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### Sexual Dimorphism and Female Reproduction in a Viviparous Snake, *Elaphe rufodorsata*

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*Elaphe rufodorsata* (Colubridae) is a viviparous water snake that is widely distributed in northeastern China; it also occurs in Russia (Primorsky Territory) and Korea (Zhao and Adler, 1993). The Morphology, karyotype, and food habits of this species have been studied (Huang and Jin, 1990), but little information on reproduction is available other than incidental notes (also see Huang and Jin, 1990). In this study, we present data on the reproductive characteristics and sexual size dimorphism of *E. rufodorsata*.

Our field site was in Dinghai, the Zhoushan Islands, Zhejiang, East China. The habitat consisted of paddy fields for double-crop rice. In the Zhoushan Islands, such habitats usually support large populations of *Rana limncharis*, *Rana nigromaculata* and *Bufo gargarizans*. These habitats are used by *E. rufodorsata* and two other colubrid snakes, *Dinodon rufozonatum* and *Sinonatrix annularis*.

Our field work was conducted from April 1993 to June 1994. Snakes were collected by hand, and then transported to Hangzhou Normal College for data collection. We recorded snout-vent length (SVL) to 0.1 mm, tail length (TL) to 0.1 mm, and body mass to 0.1 g of each snake. Twenty four gravid females were maintained in the laboratory until parturition. The remaining snakes in our sample (38 females; 23 males) were dissected in the laboratory within 36 h of capture.

Gravid females were housed 2–3 to each glass cage (40 × 30 × 30 cm) of which one half of the bottom was filled with soil and the other half was filled with water. These snakes were allowed to feed freely on frogs and fish. Temperature in the laboratory environment varied from 24 to 38 °C. Females were housed individually prior to parturition. Neonates were collected within six hours of parturition, then weighed and measured. Relative clutch mass (RCM) was calculated by using the ratio of wet clutch mass to female total body mass, including the clutch (Vitt and Congdon, 1978; Vitt, 1981; Vitt and Price, 1982; Seigel and Fitch, 1984; Seigel et al., 1986).

The size and mass of yolked follicles and oviductal eggs were recorded for dissected female snakes. Females were considered mature if they contained yolked follicles or oviductal eggs. Litter size was esti-

mated by counting the number of yolked follicles, oviductal eggs, or neonates (including infertile eggs oviposited simultaneously; eggs oviposited without embryo sacs were considered infertile). The size and mass of testes were recorded for dissected male snakes. Males were considered mature if their testes were turgid during the breeding season. The fat body mass and liver mass were recorded for all dissected snakes, and data were presented elsewhere (Ji, submitted).

To determine sexual dimorphism in TL. TLs of females and males were compared by analysis of covariance (ANCOVA) with SVL as the covariate. A Student's *t* test was used to compare the difference in mean SVL between females and males in our sample. We used a partial correlation analysis to test the effect of clutch size on offspring size and the effect of female SVL on neonate mass.

Table 1 shows the average SVL and TL of snakes in our sample. Snout-vent length showed a statistically significant sexual size dimorphism favoring females ( $t = 7.67$ ,  $df = 83$ ,  $P < 0.01$ ), whereas TL showed statistically significant sexual size dimorphism favoring males (ANCOVA;  $F = 60.39$ ,  $df = 1, 83$ ,  $P < 0.001$ ).

Gravid females stopped feeding 7–10 d prior to parturition. Parturition occurred during 1–14 August 1993. Eighteen of the 24 clutches had infertile eggs, and the proportion of infertile eggs averaged 18.5% (range 0.0–61.5%). Based on live individuals, litter size averaged 14.3 (1 SE = 1.0, range 7–24,  $N = 24$ ), wet body mass of neonates averaged 2.5 g (1 SE = 0.1, range 1.7–4.1,  $N = 238$ ), and RCM averaged 0.334 (1 SE = 0.014, range 0.241–0.451,  $N = 24$ ). Females with larger SVLs had larger clutches ( $r = 0.65$ ,  $F = 39.71$ ,  $df = 1, 54$ ,  $P < 0.01$ ; Fig. 1) and heavier neonates ( $r = 0.63$ ,  $F = 11.31$ ,  $df = 1, 17$ ,  $P < 0.01$ ; Fig. 2). No significant correlation was found between RCM and female SVL ( $r = -0.13$ ,  $P > 0.05$ ). There was a significant positive correlation between SVL and neonate mass when holding litter size constant ( $r = 0.55$ ,  $t = 2.66$ ,  $df = 16$ ,  $P < 0.05$ ). There was no significant correlation between litter size and neonate mass when holding female SVL constant ( $r = 0.10$ ,  $t = 0.39$ ,  $df = 16$ ,  $P > 0.05$ ).

