

Meal Size Effects on Antipredator Behavior of Hatchling Trinket Snakes, *Elaphe helena*

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Received: May 30, 2005

Initial acceptance: September 9, 2005

Final acceptance: September 23, 2005
(S. Foster)

doi: 10.1111/j.1439-0310.2006.01224.x

Abstract

Current foraging models limit the decision-making process of animals to the food searching and consuming phase. The post-consummatory phase of feeding may influence optimal meal size for some species as a morphologic change often results from feeding. In snakes, a single prey item can lead to abrupt increases in body mass, thus influencing locomotor performance. Identifying factors affecting locomotor performance can help predict behaviors that should maximize an animal's chance of evading predators. Although many snakes ingest large percentages of their body mass, not much work has examined the post-consummatory effects of ingesting bulky prey differing in relative mass. I examined the locomotor performance and antipredator tactics of hatchling trinket snakes (*Elaphe helena*) after subjecting snakes to mice prey varying by relative mass differences of 20–35%, 50–59% or 70–79% of an individual hatchling's body mass. Snakes in treatment groups were compared with snakes in a control group (0%). Meal size-affected locomotor parameters such as burst speed, endurance, and endurance times for hatchlings that ingested 50–59% and 70–79% of their body mass ($p < 0.001$). Recent feeding also affected the types of antipredator modes employed. Hatchlings in the 0% and 20–35% treatments exhibited behaviors that were categorized as active and threatening, while hatchlings in the 50–59% and 70–79% treatments exhibited stationary, neutral, and cryptic behaviors. Although snakes may become more reclusive following a meal, this study demonstrates that relative prey mass affects the ability of hatchling trinket snakes to flee from a predator. In turn, these results suggest that the post-consummatory effects of foraging should be considered in optimal foraging models for organisms that consume a substantial portion of their body mass during a single feeding.

Introduction

Foraging and feeding requirements shape ecologic and evolutionary patterns for many predatory organisms. The idea that organisms maximize energy intake during foraging is one of the major assumptions of foraging theories (Schoener 1971; Pyke et al. 1977). From recent studies (for review see Brown & Kotler 2004) it is apparent that foraging decisions are not strictly related to meal size but that the relationships between foraging behavior, optimal meal

size, and predator avoidance are all important for understanding decision-making processes and predator-prey interactions. Studies focusing on these complex relationships have documented the various effects of predator presence on foraging behavior (Sih 1980, 1992; Ydenberg 1998) and have shown that organisms will forage in less rewarding places when predatory risks are high (Sih 1980; Winterowd & Devenport 2004). These studies further reveal that although hunger is an internal state that drives an organism to forage, many animals exhibit

flexibility in foraging behaviors based on prior foraging experience (Devenport & Devenport 1994) and susceptibility to predation while feeding (Sih 1980; Sih & Christensen 2001; Powell & Banks 2004; Watson et al. 2004).

Although foraging models incorporate the influence of predator presence on foraging decisions, these models temporally limit the decision-making process, confining foraging decision-making to the food-seeking and food-consuming stages. Other phases of feeding such as the post-consummatory stage may influence foraging decisions. Empirical studies have revealed the effects of prey size on predatory encounter (Garland & Arnold 1983; Huey et al. 1984; Ford & Shuttlesworth 1986; Herzog & Bailey 1987; Martin 1996). In spite of these studies, optimal foraging models have yet to incorporate how post-consummatory effects of meal consumption affects foraging decisions. A possible reason for this lack of integration may be due to the conflicting results of some studies (Garland & Arnold 1983; Ford & Shuttlesworth 1986). For example, Garland & Arnold (1983) found that garter snakes (*Thamnophis elegans*), did not decrease their burst speed after feeding while Ford & Shuttlesworth (1986) discovered that *T. marcianus* decreased burst speed directly following feeding. Ford & Shuttlesworth (1986) also found that locomotor parameters did not vary when snakes were fed fish differing in relative prey mass. Another possible reason may be that an increase in predator exposure does not necessarily reflect an increase in predation rate (McNamara & Houston 1987). Organisms that are successful foragers may also be successful at escaping predators. Studies have revealed that species with broad behavioral repertoires are better able to cope with higher predation risks (Lima & Dill 1990). Regardless, it may be beneficial to include post-consummatory effects in optimal foraging models because feeding is often associated with morphologic changes as animals gain mass after feeding.

