

Maternal investment and delayed feeding in neonatal Lake Erie watersnakes: a life-history strategy

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Abstract

Neonatal growth can have lasting consequences on survival and reproduction. In many taxa, larger, faster growing neonates experience higher survival, reach sexual maturity more rapidly, and achieve higher lifetime fecundity. In contrast to their closest relatives, Lake Erie watersnakes grow slower, mature later, and may delay feeding until after their first hibernation. To determine if Lake Erie watersnakes do indeed delay feeding until after their first hibernation, we compared age class 0 (between birth and first hibernation) and age class 1 (emergence from hibernation and through the first full season) snakes in the field and in the laboratory. In the field, only 0.6% of pre-hibernation neonates were found to contain prey, while 11.9% of post-hibernation neonates contained prey. During captive feeding experiments, the probability of eating was positively correlated with age (binary logistic regression, Wald $\chi^2_1 = 25.354$, $P < 0.001$). To clarify the underlying mechanism for delayed feeding, we compared neonatal yolk and fat reserves among species with delayed feeding (Lake Erie watersnakes, Graham's crayfish-eating snakes), species that commence feeding immediately after birth (common gartersnakes, Dekay's brown snakes) and a species falling between these extremes (queen snakes). Like Lake Erie watersnakes, Graham's crayfish-eating snakes contained large energy reserves (yolk + fat body mass to carcass mass ratio = 0.39 and 0.24, respectively), common gartersnakes and Dekay's brown snakes lacked measurable reserves (0.00), and queen snakes contained intermediate reserves (0.17). Taken together, this evidence suggests that neonatal Lake Erie watersnakes do delay feeding until after their first hibernation and contain large energy reserves at birth to facilitate this behavior. While most snake life-history studies have focused on the trade-off between offspring size and number, Lake Erie watersnake females invest large amounts of energy in offspring condition.

Introduction

Early growth impacts later life-history characteristics such as survival and reproduction for many taxa (Case, 1978; Jayne & Bennett, 1990; Bronikowski, 2000; Madsen & Shine, 2000). Small neonatal size in mammals puts young at a higher risk of mortality, and juvenile mortality is one of the greatest predictors of other life-history traits like gestation length, litter size and age at maturity (Promislow & Harvey, 1990). In doctorfish *Acanthurus chirurgus*, faster growing larvae are more likely to "settle" on the reef and be recruited into the breeding population than slower growing larvae. Consequently, pre-settlement growth has a disproportionate effect on lifetime fitness (Bergecius *et al.*, 2002). Early growth in saltwater crocodiles *Crocodylus porosus*, regardless of initial hatching size, can be used to predict the risk of failing to thrive. Smaller hatchlings that exhibit compensatory growth during their first 24 days of

life can avoid early death due to "runtism" (Brien *et al.*, 2014).

Studies have shown the effects of early growth are especially pronounced in snakes, which grow continuously and can be long-lived (Shine & Bonnet, 2009). However, knowledge of neonatal life-history characteristics such as feeding, growth and survival are sparse in snakes (Rossman, Ford & Seigel, 1996; Gibbons & Dorcas, 2004). It is generally accepted that neonatal snakes have low survival rates (Shine & Bonnet, 2009; but see Pike *et al.*, 2008 for contrasting evidence), and larger, faster growing neonates have higher survival than their smaller littermates (Jayne & Bennett, 1990; Kissner & Weatherhead, 2005). Early growth can also increase later growth and fitness through a "silver spoon" advantage, where animals born into favorable conditions experience rapid early growth in their first year, leading to greater lifetime growth and final body size (Madsen & Shine, 2000).

