ARTICLE

Early experience shapes the development of behavioral repertoires of hatchling snakes

Rita S. Mehta

Abstract Snakes are obligate predatory organisms that consume prey whole, and despite their precocious nature, snakes must develop effective feeding skills, especially when encountering large prey. I conducted two experiments that document the development of behavioral repertoires for naïve hatchling trinket snakes, *Coleognathus helena*. In the first experiment, I examined how experience with prey of different relative prey mass encountered at regular feeding intervals affects hatchling feeding response. I also examined whether hatchling feeding performance improved over time. Improvement was evaluated on the frequency of the most effective behavioral states such as complex prey restraint behaviors and anterior-first ingestion. In the second experiment I tested whether feeding experience with prey of a particular size influences the way hatchlings respond to a novel prey size. All hatchlings improved their predatory behavior when prey size and number of trials were controlled. Hatchlings feeding on larger prey, however, showed greater overall improvement in their feeding behavior and were quick to integrate complex prey restraint behaviors such as constriction into their feeding repertoire. Despite the fact that early experience with one prey size seemed to shape their restraint repertoire during their first four feeding events, hatchlings remained flexible and responded to prey of a novel size with size-specific prey restraint behaviors.

R. S. Mehta
Department of Biology, University of Texas, Tyler,
TX 75719, USA

R. S. Mehta (✉)
Section of Evolution and Ecology,
University of California, Davis, CA 95616, USA
e-mail: rsmehta@ucdavis.edu

Introduction

Snakes are precocious obligate predators with complex behavioral repertoires that are innate but greatly affected by experience (Fuchs and Burghardt 1971; Arnold 1978; Waters and Burghardt 2004). How experience affects the feeding repertoire of naïve snakes has been much less studied compared to other aspects of hatchling snake development such as how experience affects their preferences for particular prey types. Although it has been shown that most organisms have some innate response to food (Burghardt 1978), an individual's early experience with prey is one of several variables that play a major role in molding foraging skills (Burghardt 1992; Morse 2000; Krause and Burghardt 2001; Waters and Burghardt 2004).

The development of prey restraint behaviors is especially illuminating in snakes because, despite their limbless nature, many snakes have more than one way of restraining prey (de Queiroz 1984; Mori 1993a, b, 1994; de Queiroz and Groen 2001; Mehta 2003), and because compared to other precocious and altricial vertebrates, feeding events are relatively infrequent. Since the duration between feeding events can range from a few days to many months, the patterns and speed by which repertoires develop may be variable and result in different developmental or maturational patterns. On the other hand, we may predict that due to infrequent feeding, each feeding experience is an opportunity to make notable improvements in feeding behavior which may, in turn, be a considerably valuable contribution to an individual's behavioral repertoire.

The predatory sequence of snakes has been categorized into the following phases: prey capture, prey restraint, prey manipulation, intraoral transport, and swallowing (Cundall and Greene 2000). Behaviors in most of these phases are further organized into two or more behavioral states. Particular behavioral states in the prey capture, prey restraint, and intraoral transport phases appear to be more effective in that they have been shown to reduce overall feeding duration (Loop and Bailey 1972) although this is highly dependent upon the predator and the type of prey (de Queiroz and de Queiroz 1987; Mori 2006).

The prey restraint phase for many snakes is developmentally complex because prey restraint behaviors take place along the snake's trunk and require motor skills such as speed and accuracy, two motor characteristics that increase with experience (Schmidt 1991). For snake taxa examined thus far, restraint behaviors are innate, and naïve snakes appear to employ behaviors best suited to handle prey based on proximate prey characteristics (Mori 1991, 1993b; Mehta 2003). Although prey restraint behaviors may be an intrinsic component of a snake's behavioral repertoire, young snakes do not handle prey with the same expertise as observed in adults of their species (Mori 1994, 1995). In light of the behavioral diversity exhibited by many colubrid snakes, I was interested in testing whether repeated experience with prey of a particular size can shape the early behavioral repertoire of hatchling trinket snakes (Coleognathus helena). Furthermore, I wanted to document how quickly trinket snakes incorporate the most effective behavioral states into their predatory sequence. Given the existing evidence that snakes respond to prey characteristics, it might be expected that continued experience with prey of a particular size will affect the development of a hatchling snake's predatory repertoire as well as how it responds to prey of a novel size. Based on what we know about colubrid snake feeding behavior, I made the following predictions about how behavioral repertoires in hatchling trinket snakes may develop when size of prey and frequency of predatory encounters are controlled. I predicted that when hatchlings consistently experience small prey at regular intervals, which may be perceived as less challenging, they would be more likely to vary their prey restraint behavior with each predatory encounter and build upon their prey restraint repertoire. When hatchlings consistently experience large prey at regular intervals, which may be perceived as more challenging, hatchlings would adopt fewer prey restraint behaviors and improve those behaviors rather than build upon their behavioral repertoire. I also predicted that repeated experience with prey of a particular size would impair the ability of hatchlings to exhibit size-specific prey responses.

