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Phenotypic effects on survival of neonatal northern watersnakes *Nerodia sipedon*

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Summary

1. Understanding the trade-off females make between offspring size and number requires knowing how neonatal size, and traits associated with size, affect survival.
2. We studied neonatal survival in the northern watersnake *Nerodia sipedon* in outdoor enclosures with artificial hibernation sites.
3. From a total of 950 neonates from 77 litters collected over 3 years, we found a survival rate of 65% between birth and hibernation and 47% during hibernation. Estimated survival from birth to the end of hibernation was 31%, comparable with indirect estimates for free-living watersnakes.
4. Consistent with the 'bigger is better' hypothesis, larger neonates and neonates heavier relative to their body length were more likely to survive both the pre-hibernation and hibernation periods.
5. Survival in the pre-hibernation period also decreased with the duration of that period and varied among years.
6. Survival during hibernation was higher in warmer winters. Mass change prior to hibernation did not affect survival during hibernation.
7. These results suggest that an optimal reproductive strategy should exist for female watersnakes, producing a 'consensus' among females on the optimal size for offspring. This expectation stands in stark contrast to the pronounced variation in offspring size observed both within and among litters.

Key-words: neonate, *Nerodia sipedon*, optimal offspring size, phenotypes, survival.

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Introduction

Life-history theory is predicated on the expectation that trade-offs between traits constrain the evolution of those traits (Roff 1992; Stearns 1992). In the case of reproduction, females with finite resources to invest must trade off the number of offspring with the size of those offspring (Smith & Fretwell 1974). Snakes have been popular subjects for research on this trade-off (Andrén & Nilson 1983; Brodie & Ducey 1989; Ford & Seigel 1989; Seigel & Ford 1991, 1992; King 1993; Gregory & Skebo 1998; Bronikowski & Arnold 1999; Weatherhead *et al*. 1999; Barron & Andraso 2001). Essential to understanding why a trade-off results in offspring of a particular size is knowledge of how neonatal size, and traits associated with size, affect survival. Our knowledge of how offspring phenotypes affect survival in neonatal snakes lags far behind what we know about variation in offspring phenotypes. In this study we determine how phenotypic variation affects neonatal survival in northern watersnakes *Nerodia sipedon* (Linnaeus).

Implicit in the hypothesis that females trade off offspring size and number is the assumption that larger offspring survive better (Smith & Fretwell 1974). Larger offspring should be able to access a greater range of prey while being vulnerable to fewer predators. Furthermore, if larger offspring benefit from their initial advantage and grow faster, they would reach sexual maturity sooner. Evidence that 'bigger is better' for snakes is limited and equivocal. Larger neonatal garter snakes (*Thamnophis* spp.) survived better in the laboratory (Bronikowski 2000), and in the field larger individuals

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survived better in 1 of 2 years (Jayne & Bennett 1990). Saint Girons & Naulleau (1981) found that larger neonatal viperids had higher survival in outdoor enclosures during their first several months of life. In contrast, Charland (1989) found no effect of size at birth on over-winter survival of neonatal western rattlesnakes *Crotalus viridis* (Rafinesque). Among snake species, larger neonates grow faster (Andrews 1982), but within species evidence is equivocal (Gregory & Prelypchan 1994; Forsman & Lindell 1996; Bronikowski 2000). The first prediction we test is that larger body size enhances neonatal survival in *N. sipedon*. Because female watersnakes are bigger than males (Weatherhead *et al.* 1995) beginning at birth (Weatherhead *et al.* 1998, 1999), we assess whether survival varies with sex.

Energy allocated per offspring can also affect body condition, which could affect survival if foraging opportunities prior to hibernation are limited and if hibernation is energetically expensive (Whitford & Creusere 1977; Blem 1981; Gregory 1982). Adult females in poor condition following reproduction suffer higher mortality (e.g. Madsen & Shine 1993; Luiselli, Capula & Shine 1996; Brown & Weatherhead 1997). Also, garter snakes *Thamnophis sirtalis* (Linnaeus) in poor condition were more vulnerable to mortality factors associated with emergence from dens (Shine *et al.* 2001). Analyses of how condition affects survival in neonatal snakes have produced equivocal results. Jayne & Bennett (1990) found a negative relationship between condition and survival in *T. sirtalis*, although this relationship was potentially confounded by effects of body size. In *T. elegans* (Baird and Girard), Bronikowski (2000) found that neonates that survived hibernation had gained more weight prior to hibernation than those that did not survive. The second prediction we test is that body condition increases survival of *N. sipedon*.

