

Influence of prey size on reproduction among populations of Diamond-backed Watersnakes (*Nerodia rhombifer*)

J.D. Chamberlain, I.T. Clifton, and M.E. Gifford

Abstract: Mean prey size often varies across landscapes, resulting in predator populations having differing access to energetic resources. Shifts in resource quality are likely to cause differences in energy allocation of reproduction. Thus, additional energy intake may lead to (i) increased offspring size, (ii) increased numbers of offspring, (iii) increased relative proportion of energy allocated to reproduction, (iv) increased absolute amount of energy allocated to reproduction or (v) increased energy allocated to growth of some other nonreproductive function, or (vi) some combination of the above outcomes. To test this hypothesis, we evaluated the reproductive allocation patterns of four populations of Diamond-backed Watersnakes (*Nerodia rhombifer* (Hallowell, 1852)) that differ in their mean prey size. Snakes at large prey sites produced longer, heavier babies compared with snakes from small prey sites. Statistical interactions among sites confounded our ability to compare differences in litter size, litter mass, and relative clutch mass. We suggest that increased prey size results in populations shifting reproductive allocation to increase offspring size. Effects of prey size on litter size, litter mass, and relative clutch mass remain unclear.

Key words: Diamond-backed Watersnake, life history, litter size, offspring size, relative clutch mass, *Nerodia rhombifer*.

Résumé : La taille moyenne des proies varie selon le paysage, ce qui se traduit par des différences d'accès aux ressources en énergie entre populations de prédateurs. Des changements de la qualité des ressources entraînent probablement des différences d'allocation d'énergie pour la reproduction. Des apports supplémentaires d'énergie peuvent ainsi mener à (i) une plus grande taille de la progéniture, (ii) une progéniture plus nombreuse, (iii) une plus grande proportion d'énergie allouée à la reproduction, (iv) une plus grande quantité absolue d'énergie allouée à la reproduction, (v) plus d'énergie allouée à la croissance de certaines autres fonctions non reproductives ou (vi) une combinaison des éléments susmentionnés. Pour vérifier cette hypothèse, nous avons évalué les motifs d'allocation d'énergie à la reproduction de quatre populations de couleuvres d'eau diamantine (*Nerodia rhombifer* (Hallowell, 1852)) caractérisées par différentes tailles moyennes des proies. Les couleuvres dans les sites caractérisés par de grandes proies produisent des bébés plus longs et lourds que les couleuvres dans les sites caractérisés par de petites proies. Des interactions statistiques entre sites nous empêchent de comparer les différences sur le plan de la taille des portées, de la masse des portées et de la masse relative des pontes. Nous proposons qu'une plus grande taille des proies amène les populations à modifier leur allocation d'énergie à la reproduction afin d'accroître la taille de leur progéniture. Les effets de la taille des proies sur la taille des portées, la masse des portées et la masse relative des pontes ne sont pas bien établis. [Traduit par la Rédaction]

Mots-clés : diamantine, cycle biologique, taille de la portée, taille de la progéniture, taille relative de la ponte, *Nerodia rhombifer*.

Introduction

Life-history theory suggests that optimizing energy allocation to competing functions of the body should maximize fitness within a population (Cody 1966; Gadgil and Bossert 1970). However, the optimal allocation strategy among populations should vary as the prey availability and quality changes (Pianka 1976; Perrin and Sibly 1993; Reznick and Yang 1993; Bronikowski and Arnold 1999). Characterizing the differences in allocation strategies among populations in the field is a major goal in life-history research (Bronikowski and Arnold 1999). Models of optimal allocation patterns in species exhibiting indeterminate growth predict that individuals (or populations) should alter their allocation to reproduction as their energy intake changes (Kozłowski 1996; Heino and Kaitala 1999; Seigel and Ford 2001). Additional energy intake may lead to (i) increased offspring size, (ii) increased numbers of offspring, (iii) increased relative proportion of energy allocated to reproduction, (iv) increased absolute amount of energy

allocated to reproduction or (v) increased energy allocated to growth of some other nonreproductive function, or (vi) some combination of the above outcomes.

Although these predictions make theoretical sense, they are rarely tested in the field. Diamond-backed Watersnakes (*Nerodia rhombifer* (Hallowell, 1852)) occurring in the aquaculture systems of the delta region of Arkansas, USA, provide a unique opportunity to study the influence of energy availability on the reproductive allocation strategy among populations. These farms raise different species of fish that vary in size while using similar culturing and pond techniques that minimize extraneous variation among the sites. Differences in the density and size of fish cultured at these sites, as well as the distribution of the size and frequency of consumed prey at each site, has been previously characterized (Korfel et al. 2015; Chamberlain 2016; Clifton et al. 2017). Diamond-backed Watersnakes occurring on farms producing larger mean fish sizes consume larger mean prey. Although

Received 13 January 2017. Accepted 22 June 2017.