The addition of mass can potentially impair an organism's ability to evade predators (Coombs 1978; Shine 1980; Taylor et al. 1980). The idea that some organisms can modify their behavior to compensate for underlying morphologic change (Shine 1980) is important and complicates decision-making models. I predict that organisms that can behaviorally compensate for morphologic change as a result of feeding, may have a wider prey breadth in terms of size. On the other hand, organisms with a limited antipredator repertoire may make foraging decisions based on their ability to evade predators after foraging and may choose smaller meals over larger ones.

Although many taxa can serve as good study subjects to test the trade-off between meal size and predatory risk, snakes have a particularly unusual feeding biology that make them amenable to such empirical studies. Most snakes are able to ingest large prey items, and some species are able to consume prey exceeding their own body mass (Greene 1997). Often, consumption of large prey leads to significant and sudden increases in body mass that may last for many days post-feeding. An abrupt change in body mass, concentrated in a particular area of the body may promote corresponding changes in ecology and behavior (Huey & Pianka 1981). The addition of a food bolus to an ectothermic organism is expected to negatively impact antipredator behavior, potentially leaving the animal more susceptible to predators (Coombs 1978; Taylor et al. 1980; Garland & Arnold 1983; Ford & Shuttlesworth 1986). A common active antipredator behavior for many snakes is escape that requires rapid locomotion (Greene 1988,1997). Therefore, the effect of meal size on locomotor performance is potentially critical to evading predators and thus survival ability in many snake species (Arnold 1983).

Young animals are often subject to predators and environmental disturbances similar to those of their older counterparts (Wren et al. 1998); however, young individuals are disadvantaged in terms of speed and endurance because of developing physiology (Pough 1977,1978). In addition, gape-limited predators unable to consume large snakes may prey upon smaller ones (Bayliss 2001). Therefore, selection may favor specialized antipredator displays other than escape, especially in juveniles.

I conducted an experiment to determine whether the post-consummatory effects of foraging on locomotor performance and antipredator behavior may influence foraging decisions of hatchling trinket snakes. I specifically tested the effects of meal size on post-prandial escape performance. Locomotor parameters such as burst speed, endurance distance, and endurance time were analyzed, as these measures are likely to be direct effects of mass change and the rigidity of the body following feeding. I also tested whether the frequency of antipredator displays, other than escape, increased when snakes consumed larger meals.

Materials and Methods

Study Species

Elaphe helena (recently proposed as a member of the Old World colubrid snake genus *Coelognathus*, see

Utiger et al. 2002), is an excellent organism with which to examine the effects of prey size on locomotor performance because it feeds on a wide variety of prey (Daniel 1983; Schulz 1996). Recent studies have demonstrated that the behavioral repertoire for *E. helena* and other members in the genus is complex, as hatchlings are able to adopt specific behaviors for different situations (Mori 1991, 1993a,b; Mehta 2003). This species is relatively easy to maintain in the laboratory, and females are capable of producing large clutches in captivity.