Materials and methods

Experimental design

Forty hatchling trinket snakes, C. helena (formerly of the genus Elaphe, see Utiger et al. 2002), the progeny of five captive born females that were housed at the University of Texas Ophidian Research Colony, Tyler, TX, were examined. Eight hatchlings were randomly chosen from each clutch 24 h after the last hatchlings emerged from their eggs. 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. Water was available ad libitum in small glass bowls. The bottom of the jars was maintained at 23–25°C with external heat tape. Overhead fluorescent lighting was set on a 12D:12 N cycle.

After the first neonatal ecdysis, which occurred between 4 and 10 days after hatching, hatchling body mass (BM) and total length (TL) were recorded. Hatchlings were weighed to the nearest 1 g and were measured for their TL by gently tracing a string from the tip of the snout to the tip of the tail. The string was then measured to the nearest 1 mm. Mean BM ($\pm$SE) was 9.48 $\pm$ 1.1 g and mean TL was 30.3 $\pm$ 1.41 cm. BM and TL did not differ among the five clutches (BM: $F_{4,39} = 2.4$, $P > 0.05$; TL: $F_{4,39} = 2.12$, $P > 0.05$).

Hatchlings were 12–15 days old at the start of the study. Hatchlings were divided into two groups ($N = 20$ each) using a balanced clutch design with each clutch represented equally across treatments. The first treatment group was fed live Mus musculus comprising a relative prey mass of 20–35% and will herein be referred to as the small prey treatment (S treatment). The second treatment group, large prey treatment (L treatment), was fed live M. musculus comprising a relative prey mass of 40–46%. Hatchlings were offered prey every 10–15 days until four feeding trials were recorded for each hatchling. This 10-to–15-day interval, following pilot studies, not only increased the chance that hatchlings would feed but also allowed time for hatchlings to undergo ecdysis. Hatchlings and mice were weighed to the nearest 0.01 g 24 h prior to each feeding to ensure relative prey mass remained between 20–35% and 40–46% of hatchling BM.

Experiment 1: effects of prey size on behavioral repertoires

Testing took place in hatchling home jars. Two hours prior to feeding, the water dish and the majority of aspen substrate were removed. Trials commenced by gently placing a live prey item in the jar with 50 cm long forceps. The following variables, which were modified from de Queiroz (1984) and Mori (1991, 1994), were recorded for the first four feeding trials.

(1) *Capture position*: the part of the prey's body first grasped by the snake. Three states were recorded: (a) anterior (head and shoulder), (b) middle (abdomen and forelegs), and (c) posterior (pelvic region, hind legs, and tail).

(2) *Prey restraint method*: the method by which the snake restrained prey. Four states were recorded: (a) simple seizing, (b) pinion, (c) hairpin loop, and (d) constriction. More detailed descriptions of these behaviors are found in Table 1.

(3) *Prey restraint time*: the elapsed time in seconds from the moment the prey was struck or seized to the commencement of swallowing.

(4) *Condition of ingestion of prey*: the condition of prey after the prey restraint phase and just before swallowing. Two states were recorded: (a) alive or (b) dead.

(5) *Direction of ingestion of prey*: there were two directions in which prey could be swallowed: (a) anterior; the head and neck region of the prey could enter the mouth of the snake first or (b) posterior; the tail end could be ingested first.

Of these five feeding variables, prey restraint method had additional behavioral states. Prey restraint methods can be performed immediately (I) after capture or delayed (D) 1 or more seconds after prey capture. I recorded the presence of delayed behavioral states in each feeding trial. All trials were recorded with an 8-mm Sharp video-recorder (VL-E43U), and the above feeding variables were documented with a check-sheet.