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prey densities among these sites differ, data suggest that farms raising larger fish at lower densities had a similar proportion of adult snakes with prey in their stomachs compared with farms raising small prey at higher densities. Therefore, Diamond-backed Watersnakes occupying farms with larger prey sizes should have increased energy intake. This system provides a unique opportunity to test the influence of increased energy availability, mediated through access to larger prey, on reproductive allocation (Forsman 1991, 1996; Arnold 1993; Forsman 1996; Cundall and Greene 2000; Chamberlain 2016).

Snakes are a fitting model for examining the influence of environmental variation on reproduction because they exhibit variation in offspring and litter traits and they are gape-limited predators (Seigel and Ford 1992; Arnold 1993; Forsman 1996; Forsman and Shine 1997; Bronikowski and Arnold 1999; Bonnet et al. 2000; Shine 2005; Ford and Seigel 2011). Previous studies provide a basis for testing hypotheses concerning the reproductive responses to changing prey characteristics. Although environmental factors can select for shifts in offspring size and litter size, such as overwinter survival, starvation risk, or size-specific predator avoidance, prey size should also influence allocation decisions during reproduction (Bonnet 1997; Shine and Downes 1999; Sun et al. 2002; Kissner and Weatherhead 2005).

The goal of this research is to determine if increased environmental energy availability alters the total or proportional energy allocation pattern to reproduction and to explore whether increasing the mean prey size available to predators results in increased offspring sizes, litter sizes, or both.

Materials and methods

Site descriptions

Four fish farms in near Lonoke, Arkansas, USA, were selected for this study: two characterized by large prey and two characterized by small prey. The large prey populations (LARGE) were Joe Hogan State Fish Hatchery (Large1) and Keo Fish Farm Inc. (Large2). Large1 was roughly 105 ha and produced approximately 80% catfish species (species of the genus *Ictalurus* Rafinesque, 1820). The remainder of production on this farm consisted of crappie (species of the genus *Pomoxis* Rafinesque, 1818) and bass (species of the genus *Micropterus* Lacepède, 1802). The maximum harvest size of catfish and crappie at Large1 was approximately 30 cm, whereas harvest size of bass is highly variable (Chamberlain 2016; Clifton et al. 2017). Large2 was approximately 100 ha but split between two properties; however, only the smaller 40 ha property was sampled for this study. This site specialized in the production of hybrid striped bass (*Morone saxatilis* (Walbaum, 1792) × *Morone chrysops* (Rafinesque, 1820)) and triploid grass carp (*Ctenopharyngodon idella* (Valenciennes in Cuvier and Valenciennes, 1844)), with 50% of the property dedicated to each fish species. The maximum harvest size for grass carp and hybrid striped bass at Large2 was 25 cm (Chamberlain 2016; Clifton et al. 2017). The two small prey sites (SMALL) were Gentry and Canterberry Fisheries LLC (Small1) and Pool Fisheries Inc. (Small2). Both sites specialized in the production of fathead minnows (*Pimephales promelas* Rafinesque, 1820) and goldfish (*Carassius auratus* (L., 1758)). However, snakes at these sites only had access to the goldfish, which are harvested at a maximum size of 7.5 cm (Chamberlain 2016; Clifton et al. 2017). Small1 was approximately 65 ha and Small2 was approximately 135 ha in size. A more complete summary of prey characteristics at all four sites can be found elsewhere (Korfel et al. 2015; Chamberlain 2016; Clifton et al. 2017).

We chose these sites because of their close proximity and environmental similarity. All sites consisted of a series of rearing ponds ranging from 0.1 to 0.8 ha with maximum depths of 3 m and exposed, grassy banks. All sites hosted avian and mammalian predators, such as Great Blue Herons (*Ardea herodias* L., 1758), Great Egrets (*Ardea alba* L., 1758), American mink (*Neovison vison*

(Schreber, 1777)), and striped skunks (*Mephitis mephitis* (Schreber, 1776)). Additionally, hybrid striped bass and catfish farmed at the LARGE populations were likely aquatic predators of neonate snakes. The maximum distance between any two sites was 15 km. However, due to lack of suitable habitat between sites, gene flow among sites was assumed to be limited.