Forty-eight hatchling *E. helena*, the progeny of four captive females from Sri Lanka were examined. I randomly chose 12 hatchlings from each clutch. Hatchling body mass (BM) averaged $8.3 \text{ g} \pm 3.44$ with snout-vent lengths (SVL) averaging $31.24 \text{ cm} \pm 5.62$. Although hatchlings were 25–33 d old at the start of the study, sex could not be determined reliably. All hatchlings were housed individually in 3.8 l glass jars (diameter, 12.5 cm; height, 23 cm). Each jar contained aspen substrate 2 cm deep and snakes had access to water in a small container, *ad libitum*. Ambient room temperature was maintained at 25°C throughout the experiment because performance capabilities of ectothermic organisms are temperature-dependent (Stevenson et al. 1985). Overhead fluorescent lighting was set on a 12D:12N cycle, and testing took place in the same room. Hatchlings had prior experience handling and ingesting live mice of variable sizes and were fasted for 10 d prior to testing. After this study, all animals were housed in the Ophidian Research Colony at the University of Texas for use in future experiments.

Meal Size and Locomotor Performance

Assessment of locomotor performance was similar to that of Garland & Arnold (1983), Arnold & Bennett (1984), and Ford & Shuttlesworth (1986). Hatchlings were pursued by a visuotactile stimulus around an oval track constructed of 15 cm tall aluminum flashing walls enclosing a 10 cm wide path covered with Astroturf. The two long sides of the track were 100 cm and one lap around the inner track was 380 cm. A trial commenced by introducing one snake into a designated 'start' area of the track using a miniature snake hook. Rapid locomotion was induced by gently tapping on the hatchling's tail with a 50 cm long cotton-tipped wooden dowel. Snake movement was constant with continual tapping at approximately 1 s interval. The time taken for a snake to cover the first 1.0 m was recorded with a hand-held stopwatch to the nearest 0.1 s

(inverse = 'burst speed' in cm/s). Total distance covered before adopting an antipredator strategy other than escape was recorded to the nearest 0.01 cm as a measure of endurance ability. Total elapsed time to antipredator behaviors other than escape was recorded as endurance time. If individuals reversed traveling direction, the trial was terminated and repeated 1 h later. Locomotor parameters and antipredator behaviors other than escape were recorded on a check-sheet.

Baseline locomotor performance for 48 hatchlings was tested over 2 d between 11:00 and 16:00 hours. Twenty-four hours after baseline testing, hatchlings were assigned to one of four groups using a split clutch design with each clutch represented equally across treatments. Three of the treatment groups ($N = 36$) were fed dead *Mus musculus*, comprising either 20–35%, 50–59% or 70–79% of their body mass 2 h prior to testing. The 12 remaining individuals served as a control and their locomotor performance was re-tested with 0% added on to their body mass. Including baseline tests, all snakes in the treatment and control groups were tested only twice to avoid behavioral habituation to the visuotactile stimulus and the arena (Burghardt 1977). Pilot studies testing adult snakes in the same apparatus revealed that after four trials snakes gradually habituated to the visuotactile stimulus.

In addition to fleeing (escape), six other antipredator behaviors presumed to be part of the antipredator repertoire for *E. helena*, were observed during the experiment. These behaviors are described and categorized from the viewpoint of whether the snake moved toward or away from the predator, whether the behavior is active or static and the apparent function of the behavior (i.e. threatening, cryptic; Mori & Burghardt 2004). When possible, names for antipredator behaviors were adopted from the literature. The behaviors were the following:

1. *S-curve with lunge* – anterior one-third of body reared upwards into the 'S-shaped' curve and was laterally compressed. In this posture the snake would throw its entire body forward and advance by a few centimeter – (category: approach, locomotive, and threatening display).
2. *S-curve with open-mouth threat* – anterior one-third of body reared upwards into the 'S-shaped' curve and was laterally compressed. The snake's mouth was open and occasionally hissing occurred in this posture – (category: approach, active-in-place, threatening display).
3. *S-curve with head-butt* – in the 'S-shaped' posture the subject abruptly struck with a closed mouth –

(category: approach, active-in-place, threatening display).

