J. Ethol. *11* : 153–156, 1993 *Short Communication*

Does Feeding Experience with Different Size of Prey Influence the Subsequent Prey-Handling Behavior in *Elaphe climacophora*?

Akira MORI
Department of Zoology, Faculty of Science, Kyoto University,
Sakyo, Kyoto, 606-01 Japan

It has been demonstrated that several factors such as prey size and type influence prey-handling behavior in snakes (e.g., de Queiroz 1984; Mori 1991; Hayes 1992). The Japanese rat snake, *Elaphe climacophora,* a powerful constrictor feeding on small mammals and birds, changes prey-handling behavior according to prey size (Mori & Moriguchi 1988; Mori in prep.). An adult *E. climacophora* usually squeezes a large mouse to kill it and swallows it headfirst, whereas the snake simply seizes a small mouse and swallows it alive without a clear preference of direction of ingestion (Mori in prep.). However, it is unknown how early or recent experiences affect the prey-handling behavior. Most studies focusing on the effects of early or recent dietary experiences on feeding behavior used chemical prey preferences or attack frequencies as variables affected by experiences (Loop 1970; Fuchs & Burghardt 1971; Arnold 1978; Dunbar 1979; Burghardt 1992). In those studies, effects of prey type were examined by using snakes raised with different types of prey. I have tested whether prey size affects subsequent prey-handling behavior and feeding durations in *E. climacophora.* In the present study, effects of recent feeding experiences on snakes that have already had a great deal of experiences with prey of various size were examined. Do snakes recently raised on large mice increase tendencies of constriction and headfirst ingestion? Do snakes recently raised on small mice reduce these tendencies? Do snakes recently raised on large mice swallow a large mouse in a shorter time than those raised on small mice?

Materials and Methods

Subjects were 18 *E. climacophora* hatched from the eggs laid by 7 wild-caught females from Gifu, Shiga, and Fukui Prefectures. The subjects were housed individually in cages made of white polypropylene corrugated board (190 × 140 × 70 mm), each containing a paper floor covering and a water bowl. The room temperature varied between 25-30°C except in winter. Illumination was provided by sunlight.

The snakes were fed a small laboratory mouse, *Mus musculus* (body mass [BM] 1.4-7.8 g) approximately twice a week. Until the final feeding just before the third winter, the size of food was not strictly controlled, but all the snakes were fed nearly the same size of mice on a given feeding day. After the third winter, these snakes were divided into 2 groups, Group L (4 males and 5 females from 6 different litters) and Group S (5 males and 4 females from 7 different litters). On each feeding day (twice a week), snakes of Group L were offered 1 "large" mouse (BM 4.0-10.0 g), and those of Group S were offered 3 "small" mice (BM 1.5-2.5 g). I offered as equal total amount of food as possible to each snake on each feeding day. The large mice corresponded to the mice that were generally constricted, killed, and swallowed headfirst, whereas the small mice corresponded to the mice that swallowed alive without constriction and without clear preference of direction of ingestion (Mori unpublished data).

After 3 months of such controlled feeding, each snake was tested with 1 large mouse (BM 9.4-16.2 g) and 1 small mouse (BM 2.5-3.1 g). Five snakes of each group were tested with the large mouse first and the remaining snakes with the small mouse first. An interval of 4 days separated the 2 tests. Feeding tests were conducted in an arena made of white polypropylene corrugated board (300 × 150 × 100 mm). The arena was composed of 2 compartments, 50 × 150 × 100 mm and 250 × 150 × 100 mm, in which a snake and a mouse were introduced, respectively, approximately 20 min before testing. Each test was initiated by removal of an insert from the arena which separated the 2 compartments. The tests were terminated if the snake did not attack the mouse within 20 min. The arena was washed with water after each test. The room temperature was maintained between 27 and 30°C during the experiment. All trials were recorded by a video camera (National VZ-C70) and a video recorder (National NV-8480).

