Prey morphology constrains the feeding ecology of an aquatic generalist predator

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Abstract. Resource availability and accessibility are primary factors guiding the distribution and abundance of organisms. For generalists, prey availability reflects both prey abundance and differences in quality among prey taxa. Although some aspects of prey quality, such as nutritional composition, are well studied, our understanding of how prey morphology contributes to overall prey quality is limited. Because snakes cannot reduce prey size by mastication, many aspects of their feeding ecology (e.g., maximum prey size, feeding performance, and the degree of postprandial locomotor impairment) may be affected by prey shape. We conducted a uniquely comprehensive comparison of prey quality for a generalist species, the banded watersnake (*Nerodia fasciata*), using prey that were similar in mass and presumably similar in nutritional composition but different in shape and habitat association. Specifically, we compared nutritional composition and shape of paedomorphic salamanders (*Ambystoma talpoideum*) and sunfish (*Lepomis marginatus*) and used a series of repeated-measures experiments to examine feeding performance (number of prey consumed, maximum prey size, and intra-oral transport time), digestive metabolism (specific dynamic action, SDA), and postprandial locomotor performance of snakes fed *Ambystoma* and *Lepomis*. Cost of digestion was similar between the prey types, likely reflecting their similar nutritional composition. However, snakes consumed larger *Ambystoma* than *Lepomis* and intra-oral transport time was much shorter for *Ambystoma*. Snakes fed *Lepomis* also suffered greater reduction in crawling speed than those fed *Ambystoma*. These differences highlight the need for behaviorally integrated approaches to understanding prey quality and support field observations of the importance of amphibian prey for juvenile watersnakes.

Key words: Ambystoma talpoideum; banded watersnakes; feeding performance; intra-oral transport; Lepomis marginatus; locomotor performance; Nerodia fasciata; prey handling; specific dynamic action.

INTRODUCTION

Classically, one of the goals of ecology is to understand factors that determine the distribution and abundance of organisms. Among the biotic and abiotic factors that can contribute to the abundance of a species, perhaps none is more obvious than the availability and accessibility of suitable food resources (White 2008). Many studies use abundance (e.g., number or biomass) of potential prey taxa exclusively as an index of habitat suitability. However, even for dietary specialists, a simple measurement of prey abundance fails to provide an adequate assessment of true resource accessibility. For example, habitat structure or complexity can influence prey encounter or capture rates such that foraging success may vary among habitats with similar numerical prey abundances (Crowder and Cooper 1982, Mullin and Cooper 2000). Assessing resource availability and accessibility is further complicated for generalist species because prey taxa may differ in quality. Prey quality represents a measure of the net gain of energy or nutrients, offset by costs, including time and energy expenditure and incurred risk of predation or injury, of prey capture, handling, processing, and digestion. Nutritional composition of prey is easily measured and can have direct effects on a variety of fitness-related traits (Mayntz et al. 2003, Wilder and Rypstra 2008). For example, young Red-legged Kittiwakes (*Rissa brevirostris*) fed low-lipid diets exhibit reduced growth and impaired learning abilities compared to those reared on high-lipid diets (Kitaysky et al. 2006). Conversely, factors that influence the costs associated with prey quality are complex and often poorly understood. In particular, few studies have examined how prey shape effects the costs incurred during prey capture, handling, and processing (Vincent et al. 2006).

Snakes provide an excellent opportunity to evaluate the effects of prey shape on various aspects of feeding ecology, physiology, and postprandial locomotor performance. All snakes are obligatory carnivores and typically cannot adjust the size of potential prey by mastication (Arnold 1993). Therefore, relative prey mass and shape ultimately determine both the maximum size of prey that can be consumed and the time and effort expended during consumption (Mori 1991, 1993, 1996, Arnold 1993, Vincent et al. 2006). Moreover, snakes are forced to consume all components of each prey item, regardless of nutritional quality or digestibility. Because snakes lack limbs, they rely solely on their jaws and body musculature for both prey handling and locomotion (Cundall 1987). Therefore, the added burden of a large meal can hinder snake locomotor performance (Garland and Arnold 1983, Ford and Shuttlesworth 1986, Shine and Shetty 2001, Mehta 2006, Mehta and Burghardt 2008). Although the effects of prey size on snake feeding behavior and performance have been examined in several species (e.g., Mori 1991, 1993, 1996, Arnold 1993, Vincent et al. 2006), few studies have compared feeding performance, digestive metabolism, or post-feeding locomotor performance of snakes fed prey that are similar in size but different in shape.

We conducted a uniquely comprehensive evaluation of the effects of prey morphology on feeding ecology in a generalist predator, the banded watersnake (*Nerodia fasciata*). Specifically, we selected two prey taxa that are similar in mass, abundant, and frequently consumed by watersnakes, paedomorphic salamanders (*Ambystoma talpoideum*) and centrarchid sunfish (*Lepomis marginatus*), that are characteristic of fishless and permanent wetlands, respectively (see Appendix). We compared nutritional composition and body shape of each prey type and used a series of repeated-measures experiments to examine feeding performance (number of prey consumed, maximum prey size, and intra-oral transport time), digestive metabolism (specific dynamic action, SDA), and postprandial locomotor performance (maximum crawling speed) of snakes fed *Ambystoma* and *Lepomis*. Because *Ambystoma* are more elongate at a specific body mass and contain fewer impediments to intra-oral transport and digestion (e.g., scales and spiny fin rays), we predicted that snakes would be able to consume more massive *Ambystoma* than *Lepomis* and consume *Ambystoma* more rapidly. Further, we expected that the large amounts of bony material present in *Lepomis* would result in a higher cost of digestion (SDA response) for *Lepomis* than *Ambystoma*. Finally, consumption of fish, which are relatively stiff-bodied, has been shown to impair locomotor performance in snakes (Garland and Arnold 1983). Thus, we expected that consumption of *Lepomis* would induce greater body distension than consumption of *Ambystoma*, resulting in reduced maximum crawling speed in snakes that consumed *Lepomis* compared to those that consumed *Ambystoma*.