Study animals

Pregnant snakes were hand-captured in late summers of 2012–2014 at all sites (total = 124; 33, 33, 29, 29 from Large1, Large2, Small1, and Small2, respectively). Snakes were brought back to the laboratory and housed individually in size-appropriate plastic cages within a rack system. They were provided a thermal gradient of 23–32 °C via thermal heating elements placed under the rear third of each cage (Vision Products, Canoga Park, California, USA). All snakes were provided aspen bedding, water, and fed once weekly ad libitum on size-appropriate goldfish. Time spent in captivity did not significantly differ among sites nested within prey type ($\text{PREY} - F_{[1,110]} = 0.0040, P = 0.9495$; $\text{PREY:SITE} - F_{[1,2]} = 1.9956, P = 0.1408$). Furthermore, a mother's time spent in captivity is expected to have little effect on reproductive output, as placental transport of organic molecules is minimal for Diamond-backed Watersnakes because this species is highly lecithotrophic (Stewart and Castillo 1984). The mean and standard deviation of days in captivity were 42 ± 25 , 44 ± 26 , 49 ± 17 , and 38 ± 16 for Large1, Large2, Small1, and Small2, respectively. Dam snout–vent length (SVL) and body mass were measured at the time of capture, henceforth called preparturient mass. Upon parturition, dam body mass was re-measured, henceforth called postparturient mass. A total of 2149 offspring were measured (621, 609, 411, 508 from Large1, Large2, Small1, and Small2, respectively). Litter size (live only), litter mass (live only), and each offspring SVL and body mass were recorded. All dams and offspring were individually marked and released to their native population within a week of birth. Animals were cared for in accordance with guidelines of the *Guide for the Care and Use of Laboratory Animals* (1996; National Academy Press, 2101 Constitution Avenue Northwest, Washington, DC 20055, USA). This project was covered under Institutional Animal Care protocol R-12-03 and Arkansas Game and Fish permit No. 031220131.

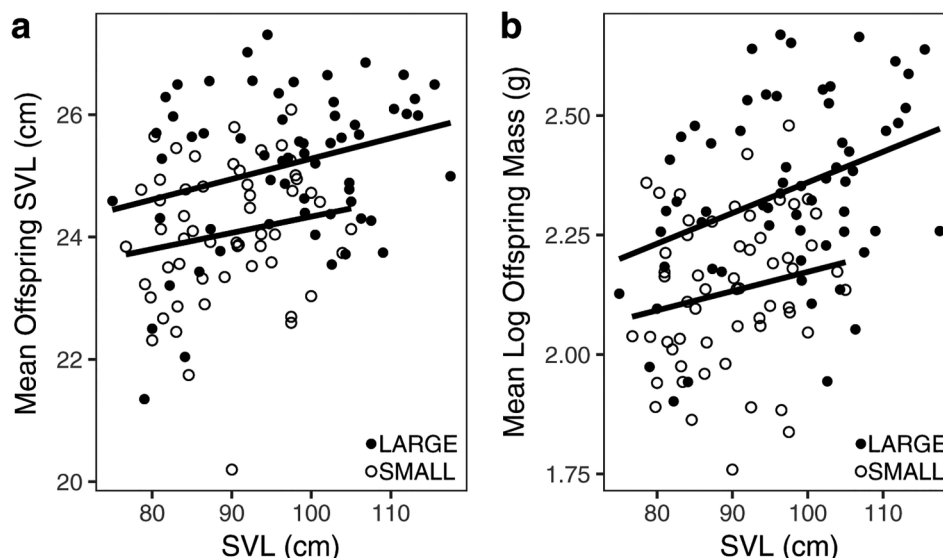
Statistical analysis

To test whether females from populations with access to differing-sized prey allocate a different proportion of their total energy to reproduction, we propose the use of relative clutch mass (RCM = litter mass/litter mass + postparturient mass), which is a measure of the relative proportion of female's total mass that is composed of reproductive material (Seigel et al. 1986). Conceptually, this measure allows comparison of reproductive investment among individuals of the same species. To test if an increased absolute amount of energy was allocated to reproduction, then there should be an increase in mean offspring size, litter size, or both among females from each site. Lastly, if additional energy is not being allocated to reproduction, then females should not differ in any of the measured reproductive traits.

Data were analyzed using the program R (R Core Team 2014). All analyses on offspring mass and offspring SVL were performed using either a mean value for each litter. Data were tested for normality to meet the assumptions of parametric testing. Data were either natural log transformed or square root transformed to meet assumptions of normality where necessary. All data were analyzed using a nested design, with sites nested within prey type.