For each treatment group, I used a Cochran's Q-test to detect differences between trials for the four matched sets (experiences) of responses (reported as frequencies) for the following behaviors: capture position, prey restraint method, condition of ingestion, and direction of ingestion (Siegel and Castellan Jr 1988). To compare responses across treatments, I used Fisher exact probability tests due to small sample sizes. The frequencies of behaviors were arranged in a 2×2 contingency table. Therefore, every individual could obtain only one of two possible scores for each behavior. Behaviors that had more than two behavioral states, capture position and prey restraint method, were further assigned to one of two categories: "adaptive" or "other" and "simple" or "complex," respectively. Anterior prey capture was assigned to the adaptive category and all the other behavioral states for capture position were assigned to "other." I used the complexity values generated for the four prey restraint methods following Bealor and Saviola (2007; see below) and assigned prey restraint behaviors as either simple or complex. Behavioral states that had complexity values of 1 and 2 were assigned to the simple category, and the remaining behavioral states that had values of 3 and 4 were considered complex.

To evaluate the effects of experience on prey restraint behavior, I compared the frequency of the least complex prey restraint behavior, simple-seizing, with the most complex behavior, constriction, across trials. I adopted a recently proposed method for assessing behavioral complexity in snakes (Bealor and Saviola 2007). This method quantifies the number of distinct functional acts that comprise a given behavior, the apparent coordination among acts, and the amount of the snake's body used during each behavior. These three measures generate a complexity score which is then used to compare the different behavioral states relative to one another.

Table 1 Descriptions of prey restraint behaviors employed by hatchling *Coleognathus helena*

Behavior	Definition	Complexity value	Assignment of points
Simple seizing	Grasping the prey in the jaws without subduing it with the body	1	A single functional act—grasping with the jaws; no part of the snake's trunk is used
Pinion	An area along the snake's trunk is used to hold down the prey and secure it to the substrate	2	Two functional acts—grasping with the jaws (1) and restraining prey with body (1)
Hairpin loop	Winding one encircling loop around prey	3	Two functional acts—grasping with the jaws (1) and restraining prey with body (1), more coordination required than pinning because prey is positioned between trunk, and trunk applies pressure to subdue prey (1)
Constriction	Using two or more fully encircling loops around prey	4	Two functional acts—grasping with the jaws (1) and restraining prey with body by two fully encircling loops around prey (1), more coordination required than hairpin loop because two coils are wound around prey (2)

Complexity values generated for each behavioral state were based on the number of distinct functional acts used during a prey restraint behavior, whether the snake's body was used, and apparent coordination among acts (after Bealor and Saviola 2007)

I pooled the responses of hatchlings in both treatments and used a Markov-Chain analysis to evaluate whether the transition to more complex behaviors is dependent upon the appearance of simple behaviors or if complex behaviors are randomly dispersed across trials. In a separate analysis I examined the frequency of immediate vs delayed prey restraint responses.

Prey restraint time data were $\log_{10}$ transformed to meet the assumption of normality prior to analyses (Sokal and Rohlf 1981). I first used a two-way repeated-measures ANOVA to test for an interaction effect between treatment and trial. I then used a repeated-measures ANOVA for each treatment separately to compare prey restraint time across trials with restraint time as the repeated measure. Tukey tests were used to perform pair-wise comparisons across trials. SPSS version 13.0 was used to obtain descriptive statistics and perform both parametric and nonparametric tests. The level of significance for all statistical tests was $P < 0.05$.

Experiment 2: responses to novel prey size

The subjects and housing were the same as in Experiment 1. Two weeks after Experiment 1, hatchlings were weighed and measured to determine whether the two feeding treatments significantly affected hatchling size. BM and TL differed between the two treatments (BM: $F_{1,19} = 6.4$, $P = 0.04$; TL: $F_{1,19} = 4.12$, $P = 0.05$), and as anticipated, hatchlings in the L treatment were larger than those in the S treatment. Body size may have effects on feeding response, and the implications of the effects of body size in this experiment are considered in the discussion.