METHODS

Experimental subjects

The banded watersnake (*Nerodia fasciata*) is an abundant, moderately large semiaquatic snake that is found in a variety of aquatic habitats throughout its range in the southeastern United States (Gibbons and Dorcas 2004). *Nerodia fasciata* is generally characterized as an opportunistic feeder and is known to consume a variety of aquatic vertebrate prey, with a particular preference for fish and amphibians (Gibbons and Dorcas 2004). Pregnant female *N. fasciata* ($n = 8$) were captured in aquatic minnow traps at various uncontaminated aquatic habitats on the U.S. Department of Energy's Savannah River Site (SRS), in South Carolina, USA, and maintained in the laboratory until parturition. Following parturition, neonates ($n = 77$) were maintained communally in 75.7-L aquaria that were lined with paper towels and equipped with large water bowls, hide boxes, and basking lamps (12 L:12 D) to provide thermal gradients within cages. Snakes were offered ad libitum fish or amphibian larvae approximately once per week between experiments. Some snakes exhibited an initial preference for amphibian prey. Thus, to minimize the effects of prior feeding experience on our results, we only included snakes that had previously consumed both prey types in our experiments. In all experiments snakes were randomly assigned to treatments to remove potentially confounding litter effects.

Prey collection, morphology, and nutritional composition

We selected prey types that are abundant and similar in weight, but very different in morphology: paedomorphic mole salamanders (*Ambystoma talpoideum*) and dollar sunfish (*Lepomis marginatus*). *Nerodia fasciata* feed on both *Ambystoma* and *Lepomis* on the SRS (J. Willson and C. T. Winne, Savannah River Ecology Laboratory, *unpublished data*) and elsewhere (Gibbons and Dorcas 2004). However, these prey types are typical of different habitats used by *N. fasciata* in the Coastal Plain of the southeastern United States (see Appendix); aquatic salamanders are the dominant prey within fishless wetlands (i.e., those that dry periodically and are isolated from permanent water bodies), whereas centrarchid fish are the dominant (by biomass) prey type in more permanent wetland habitats. Prey representing a variety of sizes were collected from uncontaminated aquatic habitats on the SRS using minnow traps. Prey were blotted dry, weighed (nearest 0.01 g), and individually frozen for use in subsequent experiments. Offering previously killed prey allowed us to focus on the effects of prey shape on feeding behavior by removing the confounding effects of prey activity or defensive behavior. Body shape of each prey type was assessed by measuring maximum body depth and maximum width (nearest 0.01 mm; measured just anterior to the dorsal fin in *Lepomis*) for 30 individuals

of each prey type and testing for differences in maximum dimensions using analysis of covariance (ANCOVA), with prey mass as a covariate. Whole-body prey samples ($n = 4$ per prey type, spanning the mass range used in the digestive metabolism experiment) were dried to constant mass in a freeze drier and analyzed for nutritional composition (protein, lipid, and energy content) at the University of Arkansas's Poultry Science Center, Fayetteville, Arkansas, USA. Although dietary values are reported on a wet mass basis, differences in nutritional content between prey types were examined using ANCOVA with absolute protein and lipid content, dry mass, and energy content (kJ) as dependent variables and prey wet mass as the covariate. In all experiments, prey rations were determined based upon the wet mass of the prey item. For all statistical analyses, we used appropriate transformations if raw data failed to meet assumptions of parametric models. We recognized statistical significance at $P \leq 0.05$ and performed all statistical analyses using SAS (version 9.0; SAS Institute 2000) or the STATISTICA for Windows software package (StatSoft 1998).

To determine whether prey type influenced post-feeding body shape of snakes, 16 snakes (18.9 ± 0.47 g; means ± SE) were randomly assigned into the two prey-type treatments and each snake was fed a prey item weighing 25.0% ± 0.4% of its body mass. This relative prey size was selected based on pilot experiments to be small enough that snakes to could consume both prey types, but large enough to substantially impact post-feeding body width and locomotor performance. Maximum snake body width (occurring at the location of the prey item within the snake) was measured 1 h post-feeding and subsequently at 24-h intervals until body distension due to prey was no longer evident (120 h post-ingestion). Effect of prey type on body distension was evaluated over time using repeated-measures MANOVA (Profile Analysis).

Experiment I: feeding performance (intra-oral transport)

We conducted a set of two experiments to examine differences in feeding performance (intra-oral transport time; Cundall and Greene 2000) between snakes fed each of the two prey types. The first experiment used a repeated-measures design to determine if the number of prey consumed differed between prey types across a range of prey sizes (20–65% of snake body mass). Because this experiment demonstrated that snakes were able to consume much larger (in terms of relative mass) salamanders than fish, a second experiment was designed, wherein snakes were offered only salamanders, to determine the maximum size of salamander that snakes could consume. Finally, data from all successful swallowing events were used to test for differences in intra-oral transport time between the prey types and prey sizes.

In the first experiment, juvenile *N. fasciata* ($n = 10$/treatment; 9.5 ± 0.61 g) were randomly assigned to a prey size treatment (20%, 35%, 50%, or 65% of the snake's body mass), and each snake was offered *A. talpoideum* and *L. marginatus* of the assigned size on separate occasions (order randomized). Snakes were offered prey in excess (2–6 individual prey items totaling >100% of snake body mass) and no snake consumed all prey offered in any trial. Number of prey consumed was compared between prey types using a Wilcoxon's matched-pairs test separately for each prey size category. In the second experiment, juvenile *N. fasciata* ($n = 8$–10/treatment; 4.9 ± 0.26 g) were randomly assigned to a prey size treatment (75%, 90%, 105%, or 120% of the snake's body mass), and each snake was offered only *A. talpoideum*.

