 1986).

Values of fecundity, RCM, and frequency of reproduction suggest that female reproductive expenditure is relatively high in *N. h. paucimaculata*. Theoretical models predict that levels of reproductive expenditure in iteroparous organisms should balance trade-offs between current and future reproductive effort (Stearns, 1976). In reptiles, these trade-offs are likely to involve fecundity and survival (Shine, 1980; Shine and Schwarzkopf, 1992). Recent evolutionary models of reptilian reproductive effort suggest that current reproductive effort should be maximized when the potential of future fecundity is low (Shine and Schwarzkopf, 1992). Demographic data for *N. h. paucimaculata* suggest survival rates of < 5% to age five for both sexes (Mueller, 1990; Whiting, 1993). Because females do not reproduce until age two or three (Greene, 1993), their number of reproductive opportunities is limited. Thus, high reproductive expenditure may be required to offset low annual survivorship in *N. h. paucimaculata*.

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