Hatchlings were 64–72 days old at the start of the experiment. The two treatments (S and L) were subdivided, and hatchlings within each treatment were randomly assigned to one of two sub-treatments: Novel Small (NS) and Novel Large (NL). Each sub-treatment group contained ten hatchlings. Hatchlings in the NS sub-treatment were offered prey comprising a relative prey mass of 10%, whereas those in the NL sub-treatment were offered prey comprising a relative prey mass of 60%. Relative prey masses of 10 and 60% were specifically chosen because the rodents that were available matched this size range and none of the hatchlings had previous experience with a prey item comprising either of these relative prey masses. Hatchlings within each sub-treatment were only tested once and experienced either small or large prey. This experimental design allowed me to test whether experience with a particular prey size has subsequent effects on responses to novel prey size without confounding prior experience. Thus, the behaviors of hatchlings within each sub-treatment (NS and NL) were compared with each other and between treatments (S and L). Testing took place in

hatchling home jars and followed the same feeding protocol as described in Experiment 1. Variables examined were same as those presented in Experiment 1.

Fisher exact probability tests were used to determine whether the frequency of behavioral states differed between sub-treatments within each treatment and between treatments. Behavioral states were organized into the same categories described in Experiment 1. Prey restraint time data were $\log_{10}$ transformed and tested for normality. I used an ANOVA to test for an interaction effect between treatment and sub-treatment. An ANOVA was then used to compare prey restraint times between the two treatments and between the two sub-treatments.

Results

Experiment 1: effects of prey size on behavioral repertoires

All hatchlings consumed prey during the experiment. Behavioral states for all trials are summarized in Table 2. Capture position for hatchlings in both treatments was significantly different across trials (S treatment: Cochran's $Q = 27.43$, $df = 3$, $P < 0.001$; L treatment: Cochran's $Q = 42.27$, $df = 3$, $P < 0.001$). As experience with prey of similar relative masses increased, the frequency by

Table 2 Development of feeding behavior of hatchling *Coleognathus helena* across four trials for snakes fed small (S) or large (L) mice, *Mus musculus*

Variables	Treatments							
	Small mouse ($N = 20$)				Large mouse ($N = 20$)			
	1	2	3	4	1	2	3	4
Capture position								
Anterior	4	6	10	15	11	16	20	20
Middle	0	2	4	4	0	4	0	0
Posterior	16	12	6	1	9	0	0	0
Restraint method								
Simple seizing	15	9	4	4	9	0	0	0
Pinion	2	5	6	4	5	10	0	0
Hairpin loop	3	3	6	6	5	3	5	2
Constriction	0	3	4	6	1	7	15	18
Ingestion condition								
Alive	20	20	12	10	20	20	12	5
Dead	0	0	8	10	0	0	8	15
Ingestion direction								
Anterior	3	8	14	20	7	15	18	20
Posterior	17	12	6	0	13	5	2	0

Small mice comprised a relative prey mass of 20–35%, and large mice comprised a relative prey mass of 40–46%

which hatchlings captured prey by the anterior (head or shoulder region) also increased in both treatments. Hatchlings from the S treatment differed in capture position strategy during all four experiences with prey ($P < 0.05$), whereas hatchlings from the L treatment differed in capture position strategy only in the first two trials. Fifteen out of the 20 hatchlings in the S treatment adopted an anterior prey capture strategy by trial 4, whereas 16 out of the 20 hatchlings in the L treatment captured prey by the anterior by trial 2. Once an individual hatchling adopted an anterior prey capture strategy, the behavior was maintained across the remaining trials for both treatments.

Four prey restraint behaviors, simple seizing, pinion, hairpin loop, and constriction, were observed across trials, and the complexity values generated for these behaviors ranged from 1 to 4 (Table 1). Simple seizing was the least complex restraint behavior, whereas pinion, hairpin loop, and constriction require varying degrees of motor coordination, involve different amounts of the snake's body (the trunk), and are more complex ways for snakes to immobilize prey. With the exception of simple seizing, hatchling snakes displayed prey restraint behaviors immediately upon capture (I), or delayed (D) 1 or more s after capture. During delayed prey restraint responses, prey was already in the snake's mouth, and the snake moved around the jar with the prey item in its jaws before using a portion of its trunk to restrain it.