In North America, natricine snakes represent a widely distributed radiation of *c.* 50 species (watersnakes, gartersnakes and allied taxa) for which knowledge of neonatal life-history characteristics is lacking (Rossman *et al.*, 1996; Gibbons & Dorcas, 2004). The Lake Erie watersnake, *Nerodia sipedon insularum*, is a New World natricine endemic to the islands of western Lake Erie. The Lake Erie watersnake was previously under federal protection because of precipitous declines in the 20th century but was delisted due to recovery (Department of the Interior & U.S. Fish and Wildlife Service, 1999, 2011; King, Queral-Regil & Stanford, 2006a; Stanford, King & Wynn, 2010). It remains listed as threatened in Ohio (Ohio Department of Natural Resources 2016).

Some natricine species begin eating and growing rapidly immediately following birth (Carpenter, 1952; Fitch, 1965; Williams, 1969; Savitzky, 1989; O'Brien, 2014) and become sexually mature by their second year (Rossman *et al.*, 1996; Stanford & King, 2004; Tuttle & Gregory, 2012). In contrast, Lake Erie watersnakes grow more slowly and delay sexual maturity until their third or fourth year (King, 1986; Stanford, 2012). Although dietary analysis of this species has been extensive (King, Ray & Stanford, 2006b), prey were never detected among neonates in the fall prior to their first hibernation. Additionally, growth does not appear to commence until the following spring (King, 1986; King *et al.*, 2016). This suggests that in contrast to other New World natricines, Lake Erie watersnakes delay feeding and growth until their first full year. Once feeding commences, young Lake Erie watersnakes can consume an average of 117% of their own body weight over a period as short as 5 days (Jones *et al.*, 2009). In light of this voracious prey consumption and the knowledge that larger, faster growing neonatal snakes tend to be more successful than their smaller counterparts, the possibility that Lake Erie watersnakes delay feeding warrants further investigation.

A few studies have documented delayed feeding in neonatal snakes. Meadow vipers *Vipera ursinii ursinii* do not feed until prey become available in the spring following their first hibernation (Baron *et al.*, 2010). Kissner & Weatherhead (2005) documented fall feeding and growth in only a small proportion (14%) of newborn northern watersnakes *Nerodia sipedon sipedon*, a conspecific of the Lake Erie watersnake. A particularly interesting study documented a dichotomy in two congeneric species (Waters & Burghardt, 2005): chemosensory prey preference experiments revealed that Graham's crayfish-eating snake *Regina septemvittata* and queen snake *R. grahamii* neonates exhibit very different feeding behaviors. Queen snakes readily ate within the first 21 days after birth, whereas most (116/123, 94.3%) Graham's crayfish-eating snake refused to eat until after emergence from their first hibernation. If feeding is delayed until the spring, snakes must utilize energy from stored fat reserves to maintain metabolic processes during the fall and winter. When comparing fat reserves between newborns of the two species, Waters & Burghardt (2005) found neonatal Graham's crayfish-eating snakes had a higher combined mass of yolk and fat bodies that was absorbed more slowly than in queen snakes. Thus, they hypothesized newborn Graham's crayfish-eating snakes must use these energy

reserves for maintenance instead of investing energy in foraging and growth before entering their first hibernation.

In this study, we performed a thorough investigation of delayed feeding in neonatal Lake Erie watersnakes in two parts. First, we determined when feeding commences through field prey studies and captive feeding trials. Second, we quantified the relative fat stores available to neonatal Lake Erie watersnakes and four other natricine species. We hypothesized that newborn Lake Erie watersnakes contain large reserves of yolks and fat bodies that allow them to delay feeding until the spring following their first hibernation.

Materials and methods

Study area

The Lake Erie watersnake is endemic to the islands of the Western Basin of Lake Erie, which is divided between Ohio, US and Ontario, Canada. Lake Erie is the southernmost, shallowest and warmest of the Great Lakes. The area's climate is characterized as temperate and humid, with an average annual temperature of *c.* 10°C and average precipitation of 86.4 cm (Herdendorf, 1987).