All feeding trails were conducted within a walk-in environmental chamber at 30°C. Feeding chambers consisted of 739-mL clear plastic containers to which we added ~10 mL of water to provide a suitable feeding environment for the watersnakes. Snakes were fasted for 10 d and allowed to acclimate in feeding chambers within the environmental chamber for 1 h prior to each trial. Following acclimation, dead, defrosted prey were added to feeding chambers, and a weighted plexiglass sheet was placed over the top of each feeding chamber, allowing detailed feeding observations. During the 1-h trial, the observer recorded the time (nearest second) at which the snake positioned the prey into swallowing position (prey position aligned with the jaws and commencement of "jaw walking") and the time at first tongue flick after swallowing. Intra-oral transport time was defined as the time elapsed between these two events (Krause and Burghardt 2001). If, after 1 h, any snake was still in the process of swallowing a prey item, that individual was not disturbed and was allowed to continue until it either successfully swallowed the meal or regurgitated and discontinued contact with the prey item.

Effects of prey type and prey size (relative mass) on intra-oral transport time were determined using a two-factor analysis of variance (ANOVA) on log-transformed transport times within prey size treatments where both prey types were represented by more than one successful swallowing event (20% and 35% of snake body mass). In cases where individual snakes consumed more than one prey item of a given prey type within a size category, the mean transport time was used to avoid pseudo-replication.

Experiment II: digestive metabolism

A repeated-measures experiment was used to compare metabolic responses of 11 juvenile *N. fasciata* fed salamanders and fish. We modified methods from Hopkins et al. (2004) to measure (1) standard metabolic rate (SMR; the metabolic rate of a resting, post-absorptive ectotherm at a specified temperature during the inactive phase of its circadian cycle; Bennett and Dawson 1976), (2) specific dynamic action (SDA; the increased energy expenditure associated with digestion,

assimilation, and biosynthesis; Kleiber 1975) after the snake had eaten a *Lepomis marginatus* of 25% of the snake's body mass, and (3) SDA after it had eaten an *A. talpoideum* of 25% of the snake's body mass. Juvenile *N. fasciata* spanning a narrow range of body masses (15.92–22.71 g) were tested to minimize the confounding effects of allometric relationships between mass and metabolic rate. Prior to respirometry trials, snakes were fasted for 10 d to ensure complete absorption of previous meals. Snakes were then placed in individual chambers (1-L Erlenmeyer flasks) within an environmental chamber (25°C, constant dark), within which all metabolic measurements were taken. A 20-mL plastic sample bottle was affixed to the bottom of the flask with Velcro to provide water to snakes throughout the experiment.

Metabolic rate was determined indirectly as O_2 consumption (adjusted for temperature and pressure) by connecting each chamber to a computer-controlled, closed-system respirometer (Micro Oxymax, Columbus Instruments, Columbus, Ohio, USA). O_2 consumption was measured every 48 min for the first 48 h to calculate SMR. After every fourth sample, chambers were refreshed with ambient air equaling four times the headspace of each chamber. Following SMR measurements, snakes were removed from the environmental chamber and fed one *A. talpoideum* or *L. marginatus* (order determined randomly) equal to ~25% (24.94% ± 0.14%) of the snake's body mass. Snakes were then returned to the environmental chamber and respirometry measurements were resumed for the following 144 h to calculate SDA parameters. During SDA trials, O_2 consumption was measured every 36 min with longer intervals (120 min) every third sample to accommodate refreshing of chambers with ambient air. At the midpoint of the SDA trial, snakes were removed, chambers cleaned, and instrumentation recalibrated. Following termination of each snake's first SDA trial, the snake was returned to its cage, where it was fed again, fasted for 10 d, and then started on its second SMR and SDA trial, during which it was fed the second prey type.

Snake SMR was estimated by calculating the mean of the lowest quartile of the O_2 measurements obtained for each snake during the 48-h SMR trial (Hopkins et al. 2004). To estimate SDA from postprandial respiration measurements, a two-part smoothing technique was used to remove the effects of spontaneous snake activity on O_2 consumption. The smoothing technique used a moving central minimum of three values, followed by a moving central median of 11 measurements (Hopkins et al. 2004). Energy allocated to SMR during digestion was estimated by extrapolating SMR measured before feeding over the digestive period. The integrated VO_2 (volume of oxygen) allocated to SMR was then subtracted from the integrated area under each smoothed postprandial curve to calculate the oxygen consumed to support SDA. Additionally, peak post-prandial O_2 consumption, digestive scope (peak O_2/SMR), time to peak O_2, time to 50% decrease from peak, and time to 75% decrease from peak were calculated for each snake. SDA was converted to energetic equivalents using a conversion factor of 19.8 J/mL O_2 (Secor and Diamond 2000), and the cost of digestion (SDA coefficient) was calculated as a percentage of total ingested energy allocated to the SDA response. Because individual snakes received both prey type treatments, individual was used as a blocking factor in a multivariate analysis of variance (MANOVA) to test for effects of prey type on SDA parameters. Because preliminary analyses revealed no overall mass effect ($F_{8,2}$ = 1.04, P = 0.576), body mass was not included as a covariate in the statistical model.

Experiment III: post-feeding locomotor performance

A repeated-measures design was used to compare the effects of prey type on locomotor behavior of snakes fed salamanders and fish. Maximum crawling speed was selected as our measure of locomotor performance because watersnakes frequent terrestrial wetland edges while basking to aid digestion. Moreover, within aquatic habitats, *N. fasciata* are most abundant in shallow, heavily vegetated wetlands (Gibbons and Dorcas 2004; J. D. Willson, *unpublished data*). In such areas, locomotion is likely more akin to crawling than swimming. Sixteen juvenile *N. fasciata* (18.9 ± 0.47 g) were randomly divided between fish and salamander treatments, and their maximum crawling speed was measured before feeding, immediately post-feeding, and subsequently at several time points during digestion using methods similar to those of Winne and Hopkins (2006). Throughout the experiment, snakes were housed at 28°C within an environmental chamber, but locomotor trials were conducted within a temperature-controlled (21.0–22.8°C) laboratory.