4. *Straight body (outstretched)* – the subject assumed a rigid outstretched posture, with very slow rectilinear travel against the aluminum flashing. Snakes would also remain stationary in this outstretched posture – (category: neutral, locomotive/static, cryptic display).
5. *Outstretched with open-mouth threat* – rigid, outstretched posture with open mouth and hissing – (category: neutral, active-in-place, threatening display).
6. *Coil with head and tail concealed* – (category: withdrawal, static, cryptic display).

Statistical Analysis

Data were analyzed using SAS software (SAS Institute Inc., 2001) and SPSS 12.0 (SPSS Inc., Chicago, IL, USA). Data satisfied the assumptions of equal variance and were analyzed with parametric tests. Accordingly, an ANOVA was used to examine maternal effects on baseline locomotor performance. Although all snakes were run only once in the treatment and control groups, a repeated measures ANOVA was used to detect differences in burst speed, endurance ability, and endurance time between each of the three treatment groups (20–35%, 50–59%, and 70–79%), the control (0%) and baseline run in an attempt to reduce variance caused from exposing the sample to both the baseline run and one other control or treatment run. A Tukey-Kramer test was used to examine paired differences between the baseline and control group because of unequal sample sizes. As there were no significant differences in burst speed, endurance ability, and endurance time between the baseline and control group, an ANOVA was used to test differences between the treatments and control. Post hoc pairwise comparisons were made using Dunnett’s test to compare each treatment mean with the control mean. Dunnett’s test enabled me to examine whether meal size impaired hatchling escape performance. I used a Kruskal–Wallis test to examine the distribution of behaviors during baseline trials and between the three treatments and control group. Tests were two-tailed and the level of significance was $p = 0.05$.

Results

Meal Size and Locomotor Performance

Baseline data

There were no maternal effects on locomotor performance [burst speed: $F(3,45) = 0.721$, $p = 0.42$;

endurance distance: $F(3,45) = 0.657$, $p = 0.583$; endurance time: $F(3,45) = 1.112$, $p = 0.35$]. Hatchlings fled when placed in the arena and on average, completed more than 1.5 laps (634.22 ± 14.2 cm; Fig. 1) before resigning to an alternative behavior. Behaviors other than escape included only the following approach active threatening displays (Mori & Burghardt 2004): S-curve with lunge, S-curve with open-mouth threat, and S-curve with head-butt.

Treatment data

Hatchling snakes in the 20–35% treatment immediately consumed their meals. Hatchlings in the 50–59% and 70–79% treatments were offered meals every 5 d for up to 20 d before they successfully