Field prey data

Neonates were collected from May to October 2014 during area-constrained searches on five islands: Kelleys, South Bass, Middle Bass, North Bass and Gibraltar. Snakes were easily classified into one of two age classes based on size (King *et al.*, 2016). Age class 0 snakes are those that are born in the fall and have not yet hibernated; they are then classified as age class 1 snakes when they emerge the following spring. Snakes were measured for snout-vent length and mass, classified by sex, and palpated for prey. If a prey item was detected, it was recovered from the snake by massaging the body in a posterior–anterior direction until the snake voluntarily regurgitated. After processing, snakes were immediately returned to their place of capture or retained for use in feeding experiments. Individuals containing prey were not used in feeding experiments. We calculated the proportion of snakes containing prey for each age class.

Feeding experiments

Laboratory feeding trials were performed in conjunction with field sampling, which allowed us to study larger numbers of snakes more frequently than would be possible in the field. Wild-caught snakes were individually housed at the F. T. Stone Laboratory research building (South Bass Island, Ohio) in 40 L aquaria with newspaper substrate, a water dish and a plastic shelter. Heat tape at one end of the aquaria provided a thermal gradient that ranged from the ambient air temperature (15–21.5°C) to a maximum of 28°C. After collection, snakes were allowed to acclimate inside their enclosures for *c.* 24 h before beginning feeding trials.

Shiners *Notropis* spp., known prey of the Lake Erie watersnake (King, 1993), were obtained from local bait shops and by seining. Fish had total lengths less than 40 mm to ensure

small watersnakes could consume them. One or two shiners were offered to each snake based on fish availability; the number of shiners offered to each snake was kept constant within each trial. Shiners were placed in a water-filled clear glass dish within each snake's aquarium. Feeding trials were started in the early afternoon, and the presence or absence of fish in the tank was recorded the following morning (mean time of exposure to prey = 21.2 h). Snakes were marked and returned to their site of capture within 24 h of the trial's termination.

Although housed and tested individually, snakes were considered to be in the same trial if they were tested during the same week. Trials consisted of 4–16 snakes. Age class 1 neonates were tested in 11 feeding trials from May 15 to June 12, 2014, and age class 0 neonates were tested in five feeding trials from September 13 to October 4, 2014. Ages of snakes are reported in "growth days." Lake Erie watersnakes are born in a synchronous pulse beginning around August 15 (King *et al.*, 2016). Therefore, the age in growth days for wild-caught age class 0 snakes (birth date unknown) was calculated as the number of days between August 15 and the date of the feeding trial. Lake Erie watersnakes are active from approximately April 27 to October 17 (King *et al.*, 2006a). Thus, the age in growth days of age class 1 snakes was the number of days between April 27 and the day of the feeding trial plus 63, the number of days between birth (August 15) and the start of hibernation (October 17). To estimate when feeding began, we performed logistic regression analysis with age in growth days as the covariate and feeding outcome as the response variable (0 = did not consume prey, 1 = did consume prey). To test for significance of the logistic regression, we used a Wald test with $\alpha = 0.05$. Analyses were performed in IBM SPSS v. 22.0 (Armonk, NY, USA).

Dissection of neonates for quantification of fat reserves

To quantify the energy reserves available to newborn Lake Erie watersnakes, we dissected nine specimens following the methods of Waters & Burghardt (2005). Specimens were stillborns born to wild-caught females in 2012 and were preserved in 70% ethanol. Only specimens with no obvious abnormalities were used, and all neonates came from separate females to control for litter effects. An incision was made on the ventral surface from the cloaca to the head, exposing the body cavity (Fig. 1). If a yolk and/or fat bodies were present, they were

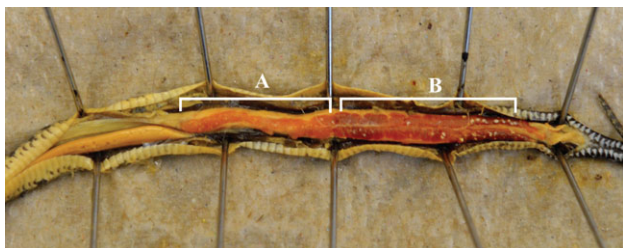


Figure 1 Dissected stillborn Lake Erie watersnake showing light colored yolk (a) overlain by darker fat bodies (b).