Because dam body size is known to correlate with most reproductive characteristics in other snake species, analyses of covariance (ANCOVA) were used to measure population differences in reproductive traits with dam SVL as a covariate (reviewed in Ford and Seigel 2011). We performed analysis of variance (ANOVA) and ordinary least-squares regression if dam SVL did not correlate

Fig. 1. LARGE and SMALL sites significantly differ in both mass (a) and length (b) of offspring Diamond-backed Watersnakes (*Nerodia rhombifer*) correcting for the effect of maternal body size. Female Diamond-backed Watersnakes at LARGE sites produce offspring that are both heavier and longer than offspring from SMALL sites. There is no significant interaction between female SVL and either offspring mass or SVL.



with a particular reproductive trait. ANCOVA models with significant interaction terms of dam SVL to factor terms were not interpreted, as they fail to meet the assumptions of common slopes. Nonsignificant interaction terms were removed from all models and only reported when their $p < 0.10$. When data were missing for a given trait, each litter with missing data was removed from the analysis. Statistical significance was determined at $\alpha < 0.05$. Significant ANCOVA, ANOVA, and linear models were further analyzed to detect population differences using post hoc analyses with a Tukey correction.

Results

Offspring size

Mean natural-log-transformed offspring mass significantly increased with female SVL and differed by prey type, with no interaction of PREY on SVL and effect of SITE nested within PREY was insignificant (SVL — $r^2 = 0.338$, $F_{[1,116]} = 32.152$, $P < 0.0001$; PREY — $F_{[1,116]} = 25.929$, $P < 0.0001$; SVL \times PREY — $F_{[1,116]} = 0.4213$, $P = 0.51276$; PREY:SITE — $F_{[1,2]} = 1.2865$, $P = 0.2803$; Fig. 1a). Snakes from LARGE sites produced heavier babies than snakes from SMALL sites ($t_{[118]} = -4.828$, $P < 0.0001$). Mean (\pm SE) offspring mass was 23% larger at LARGE sites than at SMALL sites (LARGE = 10.5 ± 0.2 g; SMALL = 8.5 ± 0.2 g).

Mean offspring SVL also significantly increased with female SVL and differed by prey type, with no interaction of PREY on SVL and effect of SITE nested within PREY was insignificant (SVL — $r^2 = 0.235$, $F_{[1,116]} = 19.696$, $P < 0.0001$; PREY — $F_{[1,116]} = 14.444$, $P = 0.0002$; SVL \times PREY — $F_{[1,116]} = 0.0692$, $P = 0.7929$; PREY:SITE — $F_{[1,2]} = 0.4484$, $P = 0.6398$; Fig. 1b). Snakes from LARGE sites produced longer babies than snakes from SMALL sites ($t_{[118]} = -3.392$, $P = 0.0010$). Mean (\pm SE) offspring length was 4.5% longer at LARGE sites than at SMALL sites (LARGE = 25.2 ± 0.2 cm; SMALL = 24.1 ± 0.1 cm).

Litter size

Litter size was square root transformed to meet the assumption of normality. Litter size strongly increased with female SVL ($r^2 = 0.3882$, $F_{[1,111]} = 66.878$, $P < 0.0001$); however, SITE nested within PREY was significant and an interaction between SVL and SITE nested within PREY was significant within the full model and made interpretations impossible because the assumption of the homogeneity of regression slopes was violated (PREY:SITE —

$F_{[1,2]} = 3.4962$, $P = 0.03388$; SVL \times PREY:SITE — $F_{[1,111]} = 4.2301$, $P = 0.01701$). The interaction of SVL with SITE nested within PREY suggested that litter size did not scale with SVL similarly among sites. This can be more easily understood by visualizing the nature of these relationships by SITE instead of PREY (Fig. 2a). It was clear from this analysis that the relationship of litter size to female SVL for snakes at Small1 had a substantially shallower slope than at Small2, whereas both LARGE sites had similar relationships of female SVL to litter size.