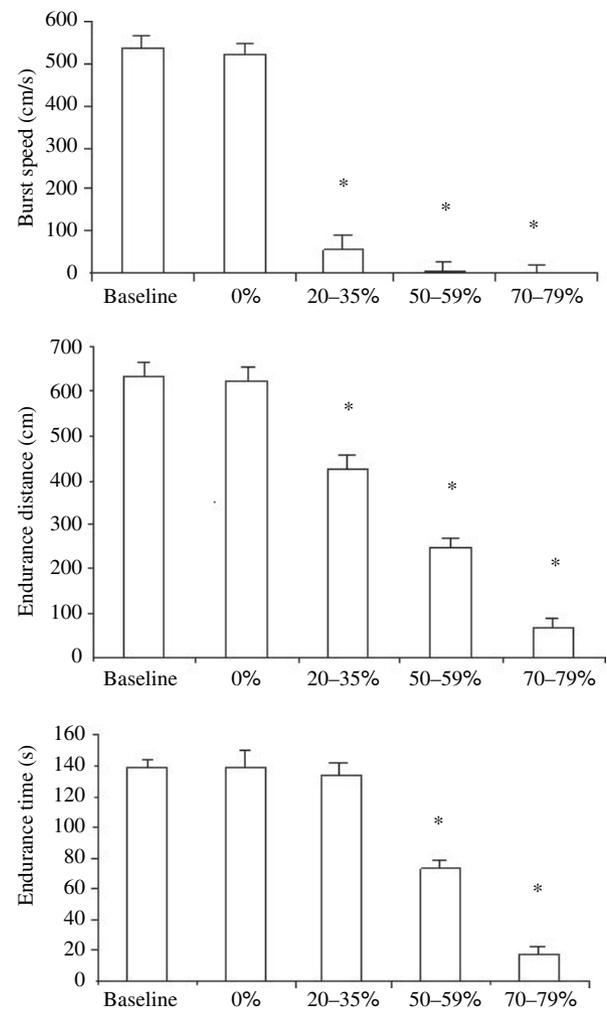


Fig. 1: Results of locomotor parameters examined for hatchling trinket snakes (*Elaphe helena*). Bars show mean \pm SE. *Significance at $p < 0.05$ when compared with control (0%) group

ingested prey and could participate in the experiment. Hatchlings in the 70–79% treatment were noticeably distended. Despite large meal sizes, no individuals regurgitated during a performance trial. Only two individuals in the 0% treatment reversed direction during trials. These individuals successfully repeated the trial 1 h later.

A repeated measures ANOVA revealed no significant differences between baseline data and the control group (0%) in burst speed [$F(1,59) = 534.22$, $p > 0.1$], endurance distance [$F(1,59) = 447.12$, $p > 0.1$], and endurance time [$F(1,59) = 218$, $p > 0.1$; Fig. 1]. As there were no significant differences between the baseline and control group, I used an ANOVA to examine differences across the treatment groups and control. All post hoc comparisons were between treatment groups and the control. Significant differences were detected in mean burst speed across the three treatment groups and control (0%) group [$F(3,44) = 43.84$, $p = 0.004$; Fig. 1]. Dunnett's comparisons revealed a significant difference in burst speed between the 0% and 20–35% treatments ($p < 0.001$). There were significant differences between the 0% and 50–59% ($p < 0.05$) and the 0% and 70–79% treatment groups ($p < 0.001$). Hatchling burst speed was fastest in the 0% and the 23–35% treatment while burst speed was slowest for hatchlings subjected to the 70–79% treatment.

Endurance distance was significantly different across the four treatments [$F(3,44) = 58.30$, $p = 0.001$; Fig. 1]. Dunnett's test indicated significant differences between all pairwise treatments [0% and 20–35% ($p < 0.023$); 0% and 50–59% ($p < 0.003$); 0% and 70–79% ($p < 0.001$)]. Hatchling endurance distance was best when snakes performed on an empty stomach or after consuming small meals (20–35%) relative to their body mass. The endurance of hatchlings in the 70–79% treatment was poor as distances covered were very short ($X = 70.0 \pm 2.4$). Three individuals in the 70–79% treatment group did not move when introduced into the arena and continual tapping with the visuotactile stimulus encouraged stationary antipredator postures over fleeing.

Endurance time differed significantly between the four conditions [$F(3,44) = 63.22$, $p = 0.001$; Fig. 1]. No difference in total endurance time was observed between the 0% and 20–35% conditions ($p > 0.05$). Significant differences were observed between the 0% and 50–59% ($p < 0.05$) and 0% and 70–79% ($p < 0.001$) conditions. Hatchlings in the 0% and 20–35% conditions fled as their main antipredator strategy.