removed and placed in separate plastic weigh boats. The yolk, fat bodies and remaining carcass were then placed in a drying oven at 50°C for 6 days. On the sixth day the dried parts were removed, weighed to the nearest milligram, and then placed back into the drying oven. This was repeated daily until there was no change in mass (± 10 mg) for 3 consecutive days. For comparison, preserved neonates of two other New World natriicine species, the common gartersnake *Thamnophis sirtalis* ($n = 6$) and Dekay's brown snake *Storeria dekayi* ($n = 6$), were also dissected. These specimens were obtained from the R. B. King research collection and consisted of stillborns with no obvious abnormalities that had been born to wild-caught mothers captured in DeKalb County, Illinois.

Dry ratios of (1) yolk mass to carcass mass; (2) fat body mass to carcass mass; and (3) combined yolk + fat body mass to carcass mass were calculated for Lake Erie watersnakes and obtained from Waters & Burghardt (2005), (Fig. 5) for Graham's crayfish-eating snakes and queen snakes. None of the common gartersnake or Dekay's brown snake neonates possessed any yolk or fat bodies, resulting in a ratio of 0 when comparing the relative masses of the energy reserves to the carcass for all of these specimens. A non-parametric analysis of variance (Kruskal–Wallace test) was used to compare the ratio of yolk + fat body mass to carcass mass among the five species. Multiple comparisons between pairs of species were then performed using independent-samples Mann–Whitney *U* tests with a Bonferroni correction to avoid an inflated Type I error rate (overall $\alpha = 0.05$).

Results

Field prey data

From May 13 to October 18, 2014, 155 age class 0 and 570 age class 1 neonates were collected. Only one age class 0 snake was found digesting a prey item (September 12), making the proportion of age class 0 neonates containing prey 0.6%. Sixty-eight age class 1 snakes contained prey over the 5-month period for a proportion of 11.9%. Prey in age class 1 snakes was lacking or rare in early and mid-May samples (prey were recovered from 0/28 and 1/51 snakes, respectively) but occurred more frequently thereafter (Table 1).

Feeding experiments

A total of 117 neonates were tested during 16 feeding trials: 49 age class 0 snakes and 68 age class 1 snakes. When trials were pooled by week, this resulted in four testing periods for age class 1 snakes from May 11 to June 14 and three testing periods for age class 0 snakes from September 8 to October 5. The proportion of snakes eating at least one fish during each trial ranged from 0.10 to 1.00 (Table 1). There was a notable increase in the proportion of snakes eating as age in growth days increased (transitioning from age class 0 to age class 1; Fig. 2). Logistic regression analysis revealed a significant positive relationship between age in growth days and the probability of eating during feeding trials (Wald $\chi_1^2 = 25.354$, $P < 0.001$).

Table 1 Results of field observations and lab feeding trials for age class 0 and age class 1 Lake Erie watersnakes (age classes differentiated by the horizontal line).

Week	Age in growth days	Field observations		Lab feeding trials	
		Snakes with prey/ Num. caught in field	Proportion with prey	Snakes eating/ Num. tested	Proportion eating
8–14 September	24	1/40	0.03	2/20	0.10
15–21 September	31	0/24	0.00	–	–
22–28 September	38	0/43	0.00	2/10	0.20
29 Sep–5 October	45	0/27	0.00	3/19	0.16
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11–17 May	87	0/28	0.00	2/14	0.14
18–24 May	94	1/51	0.02	7/19	0.37
25–31 May	93	17/103	0.17	21/25	0.84
1–7 June	108	12/127	0.09	–	–
8–14 June	115	3/26	0.12	10/10	1.00
Remainder of season	116–290	35/235	0.15	–	–

Observations were grouped by week, and age in growth days was calculated for the first day of the week.