Maximum crawling velocity for each snake was determined using a 2.3-m linear sprint track lined with pairs of photocells projecting infrared beams at 10 cm intervals interfaced with a laptop computer (Columbus Instruments, Columbus, Ohio, USA; described in detail in Holem et al. 2006). The racetrack was lined with plastic carpet to maximize crawling performance (Winne and Hopkins 2006). Prior to the experiment, snakes were fasted for 10 d and conditioned to the track by racing them twice in succession 48 h prior to the start of the experiment. Subsequently, snakes were raced twice in succession at six time intervals: 18 h before feeding and 1 h, 24 h, 48 h, 72 h, 96 h, and 120 h after consuming a *L. marginatus* or *A. talpoideum* equal to 25.0% ± 0.4% of the snake's body mass.

Prior to beginning each trial, individual snakes were placed in a box attached to the starting point of the track and left undisturbed for approximately one minute. A gate separating the start box from the sprint track was then lifted, and the snake was chased by hand down the track by lightly touching the snake's tail at
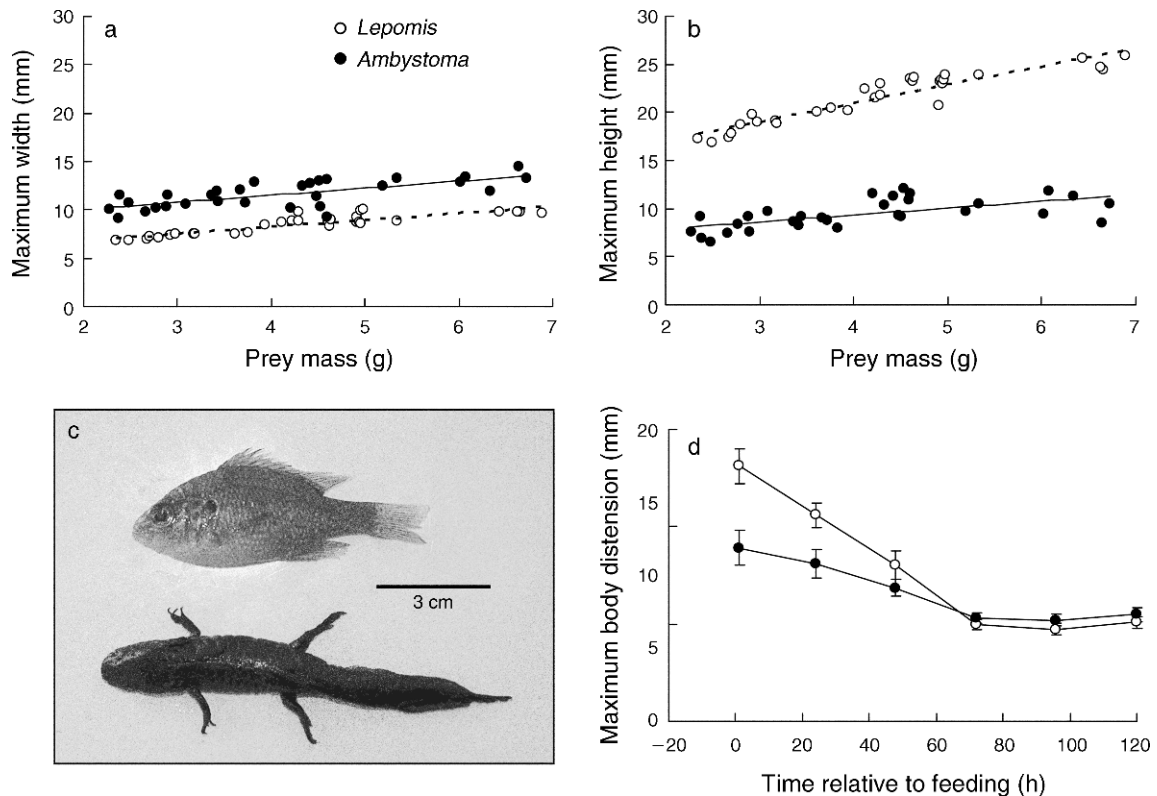
FIG. 1. Characteristics of two prey species of the generalist predator, the banded watersnake (*Nerodia fasciata*). Shown are differences in body shape between paedomorphic mole salamanders *Ambystoma talpoideum* and dollar sunfish *Lepomis marginatus*, including (a) maximum width and (b) maximum height in relation to body mass. Maximum body dimensions were at the head in *A. talpoideum* and just anterior to the dorsal fin in *L. marginatus*. (c) Morphological differences between the two prey types are shown in a photograph depicting individuals of equal mass. (d) Post-ingestion differences between the prey types are evident in a time series of body distension (maximum body width ± SE) in snakes fed prey weighing 25% of snake body mass.

approximately one second intervals to prompt a flight response (Huey et al. 1989, Winne and Hopkins 2006). The time it took for each individual to crawl 60 cm was calculated for each 60-cm segment of the track, and the single fastest velocity for each individual was used as an estimate of maximum locomotor performance in statistical comparisons. Effect of prey type on post-feeding maximum sprint velocity was evaluated using repeated-measures MANOVA (Profile Analysis). Because preliminary analyses revealed no overall effect of snake body mass ($F_{1,13} = 0.19$, $P = 0.674$), snake mass was not included as a covariate in the statistical model.