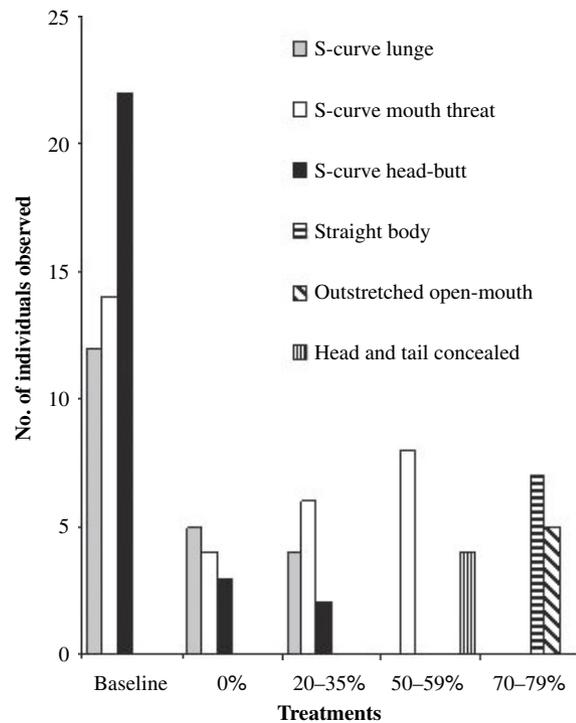


Fig. 2: Frequency of antipredator behavior observed. *Elaphe helena* hatchlings were tested for baseline antipredator repertoire ($N = 48$) and then again, after hatchlings were assigned to one of four groups: control (0%; $N = 12$), 20–35% ($N = 12$), 30–35% ($N = 12$), 50–59% ($N = 12$), and 70–79% ($N = 12$)

Defensive behaviors

A Kruskal–Wallis test revealed that the six antipredator behaviors, other than escape, were not randomly distributed across the four treatments (Fig. 2). A non-parametric multiple comparison test suggested that the frequency of these behaviors varied significantly with meal size ($Z = 5.16$, $p = 0.032$). All hatchlings in the baseline, 0% and 20–35% condition employed the S-curve posture: S-curve with a lunge, S-curve with open-mouth threat, and S-curve with head-butt. The behaviors observed in the 50–59% condition were S-curve with open-mouth threat and coiling with head and tail concealed. Eight of the 12 hatchlings in the 50–59% treatment were observed in an S-curve posture. Hatchlings in the 70–79% condition relied on static, neutral, and cryptic postures.

Discussion

The results of this study demonstrate that prey varying in relative mass have substantial effects on the escape performance and antipredator behaviors of

hatchling *E. helena*. Hatchlings in the control (0%) and 20–35% treatment exhibited fast burst speeds, relatively longer endurance times and were able to flee from the visuotactile stimulus longer before switching to another antipredator tactic besides escape. Antipredator behaviors for hatchlings in the control and 20–35% treatment were active approach displays revealing that hatchlings had more than one way to evade predators and that small meals did not impair antipredator strategies. Abrupt increases in mass resulting from the 50–59% to 70–79% treatments were difficult to overcome, as observed by the hatchling's non-threatening but cryptic antipredator postures. Hatchlings in the 70–79% treatment did not have the endurance to complete even 100 cm (one side) of the arena and exhibited the least behavioral flexibility. Therefore, the post-consummatory effects of relatively large meals may affect a hatchling snake's ability to actively evade predators in the wild.

Previous studies using colubrid snakes have demonstrated that ingestion of fish prey can affect locomotor parameters [i.e. burst speed (Garland & Arnold 1983), sprint speed, endurance (Ford & Shuttlesworth 1986)] and subsequent antipredator behavior of juvenile snakes (Garland & Arnold 1983; Ford & Shuttlesworth 1986; Herzog & Bailey 1987). In some of these studies (Garland & Arnold 1983; Ford & Shuttlesworth 1986), snakes were force-fed prey. Few studies examining the trade-offs between meal size and locomotor performance in snakes, have offered different sizes of prey to their study subjects and, with the exception of this experiment, no study to date has used bulky prey such as mice.

