



FEMALE REPRODUCTIVE OUTPUT AND NEONATE CHARACTERISTICS IN A VIVIPAROUS WATER SNAKE (*SINONATRIX ANNULARIS*)*

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Sinonatrix annularis (Colubridae) is a viviparous water snake that is endemic to China , and is widely distributed in the southern and eastern provinces of the country (Zhao *et al.* , 1993). However , except for few descriptive data on litter size and the timing of reproduction , female reproductive characteristics of the species are largely unknown . We carried out this study with a purpose to contribute the database that shows : (1) female reproductive output ; (2) the relationships among litter size , female size (snout-vent length , SVL) and neonate size ; (3) neonate characteristics .

1 Materials and Methods

Our field collection was conducted in late June 1997 in Dinghai , Zhoushan islands (30° 18' N , 122° 6' E) , Zhejiang , eastern China . The habitats consisted of paddy fields for double-crop rice . Such habitats usually support large populations of *Rana limnocharis* , *Rana nigromaculata* and *Bufo gargarizans* , and are also used by two other colubrid snakes , *Elaphe rufodorsata* and *Dinodon rufonotatum* (Ji *et al.* , 1997a ; 1997b) .

Snakes were collected by hand , and subsequently were transported to our laboratory in Hangzhou for data collection . All snakes were palpated to assess their repro-

ductive condition , and then were housed 2 ~ 3 to each terrarium (400 mm × 300 mm × 300 mm) of which the bottom was filled with water . The terraria were placed in the laboratory where snakes could be exposed to a natural light cycle and receive some direct sunlight . Temperatures in the room varied from 24 to 38 °C . Snakes were allowed to feed freely on fish (*Misgurnus anguillicaudatus*) . Pregnant females were housed individually a few days prior to parturition . We inspected the terraria twice daily , and more frequently when there was a sign of parturition , so that all neonates could be collected promptly . Pertinent body measurements of postpartum females and neonates include SVL , tail length , and body mass . We calculated relative clutch mass (RCM) using two methods (Ji *et al.* , 2000) : RCM₁ was calculated by dividing clutch mass by the female postpartum mass (Shine , 1992) , and RCM₂ by dividing clutch mass by total female (clutch plus body) mass (Seigel *et al.* , 1986) . Two pregnant females died and hence the related neonate data were not available for them .

After measuring all neonates were killed by freezing . These hatchlings were later thawed , dissected , and separated into carcass , yolk sac , and abdominal fat bodies . The three components of the hatchling were dried to con-

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stant mass in a ventilated oven at 65 °C , and then weighed.

The data on neonates were grouped by the clutch to avoid pseudo-duplications. We used regression statistics , partial correlation analysis , analysis of variance (ANOVA) and analysis of covariance (ANCOVA) to analyze data. All data were tested for normality (Kolmogorov-Smirnov test) and homogeneity of variance (F -max test) , and transformed when necessary to achieve the conditions for parametric tests. Significance level was set to $\alpha = 0.05$. Prior to testing for differences in adjusted means , the homogeneity of slopes was checked. Throughout this paper , values are presented as mean \pm standard error (SE).