A Fisher's Exact Test revealed significant differences in prey restraint behavior between treatments across all trials ($P < 0.02$). During trial 1 simple seizing exhibited the highest frequency in both treatments. As predatory experience increased, hatchlings in the S treatment gradually increased the frequency of more complex restraint behaviors, although no single behavior dominated. Hatchlings in the L treatment also employed more complex restraint behaviors with experience, and the frequency of the behaviors, simple seizing (least complex) and constriction (most complex), were significantly different across trials 1–4 (simple seizing: Cochran's $Q = 24.57$, $df = 3$, $P < 0.001$; constriction: Cochran's $Q = 20.08$, $df = 3$, $P = 0.017$). By their third predatory experience, 75% of hatchlings in the L treatment constricted prey. A Markov-Chain transition matrix was used to examine the pooled trials across both S and L treatments and revealed that the sequence of prey restraint behaviors observed, from simple to more complex, was significantly different than what would be expected by chance ($\chi^2 = 9.49$, $df = 3$, $P < 0.001$). Constriction behavior was more likely to follow pinion and hairpin loop rather than simple seizing. Only simple seizing preceded simple seizing. Thus, complex behaviors followed simple behaviors but not vice versa. In each treatment, roughly half (43–52%) of the prey restraint behaviors were delayed behaviors across all trials.

Delayed prey restraint behaviors, pinion, hairpin loop, and constriction, did not decrease with successive experience in either treatment and were randomly distributed across trials 1–4 (S treatment: Cochran's $Q = 9.32$, $df = 3$, $P > 0.05$; L treatment: Cochran's $Q = 6.14$, $df = 3$, $P > 0.05$).

With increased feeding experience, all hatchlings were more likely to kill prey prior to ingestion. By trial 4, hatchlings in the L treatment killed the majority of their prey prior to ingestion compared to 50% of prey in the S treatment. Fisher Exact tests revealed that trial 4 was the only trial that showed significant differences between the S and L treatments ($P < 0.05$). Anterior ingestion of prey gradually increased across trials for both treatments, and the proportion of prey ingested by the anterior differed across trials for both treatments (S treatment: Cochran's $Q = 38.26$, $df = 3$, $P < 0.05$; L treatment: Cochran's $Q = 23.8$, $df = 3$, $P < 0.05$). Only the first two trials differed significantly in ingestion condition between the treatments. An increase in anterior ingestion of prey across the four feeding trials revealed that hatchlings were learning the most effective direction to ingest prey.

An interaction effect between treatment and trial on prey restraint time was detected ($F_{1,3} = 16.32$, $P < 0.05$). Overall, prey restraint time was significantly shorter for hatchlings in the S treatment than those in the L treatment (Fig. 1). Average prey restraint times for hatchlings in the S treatment did not differ across trials ($F_{3,17} = 0.21$, $P > 0.05$), whereas average prey restraint times were different across trials for hatchlings in the L treatment
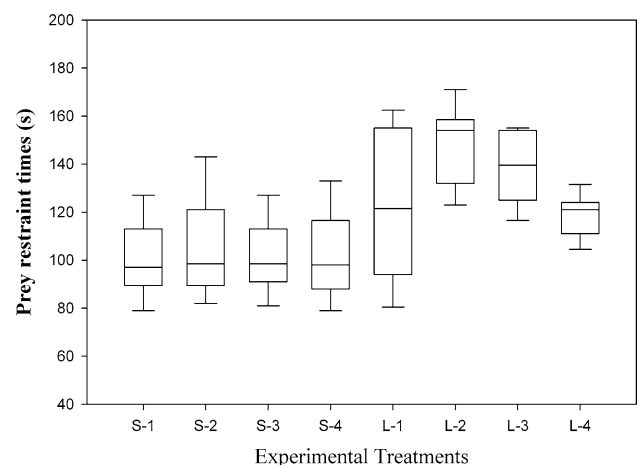
Fig. 1 Changes in prey restraint time over the four feeding trials in Experiment 1. Hatchling snakes in S treatment were offered a live mouse, *Mus musculus*, with relative prey mass of 20–35% of an individual snake's body mass. Hatchlings in L treatment were offered a mouse with relative prey mass of 40–46% of an individual snake's body mass. The *boundary of the box* closest to 0 indicates the 25 percentile, the *line within the box* marks the median, and the *boundary of the box* farthest from 0 indicates the 75 percentile. *Error bars above and below the box* indicate the 90 and 10 percentiles, respectively

