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Relationships among Mothers, Litters, and Neonates in Diamondback Water Snakes (*Nerodia rhombifer*)

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## SHORTER CONTRIBUTIONS: HERPETOLOGY

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**RELATIONSHIPS AMONG MOTHERS, LITTERS, AND NEONATES IN DIAMONDBACK WATER SNAKES (*NERODIA RHOMBIFER*).**—This paper provides reproductive information from a single population of *Nerodia rhombifer* which contributes to the understanding of the allocation of energy in the life history of the species. Previous investigators have reported on various anecdotal aspects of reproduction in *N. rhombifer* (summaries in Wright and Wright, 1957; Fitch, 1970; Ernst and Barbour, 1989), but data on the relationships among sizes of mothers, litters, and neonates are lacking.

Female *N. rhombifer* were collected at the Joe T. Hogan State Fish Hatchery at Lonoke, Arkansas, in late July 1990. Twenty-two gravid snakes were maintained in the laboratory in separate aquaria provisioned with drinking water, but not food, until parturition. Although reducing food intake is common in gravid reptiles, including many snakes (Shine, 1980), it is not specifically known whether gravid *N. rhombifer* normally reduce food intake. After parturition, mothers were measured (SVL, cm), weighed (g), and palpated to ensure that all embryos had been born. Neonates were measured (SVL, mm), weighed (g), and sexed by probing the base of the tail for hemipenes. Data were log-transformed whenever necessary to meet the assumptions of normality and homoscedasticity. Sex ratio is the proportion of males in a litter. To facilitate comparisons of relative clutch mass (RCM) in *N. rhombifer* to published values of RCM for other snakes (Seigel and Fitch, 1984), I followed Seigel and Fitch (1984) in the calculation of RCM (i.e., the mass of the litter divided by the postpartum mass of the mother plus the mass of the litter). However, for hypothesis testing, RCM was calculated by dividing the mass of the litter by the postpartum mass of the mother to avoid potential statistical problems associated with having litter mass in both the numerator and denominator.

No snake <79 cm SVL was gravid; all snakes >85 cm were gravid as were five of nine snakes (56%) between 79 cm and 85 cm SVL. Parturition occurred from 24 Aug. to 4 Oct., with 20 of 21 births (>95%) occurring before 15

Sept. One postpartum female (120.5 cm) was found by palpating to contain more embryos than the 11 that were born on 31 Aug. She was retained and fed in the laboratory until she died on 11 Jan. 1991. Subsequent dissection revealed 10 apparently normal, fully formed dead embryos within her oviducts. Data from this female were not used in the present analysis.

Reproductive characteristics of mothers and neonates are summarized in Table 1. Female neonates were slightly heavier than males (males =  $10.16 \pm 0.104$ , females =  $10.49 \pm 0.102$  g;  $t_{df=484} = -2.22$ ,  $P < 0.05$ ). Male neonates did not differ in SVL from females (males =  $246.5 \pm 0.84$ , females =  $245.8 \pm 0.84$  mm;  $t_{df=484} = 0.61$ ,  $P > 0.50$ ), but males had longer tails (males =  $77.2 \pm 0.31$ , females =  $68.8 \pm 0.28$  mm;  $t_{df=484} = 20.29$ ,  $P < 0.001$ ) and, as a consequence, had longer total lengths (males =  $323.7 \pm 1.11$ , females =  $314.5 \pm 1.07$  mm;  $t_{df=484} = 5.94$ ,  $P < 0.001$ ). Sex ratio among litters ranged from 0.27–0.69 and was independent of maternal size (for SVL,  $r = 0.216$ ,  $P > 0.30$ ,  $n = 21$ ; for mass,  $r = 0.166$ ,  $P > 0.40$ ,  $n = 21$ ), in contrast to that recently reported for the natricine *Thamnophis sirtalis* (Dunlap and Lang, 1990).

As is usually true in snakes (Seigel and Ford, 1987), maternal size had significant effects on most reproductive characteristics in *N. rhombifer*. Specifically, longer and heavier mothers produced larger and heavier litters and longer and heavier neonates (Table 2).

The proportion of variation in litter size explained by regressing litter size on maternal SVL ( $r^2 = 0.73$ ) was high relative to that found in many studies of snakes (Seigel and Ford, 1987). *Nerodia rhombifer* feed frequently in the high resource environment of the Lonoke fish hatchery ponds (Plummer and Goy, 1984). Field observations on *Vipera* (Andren and Nilson, 1983) and laboratory experiments on *Thamnophis* (Ford and Seigel, 1989b) suggest higher correlations of litter size with maternal SVL under high resource conditions.

Mean RCM (0.300) was similar to that calculated by Seigel and Fitch (1984) for *N. rhombifer* (0.289) and to that for 22 species of viviparous colubrids (0.295). In snakes, RCM is typically independent of SVL (Seigel et al., 1986). Statistically, this pattern holds true for *N. rhombifer*. However, the relationship was suf-

TABLE 1. REPRODUCTIVE CHARACTERISTICS OF MOTHERS AND NEONATES OF *Nerodia rhombifer*. Masses are expressed in g. Mass of mothers is postpartum. Sex ratio is the proportion of male neonates in a litter. Relative clutch mass (RCM) is litter mass/(mother's body mass + litter mass).