Studies that have examined factors affecting escape in squamate reptiles, have concentrated on morphologic (Garland 1985; Arnold & Bennett 1988) and abiotic correlates (temperature: Stevenson et al. 1985; Webb et al. 2001; ecology: Sinervo & Losos 1991), long-term changes related to reproduction (Shine 1980; Bauwens & Thoen 1981; Schwarzkopf & Shine 1992; Le Galliard et al. 2004) and feeding (Huey et al. 1984; Martin 1996). Feeding behavior is interesting because the majority of snake species have developed morphologic as well as behavioral innovations for ingesting large prey (Gans 1961) and the ability to consume large bulky prey such as rodents, has been attributed to the success of these vertebrates (Cundall & Greene 2000). Although some venomous species ingest meals that may exceed 100% or even 150% of their body mass (Garland & Arnold 1983; Greene 1997), these species do not rely on rapid locomotion for evading predat-

tors (Ruben 1977; Greene 1997). Many advanced colubrid snakes are slender fast snakes with unique antipredator repertoires (Greene 1988, 1997) and are more similar to lizards in terms of feeding habits (Greene 1983). In this study, hatchlings in the larger meal treatments (50–59% and 70–79%) refused to eat for up to 20 d whereas hatchlings in the 20–35% treatment immediately ingested prey. One plausible explanation for the lack of interest hatchlings had toward large meals may be associated with the cost of consuming large prey. After consuming prey in the wild, most snakes move to a place where they can digest prey undisturbed. As shown in this study, larger meals reduced hatchling locomotor performance and impaired offensive antipredator strategies, thus limiting a hatchling's movement and increasing predation risk.

Although 12 hatchling *E. helena* eventually consumed large prey items (up to 79% of their body mass), whether hatchlings consume prey of this magnitude in the wild is unknown. If the diverse antipredator strategies of *E. helena* observed in this study are true indicators of predatory pressures in the wild, hatchlings may maintain fitness by not consuming prey that exceed over half of their BM. The size range of prey items hatchlings consume in the wild is interesting because prey-handling and ingestion times increase in relation to prey size (Mehta 2003). This is important because consuming larger meals but less frequently may decrease exposure to predators over an individual's life. Although large prey can provide individuals with more nutrients, large prey are more costly food items for juvenile snakes as the possibility of prey retaliation increases with prey size. Therefore, hatchling trinket snakes may choose to consume smaller prey items (<59% of their body mass) that can be handled with minimal effort to not only reduce retaliation by the prey item but also to allow for escape if attacked by a predator.

Garland & Arnold (1983) predicted that snakes fed larger meals (50–150% of body mass), compared with meals offered in their study (18–27%), might be slower after feeding. This study supports the above hypothesis and reveals that larger meal sizes have an effect on the locomotor performance and antipredator tactics of hatchling *E. helena*. Hatchlings fed meals up to 35% of their body mass, are able to maintain fast burst speeds and long endurance times similar to hatchlings that were tested on an empty stomach. Burst speed, endurance ability, and endurance times were sacrificed when meals >35% of a hatchling's relative body mass were consumed.

In addition to the variables that may affect the reliability of optimal diet theory (ODT; for review see Sih & Christensen 2001), post-consumption effects of foraging may confound optimal foraging models as some organisms may make foraging decisions based not only on predation possibilities while foraging but also upon the chances of avoiding predators directly after a successful forage. Failure to respond quickly by fleeing or by employing a potentially threatening antipredator behavior during a predatory encounter may be fatal to a young reptile. Future studies should examine whether hatchlings prefer large meals when given choices of prey varying in relative mass. While prey size-affected escape behavior of hatchling *E. helena*, more studies examining the effects of meal size on locomotor performance are necessary to better understand selection pressures influencing foraging decision-making in vertebrates.

Acknowledgements

I thank Gordon Burghardt, Rose Carlson, Dave Cundall, Todd Freeberg, Tim Higham, Darrin Hulsey, Akira Mori, Steve Mullin, Ali Rabatsky, Vladimir Pravosudov, Jonathon Redwine, Randy Reiserer, and two anonymous reviewers for comments on the manuscript. Neil Ford provided the animals for this study. Animals were kept in captivity in accordance with the University of Texas, Tyler Animal Care Protocol.

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