Locomotive performance could also affect offspring survival. Locomotive performance is variable, repeatable, and heritable, and should affect an individual's success in predator–prey interactions (Jayne & Bennett 1990). Jayne & Bennett (1990) found that higher burst speed (corrected for body size) was associated with higher survival of both yearling and older garter snakes, but was not associated with survival of neonates. The third prediction we test is that superior locomotive performance will enhance survival of *N. sipedon*.

Time of birth is not a phenotypic trait *per se*, but should affect offspring survival and the maternal trade-off between offspring size and number. Weatherhead *et al.* (1999) proposed that small offspring born earlier might survive as well as larger offspring born later because they have more time to forage before hibernation. Here we test the prediction that, independent of body size, snakes born earlier are more likely to survive.

The dearth of information on factors affecting survival of neonatal snakes reflects the difficulty in studying small snakes (Parker & Plummer 1987). Previous researchers have used one of two approaches to deal with this problem. Charland (1989) and Jayne & Bennett (1990) took advantage of species that den communally, allowing them to study survival of neonates in the field, while Bronikowski (2000) studied survival in the laboratory. We used an intermediate approach, studying neonatal survival in outdoor enclosures. Low recapture rates of young snakes make mark–recapture methods ill suited for field studies of neonatal survival in watersnakes (Brown & Weatherhead 1999). As Bronikowski (2000) did, we also assessed survival between birth and hibernation separately from survival during hibernation to reveal when selection occurs.

Materials and methods

This study was conducted at the Queen's University Biological Station in eastern Ontario, Canada (45°37′N, 76°13′W) from 1996 to 1999.

ARTIFICIAL HIBERNATION SITES

Six 5 × 6 m enclosures were constructed at the edge of a beaver pond. Watersnakes could not climb the 75-cm high sheet metal walls that surrounded each enclosure and because the bottom of the walls were buried, they could not go under them. Each enclosure had a pond (approximately 3 × 3 × 1 m) stocked with minnows. Some replanting hastened regeneration of natural vegetation inside enclosures. Perimeter electric fencing discouraged mammals from entering enclosures, whereas birds were deterred by flagging tape tied to a monofilament line strung above the enclosures. Although predators were never observed in enclosures, we could not be certain that snakes were never subjected to predation.

Each enclosure contained a den constructed by excavating a hole approximately 1 m deep. The adjacent pond maintained a water table that resulted in standing water at the bottom of each excavation. Cement blocks stacked in each hole enclosed a space approximately 40 × 40 × 50 cm. The top of the enclosed 'box' was covered with a concrete paving stone. The lower half of each den was loosely filled with broken blocks, sticks, etc. to provide substrate and facilitate movement by snakes. This material extended well above the water table, allowing snakes to be wet or dry. An entrance to each den was constructed using paired paving stones separated by steel rods, creating a space approximately 2 cm in height from the interior to the exterior of the den. Styrofoam sheets 5 cm thick were used to insulate the sides, top, and entrance of each den. Finally, topsoil was mounded over dens and den entrances to a depth of 30–100 cm. A thermocouple in the centre of each den with leads running through den entrances allowed measurement of internal temperatures.

Preliminary trials revealed that, although neonates entered dens, their apparent urge to disperse often resulted in them leaving dens even as the weather deteriorated. To keep neonates in dens over winter and to facilitate their capture the following spring, nylon mesh bags were used to enclose each den entrance. This allowed neonates to move in and out of den entrances, but not to depart from dens. Neonates sometimes remained in the bags outside dens in fair weather, but retreated into dens as temperatures dropped. This experimental design required neonates to hibernate communally. It is unknown whether neonatal watersnakes naturally hibernate communally, although adults occasionally hibernate together (G.P. Brown, personal communication).