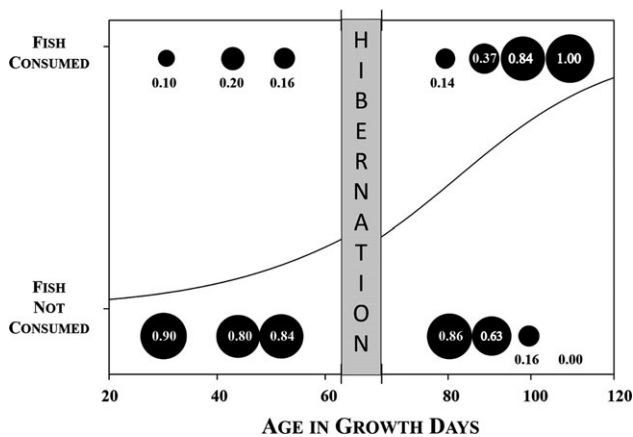


Figure 2 Feeding responses of Lake Erie watersnakes as a function of age in growth days. The diameters of the circles are scaled to represent the proportion of snakes exhibiting each response during a feeding trial period. The binary logistic regression function, $P = e^{-4.358 + 0.53x} / (1 + e^{-4.358 + 0.53x})$, estimates the proportion of snakes expected to eat as a function of age. The vertical gray bar represents the period of hibernation from October 17 to April 27, after which snakes transition from age class 0 to age class 1.

Dissection of neonates for quantification of fat reserves

Relative weights of yolks, fat bodies and carcasses varied among species (Table 2). None of the common gartersnake or Dekay's brown snake neonates possessed any yolk or fat bodies, resulting in a value of 0 for all of the ratios comparing relative masses of energy reserves and carcasses. Lake Erie watersnakes had the highest combined yolk + fat body mass to carcass mass ratio with an average of 0.39 (SE = 0.131). This ratio differed significantly among the five species (Kruskal–Wallace $\chi_4^2 = 24.79$, $P < 0.001$), and multiple comparisons revealed three homogeneous subsets: [Lake Erie watersnake +

Graham's crayfish-eating snake], [queen snake], [common gartersnake + Dekay's brown snake].

Discussion

Our results provide strong evidence for delayed feeding in age class 0 Lake Erie watersnakes. Only one age class 0 neonate was found containing prey in the field, and a very low proportion of age class 0 snakes consumed prey during laboratory feeding experiments (\bar{x} proportion = 0.15 in age class 0 vs. 0.59 in age class 1). The warm laboratory environment and readily available prey may explain why a higher proportion of age class 0 snakes ate during feeding trials than in the field. However, even under these conditions, far fewer age class 0 than age class 1 snakes consumed prey during feeding trials.

Our quantification and comparison of yolks and fat bodies in neonatal natricines may suggest the mechanism for delayed feeding. Lake Erie watersnakes had the highest energy reserves of the five species tested. Furthermore, the amounts of energy reserves available to newborns of each species corresponded to their different feeding strategies. Lake Erie watersnakes and Graham's crayfish-eating snakes had the largest relative fat stores, and both of these species appear to allocate these resources to maintenance during the fall while delaying feeding and growth until the following spring. In contrast, the common gartersnakes and Dekay's brown snakes had no yolk or fat bodies. These species are born earlier in the summer and grow significantly before entering hibernation (O'Brien, 2014). Queen snake neonates had energy reserves intermediate to the other two groups and seem to employ a hybrid survival strategy. They are born later than the common gartersnake and Dekay's brown snake, but they have lower energy reserves than the Lake Erie watersnake and Graham's crayfish-eating snake. It is not surprising that observations exist of age class 0 queen snakes consuming prey before their first hibernation (Waters & Burghardt, 2005). Although stillborns were used for our dissections, we are confident the results reflect the true amounts of yolks and fat bodies available to these species. None of the dissected neonates