	Mothers (n = 21)		Litters (n = 21)				Neonates (n = 486)	
	SVL (cm)	Mass	Number	Mass	RCM	Sex ratio	SVL (mm)	Mass
Mean	90.8	553.4	23.1	245.2	0.300	0.482	246.1	10.3
SE	2.1	38.3	2.1	25.9	0.013	0.021	0.6	0.1
Minimum	78.5	326.4	12.0	108.4	0.195	0.267	180.0	3.2
Maximum	109.0	991.3	48.0	546.3	0.408	0.688	285.0	13.6

ficiently close to be viewed as marginally significant ( $r = 0.414$ ;  $P = 0.06$ ,  $n = 21$ ).

Based on a model of an optimal relationship between size and number of offspring, Stewart (1979) made three testable predictions regarding the relationships of maternal size, litter size, and neonate size in live-bearing lizards: (1) In populations where the relationship between maternal size and litter size has a steep slope, neonate size should vary little among females; (2) In populations with a low litter size, maternal size and neonate size should be positively related; and (3) Litter size and neonate size should be negatively related within a population. I tested predictions 1 and 3 and found neither to be true for *N. rhombifer*. The relationship between litter size and maternal size in *N. rhombifer* was characteristically steep as found in most natricines. The slope was the third highest (0.85), ranking slightly below the natricines *N. taxipilota* (0.93) and *Storeria occipitomaculata* (0.86), among all snakes reported by Seigel and Ford (1987). A slope of 0.73 ( $r = 0.94$ ,  $P < 0.001$ ,  $n = 20$ ) calculated from the data of Betz (1963) for *N. rhombifer* from Missouri and Louisiana further supports this relationship. Despite the steep relationship, in *N. rhombifer* there is significant variation in neonate size which is positively related to maternal size (Table 2).

To examine Stewart's (1979) third prediction, the negative relationship between litter size and neonate size, I used partial correlation

analysis to control for the effects of maternal SVL. Partial correlation coefficients showed that neither neonate SVL ( $r = -0.030$ ;  $P = 0.45$ ,  $n = 21$ , one-tailed) nor neonate mass ( $r = -0.156$ ;  $P = 0.26$ ,  $n = 21$ , one-tailed) decreased with larger litters. For the more general question of whether any relationships exist between litter size and neonate size, the analysis clearly shows that the probability is high that there are none (SVL,  $P = 0.90$ ; mass,  $P = 0.52$ ). The lack of a negative relationship between litter size and offspring size parallels results reported by many investigators (summary in Ford and Seigel, 1989a) but contrasts those of Ford and Seigel (1989a) for three species of oviparous snakes. Ford and Seigel (1989a) argued that the reason many investigators failed to find the predicted negative relationship between clutch size and offspring size in reptiles may have resulted from the use of inappropriate statistical techniques (simple correlation) which failed to control for the effects of maternal size on reproductive characteristics. Indeed, my results of the relationship between litter size and neonate SVL, as determined from simple correlation ( $r = 0.47$ ,  $P < 0.05$ ,  $n = 21$ ) and from partial correlation ( $r = -0.03$ ,  $P > 0.90$ ,  $n = 21$ ), are in contrast.

These results, and recent results of others (e.g., Brodie and Ducey, 1989; Stewart, 1989; Stewart et al., 1990), suggest that the relationships of female body size, clutch size, and offspring size in snakes are variable among species

TABLE 2. PRODUCT-MOMENT CORRELATION COEFFICIENTS AMONG VARIOUS CHARACTERISTICS OF MOTHERS, LITTERS, AND NEONATES IN *Nerodia rhombifer*. Significance levels are indicated by \* ( $P < 0.05$ ), \*\* ( $P < 0.01$ ), and \*\*\* ( $P < 0.001$ ).

Mother	Mass of mother	Number in litter	Mass of litter	Neonate SVL	Neonate mass
SVL	0.899***	0.848***	0.869***	0.558**	0.492*
Mass	—	0.703***	0.775***	0.679***	0.599**

and still are not clearly understood (Ford and Seigel, 1989a). A potential confounding factor in these analyses that has not been considered by most researchers is the possible placental enhancement of neonate size over and above that provided by vitellogenesis (Stewart, 1989). However, such enhancement does not occur in *N. rhombifer* (Stewart and Castillo, 1984; Stewart, 1989). In Lonoke *N. rhombifer*, it appears that large females may have greater RCMs which is allocated to both larger litters and larger neonates. There does not appear to be a trade-off between litter size and neonate size as predicted by optimal offspring size models (e.g., Smith and Fretwell, 1974; Brockelman, 1975). Furthermore, when maternal SVL is held constant, partial correlation coefficients reveal that greater maternal mass yields longer ( $r = 0.49$ ,  $P < 0.05$ ,  $n = 21$ ) and heavier ( $r = 0.41$ ,  $P < 0.05$ ,  $n = 21$ ) neonates, suggesting possible phenotypic plasticity in these characteristics (Ford and Seigel, 1989b).

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SEX RATIO AND SEX-SPECIFIC GROWTH RATES OF IMMATURE GREEN TURTLES, *CHELONIA MYDAS*, IN THE SOUTHERN BAHAMAS.—Increasing our understanding of