Based on our dissected specimens, males were mature at 43.0 cm SVL, and females were mature at 48.0 cm SVL. The fact that no yolked follicles ( $\bar{x}$  length = 0.56 cm) were found in adult females ( $N = 7$ ) in late November and the presence of medium sized yolked follicles ( $\bar{x}$  length = 1.28 cm) in all adult females ( $N = 8$ ) in late April indicated that vitellogenesis began in late March when *E. rufodorsata* emerged from hibernation. All females of mature size ( $N = 19$ ) dissected in June contained oviductal eggs ( $\bar{x}$  length = 2.10 cm). Litter size of the dissected females averaged 11.2 (1 SE = 0.5, range 6–18,  $N = 32$ ).

Sexual size dimorphism has been described in many reptiles. Sexual dimorphism may be caused by sexual selection (Trivers, 1972, 1976) and other causes (Schoener, 1967; Dunham, 1981; Powell and Russell, 1985; Best and Paffenberger, 1987; Cooper and Vitt, 1989; Hedrick and Temeles, 1989; Anderson and Vitt, 1990). We are not aware of any accurate way to deter-

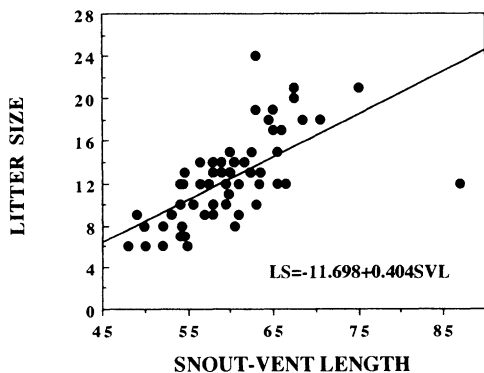
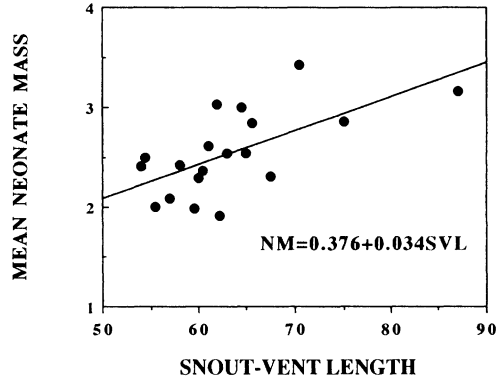
TABLE 1. Sexual dimorphism in body size and tail length of *Elaphe rufodorsata* in this study.

	Female		Male	
	Snout-vent length (cm)	Tail length (cm)	Snout-vent length (cm)	Tail length (cm)
Mean	60.2	10.7	48.6	11.2
N	62	62	23	23
1SE	0.8	0.1	0.9	0.2
Range	48.0–87.0	7.5–13.5	43.0–60.0	10.1–13.0

mine the proportion of sexual differences in body size or other morphological characters attributable to a specific selection pressure. Our data are not sufficient to explain the sexual size dimorphism seen in *E. rufodorsata*. However, selection should favor large body size in female *E. rufodorsata*, as our data indicate a female can increase her reproductive output through the production of more or heavier offspring by increasing body size.

In many reptile species, larger females allocate more energy to reproduction (Fitch, 1970; Shine, 1977). Larger female *E. rufodorsata* allocated more energy to reproduction by increasing clutch size as well as neonate mass. In our sample, only female size had a significant effect on neonate mass and clutch size did not. This finding is similar to those of Ford and Karges (1987) for the checkered garter snake, *Thamnophis marci*. However, our findings do not support the results of Ford and Seigel (1989) that showed clutch size was inversely related to off-spring size.