RESULTS

Prey shape and nutritional composition

Substantial differences in shape were evident between salamanders and fish (Fig. 1). Although *A. talpoideum* had a slightly larger maximum body width than *L. marginatus* at a given mass ($F_{1,57} = 293.7$, $P < 0.001$; Fig. 1a), *L. marginatus* had substantially greater maximum height than *A. talpoideum* at all body sizes ($F_{1,57} = 1\,224.9$, $P < 0.001$; Fig. 1b). Snakes generally oriented *L. marginatus* laterally (side down) during

swallowing, whereas *A. talpoideum* were generally consumed dorsoventrally (vent down). Thus, the most meaningful comparison of shape between the prey types is between body width in *A. talpoideum* and body height in *L. marginatus*. Even considering the differences in swallowing position, however, *L. marginatus* had a substantially greater maximum body dimension than *A. talpoideum* (*L. marginatus* height vs. *A. talpoideum* width; $F_{1,57} = 1\,200.03$, $P < 0.001$; Fig. 1). Additionally, although we considered only dead prey, it is important to consider that dorsal spines, which would be erected by live *Lepomis* in response to attack by a predator, would further increase body height in *L. marginatus*. Following feeding, snakes fed *L. marginatus* exhibited much greater body distension (maximum body width) than those fed an equivalently sized *A. talpoideum* (time-by-prey type interaction, $F_{5,70} = 8.35$, $P = 0.003$; Fig. 1d).

Overall, nutritional composition was similar between the two prey types (Table 1). Energy content per unit mass and lipid content did not differ between the prey types. Although *L. marginatus* had a slightly (2.4%) higher protein content per unit mass than *A. talpoideum*, the most substantial difference between the prey types

TABLE 1. Nutritional composition (mean $\pm$ SE) relative to prey wet mass of *Ambystoma talpoideum* and *Lepomis marginatus*.

Component	Ambystoma	Lepomis	$F_{1,5}$	P
H_2O (%)	81.33 $\pm$ 0.32	75.93 $\pm$ 0.42	59.59	**<0.001**
Protein (%)	12.22 $\pm$ 0.35	14.62 $\pm$ 0.37	15.17	**0.011**
Lipid (%)	2.23 $\pm$ 0.18	2.37 $\pm$ 0.25	0.11	0.749
Energy content (kJ/g)	4.06 $\pm$ 0.12	4.63 $\pm$ 0.14	3.59	0.117

Note: Significant differences between prey types (ANCOVA) are indicated in boldface.

was in water content, with *A. talpoideum* having 6% greater water content than *L. marginatus*.

Feeding performance (intra-oral transport)

Snakes showed substantial differences in feeding performance between the two prey types. Although the maximum size of *L. marginatus* consumed by a juvenile *N. fasciata* was 50% of the snake's body mass, three of 10 snakes were able to consume *A. talpoideum* equal to 105% of the snake's body mass (Fig. 2). Within the smallest prey size category (20% of snake body mass), snakes consumed an average of 1.5 prey items, regardless of prey type (Wilcoxon's matched pairs test; $Z = 1.60$, $P = 0.109$). However, snakes consumed significantly more *A. talpoideum* than *L. marginatus* within all larger prey size categories tested: 35% of snake body mass ($Z = 2.20$, $P = 0.028$), 50% of snake body mass ($Z = 2.80$, $P = 0.005$), 65% of snake body mass ($Z = 2.67$, $P = 0.007$).

Within prey size categories where both prey types could be consumed (20% and 35% of snake body mass), prey type had a significant effect on intra-oral transport time ($F_{1,30} = 120.60$, $P < 0.001$; Fig. 3). At 35% of snake body mass, mean transport time for *L. marginatus* (20.6 min) was nearly 15 times higher than that of *A. talpoideum* (1.5 min). Even transport time of *A. talpoideum* of 105% of snake body mass (9.0 min) was only half as long as that of *L. marginatus* of 35% of

snake body mass (20.6 min). Prey size also had a significant effect on intra-oral transport time ($F_{1,30} = 18.2$, $P < 0.001$), with larger prey taking longer to transport in both prey types.

Digestive metabolism

Juvenile *N. fasciata* weighing 18.47 $\pm$ 0.29 g had SMRs of 0.66 $\pm$ 0.04 mL O_2/h, and SMR did not differ between treatments (Table 2). After consuming meals of 25% of their body mass, snakes exhibited classic SDA response curves (Fig. 4). Overall, SDA curves were similar between the two prey types ($F_{8,3} = 7.49$, $P = 0.063$), with only subtle differences in the shapes of the curves (Fig. 4). Individual comparisons revealed no effect of treatment on total VO_2 consumed, peak O_2, digestive scope, SDA coefficient (proportion of ingested energy allocated to SDA), and time to peak O_2 consumption (Table 2). However, treatment did significantly affect time to 50% and 75% decrease from peak O_2 consumption (Table 2), with snakes fed *A. talpoideum* declining more steeply towards baseline O_2 consumption rate than snakes fed *L. marginatus* (Fig. 4).

Post-feeding locomotor performance

Prior to feeding, snakes in both treatment groups exhibited maximum crawling speeds of ~25 cm/s (Fig. 5). Following consumption of prey, snakes in both treatment groups exhibited significant reductions in
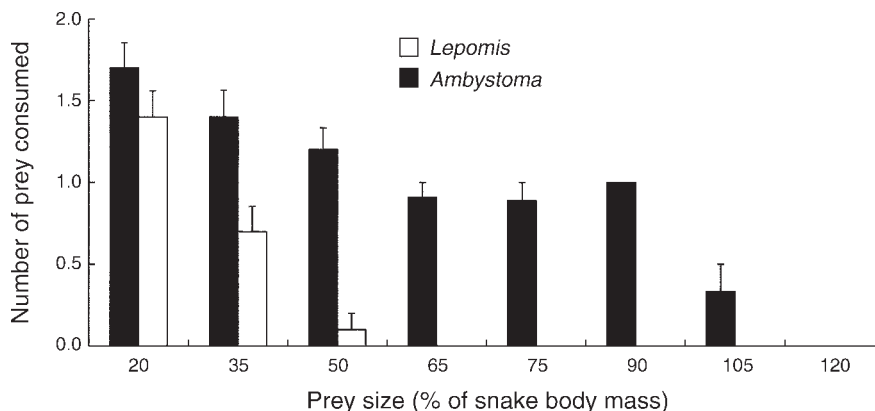

