

Swimming and pregnancy in Tiger snakes, *Notechis scutatus*

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Reduced locomotor ability may increase susceptibility to predation and hence may represent a proximate mechanism by which “costs” of reproduction are expressed (Shine, 1980). In squamate reptiles, many examples of such effects have been documented, where non-gravid females and/or males showed higher survival rates than gravid females (Shine, 1980; Andren, 1982, 1985; Madsen, 1987). For instance, pregnancy may entail a reduction in locomotor performances in lizards and snakes (Shine, 1980; Shine, 2003; Bauwens and Thoen, 1981; Garland and Else, 1987; Seigel et al., 1987), including decreased burst speed by 12 to 30%, and endurance by 52 to 55%. Because fleeing from predators or foraging ability depends on speed and/or stamina, reduced locomotor performance resulting from carrying offspring may result in increased risk of predation and/or decreased energy intake compared to non-gravid females.

However, less clear is the effect of pregnancy on aquatic locomotion. Many snakes inhabit aquatic environments such as rivers, lakes, swamps, mangroves, or oceans (Voris and Jayne, 1979; Voris and Karns, 1996; Jayne et al., 1988; Shine and Shetty, 2001) and may rely on water for feeding, and/or as an escape route from predators (such as sharks for sea kraits; Weatherhead and Robertson, 1992;

Heatwole, 1999). Reproductive investment in aquatic snakes may be constrained by the important locomotory role of the posterior part of the body during swimming, and to a larger degree than during crawling on land (Jayne, 1985; Gans, 1986; Shine, 1988). Indeed, clutches of aquatic snakes are located more anterior in the body, and overall reproductive investment is reduced compared to terrestrial species (Shine, 1988). If such modifications are genuinely related to a reduction of the “costs” associated with pregnancy in swimming snakes, then it may be possible to record an impairment in swimming performances in pregnant snakes compared to non pregnant individuals, either in terms of stamina or swimming speed. To date however, no study has specifically evaluated the effect of pregnancy in swimming snakes; therefore, it is important to determine if pregnancy alters aquatic locomotion in snakes as it may do in terrestrial locomotion. We studied the effect of pregnancy on swimming performance of Tiger snakes (*Notechis scutatus*), a viviparous species that contains populations that exhibit aquatic habits to escape predators or to forage on amphibians (Mirtschin and Davis, 1992).

Twenty-two adult females (table 1) were caught on Carnac Island (32°07'S, 115°39'E) in Western Australia in January and February 2002; including 13 pregnant and 9 non-reproductive females (see Bonnet et al., 1999 and Aubret et al., 2004 for details on study site). Females were measured in snout-vent length (SVL), body length (BL) to the nearest ± 0.5 cm and weighed to the nearest ± 0.1 g (Body mass; BM). Reproductive status was determined by gentle abdominal palpation and eggs/embryos counted (January-February correspond to mid-pregnancy, unpublished data). All females were maintained under similar conditions. They were housed individually in plastic boxes (50 × 40 × 30 cm) with towel paper, water dish

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Table 1. Body size and swimming performances in pregnant and non-reproductive female tiger snakes. Comparisons between the groups of females were performed using ANOVAs with reproductive status as the factor and the trait under focus as the dependent variable. Snake's body size or body mass influenced several traits (see text), therefore we use ANCOVAs with SVL* or BM** as a covariate. Means and adjusted means (to SVL*, to BM**) are expressed ± 1 SD. Df: degree of freedom. F: F value from ANOVAs and ANCOVAs. Significant results are in bold face.

