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Speed and Endurance of Gravid and Nongravid Green Snakes, *Ophedrys aestivus*

MICHAEL V. PLUMMER

The documented costs of reproduction in reptiles include possible decreased survival resulting from behavioral and physiological changes associated with reproduction (Shine, 1980). For example, if escaping from predators depends on a snake's speed or endurance, then reduced locomotor performance of females carrying eggs or embryos could increase the risk of predation (Seigel et al., 1987), assuming that antipredator behaviors are not modified (Brodie, 1989). Locomotor performance is subject to selection in adult snakes because it is repeatable, heritable, and correlated with survivorship (e.g., Garland, 1988; Brodie, 1993a; Jayne and Bennett, 1990a). Both speed and endurance are impaired in gravid viviparous garter snakes, *Thamnophis marcianus* (Seigel et al., 1987) and *T. ordinoides* (Brodie, 1989), but data on locomotor performance are not available for any other gravid viviparous snake species, and none are available for an oviparous species. Because gravid oviparous colubrid snakes have an approximately 17% greater relative clutch mass compared to gravid viviparous colubrids (Seigel and Fitch, 1984), the greater physical burden in oviparous forms might result in greater impairment of locomotor performance. In this paper, I examine whether gravid oviparous green snakes (*Ophedrys aestivus*) decrease locomotor performance (crawl speed and endurance) relative to nongravid snakes.

Materials and methods.—Green snakes were hand collected from 25 June to 16 July 1990, in the thick shoreline vegetation surrounding Ransom Lake, a 21 ha lake impounded in 1972 and located 2 km west of Denmark, White County, Arkansas. Captured snakes were individually bagged and taken to the laboratory where they were either marked, or identified if previously marked, using Brown and Parker's (1976) system, sexed, and measured (SVL in mm; weight in g). I counted the number of eggs in gravid snakes by palpation. Finally, I measured the locomotor ability of each snake and returned it to the field. Locomotor ability was measured on a 2 m linear race track (23 cm H × 14 cm W) with a floor covered with coarse plastic carpet material. Snakes were retained in the laboratory

at ambient temperatures similar to those at testing for at least one day prior to testing and for an additional day if snakes had food in their stomachs that could be detected by palpation. Body temperatures of snakes at testing (26.6–28.8 C) were within the normal range of body temperatures for active snakes in the field (Plummer, 1993). I conducted each trial by releasing a snake at the starting gate where its head was detected by an infrared sensor. I stimulated each snake to crawl rapidly for the length of the track by lightly prodding it at the base of the tail with a small hand-held brush. As soon as the snake's head passed through the finish gate where it was detected by another infrared sensor, I collected the snake and immediately placed it at the starting gate for the next trial. I conducted 10 such trials on each snake in rapid succession. The time between a snake's head passing through the finish gate and passing through the starting gate for the next trial was less than three seconds. The time from start to finish in each trial was measured to the nearest 0.01 sec, using Precision Timer III (Vernier Software, Portland, OR). Because some gravid snakes essentially refused to crawl in the later trials, thereby reducing sample size, I did not use data from all trials in the endurance analyses. Female snakes classified as nongravid were estimated to be 1–2 weeks postovipository, and those classified as gravid were in the late stages of gravidity likely within 1–1.5 weeks of oviposition.

Statistical analyses were conducted with SYSTAT Version 5 (SYSTAT, Inc., Evanston, IL, 1992, unpubl.) or SigmaStat (E. Fox, J. Kuo, L. Tilling, and C. Ulrich, Jandel Scientific, San Rafael, CA, 1994, unpubl.). For parametric tests, I ensured that the data were normally distributed and the variances were homogeneous. For independent *t*-tests, each snake was tested one time, either when gravid or postovipository. For paired comparison *t*-tests, each snake (designated BA) was tested two times, once before and once after oviposition. Gravid snakes were released in the field after initial testing and, if they were recaptured after oviposition, were brought back to the lab and retested. Because I returned snakes to the field soon after testing, I was not able to conduct additional testing of individual snakes which would allow the calculation of repeatabilities in behavior. Performance of individual garter snakes using similar methods is known to be repeatable (Garland, 1988; Brodie, 1989, 1993a). I defined crawl speed as the mean speed (m/sec) for the first three trials and endurance as the slope of the line resulting from regressing speed on trial

TABLE 1. DESCRIPTIVE STATISTICS OF SVL, BODY MASS, AND CRAWL SPEED OF GRAVID AND NONGRAVID GREEN SNAKES IN BOTH INDEPENDENT AND PAIRED-COMPARISONS GROUPS. Indicated are sample size, mean \pm 1 SD, minimum and maximum.