Videotape analyses were done to record following variables. 1) Prey handling method: the snake grasped the mouse in the jaws without subduing it with the body (simple seizing); the snake squeezed the mouse with its body or coiled around it immediately after striking (immediate constriction); or the snake squeezed or coiled around the mouse but with a delay of more than 1 s after striking (delayed constriction). Detailed descriptions of the prey-handling methods were presented in Mori (1991). 2) Direction of prey at ingestion: the snake swallowed the mouse headfirst or tail first. 3) Condition of mouse at ingestion: the mouse was swallowed alive or dead. 4) Handling duration: time in s from the moment the snake grasped the mouse until just before the snake initiated swallowing in the direction in which the mouse was subsequently swallowed. 5) Swallowing duration: time in s from the commencement of swallowing until the mouse was no longer visible. 6) Total feeding duration: handling duration + swallowing duration. Fisher exact probability tests and Mann-Whitney U-tests were used for statistical analyses.

Results

One snake of Group S died before testing. Snout-vent length (SVL) and head width (HW) of snakes measured just before the experiment did not significantly differ between Groups L and S (SVL; Group L, $\bar{x} = 742$ mm, Group S, $\bar{x} = 725$ mm, $z = 1.33$, $P > 0.10$: HW; Group L, $\bar{x} = 15.4$ mm, Group S, $\bar{x} = 14.6$ mm, $z = 1.85$, $P > 0.05$). All snakes of Group L ate the large mouse, and 6 out of 8 snakes of Group S ate the large mouse. The frequency of acceptance of the large mouse was not significantly different between Groups L and S ($P > 0.10$). In both groups, all but 1 snake ate the small mouse. The frequency of acceptance of the small mouse was not significantly different between Groups L and S ($P > 0.10$).

In each group, 5 snakes constricted the large mouse immediately after striking (Table 1). One and 3 snakes of Groups S and L, respectively, exhibited delayed constriction in the large mouse test. The remaining snake of Group L pressed the large mouse against the substrate with its body (pinion) immediately after striking. Prey-handling method was not significantly different between Groups L and S in the large mouse test ($P > 0.10$). All snakes, in both groups, simply seized the small mouse.

All large mice were swallowed headfirst in both groups (Table 1). One and 3 small mice were swallowed headfirst in Groups S and L, respectively, and the others were swallowed tail first. The frequency of headfirst ingestion of the small mouse was not significantly different between Groups L and S ($P > 0.10$).

In both groups, all large mice were killed before swallowing and all small mice were swallowed alive (Table 1).

There were no significant differences in handling, swallowing, and total feeding durations between Groups L and S in both large and small mouse tests (handling: small mouse, $z = 0.29$, $P > 0.10$, large mouse, $z = 0.45$, $P > 0.10$; swallowing: small mouse, $z = 0.75$, $P > 0.10$, large mouse, $z = 0.52$, $P > 0.10$; total: small mouse, $z = 0.35$, $P > 0.10$, large mouse, $z = 0.71$, $P > 0.10$: Table 2).

Discussion

It has been demonstrated that in some snakes feeding responses to particular prey can be altered by experiences. For instance, feeding

Table 1. Comparisons of feeding behavior of *Elaphe climacophora* on small and large mice between snakes raised on small (Group S) and large mice (Group L). See text for detailed description of variables.

Variables	Small mouse		Large mouse	
	Group S	Group L	Group S	Group L
Prey-handling method				
Simple seizing	7	8	0	0
Immediate constriction	0	0	5	6*
Delayed constriction	0	0	1	3
Direction of ingestion				
Headfirst	1	3	6	9
Tail first	6	5	0	0
Condition of mouse at ingestion				
Alive	7	8	0	0
Dead	0	0	6	9

*Including a snake that did not constrict the mouse but pressed it against the substrate with its body.

Table 2. Comparisons of feeding durations of *Elaphe climacophora* on small and large mice between snakes raised on small (Group S) and large mice (Group L). Figures in table are mean ± SE in s.

	Small mouse		Large mouse	
	Group S (N = 7)	Group L (N = 8)	Group S (N = 6)	Group L (N = 9)
Handling duration	24 ± 10.5	24 ± 11.1	513 ± 265.5	364 ± 116.3
Swallowing duration	54 ± 8.0	48 ± 6.9	488 ± 29.7	537 ± 78.3
Total feeding duration	78 ± 12.7	72 ± 14.5	1001 ± 272.3	940 ± 109.8

experience with live fish enhanced subsequent responsiveness to dead, motionless fish (Arnold 1978). Feeding experience with one type of prey can inhibit responses to another type of prey, but this is not always the case. Fuchs & Burghardt (1971) found that chemoreceptive responses to redworms decreased progressively during feeding experience with fish, and that inhibition of responses to fish occurred during feeding experience with redworms. In contrast, Arnold (1978) demonstrated that feeding experience with fish does not inhibit responses to anurans.