Litter mass

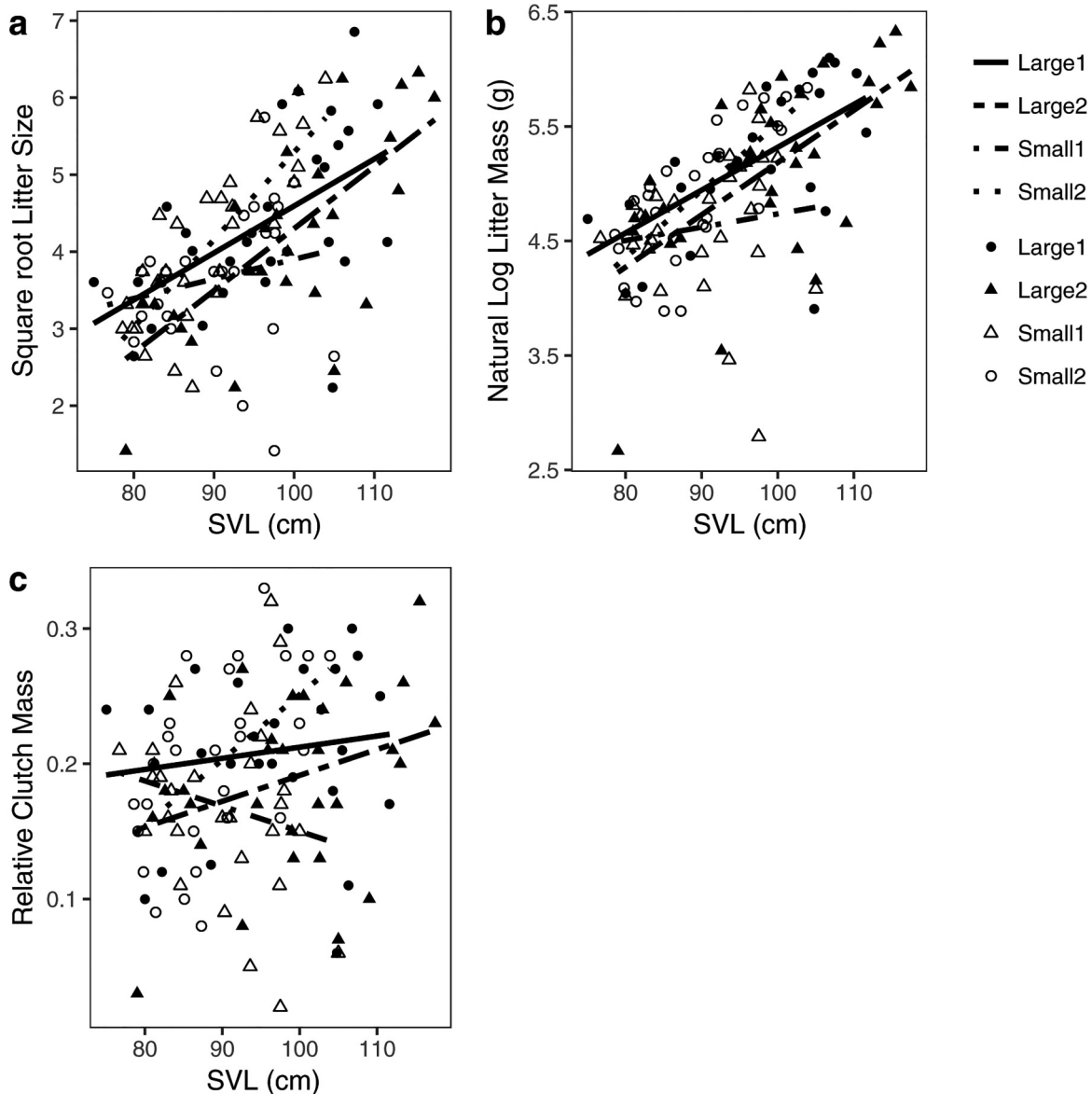
Natural-log-transformed litter mass significantly increased with female SVL; however, the significant interaction between SVL with SITE nested within PREY made interpretation impossible because the assumption of the homogeneity of regression slopes was violated (SVL — $r^2 = 0.376$, $F_{[1,111]} = 58.326$, $P < 0.0001$; PREY:SITE — $F_{[1,2]} = 2.8137$, $P = 0.0609$; SVL \times PREY:SITE — $F_{[2,111]} = 2.8978$, $P = 0.05952$). Similarly, visualizing this interaction in terms of SITE instead of PREY helped to decipher patterns (Fig. 2b). Again, the relationship of litter mass to female SVL at Small1 had a substantially shallower slope than the other SMALL site, as well as both LARGE sites.

Relative clutch mass

Relative clutch mass significantly correlated with female SVL; however, SITE nested with PREY was significant and an interaction between female SVL and SITE nested within PREY was significant within the full model and made interpretations impossible because the assumption of the homogeneity of regression slopes was violated (SVL — $r^2 = 0.1625$, $F_{[1,111]} = 5.5961$, $P = 0.01982$; PREY:SITE — $F_{[1,2]} = 2.9991$, $P = 0.05408$; SVL \times PREY:SITE — $F_{[1,108]} = 3.001$, $P = 0.01404$). Again, visualizing by SITE rather than PREY, as with litter size and litter mass, helped clarify this relationship (Fig. 2c). Relative clutch mass scaled negatively with SVL at Small1, whereas it scaled positively at Small2.