	Independent		Paired comparisons	
	Gravid (n = 17)	Nongravid (n = 19)	Gravid (n = 6)	Nongravid (n = 6)
SVL (mm)	465 \pm 35.9 407–525	455.6 \pm 49.4 365–525	454.7 \pm 24.7 422–490	454.3 \pm 24.5 420–489
Body mass (g)	30.4 \pm 5.7 19.8–37.7	19.7 \pm 5.6 9.9–35.8	30.3 \pm 3.8 23.4–34.6	19.6 \pm 2.9 14.1–22.4
Crawl speed (cm/sec)	3.11 \pm 0.41 2.15–3.78	4.15 \pm 0.72 2.73–5.13	2.88 \pm 0.23 2.53–3.17	3.72 \pm 0.55 2.97–4.39

number. I used repeated measures ANOVA to examine the relationship of speed and trial number. Unless stated otherwise, means are presented with their standard deviations.

Results.—Crawl speeds of independent gravid and nongravid snakes (Table 1) were significantly different ($t = -5.22$, $P < 0.001$, $df = 34$). Gravid snakes crawled 25.1% slower than nongravid snakes and weighed 54.3% more ($t = 5.28$, $P < 0.001$, $df = 34$) because of the mass of the eggs and tissue/fluid which would be lost at oviposition. Crawl speed of six BA snakes in the gravid and nongravid condition were significantly different in a paired-comparison analysis (Table 1; $t = -4.50$, $P < 0.01$, $df = 5$). Gravid BA snakes crawled 22.6% slower than when nongravid and weighed 54.6% more ($t = 18.37$, $P < 0.001$, $df = 5$) because of the mass of the eggs and tissue/fluid which would be lost at oviposition.

Snout-vent length did not differ between gravid and nongravid snakes in the independent analysis (Table 1; $t = 0.65$, $P > 0.50$, $df = 34$). For gravid snakes, crawl speed was unrelated to either SVL ($r = 0.25$, $P > 0.30$, $n = 17$) or body mass ($r = 0.30$, $P > 0.20$, $n = 17$). However, for nongravid snakes, crawl speed was positively related to both SVL ($r = 0.68$, $P < 0.01$, $n = 19$) and body mass ($r = 0.59$, $P < 0.01$, $n = 19$). Because of the significant relationship between crawl speed and SVL in nongravid snakes, I used ANCOVA to check for possible interaction between the slopes of speed on SVL for gravid and nongravid snakes. The slopes were homogeneous ($F_{1,32} = 2.95$, $P < 0.096$), but the intercepts were different ($F_{1,33} = 43.33$, $P < 0.001$), thus corroborating the results of the t -test analysis.

For BA snakes in the gravid condition, crawl speed was unrelated to SVL ($r = 0.45$, $P > 0.30$, $n = 6$) but was affected by body mass ($r = 0.86$, $P < 0.05$, $n = 6$). For BA snakes in the non-

gravid condition, crawl speed was not significantly related to either SVL ($r = 0.70$, $P > 0.10$, $n = 6$) or body mass ($r = 0.67$, $P > 0.10$, $n = 6$). Because the correlation coefficients between speed and size for snakes in the nongravid condition were similar in value to those obtained in the independent analysis (SVL, 0.70 vs 0.68; mass, 0.67 vs 0.59), it is likely that the lack of significance resulted from low power in both tests ($< 35\%$) because of low sample sizes ($n = 6$).

Reproductive characteristics such as relative clutch mass (RCM) and clutch size may directly affect locomotor performance in viviparous snakes (Seigel et al., 1987). I was not able to measure clutch mass directly because I released gravid snakes in the field soon after testing them. However, because the mass carried by gravid females includes not only the mass of offspring but also that of fluids and tissues such as extraembryonic membranes, the total mass gain resulting from reproduction may be more representative of the actual physical burden experienced by a gravid female than RCM alone (Brodie, 1989). The total mass resulting from reproduction (= effective relative clutch mass of Brodie, 1989), measured in BA snakes as the proportion of the mass lost by a snake between gravid testing and postovipository retesting to the mass of the gravid snake, varied from 0.309–0.397 ($\bar{x} = 0.356 \pm 0.032$, $n = 6$) and was unrelated to speed ($r = -0.012$, $P > 0.90$, $n = 6$). Clutch size varied from 4–11 eggs ($\bar{x} = 6.4 \pm 1.5$) and also was unrelated to speed ($r = 0.116$, $P > 0.60$, $n = 17$).