RCM is an important life history characteristic of reptiles and is apparently related to reproductive mode, foraging mode, and predator-escape strategy (Vitt and Congdon, 1978; Vitt and Price, 1982; Seigel and Ford, 1987). Seigel and Fitch (1984) and Seigel and Ford (1987) indicated that the RCM of viviparous snake species was significantly less than that of oviparous species. Theoretically, a viviparous species reduces mortality during gestation by remaining fairly mobile due to low RCM (Seigel and Ford, 1987). We found the RCM (0.334) of *E. rufodorsata* in our sample to be higher than the mean RCM (0.295) for the 22

FIG. 1. The relationship between litter size (LS) and SVL (cm) in adult female *Elaphe rufodorsata*.FIG. 2. The relationship between mean neonate mass (g) per clutch and SVL (cm) in adult female *Elaphe rufodorsata*.

populations of viviparous colubrid snakes reviewed by Seigel and Fitch (1984). This may be due to the lack of major predators (*Naja naja atra* and *Elaphe carinata*), higher food availability in paddy fields, and the foraging behavior of *E. rufodorsata*. However, additional data will need to be collected to substantiate these claims.

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### Calorimetric Analysis of Neonatal Water Snakes, *Nerodia sipedon*

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Models of life history evolution center on the trade-offs between current reproductive effort and the ex-

pectation of future reproduction, and between effort per offspring and offspring number (Roff, 1992). Generally, reproductive effort is estimated by the ratio of propagule mass to female mass (termed "relative clutch mass," or RCM), and effort per offspring is estimated by offspring mass. It is therefore interesting to determine the extent to which these estimates of effort truly reflect actual caloric investment by the female.

Analyses of caloric investment are scarce for squamate reptiles. Although several studies of caloric investment in lizards were published in the 1970s (Ballinger and Clark, 1973; Tinkle and Hadley, 1973, 1975; Vitt, 1974; Vitt and Ohmart, 1975; Congdon et al., 1978; Vitt, 1978), only one of these included caloric data for snakes (Vitt, 1978). In the latter case, data are presented for only one gravid female from each of four species (Vitt, 1978).

Most of the studies above focused primarily on the concordance of caloric estimates of total reproductive effort (calories per clutch/calories in soma) with wet-mass estimates (i.e. relative clutch mass: mass of clutch/mass of soma) in comparisons across species. The consensus was that the two ratios are highly correlated and result in essentially identical conclusions (Ballinger and Clark, 1973; Vitt, 1978). Additionally, caloric densities and percent water of both eggs and bodies (of adult females) were very similar among species (but see Tinkle and Hadley, 1975), prompting Vitt (1978) to propose general formulae for the linear conversion of wet-mass data to calories, applicable to both lizards and snakes. It may be that the striking concordance of wet mass and calories, even among species, has discouraged subsequent investigators from going to the trouble of either estimating or empirically determining actual caloric investment. This concordance of wet mass and calories would account for an apparent lack of published caloric estimates for squamates from 1978 to the present.

The current study adds caloric investment data from a lecithotrophic, livebearing snake, *Nerodia sipedon*, to the somewhat limited (especially with respect to snakes) data base above. The purpose of this study is twofold: (1) to describe the energetic and hydric content of neonatal *Nerodia sipedon* and compare these values with those published for other squamates; and (2) to examine the relationships between commonly used estimates of effort per offspring (i.e. offspring mass and length) and caloric measurements.

From 1990 to 1993, a four-year field study of reproductive ecology of the northern water snake, *Nerodia sipedon*, was performed in south-central Indiana. Each year, gravid females were collected in July and held in the lab until parturition in August. While in the lab, females were housed in plastic sweater boxes, and fed green frogs (*Rana clamitans*) and/or goldfish (*Carassius auratus*) weekly to satiety. Each female had fresh water available at all times. Within 24 h of birth, each maternal female was weighed to the nearest 5.0 g with a Pesola spring scale, and measured to the nearest 0.5 cm; each offspring was sexed, weighed to the nearest 0.001 g on a Sartorius electronic balance, and measured to the nearest 1.0 mm.

In 1992, all offspring from six females were measured, weighed, and immediately euthanized by freezing (Stewart et al., 1990). Random samples (in

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