2 Results

The smallest reproductive female in our sample was 486 mm SVL , and all females surpassing this size reproduced a single clutch per breeding season. Reproductive females ($n = 19$) averaged 629.4 mm ($SE = 20.2$, range = 486 ~ 771) SVL and 136.6 mm ($SE = 7.6$, range = 60 ~ 170) tail length. Parturition occurred between 30 August and 30 September. Litter size was positively correlated with female SVL ($r^2 = 0.647$, $F_{1,17} = 31.165$, $P < 0.0001$; Fig. 1 = , and averaged 11.7 ($SE = 0.8$, range = 6 ~ 18 , $n = 17$). There was no relationship between mean neonate mass and female SVL ($r^2 = 0.004$, $F_{1,15} = 0.064$, $P < 0.803$). RCM_1 and RCM_2 averaged 0.495 ($SE = 0.030$, range = 0.288 ~ 0.765 , $n = 17$) and 0.327 ($SE = 0.014$, range = 0.224 ~ 0.433 , $n = 17$), respectively. Both RCM_1 ($r_2 = 0.077$, $F_{1,15} = 1.248$, $P < 0.282$ = and RCM_2 ($r^2 = 0.096$, $F_{1,15} = 1.588$, $P < 0.227$) were independent of female SVL. A partial correlation analysis confirmed the positive relationship between litter size and female SVL ($r = 0.841$, $t = 5.817$, $df = 15$, $P < 0.0001$) and the absence of the relationship between neonate mass and female SVL ($r = -0.331$, $t = 1.313$, $df = 15$, $P = 0.209$). The analysis also showed that there was no relationship between litter size and neonate mass ($r = 0.354$, $t = 1.418$, $df = 15$, $P = 0.176$). When employing a partial correlation analysis to test the relationships among female SVL , female condition (as estimated using the residuals derived from the regress \log (female postpartum mass) on

\log (female SVL) ; van Damme *et al.* , 1992 , and litter size (\log transformed) , we again found a positive relationship between litter size and female SVL ($r = 0.824$, $t = 5.824$, $df = 17$, $P < 0.001$). The analysis also showed that there was no relationship between litter size and female condition ($r = 0.162$, $t = 0.658$, $df = 17$, $P = 0.519$).

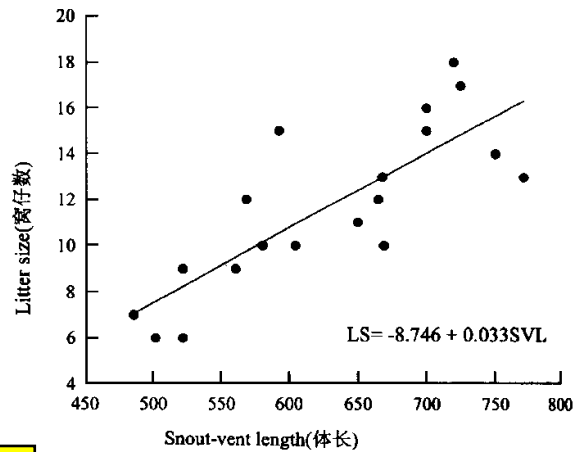


Fig. 1 The relationship between litter size (LS) and snout-vent length (SVL) (mm) in adult female *Sinonatrix annularis*

图 1 窝仔数与雌性赤链华游蛇体长 (mm) 之间的关系

Table 1 Neonate characteristics of *Sinonatrix annularis* ($n = 17$ clutches)

表 1 赤链华游蛇的初生幼体 ($n = 17$ 窝) 特征

	Mean	SE	Range
	平均值	标准误	范围
Body wet mass(体湿重 \bar{X} g)	4.37	0.16	3.50 ~ 5.93
Snout-vent length(头体长 \bar{X} mm)	171.0	1.9	158 ~ 189
Tail length(尾长 \bar{X} mm)	44.7	0.9	38.0 ~ 50.0
Body dry mass(体干重 \bar{X} g)	1.18	0.05	0.90 ~ 1.64
Carcass dry mass(躯干干重 \bar{X} g)	0.74	0.03	0.58 ~ 1.02
Yolk-sac dry mass(卵黄囊干重 \bar{X} g)	0.24	0.02	0.14 ~ 0.36
Fatbody dry mass(肪体干重 \bar{X} g)	0.21	0.01	0.15 ~ 0.29

Data on neonate characteristics are given in Table 1 . An ANCOVA with neonate SVL as the covariate showed significant between-individual variations in adjusted mean dry masses of carcass ($F_{16,106} = 28.092$, $P < 0.0001$) , fat bodies ($F_{16,106} = 8.056$, $P < 0.0001$) and yolk sac ($F_{16,106} = 15.157$, $P < 0.0001$). A partial correlation analysis on carcass dry mass , yolk sac dry mass , and fat-body dry mass showed that carcass dry mass was negatively correlated with residual yolk dry mass ($r = -0.916$, t

= 8.562, $df = 13$, $P < 0.0001$) and fatbody dry mass ($r = -0.557$, $t = 2.511$, $df = 13$, $P < 0.024$). The analysis also showed that residual yolk dry mass was independent of fatbody dry mass ($r = 0.178$, $t = 0.677$, $df = 13$, $P < 0.509$).

