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Prey Handling Behavior of the Young Rat Snake, *Elaphe taeniura* (Squamata: Reptilia)

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Abstract The feeding behavior of the Asian rat snake, *Elaphe taeniura*, which was raised on mice, was observed when they were approximately one year old (yearlings) and two years old (juveniles). Clear preference for head first ingestion of large mice was observed in juveniles but not in yearlings. Smaller mice tended to be simply seized whereas larger ones tended to be constricted immediately after striking both in yearlings and juveniles, but this tendency was clearer in juveniles than in yearlings. Smaller mice were swallowed alive whereas larger ones were killed before ingestion in both age classes.

INTRODUCTION

Many snakes are known to change prey handling behavior according to prey size (e.g., Radcliffe et al., 1980; Kardong, 1986; Barr et al., 1988; Mori, 1991), and the different responses to different prey size are considered to have adaptive functions (e.g., Diefenbach and Emslie, 1971; de Queiroz and de Queiroz, 1987; Mori, 1991). However, most of the studies on prey handling behavior are based on adult snakes, and the ability of neonatal snakes to switch prey handling behavior according to prey size or early development of prey handling behavior are poorly investigated (Halloy and Burghardt, 1990; Mori, 1993, 1994). An Asian rat snake, *Elaphe taeniura*, is a true constrictor feeding on endothermic animals (Pope, 1935; Kuntz, 1963). Mori (1993) demonstrated that neonatal *Elaphe taeniura* showed prey-size dependent switching in some aspects of prey handling behavior such as constricting but not in other aspects such as direction of ingestion. This study investigates subsequent development of prey handling behavior of young *E. taeniura* that hatched in captivity and was reared under the controlled feeding schedule.

MATERIALS AND METHODS

Eight snakes hatched from the eggs oviposited by a wildly-caught gravid female were used as subjects. All snakes were housed individually in plastic cages (190 × 140 × 70 mm). Each cage was provided with a paper floor covering and a water bowl. The temperature varied between 25–30C except in winter. Illumination was provided by sunlight. The snakes were fed on a small laboratory mouse, *Mus musculus* (body mass 1.5–11.5 g) approximately twice a week from their first meal. No food was offered to them during winter. The size of mice offered depended on the size of the snake.

The snakes were tested when they were approximately 11 months old (referred as yearlings) and 23 months old (referred as juveniles). The testing arena was made of polypropylene corrugated board (300×150×100 mm) with transparent plastic ceiling. The arena was divided into two compartments by a plastic insert across the floor (larger 250×150×100 mm and smaller 50×150×100 mm). About 20 min prior to each trial, a snake and a prey animal were introduced into the smaller and the larger compartments of the arena, respectively. Each trial was initiated by removal of the insert from the arena by sliding it out through a slit in the front wall. After each trial, the arena was washed with water. During the experiment room temperature was maintained between 27 and 30C. The snakes were starved for seven to ten days before the experiment. Snout-vent length, head width (HW), and body mass of the snakes were measured within a week before trials.

Each yearling and juvenile was tested with one "small" mouse and one "large" mouse. The small mouse corresponded to a mouse whose relative prey size (HW of the mouse/HW of the snake) ranged from 0.50–0.83. The large mouse corresponded to a mouse with a relative prey size of 0.85–1.15. Half of the yearlings and juveniles were tested with a small mouse first, and the remaining were tested with a large mouse first. Small and large mouse trials for each snake were carried out at an interval of three days. All trials were recorded using a video camera (National VZ-C70) and a video monitor (National NV-8480, VHS type).

To examine effects of prey size on prey handling behavior, the following three variables were recorded.

1) Direction of prey ingestion: head first or tail (hind legs) first.

2) Prey handling method: simple seizing, grasping the prey in the jaws without subduing it with the body; pinion, pressing the prey against the substrate by the snake's body; a hairpin loop, squeezing the prey between non-overlapping portions of the snake's body; and coil, constricting the prey by fully encircling loop. The latter three prey handling methods were further subdivided into two categories: performed immediately after attacking as a continuation of the striking motion or performed after a delay of more than one second.

3) Condition of prey at ingestion: swallowed alive or dead. A detailed description of the above three variables was presented in Mori (1991).