($F_{3,17} = 49.31$, $P < 0.05$). Average prey restraint times for hatchlings in the L treatment decreased across trials (Fig. 1). Multiple pair-wise comparisons revealed differences between trial 1 and all other trials in the L treatment ($P < 0.01$). To determine whether the decrease in prey restraint time may be due to an increase in experience with constriction behavior or a general change in the direction of more complex prey restraint behavior, I re-examined the prey restraint times of a sub-sample of hatchlings from the L treatment. Specifically, I chose to compare the prey restraint times for seven hatchlings that repeated prey restraint behaviors in only two out of the four trials with the prey restraint times of seven hatchlings that constricted prey in trial 3 out of the four trials. A repeated-measures ANOVA indicated that there was an interaction effect between prey restraint method and trial ($F_{1,3} = 22.23$, $P < 0.05$). Hatchlings in the L treatment that predominantly employed constriction behavior exhibited average prey restraint times that were much shorter for trials 3 and 4 than those hatchlings that mostly changed prey restraint behaviors across trials.

Experiment 2: responses to novel prey size

Two snakes within the S treatment did not consume NL prey during the experimental period and were removed from the analysis. All snakes within the L treatment consumed NS or NL prey. Prior experience with small and large relative prey mass affected the subsequent responses to NS and NL prey (Table 3).

Hatchlings in the two treatments differed in the way in which they captured NS prey ($P < 0.05$). Hatchlings from the S treatment captured NS prey by the anterior, whereas hatchlings in the L treatment captured NS prey by the anterior or posterior. Hatchlings in both S and L treatments captured NL prey by the anterior. Although hatchlings in the S treatment did not respond differently towards NS and NL prey ($P > 0.05$), L treatment hatchlings responded differently toward the two novel prey sizes ($P < 0.05$).

Hatchlings in the S and L treatments exhibited different strategies for restraining NS prey ($P < 0.05$) and NL prey ($P < 0.05$). Hatchlings from the S treatment mostly pinioned NS prey, whereas NL prey were pinioned, looped, or constricted. Hatchlings from the L treatment pinioned or constricted NS prey, whereas all NL prey were constricted.

No significant differences in ingestion condition were detected between hatchlings for each sub-treatment ($P > 0.05$). The majority of hatchlings in both treatments killed prey prior to ingestion. All hatchlings consumed prey head-first.

There was a significant interaction effect between treatment and sub-treatment on prey restraint time ($F_{1,1} = 8.11$, $P < 0.05$). Prey restraint time for NL prey

Table 3 Feeding responses of hatchling *Coleognathus helena* on novel small (NS) and novel large (NL) mouse, *Mus musculus*

| Variables	S treatment		L treatment	
	NS ($N = 10$)	NL ($N = 8$)[a]	NS ($N = 10$)	NL ($N = 10$)
Capture position				
Anterior	9	8	5	10
Middle	0	0	0	0
Posterior	1	0	5	0
Restraint method				
Simple-seizing	2	0	0	0
Pinion	6	4	5	0
Hairpin loop	1	2	0	0
Constriction	1	2	5	10
Ingestion condition				
Alive	2	0	2	0
Dead	8	8	8	10
Ingestion direction				
Anterior	10	8	10	10
Posterior	0	0	0	0

Comparisons were made across snakes experienced with small (S) and large (L) prey. NS mice comprised a relative prey mass of 10%, and NL mice comprised a relative prey mass of 60%

[a] Two snakes from the S treatment did not consume NL prey and were removed from the analysis

was significantly longer than that for NS prey in both treatment groups (S treatment: $F_{1,9} = 12.62$, $P < 0.05$; L treatment: $F_{1,9} = 16.26$, $P < 0.001$). Hatchlings in the S treatment took significantly longer to handle both NS and NL prey when compared to hatchlings in the L treatment (NS prey: $F_{1,18} = 7.31$, $P < 0.05$; NL prey: $F_{1,18} = 14.63$, $P < 0.05$; Fig. 2).