A consistent pattern was evident in the relationships of litter size, litter mass, and relative clutch mass to maternal SVL; the regressions for Small1 scaled with shallower slopes than those regressions from the corresponding Small2. Meanwhile, both LARGE sites behaved similarly when comparing their slopes of litter size, litter mass, and RCM to female SVL. In an effort to explain the SMALL site pattern in the scaling of each reproductive

Fig. 2. Strong interactions of female Diamond-backed Watersnake (*Nerodia rhombifer*) body length and site exist for litter size (a), litter mass (b), and relative clutch mass (c). In all three panels, Small1 consistently behaves differently than its corresponding SMALL site Small2, whereas both LARGE sites behave similarly for all three traits. This suggests that the significance of these interactions may be driven by Small1.



trait to female SVL, we tested whether they differed in variability of these traits. We specifically tested whether shallower slopes at Small1 were associated with increased variation in these traits for larger females compared with those at Small2. We calculated the absolute value of the residuals of each reproductive trait regressed on female SVL for both populations and tested for a correlation between these residuals and female SVL for the three reproductive traits separately. Absolute values of residuals were used because we were strictly interested in measuring the absolute deviation from the regression line and not whether these values were above or below the regression line, thus avoiding the effect of regression towards the mean. Therefore, if a positive correlation exists at a site between SVL and absolute value of residuals of a particular reproductive trait regressed on female SVL, then the deviations from the mean regression line increases with female body size.

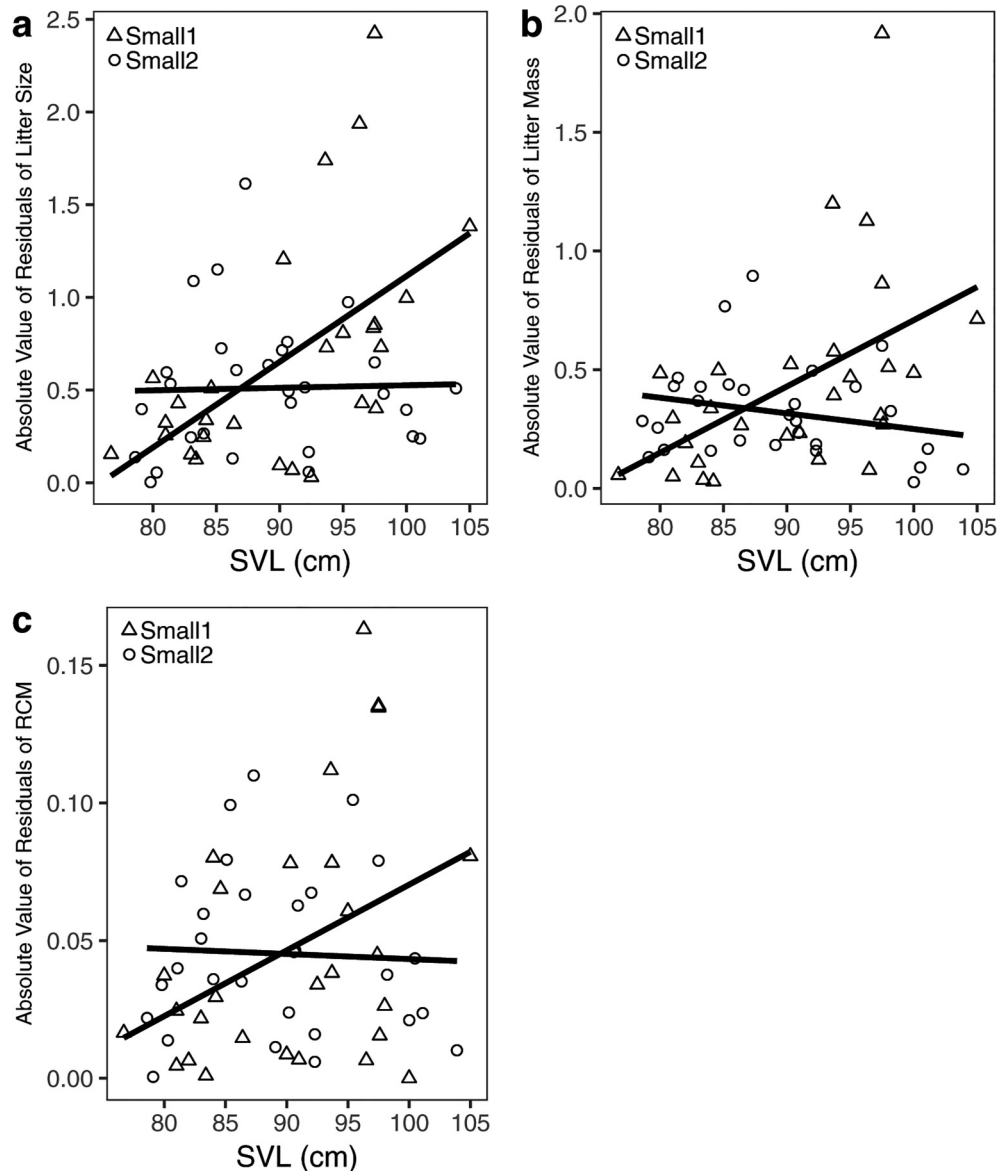
The relationship between variation in litter size and female SVL differed between Small2 and Small1; Small1 exhibited a positive