Table 2 Relative masses of yolk/carcass, fat bodies/carcass, and combined yolk and fat bodies/carcass for neonates from five natricine species

Species	<i>N</i>	Yolk:Carcass, mean (sd)	Fat bodies:Carcass, mean (sd)	Combined:Carcass, mean (sd)
Lake Erie watersnake	8	0.29 (0.121)	0.11 (0.032)	0.39 (0.131) ^a
Graham's Crayfish-eating snake	4	0.05 (0.004)	0.19 (0.003)	0.24 (0.009) ^a
Queen snake	4	0.06 (0.004)	0.11 (0.028)	0.17 (0.023) ^b
Common gartersnake	6	0.00	0.00	0.00 ^c
Dekay's Brown snake	6	0.00	0.00	0.00 ^c

Common gartersnakes and Dekay's brown snakes did not contain any fat reserves, leading to relative masses of 0. Relative masses for queen snakes and Graham's crayfish-eating snakes were estimated from Figure 5 in Waters & Burghardt (2005). Superscripts indicate homogeneous subsets based on the Combined yolk + fat bodies:carcass ratio.

showed any visible deformities, and stillborn Lake Erie watersnakes still contained yolks and fat bodies. As the Lake Erie watersnake is a protected species, it did not seem prudent to sacrifice animals for this study when stillborns were readily available. However, future studies could utilize young snakes found dead in the field as a way to confirm these results.

In the congeneric northern watersnake, Kissner & Weatherhead (2005) directly measured neonatal overwinter survival in outdoor enclosures and found it varied from 40 to 53% for three annual cohorts. They also determined neonates that were longer, heavier, or in better condition were more likely to survive. Absolute loss of mass during hibernation did not differ between small and large neonates. However, relative loss of mass was much lower for larger snakes, meaning larger snakes lost less in relation to their total mass. In light of our results, we can hypothesize these larger snakes had larger amounts of yolk and fat reserves to sustain them through the winter, resulting in a more favorable condition upon egress.

Although delayed feeding sometimes occurs because of limited prey availability (such as the meadow viper, *Vipera ursinii ursinii*; Baron *et al.*, 2010), this is unlikely to be the case for the Lake Erie watersnake. Lake Erie watersnakes mainly prey upon the round goby *Neogobius melanostomus*, an invasive fish found in extraordinary numbers in the Western Basin of Lake Erie (Johnson *et al.*, 2005; Jones *et al.*, 2009). In addition to abundance, a prolonged spawning season ensures gobies small enough to be eaten by neonatal watersnakes are available throughout the fall (Macinnis & Corkum, 2000; Thompson & Simon, 2015). In the conspecific northern watersnake, Kissner & Weatherhead (2005) also found only a small proportion (14%) of age class 0 neonates gained mass (and presumably ate) before entering hibernation despite being provided with an abundance of small fish in their enclosures *ad libitum*.

Delayed feeding in Lake Erie watersnakes may be adaptive for other reasons. Considering the short time between birth and ingress and the sudden onset of cold spells in the Great Lakes region, snakes may be unable to thermoregulate sufficiently to digest prey, possibly resulting in sepsis. However, Lake Erie watersnakes digest prey rapidly (90% of prey digested after 20 h; Jones *et al.*, 2009), and adults have been found containing prey as late as mid-September (R.B. King, pers. obs.). Furthermore, the thermal inertia of Lake Erie moderates the climate of the islands, resulting in warmer fall temperatures than at sites farther inland (Schertzer *et al.*, 1987).

It is possible the lack of prey recovered from wild-caught age class 0 snakes reflects the need to improve foraging techniques over time. This is less likely to be true of our feeding trials as opportunities for prey to escape were restricted. At least some neonates are able to catch and consume prey soon after birth (two age class 0 neonates consumed prey during a feeding trial on September 14). However, we were unable to observe any stalking, capture attempts or other foraging behaviors because the snakes would hide under their shelters (for hours at a time) when we attempted to observe them interacting with the fish.