Traits	Non pregnant (n = 9)	Pregnant (n = 13)	Df; F	P
<i>Morphological traits</i>				
Body Mass (g)	278.6 \pm 90.8	410.8 \pm 78.3	1, 20; 13.5	0.002
Snout Vent Length (cm)	76.9 \pm 8.3	83.9 \pm 4.2	1, 20; 6.5	0.019
Body Length (cm)	91.1 \pm 9.8	98.2 \pm 4.5	1, 20; 5.2	0.033
Body condition (g)*	316.2 \pm 90.8	373.3 \pm 78.3	1, 19; 6.7	0.018
<i>Free swimming trial</i>				
Time spent swimming (s)	561.3 \pm 35.9	365.4 \pm 167.7	1, 18; 11.7	0.003
Distance swum (m)	66.1 \pm 17.9	43.3 \pm 24.4	1, 18; 6.1	0.023
Distance swum (BL)	73.3 \pm 21.6	44.0 \pm 25.8	1, 18; 8.2	0.010
Average speed (cm.s ⁻¹)**	22.5 \pm 5.4	24.4 \pm 5.1	1, 17; 0.1	0.715
Average speed (BL.s ⁻¹)	0.3 \pm 0.1	0.2 \pm 0.1	1, 18; 0.5	0.490
<i>Forced swimming trial</i>				
Shaking time (s)	16.6 \pm 18.8	21.6 \pm 19.3	1, 20; 0.2	0.630
Underwater swimming (s)**	42.5 \pm 60.3	15.5 \pm 11.7	1, 19; 4.2	0.053
<i>Sprint swimming speed</i>				
Sprint speed (cm.s ⁻¹)	60.3 \pm 16.5	60.7 \pm 10.4	1, 20; 0.1	0.840
Sprint speed (BL.s ⁻¹)	0.7 \pm 0.2	0.6 \pm 0.1	1, 20; 0.3	0.570
<i>Voluntary apnea</i>				
Apnea duration (s)**	194.5 \pm 220.5	76.94 \pm 77.2	1, 19; 1.2	0.287

and shelter in a controlled temperature room, at 27.5°C by day and 20°C by night. A heat source provided basking opportunity four times 15 minutes per day (High pressure Na+ lamp; 600 Watts). Food (dead adult mice previously euthanased) was offered approximately every three weeks and water provided *ad libitum*. Although all pregnant females carried eggs/embryos at the time of the experiments, a significant proportion “reabsorbed” (i.e. the eggs were no longer detectable) them long after the end of our experiment: only 7 out of the 13 pregnant females gave birth between two and three months after completion of the experiments, after what all were released at their exact capture location. Post reproduction BM was recorded after ventral palpation confirmed that all oviductal items had been expelled. Litter size included fully formed neonates, aborted embryos, and non-developed eggs. Litter mass was determined by weighing all those items. Relative litter mass (=RCM) was calculated by dividing litter mass by post-parturition maternal mass. All snakes were tested with an empty stomach (Garland and Arnold, 1983).

A rectangular swimming pool 370 cm long, 64 cm width, and 100 cm high was lined with black plastic. The 64 cm width was adjusted to allow normal swimming waves of the largest snake involved in the study. Water depth (40 cm) prevented the largest snake from touching the bottom.

Two observers (located at each end of the pool) recorded the different parameters. Each of the following tests was separated by two days and performed in the same order for each individual, as follows:

1. *Free swimming trial* — snakes were gently manipulated (i.e. slowly lifted up with a hook from their cage) and smoothly dropped above the water level at one end of the pool. All snakes immediately swam toward the other end (Shine and Shetty, 2001), a behaviour commonly observed in many “terrestrial” snake species (XB, pers. obs.). During a 5-minute trial, we recorded the total time spent swimming *versus* resting and the distance travelled by each snake (cumulative number of lengths of the pool). No snakes swam in random trajectories in the pool, but all showed stereotypic patterns: fast swimming along the length of pool and turns at each ends. Thus, the total distance swum by each snake was measured relatively accurately. The distance swum and the average speed were expressed either in absolute terms (cm.s⁻¹) or relative to the snake body size (BL.s⁻¹). We also recorded the occurrence of shaking (instability in swimming *versus* fluid and regular movements, Jayne, 1985) and the occurrence of underwater swimming.

2. *Forced swimming trial* — the 5 minute trial was repeated but when snakes became tired, they were kept swimming

by gently touching their tail with a stick each time they stopped. We recorded the cumulative time periods during which the snakes displayed unstable swimming (shaking), and underwater swimming.

3. *Sprint swimming speed* — maximum swimming speed was recorded by placing each snake in a situation where they were made to flee under stress: snakes were picked up by the head and suddenly dropped in the water at one end of the pool. For accuracy, two observers independently recorded the time taken to cross the pool and a mean value was used in the analyses.

4. *Voluntary apnea* — we used an opaque PVC tube (40 cm long with a diameter of 8 cm), closed at one end. The diameter of the tube was large enough to allow easy movement of the snake inside it. As we suspected that snake's stress level may influence the time spent underwater, we attempted to minimise stress to the snakes prior to testing. Snakes were removed from their cage, and the open end of the PVC tube was presented to them. In each case, the snake voluntarily entered the tube (i.e. snakes normally feel safe in confined environments). Time recording started when the tube was fully immersed in the pool and ceased when snakes chose to move to the surface. To our knowledge, this study provides the first report of such apnoea durations, a trait that may well play a role in natural conditions. When pursued by a predator, a snake that escaped by taking refuge underwater must remain hidden as long as possible. All experiments were performed at 27°C, close to the average body temperature chosen by tiger snakes in captivity (26.8±0.7°C; Ladyman and Bradshaw, 2003). Times were recorded using digital stopwatches (0.1 s). All data were log transformed prior to analysis.