FIG. 2. Number of prey consumed (mean + SE) by juvenile *Nerodia fasciata* fed *Ambystoma talpoideum* or *Lepomis marginatus* of varying sizes. For prey sizes between 20% and 65% of snake body mass, snakes were offered both *A. talpoideum* and *L. marginatus*, on separate occasions. For prey sizes >65%, snakes were offered only *A. talpoideum* of larger size. In all cases snakes were offered prey in excess, and no snake consumed all prey offered.
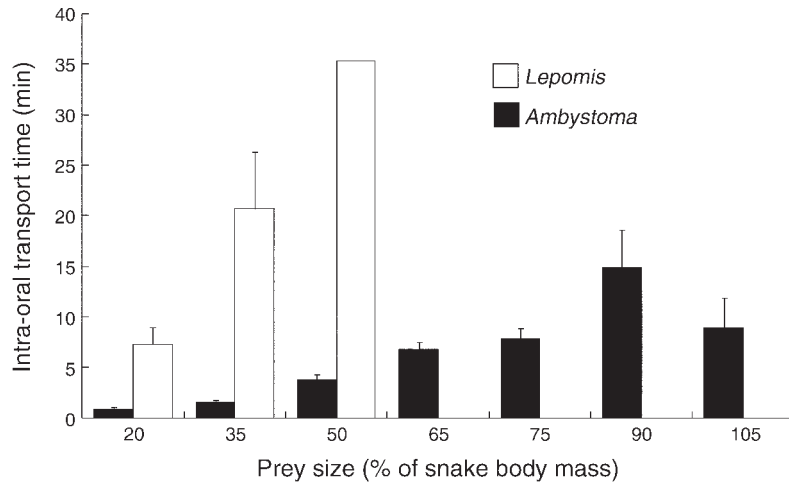
FIG. 3. Mean (+SE) intra-oral transport times (time from commencement of jaw walking to first tongue flick after swallowing) of juvenile *Nerodia fasciata* fed *Ambystoma talpoideum* or *Lepomis marginatus* of varying sizes. Lack of error bars for *Lepomis* in the 50% size category reflects the fact that only one snake consumed a *Lepomis* of that size.

maximum sprint speed (time, $F_{6,84} = 16.71$, $P < 0.001$). This reduction, however, was much more pronounced in snakes fed *L. marginatus* than in snakes fed *A. talpoideum* (time-by-prey type interaction, $F_{6,84} = 2.67$, $P = 0.020$). When tested 1 h post-feeding, snakes fed *L. marginatus* displayed an average maximum sprint velocity of 13 cm/s, a reduction of nearly 45% from pre-feeding speed, whereas snakes fed *A. talpoideum* displayed a maximum sprint velocity of 21 cm/s, a reduction of only 23% from pre-feeding speed. Snakes gradually increased in mean sprint velocity during digestion. However, snakes that had consumed *L. marginatus* did not attain preprandial crawling velocities until ~100 h after feeding.

DISCUSSION

Our results suggest that the shape of aquatic salamanders (e.g., *Ambystoma talpoideum*) make them a more desirable prey for juvenile watersnakes than centrarchid fish (e.g., *Lepomis marginatus*). Energetic content per unit prey mass did not differ between the prey types and only slight differences existed in nutritional content; *Lepomis* was 2.4% higher in protein content than *Ambystoma*. However, the slight advantage of *Lepomis* in terms of protein content was offset by the fact that juvenile *N. fasciata* were able to consume much larger *Ambystoma* than *Lepomis* and consumed more *Ambystoma* at sizes where both prey types could be consumed. Although cost of digestion (SDA response) was similar between the prey types, likely reflecting their similar nutritional composition, other costs associated with consumption were higher for *Lepomis* than for *Ambystoma*. Specifically, *Lepomis* induced greater post-prandial body distension in snakes than did *Ambystoma*, resulting in severely impaired locomotor performance. These differences highlight the complexity of evaluating prey quality for generalist predators and highlight the advantages of elongate prey (such as amphibians) for snakes.

TABLE 2. Metabolic parameters (mean ± SE) of *Nerodia fasciata* fed *Ambystoma talpoideum* and *Lepomis marginatus* equal to 25% of snake body mass at 25°C.

Parameter measured (units)	*Ambystoma*	*Lepomis*	$F_{1,10}$	P
N (number of snakes fed)	11	11		
Mass (g)	18.63 ± 0.49	18.31 ± 0.34		
SMR (mL O_2/h)	0.65 ± 0.06	0.67 ± 0.06	0.59	0.46
Peak O_2 rate (mL O_2/h)	4.00 ± 0.14	4.02 ± 0.09	0.00	0.98
Digestive scope (peak O_2/SMR)	6.53 ± 0.40	6.54 ± 0.65	3.23	0.10
Time to peak O_2 (h)	31.75 ± 2.91	24.91 ± 2.00	2.22	0.17
Time to 50% decrease from peak (h)	68.27 ± 1.53	74.33 ± 2.19	5.77	**0.04**
Time to 75% decrease from peak (h)	81.21 ± 1.72	95.94 ± 5.95	5.66	**0.04**
SDA				
Total O_2 consumed (mL)	229.54 ± 7.01	242.67 ± 8.88	0.49	0.50
Total energy expended (kJ)	4.54 ± 0.18	4.80 ± 0.18		
SDA coefficient (% ingested energy utilized)	23.83 ± 0.47	22.98 ± 0.66	0.03	0.87