MEASUREMENT OF GROWTH AND SURVIVAL

Neonates were obtained from wild-caught females that gave birth in the laboratory in 1997, 1998, and 1999. Some females had mated prior to capture while others mated in captivity. Ten offspring were chosen from each of 24 litters in 1997 and 10–12 offspring from each of 23 litters in 1998. Offspring were selected randomly except to include equal numbers of males and females within litters to the extent possible. In 1999 we used 30 complete litters ranging from four to 32 offspring. Neonates were marked by a PIT tag or by clipping a unique combination of ventral scales. All neonates chosen from a litter were placed in the same enclosure. The number of litters per enclosure per year varied from four to eight. Once neonates were released in enclosures their movement within enclosures was unrestricted. Any feeding relied on prey occurring naturally within enclosures and on minnows stocked in ponds. Some snakes grew between being released and hibernation (see Results), so food was available.

For 2 weeks beginning in late September, just prior to the start of hibernation by adult watersnakes in the wild (Brown & Weatherhead 2000), neonates were recaptured by visual searches and by scanning for PIT tags. Remains of many snakes that had died were found but could only be identified if they had been PIT tagged. Any snakes not accounted for were assumed to have died. Probability of recapture was independent of whether a snake was scale clipped or PIT tagged ($\chi^2 = 0{\cdot}13$, d.f. = 1, $P = 0{\cdot}71$). Recaptured individuals were re-measured and put into dens. Temperatures inside dens were measured monthly from October to April in 1997 and 1999. More frequent measurement was unnecessary because dens were buffered from above-ground fluctuations in temperature. Ambient temperatures were recorded at a nearby weather station at the Queen's University Biological Station.

Beginning in mid-March, mesh bags were checked daily to collect neonates as they emerged from hibernation. Each snake was re-measured and its emergence date recorded. Monitoring continued until mid-June, well after the last neonate had emerged. We assumed that neonates that did not emerge died during hibernation. In 1998 and 1999, dens were opened in late summer by excavating and removing the top paving stones. Some remains were recovered and identified if PIT tagged, but because excavation was incomplete, many individuals remained unaccounted for. Because the mesh bags precluded snakes from leaving the dens, we are confident that snakes that did not emerge in spring perished over the winter. Neonates were released where their mothers were captured either following emergence or after use in a study on juvenile growth.

BEHAVIOURAL AND MORPHOLOGICAL MEASURES

Neonates were weighed and snout–vent length (SVL) measured within 48 h after birth. Changes in mass during the pre-hibernation and hibernation periods were determined both as absolute values and as proportions of mass at birth or mass prior to hibernation, respectively. Body condition was estimated as residuals from a regression of ln-transformed mass on ln-transformed SVL. Swimming speed was measured by 'chasing' neonates the length of a trough of water 2 m long and 14 cm wide maintained at 25 °C. Each individual was tested twice and its burst speed determined as the faster of the two trials. Swimming speed relative to body length was calculated using residuals from a regression of speed on SVL ($r = 0{\cdot}32$, $P < 0{\cdot}0001$).

STATISTICAL ANALYSIS

Data were first analysed without considering which litter individuals were from, using logistic regression with status (survived/did not survive) as the binary response variable, and offspring traits as quantitative predictor variables. Analyses were also performed using mean traits of individuals that survived and did not survive within litters, using the general linear model procedure (PROC GLM) in SAS (SAS 1999), with the proportion of offspring surviving as the response variable and mean traits of offspring as predictor variables. Because the two methods produced results that were qualitatively the same in all but one case, only results of analyses based on individuals are presented for one important reason. Our interest is in how individual phenotypes affect survival. Within-litter variation in SVL and mass is almost as extensive as variation among litters, accounting for 72% and 63% of among-litter variation, respectively (Weatherhead *et al.* 1999). Thus, use of litter means masks much of the variation of interest.