slope compared with Small2, which had a slope that did not differ from zero ($SVL - F_{[1,53]} = 9.196, P = 0.0037$; $SVL \times SITE - F_{[1,53]} = 7.666, P = 0.0077$; Fig. 3a). This suggested that at larger SVLs, females from Small1 produced litters that varied more in size than did females from Small2. Similar relationships occurred for litter mass and RCM; Small1 snakes had larger absolute residuals at longer SVLs compared with snakes from Small2 (litter mass: $SVL - F_{[1,53]} = 4.251, P = 0.0442$; $SVL \times SITE - F_{[1,53]} = 9.980, P = 0.0026$; RCM: $SVL - F_{[1,53]} = 3.981, P = 0.0512$; $SVL \times SITE - F_{[1,53]} = 9.789, P = 0.0029$). These results suggest increased variation in litter mass and RCM at larger body sizes at Small1, which resulted in a steeper positive slope for these relationships compared with individuals from Small2 (Figs. 3b, 3c).

Discussion

Here we present evidence that prey-size variation can have a profound influence on reproductive allocation patterns in

Fig. 3. Variation in the absolute value of residuals of litter size to female Diamond-backed Watersnake (*Nerodia rhombifer*) body size (a), absolute value of residuals of litter mass to female body size (b), and the absolute value of relative clutch mass to female body size (c) all increase with female body length at Small1, resulting in a positive correlation. Small2 residuals do not correlate with female body length, resulting in near-flat slopes.



Diamond-backed Watersnakes. Snakes feeding on larger prey had longer and heavier babies compared with similarly sized snakes from sites that had access only to small prey (Figs. 1a, 1b). The influence of prey size on litter size, litter mass, and relative clutch mass is less clear because of significant interactions suggesting that, for these traits, factors of prey type and sites within prey type did not scale similarly with female SVL (Figs. 2a–2c). Post hoc examination suggests these interactions are likely due to a high degree of variation in reproductive traits in snakes with longer body sizes at Small1, which resulted in a similar shallow slope in the three regressions of litter size, litter mass, and RCM on female SVL (Figs. 3a–3c). The increase in offspring size at LARGE sites and lack of clear pattern in differences of litter size between SMALL and LARGE sites provide marginal support for an increase in total energy allocation to reproduction at LARGE sites. We are unable to determine if prey-size changes influence the relative proportion of energy allocated to reproduction because of the inability to resolve patterns of RCM between SMALL and LARGE sites.

The strongest effect of increasing prey size was a dramatic increase in mass and length of offspring. Although size-specific predation, starvation risk, and overwinter survival (Bonnet 1997; Shine and Downes 1999; Sun et al. 2002; Kissner and Weatherhead 2005) favor larger offspring size and could be influencing these sites, it is likely that snakes occupying all fish farms experience these environmental variables to a similar degree. We therefore conclude that the major selective force on offspring size in these populations is driven by differences in prey size.

Previous work has shown that mean adult body size within a population is selectively driven by differences among populations in mean prey size. Snakes colonizing islands with mean prey sizes larger or smaller than the ancestral mainland population, for example, often result in gigantism or dwarfism (Forsman 1991; Boback 2003; Keogh et al. 2005; Aubret and Shine 2007). Unfortunately, these studies typically examine prey-size effects on adult body size and do not consider the effect of prey size on reproductive allocation or the response of offspring to increasing the mean

prey size. However, we are not the first to document that prey size can result in increasing mean offspring size in snakes. Sun et al. (2002) showed that mean size of offspring in insular vipers was larger than mainland counterparts. These authors argued that the increase in offspring size was due to the need for neonatal vipers to quickly attain sizes that allowed them to forage on proportionally large birds that stopover during migration on their study island. Gape limitation produces a strong selective pressure for increased SVL size of neonates. Mainland vipers, in contrast, feed on diverse prey with variable body sizes and produce offspring that are less than half the length of offspring from the insular population.

Thus, larger offspring may be an indirect effect of prey size. The ability to eat large prey is limited by gape elements of the skull in macrostomatan snakes (Cundall and Greene 2000). Longer gape elements increase the ability of macrostomatan snakes to swallow larger prey by aiding in the biomechanics of handling and swallowing prey (Cundall and Greene 2000; Vincent et al. 2006). If cranial gape elements are unable to respond to selection of larger prey independently, then selection for an overall larger body size would achieve the same results as a function of positive allometries.