In the present experiment, no effects of recent experience with large or small prey could be detected on the subsequent prey-handling behavior in *E. climacophora* that had long experienced a variety of prey sizes. Although sample size of the present study may not be enough to detect small effects, it would presumably have allowed detection of any major alteration in feeding behavior. However, neither increase nor decrease of tendencies of constriction, prey killing, and headfirst ingestion occurred after feeding on particular size of prey: snakes of both groups exhibited virtually similar prey-handling behavior. In addition, feeding durations were not affected by early experience. The snakes raised on small mice could handle and swallow large mice as easily as those raised on large mice.

Hatchlings of *E. climacophora* change prey-handling behavior less clearly than adults, and it is likely that some years are needed to attain an adult pattern (Mori in prep.). The snakes used in the present study, which were approximately 3 years old, were already exhibiting prey-handling behavior similar to that of adult snakes before the different feeding regimens were initiated. After 3 months of controlled feeding, they retained the same pattern of prey-handling behavior as before. Hence, in *E. climacophora,* modification of prey-handling behavior by feeding experience with different size of prey seems unlikely, at least after behavior has fully developed. It has been suggested that different responses to different sizes of prey have adaptive functions such as avoidance of retaliatory injury or decrease of handling time (e.g., Diefenbach & Emslie 1971; de Queiroz & de Queiroz 1987; Mori 1991). The present results suggest that *E. climacophora* can exhibit the most adaptive prey-handling behavior even after they have been fed prey of limited size range for some time. Similar experiments using newborn snakes are desireable to examine the effects of feeding experience with different size of prey on early development of the prey-handling behavior.

Acknowledgements — I wish to thank H. Moriguchi for providing snake eggs. I also thank M. Amano, T. Hayashi, C. Koshio, and Y. Mori for their assistance in keeping the animals. The comments of H. Ota on the manuscript are greatly appreciated. This study was partly supported by Grants-in-Aid from the Japan Ministry of Education, Science, and Culture, and the Japan Society for the Promotion of Science to AM.

References

Arnold, S.J. 1978 Some effects of early experience on feeding responses on the common garter snake, *Thamnophis sirtalis. Anim. Behav. 26* : 455-462.

Burghardt, G.M. 1992 Prior exposure to prey cues influences chemical prey preference and prey choice in neonatal garter snakes. *Anim. Behav. 44* : 787-789.

de Queiroz, A. 1984 Effects of prey type on the prey-handling behavior of the bullsnake, *Pituophis melanoleucus. J. Herpetol. 18* : 333-336.

de Queiroz, A. & K. de Queiroz 1987. Prey handling behavior of *Eumeces gilberti* with comments on headfirst ingestion in squamates. *J. Herpetol. 21* : 57-63.

Diefenbach, C.O. & S.G. Emslie 1971 Cues influencing the direction of prey ingestion of the Japanese snake, *Elaphe climacophora* (Colubridae, Serpentes). *Herpetologica 27*: 461-466.

Dunbar, G.L. 1979 Effects of early feeding experiences on chemical preference of the northern water snake, *Natrix s. sipedon* (Reptilia, Serpentes, Colubridae). *J. Herpetol. 13* : 165-169.

Fuchs, J.L. & G.M. Burghardt 1971 Effects of early feeding experiences on the responses of garter snakes to food chemicals. *Learn. Motiv. 2* : 271-279.

Hayes, W.K. 1992 Prey-handling and envenomation strategies of prairie rattlesnakes *(Crotalus v. viridis)* feeding on mice and sparrows. *J. Herpetol. 26* : 496-499.

Loop, M.S. 1970 The effects of feeding experience on the response to prey-object extracts in rat snakes. *Psychon. Soc. 21* : 189-190.

Mori, A. 1991 Effects of prey size and type on prey-handling behavior in *Elaphe quadrivirgata. J. Herpetol. 25* : 160-166.

Mori, A. & H. Moriguchi 1988 Food habits of the snakes in Japan: a critical review. *Snake 20* : 98-113.

(Received 19 Apr. 1993 ; Accepted 24 Jun. 1993)

Published by Japan Ethological Society, Department of Zoology, Kyoto University, Sakyo, Kyoto, 606 Japan