Analyses were carried out using SAS statistical software (SAS 1999). Interaction terms among all variables were dropped from logistic regression models when not significant. Coefficients of logistic regressions (β) and Wald χ^2 values were obtained from Type III SS results. Goodness-of-fit of logistic models was examined using the Hosmer and Lemeshow test (Hosmer & Lemeshow 2000). In the three cases (of 10) where the fit of models was poor, transformations did not improve the fit of the models. We did not run alternative models because we needed to include main effects and other variables that could have confounded our results (e.g. year). Thus, we simply report the results of these models but indicate where the fit was poor. Statistical significance was assessed at $\alpha = 0{\cdot}05$.

Results

We released a total of 903 neonatal watersnakes into enclosures, of which 591 (65·4%) were recaptured and put into dens. An additional 47 neonates (from three litters) born late in the season were put directly into dens. Of all snakes put into dens, 302 (47·3%) emerged in the spring. Combining survival rates from both phases of the experiment, the estimated survival of snakes from birth to the following spring was 31%.

PRE-HIBERNATION SURVIVAL

More snakes survived during pre-hibernation in 1997 than in other years (χ^2 = 75·96, d.f. = 2, P < 0·001). Therefore, we included year as a categorical variable in analyses of phenotypic effects. Neonates in enclosure 5 were more likely to survive through the pre-hibernation period (χ^2 = 19·37, d.f. = 5, P = 0·002). Excluding data from enclosure 5, there were no differences in pre-hibernation survival in the remaining enclosures (χ^2 = 6·10, d.f. = 4, P = 0·19). There were no recorded differences among snakes in this enclosure that appeared to account for the difference in survival. Because controlling for enclosure and its interactions with other variables made analyses cumbersome, we excluded data from enclosure 5 from analyses of pre-hibernation survival, although doing so did not qualitatively alter results.

Pre-hibernation survival was higher for snakes released in enclosures later (β = 0·09, χ^2 = 80·42, d.f. = 1, P < 0·0001). Therefore, we included the date snakes were put in enclosures (expressed as number of days since 1 January) to control for this effect in subsequent analyses.

Several attributes of neonates enhanced survival during the pre-hibernation period (Table 1). Neonates that were longer and heavier at birth were more likely to survive (Table 1). The larger effect size for mass and the better fit of the model, suggests that mass was more important to pre-hibernation survival than length (Table 1), although the two variables are highly correlated (r = 0·83, P < 0·0001). There was a strong trend for neonates in better body condition at birth to have higher survival (Table 1). Neonates that swam faster were more likely to survive, even after controlling for the effects of SVL (Table 1). The lack of relationship between swimming speed and either absolute change in mass ($F_{1,432}$ = 0·96, P = 0·33) or change in mass relative to body size ($F_{1,432}$ = 0·07, P = 0·78) suggests that faster snakes did not survive better as a result of higher foraging success.

OVER-WINTER SURVIVAL

Survival differed significantly among years (44·5%, 37·9%, and 53·0%, in 1997, 1998, and 1999, respectively; χ^2 = 8·68, d.f. = 2, P = 0·01) due to higher survival of neonates in 1999. Survival of neonates in 1997 and 1998 did not differ (χ^2 = 1·34, d.f. = 1, P = 0·25). Mean (± SD) outside air temperatures during hibernation (15 October to 31 March) were 0·04 (± 5·58) °C in 1997, −0·86 (± 7·64) °C in 1998 and 1·34 (± 7·23) °C in 1999. Mean air temperature was significantly higher in 1999 when survival was highest, than in 1998 when survival was lowest ($F_{2,431}$ = 3·69, P = 0·03). We included year as a categorical variable in analyses of phenotypic effects on survival.

Survival of neonates also differed among dens (χ^2 = 18·35, d.f. = 5, P = 0·003) as a consequence of low survival in den 2; neonates in the remaining dens did not differ significantly in overall survival (χ^2 = 2·77, d.f. = 4, P = 0·60). There were no obvious phenotypic differences between neonates in den 2 and those in other dens. Across dens, the overall mean (± SD) internal temperature was 2·9 (± 3·7) °C in 1997 (n = 28, range −0·1–10·0 °C) and 4·3 (± 4·3) °C in 1999 (n = 20, range 0–11·6 °C). Temperatures were not significantly different among dens in 1997 ($F_{5,22}$ = 0·06, P = 0·99) or in 1999 ($F_{3,16}$ = 0·00, P = 0·99), so lower survivorship in den 2 was not a consequence of it being colder. To avoid analytical problems associated with controlling for den effects and their interactions, we excluded data from den 2 from further analyses but note that analyses with and without those data were qualitatively similar.