Effects of prey size on direction of ingestion, prey handling method, and prey condition at ingestion were analyzed with binomial tests (Siegel and Castellan, 1988). For this analysis, prey handling methods were divided into two categories, simple seizing and the others. I predicted that large mice would be constricted, killed and swallowed head first, whereas small mice would be simply seized, and swallowed either head or tail first without being killed. Binomial tests were based on the null hypothesis of equal probability of change of direction. Binomial tests were also employed separately for small and large mouse trials for each age class to determine whether head and tail first ingestion was significantly different from random. The level of statistical significance was set at $P=0.05$.

RESULTS

Both yearlings and juveniles did not seem to change direction of ingestion between small and large mice (Table 1). Because few individuals of both age classes changed direction of ingestion according to prey size, no statistical analyses of prey size effects were carried out.

No significant preference for head first ingestion was observed in both small and large mice for yearlings (Table 1). On the other hand, juveniles showed significant preference for head first ingestion with both small and large mice (small, $P<0.05$; large, $P<0.005$).

In yearlings, there were no significant effects of prey size on prey handling method ($P=0.062$; Table 2). On the other hand, juveniles changed prey handling method from simple seizing for small mice to the others for large mice significantly more frequently than vice versa ($P<0.01$). In one case out of 14 where snakes coiled around a mouse immediately after striking, the juvenile snake released its coils from around the prey and

Table 1. Relationship between size of mice and direction of ingestion in feeding trials for yearling and juvenile *Elaphe taeniura*. Values in table are the number of mice.

Direction of ingestion	Yearling		Juvenile	
	Small	Large	Small	Large
Head first	4	6	7	8
Tail first	4	2	1	0

Table 2. Relationship between size of mice and prey handling method in feeding trials for yearling and juvenile *Elaphe taeniura*. Values in table are the number of mice.

Prey handling method	Yearling		Juvenile	
	Small	Large	Small	Large
Simple seizing	4	0	7	0
Delayed pinion	1	0	0	0
Delayed hairpin loop	0	1	0	0
Delayed coil	0	0	0	0
Immediate pinion	3	0	0	1
Immediate hairpin loop	0	1	0	0
Immediate coil	0	6	1	7

Table 3. Relationship between size of mice and condition of prey at ingestion (alive or dead) in feeding trials for yearling and juvenile *Elaphe taeniura*. Values in table are the number of mice.

Condition at ingestion	Yearling		Juvenile	
	Small	Large	Small	Large
Alive	8	0	8	0
Dead	0	8	0	8

coiled around it again. In the other 13 cases, the snakes maintained the initial coils, and no such re-constricting behavior was observed. Failure of initial coil application immediately after striking, which was observed in some neonatal rat snakes (Mori, 1994), was not observed.

Large mice were significantly more frequently killed before ingestion than small mice in both yearlings and juveniles (both $P<0.005$; Table 3).

DISCUSSION

Head first ingestion of large prey has been considered to be associated with decrease of prey handling time and energy expenditure (Diefenbach and Emslie, 1971; de Queiroz and de Queiroz, 1987). Innate preference for head first ingestion of large prey has been observed for *E. obsoleta* and *Lampropeltis calligaster* (Klein and Loop, 1975) but not for *E. taeniura, E. climacophora, E. quadrivirgata*, and *E. dione* (Mori, 1993, 1994). The present study showed that only juvenile *E. taeniura* has clear preference for head first ingestion of large prey. Therefore, it is suggested that in *E. taeniura* adaptive switching for direction of ingestion may develop during the first two years after hatching.

On the other hand, proficient constricting behavior was observed in hatchlings of *E. taeniura* (Mori, 1993). They constricted and killed large mice more frequently than small mice, and their coiling behavior seemed to be nearly as proficient as adult snakes (Mori, 1993, 1994). These trends seem to persist during the first two years after hatching. Only exception was no significant prey size effect (but nearly reached a significant level, $P=0.062$) on prey handling method in yearlings. This may due to the small sample size of the present experiment. Therefore, coupled with an earlier study (Mori, 1993), it is suggested that *E. taeniura*, a specialist on endotherms, has an ability of performing efficient constricting, which is crucial for handling endotherms, from its early developmental stage.

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