The dichotomy in neonatal feeding strategies demonstrated here among Lake Erie watersnakes and other natricine species is also present between some *Vipera* species. The meadow viper in France *Vipera ursinii ursinii* delays neonatal feeding until after the first hibernation (Baron *et al.*, 2010). In contrast, conspecific Hungarian meadow viper neonates *Vipera ursinii rakosiensis* show evidence of some growth, and presumably feeding, between birth and egress (Fig. 1 in Ujvari, Korsos & Pechy, 2000). Ujvari *et al.* (2000) also performed feeding experiments with age class 0 vipers and found them to readily consume prey, evidenced by large body mass gains in captive neonates during the winter. Parturition date does not seem to be the deciding factor for these species, as both give birth in late August or early September. Based on this evidence and our results, it is possible the meadow viper in France has larger energy reserves at birth than the Hungarian meadow viper, facilitating delayed feeding.

The variation in maternal provisioning and neonatal feeding we report has relevance to the larger topic of life-history variation. Within reptiles, research has focused on litter size vs. offspring size trade-offs and subsequent neonatal survival. At the extremes, females are expected to produce either a large litter of small offspring or a small litter of larger, more robust offspring (Stearns, 1992; King, 1993; Olsson, Wapstra & Olofsson, 2002; Radder *et al.*, 2007). The majority of these studies examine species whose young feed soon after birth. Therefore, conclusions may be less applicable to species exhibiting the delayed feeding behaviors we describe. For example, manipulation of yolk levels in hatchling jacks dragons *Amphibolurus muricatus* did not affect their size, physiological performance or survival (Radder *et al.*, 2007). These results, however, are the byproducts of a life history much different than that of the Lake Erie watersnake. Jacky dragons began eating immediately

after hatching, and lizards in the reduced-yolk treatment exhibited compensatory growth that allowed them to “catch up” to their untreated siblings. Our results highlight the importance of a third variable in reproductive strategies: offspring condition as a consequence of female investment in energy reserves (Weatherhead *et al.*, 1999; Waters & Burghardt, 2005). In addition to having large litters (up to 50 offspring; King, 1986), Lake Erie watersnake females may increase overwinter neonatal survival by provisioning their young with large fat stores. As well as being a buffer during the short foraging period available between birth and ingress, this may reduce the likelihood of depredation during foraging. We hypothesize that like the northern watersnake (Kissner & Weatherhead, 2005), Lake Erie watersnake neonates with larger fat reserves are more likely to survive their first hibernation and then emerge in the spring in a more advantageous condition.

Many animals exhibit unique nourishment strategies that function to increase neonatal survival. Fire salamander *Salamandra salamandra* females are either ovoviviparous with neonates being solely nourished by egg yolk or viviparous with both yolk and maternal provision of nutrients through a uterine secretion (Buckley *et al.*, 2007). Ovoviviparous clutches are large and made up of small young, whereas viviparous clutches consist of only a few, large neonates. Many neonatal fish go through a “yolk-sac larvae” stage where nourishment for growth and metabolism is solely provided by an internalized yolk. During this early period of growth, larval fish avoid energy-consuming and potentially dangerous situations such as foraging, excretion, extensive locomotion, and social interactions (Kamler, 2008). In viviparous fishes, neonates are nourished with ovarian fluids or reabsorbed ova in addition to yolk (Kamler, 2008). Even primitive mammals like the platypus *Ornithorhynchus anatinus* use a multi-factor strategy for nourishing their young, combining energy from egg yolk with lactation after hatching (Nowak, 1999). The large variation in neonatal feeding strategies of temperate snakes presented here, and their implications for later life-history traits, warrant further investigation. Future studies on maternal provisioning should include a larger diversity of taxa which cover a broad range of life-history strategies.

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