The selective force of prey size may operate at multiple levels in ontogeny to increase offspring size. If small preys are rare or unavailable at birth due to timing of life histories of the prey or, in our case, because of anthropogenic interference associated with culturing fish stock, then selection should favor increasing neonate size to a point where neonates can begin to immediately forage. If prey is still too large at the time of birth, then increasing offspring mass could fuel postnatal growth from energetic reserves until neonates are large enough to begin foraging on available prey (Madsen and Shine 2002; Sun et al. 2002). Even if small preys are available to neonates, then selection may still favor longer or heavier offspring if larger, more energetically rich prey are available but are unattainable due to their size (Sun et al. 2002). Increasing both initial offspring mass and length should shorten the growth time necessary for neonates to access these more favorable preys.

Either or both of these explanations may be operating among our sites to drive differences in offspring size. While both LARGE sites stock small fish fry between April and July, small prey at the time of birth of neonate snakes in August to October are rare because only those fish stocked in June or July will not have grown beyond what neonate snakes can physically handle. Because of this time delay of stocking, differential feeding of fish among ponds, and the retention of larger size classes of fish awaiting sale and shipment, larger and more calorically valuable preys are always more abundant. Thus, larger neonates at LARGE prey sites have access to more prey both immediately and through ontogeny. To further support this argument, observations of snake diet through ontogeny, including that of Diamond-backed Watersnakes, show that as snakes grow larger, individuals (particularly females) preferentially drop smaller prey items from their diet (reviewed in Arnold 1993, but see also Mushinsky et al. 1982 and Plummer and Goy 1984).

The advantage of larger offspring to access larger prey is greatly diminished at SMALL sites because these sites have abundant small prey on which neonates can immediately begin foraging. But, there are still larger prey available, which might offer an energetic advantage, suggesting a benefit to starting life at a larger size. However, two factors may diminish this advantage compared with LARGE sites. First, the maximal prey size at SMALL sites is smaller, meaning that intermediate-sized snakes quickly lose a size advantage, and large snakes are likely to be constrained by needing to feed on relatively small prey. Slowing the rate at which larger body sizes are reached may be advantageous, which could be achieved by beginning as a smaller neonate. Secondly,

the largest prey sizes at SMALL sites are rarer than smaller prey sizes due to commercial demand.

We were unable to interpret of the effect of prey size on litter size, litter mass, and RCM initially due to the increased variation in these traits at Small1. Why did variation in litter size, litter mass, and RCM increase with body length at this site and not the other SMALL site (Small2)? We have identified two potential explanations that may address this discrepancy. (1) Although these sites raise the same fish species to approximately the same sizes, they might not raise them at the same frequency. If Small1 does not use all of its rearing capacity, either by not stocking as many ponds at one time or by not stocking at the same level throughout the year, then prey may become more patchily distributed and harder to acquire for pregnant females. (2) Even if sites have the same-sized fish, raised at the same frequencies, then these sizes may not be available in the same proportions. Small1 might raise the largest fish at a lower proportion of its total. This would require large females to either begin foraging on smaller prey more often, or move more frequently to find ponds with large prey.

In either explanation, larger females that need more fuel to supply greater reproductive demands (since reproductive output is correlated with body size) will suffer a greater cost than smaller females when large prey become scarce. Both mechanisms would result in some large females successfully foraging, while others would fail to locate appropriate food resources. Consequently, some large females will be able to fuel reproduction, while others will not, leading to increased variation in reproductive output as female body size increases (van Noordwijk and de Jong 1986). In a similar scenario between two populations of Checkered Gartersnakes (*Thamnophis marcianus* (Baird and Girard, 1853)), Seigel and Ford (2001) found that populations differed in phenotypically plastic response of reproductive traits in response to prey availability. A population with access to constant prey showed little variation in reproduction, which they suggest is a response to the lack of selective pressure to respond to variation in prey availability. However, a population with dramatic seasonal variation in prey availability showed substantial variation in reproductive traits in response to sudden bursts of prey of high food availability. Similar selective pressures could push Small1, but not Small2, to exhibit similar plasticity in reproductive traits.

Acknowledgements

We thank A. Anderson, T. Clay, C. Korfel, M. Pollett, A. Winters, and numerous other volunteers for their assistance in collecting and housing snakes. Additionally, we thank Gentry and Canterbury Fisheries LLC, Keo Fish Farm, Pool Fisheries Inc., and Arkansas Game and Fish Commission for generously allowing us to sample their properties. We also thank R. Sikes, W. Baltosser, D. Jones, and J.D. Willson for reviewing the manuscript. Finally, we thank the Basic Animal Services Unit at the University of Arkansas at Little Rock for allowing use of their facilities.

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