Snakes were captured in enclosures and put into dens over a period of approximately 2 weeks. Snakes placed in dens later were more likely to survive (β = 0·06, χ^2 = 8·17, P = 0·004). The time snakes went into dens

Table 1. Probability of a neonatal watersnake being recaptured prior to hibernation based on its phenotype. Results are based on logistic regression with β representing the coefficient from the regression for the phenotypic variable. Means (SD) for phenotypic data are uncontrolled for other variables in the models. Condition was calculated as the residuals from a regression of ln-transformed mass on ln-transformed snout–vent length (SVL). Relative speed represents swimming speed relative to body length, calculated as residuals from a regression of speed on SVL. The odds ratio indicates the increase in probability of survival with every unit increase in the phenotypic variable. Goodness-of-fit of models use the Hosmer and Lemeshow test (Hosmer & Lemeshow 2000). *Indicates the regression model was not a good fit to the data

	Mean value (± SD)							
Offspring trait	Survived	Died	n	Odds ratio (95% CI)	β	Wald χ^2 (d.f. = 1)	P	Goodness of fit of logistic model (d.f. = 8)
SVL (cm)	16·9 (1·0)	17·2 (1·0)	715	1·27 (1·05, 1·53)	0·24	6·04	0·014	21·37*
Mass (g)	4·3 (0·6)	4·3 (0·6)	715	1·48 (1·12, 1·96)	0·39	7·44	0·006	13·62
Body condition	0·003 (0·35)	−0·103 (0·33)	715	1·61 (0·96, 2·69)	0·47	3·24	0·072	12·40
Speed (m s^{-1})	0·62 (0·15)	0·59 (0·16)	711	5·18 (1·50, 17·84)	1·64	6·78	0·009	16·38*
Relative speed	0·014 (0·14)	−0·031(0·15)	711	3·63 (0·99, 13·28)	1·28	3·78	0·052	17·82*

Table 2. Probability of a neonatal watersnake surviving hibernation based on its phenotype. Results are based on logistic regression with β representing the coefficient from the regression for the phenotypic variable. Means (SD) for phenotypic data are uncontrolled for other variables in the models. Condition was calculated as the residuals from a regression of ln-transformed mass on ln-transformed snout–vent length (SVL). Relative speed represents swimming speed relative to body length, calculated as residuals from a regression of swimming speed on SVL. Odds ratio indicates the increase in probability of survival with every unit increase in the phenotypic variable. Goodness-of-fit of models use the Hosmer and Lemeshow test (Hosmer & Lemeshow 2000). All models provided acceptable fits to the data

Offspring trait	Mean value (± SD) Survived	 Died	*n*	Odds ratio (95% CI)	β	Wald χ^2 (d.f. = 1)	*P*	Goodness of fit of logistic model (d.f. = 8)
SVL (cm)	17·1 (1·0)	16·8 (1·1)	514	1·30 (1·08, 1·56)	0·26	7·63	0·006	6·15
Mass (g)	4·4 (0·6)	4·2 (0·6)	514	1·68 (1·25, 2·26)	0·52	11·95	0·0005	6·26
Body condition	0·027 (0·33)	−0·034 (0·34)	514	2·00 (1·16, 3·43)	0·69	6·23	0·013	6·09
Speed (m s^{-1})	0·64 (0·13)	0·62 (0·16)	513	4·45 (1·25, 15·81)	1·49	5·31	0·021	11·29
Relative speed	0·025 (0·12)	0·015 (0·15)	513	2·90 (0·75, 11·22)	1·07	2·39	0·12	9·94

was not significantly related to any phenotypic traits after controlling for year (all $P > 0·10$), so the relationship between survival and time in hibernation was not confounded by any relationship between phenotypes and the time that snakes went into hibernation (e.g. had faster babies been harder to capture they would have been put in dens later). We included timing of placement in hibernation (expressed as the number of days since 1 January) in further analyses.