3 Discussion

As in many other reptiles (Fitch, 1970), larger female *S. annularis* allocated more energy for reproduction than did smaller ones. In our sample, only female size was the main determinant of litter size and neonate mass was not. This result is somewhat similar to that reported for some other viviparous snakes, e. g., *Thamnophis marcianus* (Ford *et al.*, 1987) and *Elaphe rufodorsata* (Ji *et al.*, 1997b). Female *S. annularis* increase reproductive output solely through increasing litter size. This pattern is different from that reported for *T. marcianus* and *E. rufodorsata*, which allocate more energy to reproduction by increasing litter size as well as neonate mass (Ford *et al.*, 1987; Ji *et al.*, 1997b). Our findings do not support the results reported for some snakes (Ford *et al.*, 1989; Ford *et al.*, 1983) and lizards (Stewart, 1979; Nussbaum, 1981) that showed an inverse relationship between clutch size and offspring size.

An inverse relationship between carcass dry mass and yolk sac dry mass suggests the transformation of resources in the yolk sac to the carcass. The result is somewhat similar to that reported for some studied oviparous

colubrid snakes, e. g. *Elaphe carinata* (Ji *et al.*, 1997a), *E. taeniura* (Ji *et al.*, 1999a), *Dinodon rufozonatum* (Ji *et al.*, 1999b) and *Ptyas korros* (Ji *et al.*, 2000). In these snakes, resources in the yolk sac can be mobilized to support carcass growth during the first days of a neonate's life.

Previous studies have showed that RCM varies considerably amongst reptiles [see the review by Seigel *et al.* (1984)]. Viviparous species allocate relatively less amount energy for reproduction than do oviparous species, so as to reduce mortality during gestation by remaining fairly mobile due to low RCM (Seigel *et al.*, 1984; Seigel *et al.*, 1987). RCM₂ (0.327) of *S. annularis* in our sample falls within the range (0.112 ~ 0.614) reported for the 22 populations of viviparous colubrid snakes (Seigel *et al.*, 1984), and is very similar to that (0.334) reported for *E. rufodorsata* (Ji *et al.*, 1997b). The similarity in RCM of *S. annularis* and *E. rufodorsata* presumably resulted from the similarities in female size and dimension, food habits and habitat requirements of the two species. However, we need data from more species to substantiate our claim that morphologically and ecologically similar snakes may have similar RCM.

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中文摘要

赤链华游蛇的雌性生殖输出和初生幼体特征*

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研究浙江舟山产赤链华游蛇窝仔数、幼体大小和雌体大小之间的关系以及初生幼体特征。产仔雌体的最小体长 (SVL) 为 486 mm, 大于最小 SVL 的雌体均年产单窝仔, 产仔期为 8 月 30 日 ~ 9 月 30 日。窝仔数与雌体 SVL 呈正相关, 平均值为 11.7。初生幼仔重与雌体 SVL 和窝仔数无关。窝仔数与产后雌体的状态无关。赤链华游蛇主要通过增加窝仔数来增加繁殖输出。初生幼仔湿重、干重、SVL 和尾长平均值分别为 4.37 g、1.18 g、171.0 mm 和 44.7 mm。幼体躯干、剩余卵黄和脂肪体的干重有显著的窝间差异。偏相关分析显示, 幼体躯干干重与剩余卵黄及脂肪体干重呈负相关, 剩余卵黄干重与脂肪体干重无关。

关键词 游蛇科 赤链华游蛇 生殖输出 窝仔数 初生幼体

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