A repeated-measures ANOVA indicated that crawl speed was dependent on trial ($F_{8,256} = 311.09$, $P < 0.001$) and was greater in nongravid snakes (Fig. 1; $F_{1,32} = 20.78$, $P < 0.001$). Because there was no interaction between trial and reproductive condition ($F_{8,256} = 1.29$, $P > 0.20$), the similar slopes of speed on trial suggested similar rates of endurance (Fig. 1). A repeated-

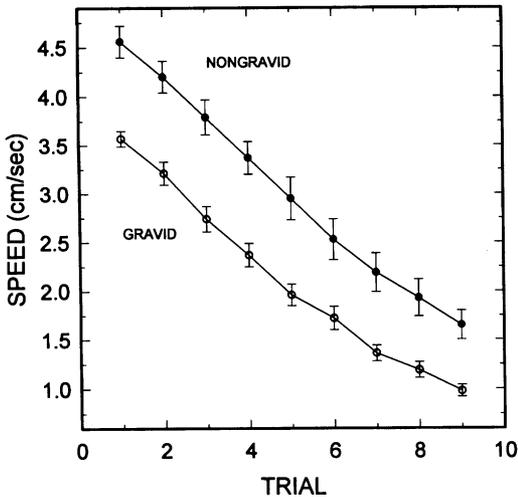


Fig. 1. The relationship of crawl speed and trial number for gravid and nongravid green snakes. Indicated are mean \pm 1 SE. For each trial, $n = 19$ for nongravid snakes. For gravid snakes, $n = 17$ (trials 1–2), $n = 16$ (trial 3), $n = 15$ (trials 4–7), $n = 14$ (trial 8), and $n = 13$ (trial 9).

measures ANOVA on BA snakes also indicated that speed was dependent on trial ($F_{9,72} = P < 0.001$) and was greater in nongravid snakes ($F_{1,8} = 9.25$, $P < 0.05$). The similar slopes of speed on trial for gravid and nongravid BA snakes ($F_{9,72} = 0.54$, $P > 0.80$) likewise suggested similar rates of endurance. Four females, in each of which oviposition was imminent, essentially refused to move down the track after only 2, 3, 7, and 8 trials, respectively.

Discussion.—The results of this study, the first reported for an oviparous snake, in part support and extend those of Seigel et al. (1987) and Brodie (1989) who showed that pregnancy in viviparous garter snakes decreases locomotor performance, especially crawl speed. This reduction is ecologically significant because locomotor performance in snakes is repeatable and heritable (Brodie, 1989, 1993a, 1993b), correlated with survivorship in adult snakes (Jayne and Bennett, 1990a), and thus is subject to selection (Garland, 1988; Jayne and Bennett, 1990a, 1990b). Because reduction in speed is greatest in the late stages of pregnancy (Seigel et al., 1987; Brodie, 1989), my results should reflect maximum locomotor reduction. Assuming the increase in speed after oviposition is a direct function of the decrease in the mass of reproductive material, one might predict that green snakes should exhibit a greater proportional increase in speed because of their greater mass burden (RCM = 0.372, Seigel and Fitch, 1984)

compared with that in either *T. marcianus* (RCM = 0.240, Seigel et al., 1987) or *T. ordinoides* (RCM = 0.310, Brodie, 1989). Speed in postovipository green snakes increased 29–33% over that of gravid snakes, whereas comparable speed increases in garter snakes ranged from 16–25% (Seigel et al., 1987) to 49% (Brodie, 1989). It appears that change in speed resulting from oviposition or parturition is a more complex function than just that of the extra mass lost. For example, changes in certain physiological and behavioral traits may also accompany parturition (Birchard et al., 1984; Brodie, 1989). In green snakes, the lack of relationship between speed and either total mass loss at oviposition or clutch size supports this notion. Speed is reduced in gravid garter snakes independent of the burden associated with carrying a clutch (Brodie, 1989).

Interestingly, my data suggested that locomotor endurance in green snakes was not affected by gravidity, an unexpected result considering that both Seigel et al. (1987) and Brodie (1988) found that pregnancy in garter snakes decreases endurance. This discrepancy may reflect differences in methodology because both Seigel et al. (1987) and Brodie (1988) used total distance traveled to measure endurance. My method of using the rate of reduction in speed over successive trials may not have been an adequate measure of endurance. Alternatively, it might be argued that, because nongravid snakes moved as fast after nine trials as gravid snakes did after only six trials, the former had greater absolute endurance than the latter. The aforementioned tendency of gravid snakes to refuse to crawl in later trials also suggests either a lack of motivation or decreased endurance.

After observing an apparent high rate of predation on telemetered gravid green snakes during their nesting migrations, I suggested (Plummer, 1990) that implanted transmitters, adding 25% to the mass burden of an average clutch, may have decreased an already lowered locomotor performance rendering the snakes more susceptible to predation. Because crawl speed and perhaps endurance of green snakes was decreased by gravidity but was not directly related to total mass lost at oviposition, this hypothesis is only weakly supported by the present data. Locomotor performance of garter snakes was not affected by either implanted transmitters up to 10% of body mass or by the surgical procedures associated with the implantation itself (Lutterschmidt, 1994).

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