Notes: Significant differences between prey types (MANOVA; individual as blocking factor) are indicated in boldface. Abbreviations are: SMR, standard metabolic rate; and SDA, specific dynamic action.
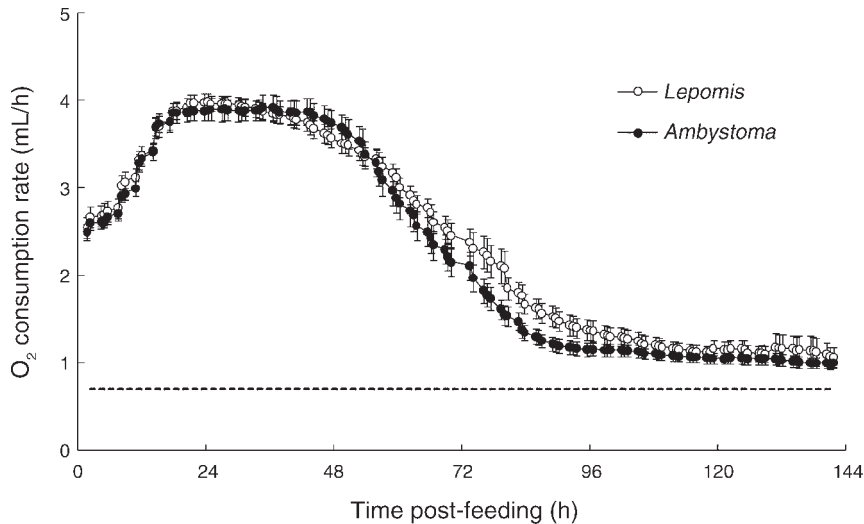
Fɪɢ. 4. Oxygen consumption (mean ± SE) by juvenile *Nerodia fasciata* fed an *Ambystoma talpoideum* or *Lepomis marginatus* equal to 25% of the snake's body mass at 25°C. The dashed line represents *Nerodia fasciata's* standard metabolic rate (SMR).

Feeding performance (intra-oral transport)

Although snakes are well known for their ability to consume massive meals relative to their body size, our understanding of how prey shape contributes to feeding performance is limited (but see Mori 1991, 1997, Kley and Brainerd 2002, Vincent et al. 2006). We found that prey shape was extremely important in determining the maximum size of prey that could be consumed by snakes; the maximum size of *Ambystoma* that snakes could consume (105% of snake mass) was over twice the maximum size of *Lepomis* (50% of snake mass). This result corroborates the findings of Vincent et al. (2006), who concluded that prey with greater maximum dimensions were more difficult for snakes to consume than more elongate prey. Interestingly, the upper size of *Ambystoma* that snakes were able to consume was apparently not dictated by gape limitation. In fact, three snakes attempting to swallow very large *Ambystoma* (105% or 120% of their body mass) all managed to get well past the widest point of the prey item (head) before regurgitating. This observation suggests that snakes may be limited by the volume of their stomach, rather than their gape, when consuming elongate prey such as *A. talpoideum*. Alternatively, these large prey may have filled the snake's body cavity so completely that cardiovascular or respiratory function would have been impaired had the snake not regurgitated. Other authors have noted that elongate, but massive, prey represent the ideal prey shape for snakes and it has been suggested that a switch to elongate prey was a precursor to the success, and subsequent diversification, of ancestral snakes (Greene 1983). Our results support this conclusion by demonstrating that, for snakes, feeding on large, elongate prey can alleviate the constraints of gape limitation.

We also observed striking differences in intra-oral transport time between the two prey types. Transport time was always longer for *Lepomis*, and even *Ambystoma* of over 100% of snake body mass took less than half as long to transport as *Lepomis* weighing 35% of snake body mass. These results confirm the findings of Vincent et al. (2006) that prey shape, independent of prey mass, can be an important determinant of snake feeding performance. Vincent et al. (2006) suggested that wide or bulky prey may interfere with a snake's ability to use anterior vertebral bending to transport prey past the jaws. It is likely that the narrow, high shape and stiff structure of *Lepomis* contributed to the longer transport times we observed by forcing snakes to rely primarily on jaw protractions to transport fish (Kley and Brainerd 2002). Alternatively, it is likely that the elongate shape of *Ambystoma* placed the anterior portion of the prey item far enough past the cranium
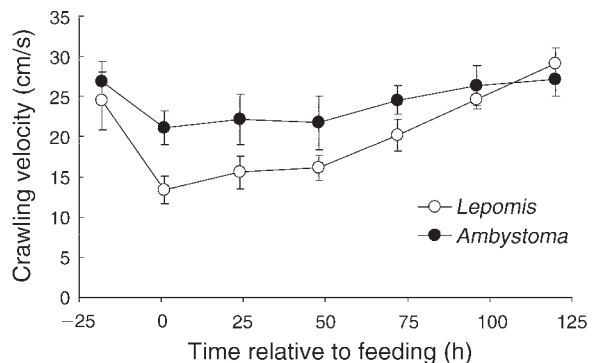

Fɪɢ. 5. Post-feeding locomotor impairment of juvenile *Nerodia fasciata* fed *Ambystoma talpoideum* and *Lepomis marginatus*. Plots represent maximum crawling speeds (mean ± SE) over a 60-cm interval 18 h prior to feeding and 1 h, 24 h, 48 h, 72 h, 96 h, and 120 h after consuming prey equal to 25% of the snake's body mass.

to permit the use of concertina-like movements of the anterior portion of the snake's trunk to aid in intra-oral transport (Cundall and Greene 2000, Kley and Brainerd 2002), resulting in rapid transport times, even for very large prey. Further, although we tested only dead prey, transport of live *Lepomis* would likely be further hindered by the erection of sharp dorsal spines, increasing body height of *Lepomis* relative to *Ambystoma*. Although the energetic cost of prey transport and swallowing in snakes is likely small in relation to the net energy gained from the meal (Feder and Arnold 1982, Cruz-Neto et al. 2001), differences in transport time are important. Increased prey handling time may increase predation risk, especially in juvenile snakes (Arnold 1993, Vincent et al. 2006). Many animals, including snakes, are known to make foraging vs. risk decisions (Sih 1992, Lima 1998, Aubret et al. 2007). Thus, snakes may avoid prey that incur an increased risk of predation. Alternatively, snakes inhabiting habitats where the only prey available require lengthy transport times (e.g., permanent wetlands) may be subject to elevated levels of predation.