Results of this study are summarized in table 1.

Body size and Swimming performance: because of the potentially confounding effect of pregnancy we restricted these analyses to non-reproductive females. Average swimming speed was negatively correlated with both BL and BM (respectively $n = 6$; $r = -0.91$, $P < 0.02$ and $r = -0.89$, $P < 0.02$). In contrast, apnea duration was positively correlated with BL and BM (respectively $n = 7$; $r = 0.76$, $P < 0.05$ and $r = 0.82$, $P < 0.03$). For all other traits, there was no significant correlation (all $r < 0.68$, all $P > 0.09$).

Pregnancy and swimming performances: litter mass ($n = 6$, $r = -0.88$; $P < 0.02$) and relative litter mass negatively affected average swimming speed ($n = 6$, $r = -0.83$, $P < 0.04$). Apnea duration was positively correlated with litter mass ($n = 7$, $r = 0.82$, $P < 0.03$) and with relative litter mass ($n = 7$,

$r = 0.93$, $P < 0.01$). Pregnant females spent less time swimming and consequently travelled shorter distances during the free-swimming experiments than did the non-pregnant females (table 1). However, pregnancy did not reduce significantly average or sprint swimming speed (table 1). We did not find any significant difference between pregnant and non-pregnant females for the other swimming performance traits (table 1).

A decrease in locomotor performance due to pregnancy has been reported for terrestrial locomotion in reptiles (Shine, 1980; Bauwens and Thoen, 1981; Garland, 1985; Seigel et al., 1987). Our study provides the first example of a similar analysis applied to swimming snakes. Activity levels strongly decreased (35% in absolute terms, 40% relative to body length) in pregnant females during the free-swimming tests leading to a marked reduction in the total distance swum. Pregnancy had no effect on apnea duration and underwater swimming (close to significance for this later trait), although it may well be that with larger sample sizes, significant effects might be seen. It is possible that buoyancy changes due to the litter might affect these variables (Jayne, 1985). Alternatively, the pregnant females may have tolerated less physiological stress (i.e. anoxia when underwater) to protect their developing, and perhaps fragile, embryos. Overall, the differences observed between pregnant and non-pregnant females may be related either to the physical burden of the litter, or to physiological and behavioural modifications of the maternal organism in response to the physiological requirements of the embryos; or to a combination of both kinds of factors (Sinervo et al., 1991; Olsson et al., 2000; Shine, 2003). Surprisingly, burst (=sprint) and average swimming speed remained unaffected by pregnancy. This last result is counterintuitive and opposes a common finding in snakes and lizards where pregnancy decreases terrestrial burst speed (Shine, 1980, 2003; Bauwens and Thoen, 1981; Garland and Else 1987; Seigel et al., 1987; Sinervo et al., 1991; Olsson et al.,

2000). This result also supports the notion that physiological/behavioural modifications played a role in the decrease in time-spent swimming by pregnant females (Sinervo et al., 1991; Olsson et al., 2000).

High variances recorded in most traits, and relatively small sample size, make it difficult to interpret some of our results. Hence, the evolutionary significance of our results and their potential impact on female survivorship remain unclear. Further studies are needed to test the hypothesis that a reduction in reproductive investment or a shift in location of the litter (clutch) more anteriorly in the body would improve swimming performances. This could well be the case, as in our study litter mass and RCM were both negatively correlated with average swimming speed. Apnea duration was nonetheless positively correlated with litter mass, highlighting the importance of measuring various traits simultaneously when we attempt to interpret complex phenomena.

Acknowledgements. We thank the region Poitou-charentes (France), the Conseil Général des Deux-Sèvres, and the University of Western Australia for funding. We are also very grateful to D. Bradshaw, W. Gibb, Z. Lechat, and R. Cambag helped with animal handling. R. Avery and an anonymous referee provided useful comments. The Animal Ethics Committee of UWA approved all procedures and the Department of Conservation and Land Management (WA) issued fauna collection permits.