Controlling for year and time in hibernation, neonates that were longer and heavier were more likely to survive (Table 2). When length and mass were included in the same analysis, only mass significantly affected survival (SVL: $\chi^2 = 0·12$, d.f. = 1, $P = 0·73$; mass: $\beta = 0·60$, $\chi^2 = 4·60$, d.f. = 1, $P = 0·03$). Neonates in better condition had higher survival (Table 2). Faster neonates were more likely to survive, but after controlling for SVL, locomotive performance did not affect survival (Table 2).

Most (86%) snakes lost mass during the pre-hibernation period. Mean (± SD) size of snakes at birth was 4·3 (± 0·7) g and 4·1 (± 0·6) g just prior to hibernation. After controlling for year and days in hibernation, snakes that lost absolutely less mass (or gained absolutely more) prior to hibernation did not have a higher probability of survival ($\chi^2 = 0·42$, $P = 0·51$). Mean (± SD) change in mass before hibernation of individuals that survived was 0·24 (± 0·19) g and that died was 0·24 (± 0·24) g.

Across all individuals, loss in mass during hibernation varied from 0 to 1·3 g, accounting for 0–25% of their mass entering hibernation (mean = 8·0%, SD = 5·3%). After controlling for year and days in hibernation, absolute mass loss during hibernation increased with SVL ($F_{1,214} = 6·00$, $P = 0·02$) and mass ($F_{1,214} = 12·58$, $P < 0·0005$). After controlling for year and days in hibernation, mass loss relative to mass entering hibernation did not vary with SVL ($F_{1,214} = 0·08$, $P = 0·78$) or mass ($F_{1,214} = 0·24$, $P = 0·62$).

Sexual dimorphism in mass of watersnakes at birth is small (average difference approximately 0·1 g), particularly relative to variation in mass among all neonates (Weatherhead *et al.* 1998, 1999). Not surprisingly, over-winter survival did not differ between the sexes ($\chi^2 = 0·99$, d.f. = 1, $P = 0·32$).

Contrary to previous data from the same population (Weatherhead *et al.* 1999), mean neonatal size of watersnakes decreased with birth date of the litter ($r = -0·34$, $n = 34$, $P = 0·01$). Thus, higher survival of larger neonates could be associated with them having been born earlier, rather than an effect of size *per se*. However, survival was unrelated to timing of birth ($\chi^2 = 0·07$, d.f. = 1, $P = 0·80$), so size alone accounted for enhanced over-winter survival of larger neonates.

Discussion

Low survival of neonates during hibernation has been reported for several snake species (Gregory 1982; Bronikowski 2000). Our empirical measures of neonatal survival in enclosures and artificial hibernacula (31%) fall within the range estimated by Brown & Weatherhead (1999) for free-ranging watersnakes in the same population. This level of survival, combined with the fact that snakes in our study enclosures and hibernation sites had to deal with many of the same factors confronted by neonates in the wild (i.e. avoiding starvation, freezing), gives us confidence that our results reasonably reflect the natural state for neonatal watersnakes. Given high mortality, traits that influence survival should be under strong selection and ultimately, this selection should shape the trade-off made by females between their fecundity and survivorship of their offspring. We review our specific results, and then return to the issue of trade-offs.

Our results supported the general view that for offspring, 'bigger is better' (reviewed by Packard & Packard 1988). Larger neonates and neonates that were heavier relative to their body length were more likely to survive between birth and hibernation, and over winter. Smaller neonates may have lower survival during hibernation because relative mass loss during winter is typically greater for smaller animals (Gregory 1982). Proportionally, mass loss during hibernation did not vary with body size. Larger neonates lost absolutely more mass during hibernation, possibly because metabolic costs during hibernation are higher for larger individuals (Bennett 1982). Consequently, for mass loss during hibernation to explain differences in survival among large and small neonates, the consequences for smaller neonates of losing a given proportion of their mass must be more detrimental for survival than the same relative mass loss for larger neonates. Dehydration might also contribute to mortality during hibernation (Costanzo 1989; Prior & Shilton 1996), but because dens had standing water in the bottom, dehydration should not have been a problem in our study.