Cost of digestion

Previous studies suggest that nutritional composition, particularly protein content, is the primary driver of the SDA response in ectotherms (McCue et al. 2005). This conclusion is based primarily on observations that SDA response correlates strongly with protein content of meals (Hailey 1998). Moreover, inhibition of protein synthesis has been shown to disable the SDA response in both fish (Brown and Cameron 1991*a*, *b*) and snakes (McCue et al. 2005). However, little is known about the effects of prey shape or other morphological attributes on digestive physiology, and few studies have compared SDA responses of ectotherms fed natural prey types that are similar in nutritional composition, but different in morphology.

Although *Ambystoma* and *Lepomis* are similar in nutritional composition, we hypothesized that *Ambystoma* would be less costly to digest than *Lepomis* because *Ambystoma* lack scales, spiny fin rays, or other presumably difficult to digest materials. Surprisingly, we found that SDA profiles were similar for snakes digesting the two prey types. This result is consistent with the general conclusion that nutritional composition of prey is the strongest determinant of SDA in snakes. However, we did detect slight differences between the prey types in the shapes of the SDA curves (time to 50% and 75% decrease from peak O_2 consumption), with digestion being completed slightly more rapidly in snakes fed *A. talpoideum*. Although the biological relevance of these slight differences is debatable, it is possible that the slightly faster digestion of *A. talpoideum*, combined with the lack of post-feeding locomotor impairment, could allow for a greater turnover rate of prey items, and consequently faster growth of snakes.

Post-feeding locomotor performance

Snakes with slim, elongate morphology generally exhibit faster maximum crawling speeds than those with stouter body forms (Ruben 1977, Shine and Shetty 2001, Shine et al. 2003). It follows that changes in relative snake mass and body width have direct effects on locomotor performance. For example, female snakes suffer reduced locomotor performance during pregnancy, due in part to the added burden of offspring (Seigel et al. 1987, Winne and Hopkins 2006). Likewise, consuming a large meal comes at a cost to locomotor performance, both on land (Garland and Arnold 1983, Mehta 2006) and in the water (Shine and Shetty 2001). For example, Ford and Shuttlesworth (1986) found that checkered garter snakes (*Thamnophis marcianus*) fed large meals exhibited reduced maximum sprint speed, average crawling speed, and endurance. However, our study is the first to report differences in locomotor performance associated with differences in prey shape, independent of prey mass. We found that snakes fed *Lepomis* exhibited much more impaired crawling speeds than those fed *Ambystoma*. Our results are not unexpected given that *Lepomis* induced a much greater distortion of normal body form than did *Ambystoma*.

Presumably, reduction in sprint speed is associated with increased exposure to predators and subsequent reduction in survivorship (Shine 1980, Jayne and Bennett 1990, Husak 2006*a*, *b*). Thus, all else being equal, juvenile *N. fasciata* feeding on centrarchid fish could experience reduced survivorship compared to those feeding on aquatic salamanders. Additionally, impaired locomotor ability may reduce snake's abilities to procure sequential prey items, ultimately reducing individual growth rates, slowing time to maturity, and retarding population growth.

Conclusions

Our results suggest that using resource availability as an index of habitat quality for generalist predators is complex, requiring consideration of more than simple prey abundance or even nutritional composition. Although the prey types we considered were similar in size and nutritional composition, differences in shape lead to substantial differences in overall prey quality. Further, the prey we considered are characteristic of different aquatic habitat types. Whereas centrarchid fish are abundant in permanent water bodies, paedomorphic salamanders are the dominant prey type (by biomass) within fishless, often temporary, wetlands (Appendix).

In South Carolina, *N. fasciata* are abundant in fishless wetlands, despite the fact that they experience precipitous declines in these habitats during periodic extreme droughts (Seigel et al. 1995, Willson et al. 2006). However, following drought-induced population declines, *N. fasciata* populations rebound rapidly, driven by high fecundity of surviving females and subsequent rapid growth to maturity of juveniles (Winne 2008). This rapid recovery may be fueled in part by the remarkable

productivity of amphibians in these habitats. Moreover, the ability of snakes to consume very large salamanders with relatively minor impediments to locomotor performance, may facilitate the high abundances and rapid individual and population growth of *N. fasciata* observed in fishless wetland habitats (Winne 2008). Conversely, consuming centrarchid fish imposes constraints on maximum prey size and induces lengthened transport times and impaired crawling speeds that presumably increase a snake's risk of predation. Thus, in more permanent aquatic habitats, juvenile snakes may be forced to either persist on a lower quality diet or resort to alternative prey types. Alternative prey could include those that are abundant but so small that they must be captured in large quantities to meet energetic demands (e.g., *Gambusia* and *Fundulus*) or those that are large but less abundant (e.g., adult anurans; see Appendix). In permanent cypress swamp habitats in Louisiana, juvenile *N. fasciata* fed predominantly on *Gambusia*, while adults fed predominantly on frogs (Mushinsky et al. 1982), with neither demographic preying extensively on centrarchid fish, despite their availability (Mushinsky and Hebrard 1977). Thus, the abundance of amphibians within fishless wetlands may make these habitats particularly important for aquatic snakes.

Our results highlight the importance of considering various aspects of prey quality when attempting to use prey abundance as an indicator of overall habitat suitability. When attempting to assess prey quality, the energetic and nutritional content of potential prey must be measured against the costs associated with prey ingestion, transport, swallowing, and processing. Although we have focused on snakes, our findings apply to many groups of organisms, especially predators that do not reduce prey size by mastication and thus are limited in the sizes and shapes of prey they can consume. Such predators include amphibians, most lizards and fishes, some birds, and a wide variety of aquatic invertebrates. For such organisms, variation in prey morphology, including shape, may lead to substantial costs in terms of handling and processing time, increased predation risk, or post-feeding performance.

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APPENDIX

Availability of prey for juvenile banded watersnakes (*Nerodia fasciata*) in permanent and periodically dry wetlands in South Carolina, USA (*Ecological Archives* E092-062-A1).