Discussion

It is clear from the present study that hatchling trinket snakes incorporated more adaptive behavioral states into their predatory sequence with experience. For example, the frequency by which hatchlings captured prey by the anterior and ingested prey anteriorly increased. Although it was difficult to determine whether capturing prey by the anterior reduced overall feeding time because other behaviors in the predatory sequence were also changing with experience, hatchlings that captured prey by the anterior do not need to pause to re-orient their prey prior to swallowing. Anterior ingestion of prey has been suggested to be more adaptive than posterior ingestion of prey (Diefenbach and Emslie 1971; Loop and Bailey 1972; Greene 1976; de Queiroz and de Queiroz 1987; Cundall and Greene 2000), although this is dependent upon prey type and dietary
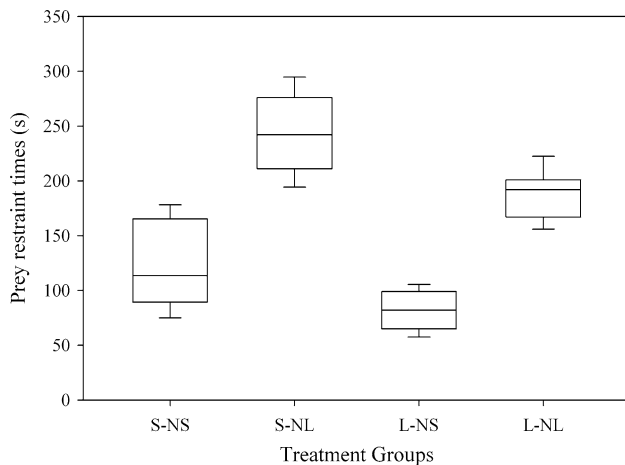
Fig. 2 Variation in prey restraint time observed in the two sub-treatments in Experiment 2. Hatchlings from each of the treatments (S: small, L: large) in Experiment 1 were further divided into two sub-treatments: novel small (NS) and novel large (NL). Hatchlings in the NS sub-treatment were offered prey comprising 10% of an individual snake's body mass, and those in the NL sub-treatment were offered prey comprised 60% of an individual snake's body mass. The *boundary of the box* closest to 0 indicates the 25 percentile, the *line within the box* marks the median, and the *boundary of the box* farthest from 0 indicates the 75 percentile. *Error bars above and below the box* indicate the 90 and 10 percentiles, respectively

specialization of the predator (Mori 2006). In this study, ingesting mouse prey posterior-first seemed to increase resistance while swallowing because the prey's appendages were not pressed up against the prey's body. Once an individual hatchling adopted an anterior ingestion strategy, the behavior was maintained, further supporting the idea that cues involving anterior ingestion may be learned and that anterior ingestion can potentially reduce overall feeding duration.

The three other variables recorded in the present study, prey restraint method, ingestion condition of prey, and prey restraint time, revealed clear developmental patterns influenced by both predatory experience and prey size. In Experiment 1, the frequency of complex prey restraint methods increased with predatory experience as did the ingestion of dead prey. Hatchlings in the S treatment retained simple seizing in their predatory repertoire across the four trials, whereas hatchlings in the L treatment only employed complex prey restraint behaviors after the first feeding trial. Prey restraint time did not decrease with experience in the S treatment, whereas a significant decrease in prey restraint time was observed in the L treatment. These results reveal that hatchlings employ adaptive behavioral states relatively early in development and support the hypothesis that small prey elicits greater prey restraint variation compared to large prey.

Experience with prey of a particular relative mass also affected the speed by which adaptive behavioral states

were incorporated in the feeding sequence and the development of prey restraint behaviors. These results suggest that small prey does not elicit a learning curve as steep as large prey. Large prey may present more risk, and this perceived threat of prey retaliation may motivate young hatchlings to handle prey more effectively as exemplified by the employment of complex restraint behaviors and the increase in dead prey prior to ingestion.

The present study also provides insight into another important developmental phenomenon, maturation. Maturation and experience are interconnected physiological processes and are often inextricable since experience can affect the timing of maturation initially and maturation can affect how an organism responds to experience (Morse 1980). Hatchlings within the two treatments differed in overall size by the end of Experiment 1. Although the size differences were not great, hatchling size may have had an effect on the latter trials in Experiment 1 and subsequent responses to novel prey size in Experiment 2. Other studies have shown that body size and maturation can influence performance patterns for many snake species (Pough 1978; Lind and Welsh Jr 1994; Savitsky and Burghardt 2000; Moon and Tullis 2006). As prey restraint behavior requires muscular movements, the maturation of the epaxial muscles, which has been shown to be active during prey restraint behaviors such as constriction (Moon 2000), may greatly affect the ability of hatchlings to constrict prey as well as the effectiveness of constriction. Thus, the findings that the frequency of more complex prey restraint behaviors (behaviors requiring more than 50% of the trunk) increased across trials and that more complex behaviors were employed by hatchlings in the L treatment in both experiments suggests that regular experience with large prey and/or muscle maturation are important in the development of predatory behavior. The increased frequency of dead prey further supports the idea that maturation plays an important role in the development of behavioral repertoires and affects the effectiveness of constriction behavior in some snake species. A previous experiment also revealed that hatchlings that employed constriction behavior to immobilize and kill prey on their first predatory encounter were significantly larger than hatchlings that used other restraint tactics that did not result in prey death prior to ingestion (Mehta 2003). The fact that delayed prey restraint behaviors did not decrease across trials suggests that more predatory experience may be needed for hatchlings to exhibit the behavioral expertise observed in subadult and adult snakes.