Despite the survival advantage of being heavier at birth, we found no evidence that weight gain (or loss) prior to hibernation affected over-winter survival. This result differs from that of Bronikowski (2000), who found that neonatal *T. elegans* that survived the winter in captivity gained significantly more mass during the pre-hibernation period than those that died. We did find that neonates in better condition at birth had higher survival, particularly during hibernation. Similar to many other reptiles, watersnakes are born with internal yolk reserves that fuel their activity early in life (Gregory 1982; Bobyn & Brooks 1994). If condition reflects the size of yolk reserves, then those reserves may be important in sustaining watersnakes for the first 6 months of their life. Bobyn & Brooks (1994) found that hatchling snapping turtles *Chelydra serpentina* (Linnaeus) with larger yolk reserves had higher survival in captivity. Bellairs, Griffiths & Bellairs (1955) suggested that the yolk reserves of neonatal *Vipera berus* (Linnaeus) provide enough energy for several months of activity and for survival over winter.

Results for locomotive performance were ambiguous. Although faster snakes survived better during prehibernation, the fit of the model was poor, whereas during hibernation, survival was unrelated to swimming speed. Under natural conditions, faster individuals should be more successful avoiding predation and capturing prey (Miller, Packard & Packard 1987; Janzen, Tucker & Paukstis 2000). Predators were largely or completely excluded from our enclosures, so any benefit of increased performance for survival prior to hibernation seems unlikely to have been associated with predator avoidance. Also, the lack of relationship between change in mass prior to hibernation and swimming speed suggested that faster individuals were not more successful in capturing prey in enclosures.

Contrary to our prediction that earlier-born snakes should be more likely to survive, and empirical evidence in other reptiles supporting this prediction (Olsson & Shine 1997), neonates that spent less time in enclosures between birth and hibernation were more likely to survive. Most snakes lost mass prior to hibernation, suggesting they fed little during this period. Whether this pattern is typical of neonatal watersnakes prior to hibernation under natural conditions is unknown, although fasting prior to hibernation is common in many reptiles (Gregory 1982; Charland 1989). Timing of birth had no effect on probability of survival over winter. However, most neonates that entered hibernation were those born late because early born snakes survived poorly in the pre-hibernation period. Consequently, there was little variation in timing of birth among individuals put into hibernation. These results might indicate that it is advantageous for female watersnakes to give birth as late in the season as possible. This would require either that the factors that cause mortality in the autumn are less prevalent the following spring, or that neonates mature during hibernation so they are less vulnerable to those factors in the spring. Otherwise, any advantage from being born late might be lost the following spring. Resolving this issue will require determining the fate of neonates after emergence from hibernation.

Given the factors we have identified that affect survival of neonatal watersnakes, what are the implications for female reproductive strategies? Collectively, our results suggest that females would maximize survival of individual offspring by producing larger offspring that are in better body condition and born late in the season. As discussed above, the value of giving birth late depends on the extent to which this simply delays exposure of neonates to various mortality factors. Delaying birth would also limit the time available for neonates to locate suitable hibernation sites, a cost that might outweigh any survival advantage prior to hibernation.

Independent of when a female gives birth, maximizing offspring survival by increasing their size and body condition could only be accomplished at the expense of offspring number. In general then, the best strategy for a female should be to optimize the trade-off between offspring size and number such that the number of offspring that survive is maximized (Smith & Fretwell 1974). Whatever the optimal size, there should be 'consensus' among females, evidenced by uniformity of offspring size. Watersnakes show no such consensus (Weatherhead *et al.* 1999), however, as is true for many animals (Bernardo 1996). Variation in offspring size is substantial and much of that variation is evident within litters. Physiological constraints on provisioning might account for some of the variation among females (Bernardo 1996; Weatherhead *et al.* 1999), but would still leave within-female variation unexplained. It is possible that allocating substantial resources to some offspring and much less to others is a form of bet hedging that maximizes female fitness over the long-term when dealing with variable and unpredictable environments. Better understanding of female reproductive strategies must await data on long-term survival of neonates produced in multiple years.

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