References

- Andr n, C. (1982): Effect of prey density on reproduction, foraging and other activities in the adder, *Vipera berus*. *Amphibia-Reptilia* **3**: 81-96.
- Andr n, C. (1985): Risk of predation in male and female adders, *Vipera berus* (Linn ). *Amphibia-Reptilia* **6**: 203-206.
- Aubret, F., Bonnet, X., Maumelat, S., Bradshaw, S.D., Schwaner, T. (2004): Diet divergence, jaw size and scale counts in two neighbouring populations of tiger snakes (*Notechis scutatus*). *Amphibia-Reptilia* **25**: 9-17.
- Bauwens, D., Thoen, C. (1981): Escape tactics and vulnerability to predation associated with reproduction in the lizard *Lacerta vivipara*. *J. Anim. Ecol.* **50**: 733-743.
- Bonnet, X., Bradshaw, S.D., Shine, R., Pearson, D. (1999): Why do snakes have eyes? The (non-) effect of blindness in island tiger snakes. *Behav. Ecol. Sociobiol.* **46**: 267-272.
- Gans, C. (1986): Locomotion of limbless vertebrates: pattern and evolution. *Herpetologica* **42**: 33-46.
- Garland, T.Jr. (1985): Ontogenic and individual variation in size, shape and speed in the Australian agamid lizard *Amphibolurus nuchalis*. *J. Zool., Lond.* **207**: 425-439.
- Garland, T.Jr., Arnold, S.J. (1983): Effects of a full stomach on locomotor performance of juvenile garter snakes (*Thamnophis elegans*). *Copeia* **1983**: 1092-1096.
- Garland, T.Jr., Else, P.L. (1987): Seasonal, sexual, and individual variation in endurance and activity metabolism in lizards. *Am. J. Physiol.* **252**: R439-R449.
- Heatwole, H.F. (1999): Sea snakes. Sydney. University of New South Wales Press.
- Jayne, B.C. (1985): Swimming in constricting (*Elaphe guttata*) and non constricting (*Nerodia pictiventris*) colubrid snakes. *Copeia* **1985**: 195-208.
- Jayne, B.C., Voris, H.K., Heang, K.B. (1988): The diet, feeding behavior, growth and numbers of a population of *Cerberus rynchops* (Serpentes: Homalopsinae) in Malaysia. *Fieldiana (Zool.)* **50**: 1-15.
- Ladyman, M., Bradshaw, S.D. (2003): The influence of dehydration on the thermal preferences of the Western tiger snake, *Notechis scutatus*. *J. Comp. Physiol. B* **173**: 239-246.
- Madsen, T. (1987): Cost of reproduction and female life history tactics in a population of grass snakes, *Natrix natrix*, in Southern Sweden. *Oikos* **49**: 129-132.
- Mirtschin, P., Davis, R. (1992): Snakes of Australia: dangerous and harmless. Melbourne. Hill of Content Publ.
- Olsson, T., Shine, R., Bak-Olsson, E. (2000): Locomotor impairment of gravid lizards: is the burden physical or physiological? *J. Evol. Biol.* **13**: 263-268.
- Seigel, R.A., Huggins, M.M., Ford, N.B. (1987): Reduction in locomotor ability as a cost of reproduction in gravid snakes. *Oecologia* **73**: 481-485.
- Shine, R. (1980): "Costs" of reproduction in reptiles. *Oecologia* **46**: 92-100.
- Shine, R. (1988): Constraints on reproductive investment: a comparison between aquatic and terrestrial snakes. *Evolution* **42**: 17-27.
- Shine, R. (2003): Effects of pregnancy on locomotor performance: an experimental study on lizards. *Oecologia* **136**: 450-456.
- Shine, R., Shetty, S. (2001): Moving in two worlds: aquatic and terrestrial locomotion in sea snakes (*Laticauda colubrina*, Laticaudidae). *J. Evol. Biol.* **14**: 338-346.
- Sinervo, B., Hedges, R., Adolph, S.C. (1991): Decreased sprint speed as a cost of reproduction in the lizard *Sceloporus occidentalis*: variations among populations. *J. Exp. Biol.* **155**: 323-336.
- Voris, H.K., Jayne, B.C. (1979): Growth reproduction and population structure of a marine snake, *Enhydryna schistosoma* (Hydrophiidae). *Copeia* **1979**: 307-318.
- Voris, H.K., Karns, D.R. (1996): Habitat utilization, movements, and activity patterns of *Enhydryn plumbea* (Serpentes: Homalopsinae) in a rice paddy wetland in Borneo. *Herpetol. Nat. Hist.* **4**: 111-126.

Weatherhead, P.J., Robertson, I.C. (1992): Thermal constraints on swimming performance and escape response of northern water snakes. Can. J. Zool. **70**: 94-98.

Received: November 12, 2003. Accepted: June 30, 2004.