In addition, maturation and experience presumably played a role in keeping prey restraint time relatively constant throughout early development for hatchlings in the S treatment, while facilitating the employment of more complex prey restraint behaviors. All hatchlings in

Experiment 1 had limited experience with prey. However, within their limited experience, new prey restraint behaviors were employed by hatchlings in the S treatment. Motor skill studies have revealed that changes in performance increase rapidly, at first, and then gradually level off as a function of practice time (Annett 1985). Hatchlings that consistently experienced small relative prey masses continued to develop a broad prey restraint repertoire which resulted in less practice time for each behavior and may explain why mean prey restraint times did not decrease across trials for these hatchlings. Changes in performance, particularly with characters such as speed, may be evident after several trials. In contrast, hatchlings in the L treatment focused on fewer prey restraint behaviors which presumably increased their effectiveness for each behavior as exemplified by their reduction in prey restraint times and success in killing prey prior to ingestion. Thus, during the course of their development, snakes with more than one prey restraint behavior can either continue to expand their repertoire or improve a particular restraint behavior with each predatory experience. A comparison of a sub-set of average prey restraint times for L treatment hatchlings that predominantly constricted prey with those that varied their prey restraint behaviors support this idea. The development of behavioral repertoires will be affected by the size of prey encountered and the frequency of prey encounters. The former, especially, will dictate which behaviors are employed.

Experiment 2 revealed that experience with prey of a constant relative size has subsequent effects on predatory behavior. Overall, hatchlings in the L treatment exhibited less variability in their feeding repertoires with both NS and NL prey compared to hatchlings in the S treatment. The reduction in variability suggests that previous experience with large prey may have narrowed the behavioral possibilities available for young snakes. Whether the hatchlings in the L treatment abandon less complex behaviors from their repertoire or become more proficient constrictors as adults will necessitate long term examination. Despite the fact that hatchlings in the S and L treatments differed in the ways they responded to the two sub-treatments, hatchlings within both treatments responded differently towards NS and NL prey. These results reveal that experiences with prey of a constant size need not affect the overall ability of hatchling snakes to respond to differences in prey size. However, early experience with larger prey increases the frequency by which hatchlings employ more complex prey restraint behaviors when faced with prey of different size.

Adults of this species also have more than one way of restraining prey. In a previous laboratory study, adults of *C. helena* were observed pinioning and constricting large prey (R.S. Mehta, unpublished data). In a few of the trials

in which pinion was employed, prey escaped from underneath the snake's body. There was also much variation observed in adult constriction patterns. Some adults constricted with non-overlapping loops while others looped haphazardly around prey. Early experiences with prey may account for some of the variation observed in adult snakes.

Mori (1993a) did not detect any effects of recent experience with large or small prey on the subsequent restraint behaviors for *E. climacophora*. However, the snakes used in his study were 3 years old and exhibited similar behaviors to those of adult snakes. The present study is the first to document the development of complex motor repertoires in naive hatchling snakes while controlling for early feeding experience. The prey restraint behavior of snakes provides an opportunity to examine the development of complex motor patterns because behaviors such as pinion and constriction are performed only during feeding. Feeding hatchlings either small or large prey as in this study, may have forced hatchlings down a different developmental trajectory. Encountering small prey at regular intervals may have released the constraints on developing one particular prey restraint behavior leading to employ different prey restraint tactics for small prey. On the other hand, early experience with relatively large prey may facilitate the employment of complex prey restraint behaviors in snakes. Overall, the present study supports the idea that the effects of prey size on behavioral development may be more critical in neonates or hatchlings due to changing predator-prey body size relationships (Mushinsky 1987; Arnold 1993; Krause and Burghardt 2001). Future studies are necessary to better understand how experience with prey of a particular size may influence adult behavioral repertoires.

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