SOME EFFECTS OF EARLY EXPERIENCE ON FEEDING RESPONSES IN THE COMMON GARTER SNAKE, *THAMNOPHIS SIRTALIS*

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Abstract. The effects of early experience on chemoreceptive and feeding responses were studied using 224 naïve, newborn snakes (*Thamnophis sirtalis*) from a single locality in California. The effect of experience depends on the kind of prey. Responses to some prey (fish) can be modified by early experience. Response to dead, motionless fish can be enhanced by a single experience with a live, moving fish. Responses to other prey were not affected by experience. Snakes attacked and ate frogs and tadpoles on nearly all occasions regardless of prey movement and experience with other prey.

There is now considerable evidence indicating that naïve newborn snakes are prone to attack some prey more than others, and that chemoreception is a major sensory modality in prey recognition (Burghardt 1966, 1967, 1969, 1975; Burghardt & Abeshaheen 1971; Gove & Burghardt 1975). Odiferous particles are apparently transported to the chemoreceptive epithelium of the Jacobson's organ, in the roof of the mouth, by the tongue (Wilde 1938; Burghardt & Pruitt 1975). The feeding biases of naïve, newborn snakes are mediated by Jacobson's organ in large part and are apparently unaffected by the diet of the mother during gestation (Burghardt & Hess 1968; Burghardt 1971). In the case of some dietary specialists (e.g. the crayfish specialists, *Regina grahamii* and *R. septemvittata*) naïve young appear to be programmed to attack those prey most often eaten by wild snakes, e.g. crayfish (Burghardt 1968). The naïve young of snakes with more catholic diets, e.g. *Thamnophis sirtalis*, show strong chemoreceptive responses to prey that predominate in the natural diet as well as to prey that form only a small fraction of the natural diet (Burghardt 1970). The feeding biases of naïve dietary specialists probably focus attacks on species characteristic prey in the wild. The ecological significance of feeding biases in the naïve young of species with more diverse diets is less apparent. While it is clear that at least some chemoreceptive responses can be modified by experience in the laboratory (Fuchs & Burghardt 1971; Burghardt et al. 1973), we do not know whether experience plays an important role in shaping the natural diet of snake populations.

The purpose of the present study is to determine whether experiences of the kind likely to occur in nature can modify chemoreceptive and attack responses to prey. This study focuses on the effects of prey movement and diets of limited variety. The tendency to actually attack and eat prey was used as a measure of feeding propensity, since from an ecological point of view we want to know whether experience can cause a snake to add or delete prey species from its diet as well as modify chemoreceptive response.

Anurans and earthworms predominate in the diets of natural populations of *T. sirtalis*, but arthropods, birds, fish, leeches, mammals, reptiles, salamanders and slugs are also eaten (Fitch 1965; White & Kolb 1974). *Thamnophis sirtalis* shows considerable geographic variation in natural diet (Fitch 1965), and the complete spectrum of prey indicated above has not been reported from any single locality.

General Methods

Twenty-four gravid female *T. sirtalis* were collected 8 km SSW. of Orick, Humbolt Co., California on 20 July 1974. All snakes used in this study (224) were captive-born progeny of these females. The litters were born from 26 July to 29 August (median date = 6 to 7 August). The gravid females were not fed during the period of gestation in the laboratory.

Snakes were kept in a room with a natural photoperiod and with a temperature of 24 to 27 C. Gravid females and newborn young were individually housed in clear plastic boxes (15 × 30 × 9 cm). Paper towels were used as a substrate, and ventilation was provided by holes drilled in each end of the box. Each snake was provided with a water dish.

Newborn snakes were separated from their mother within 18 h of birth. After separation each litter was kept in a single box. On the day after separation littermates were weighed and moved to individual boxes.

All prey were presented to snakes by placing the prey on the paper towel substrate of the box. Prey were left in the boxes for 24 h. Uneaten prey were then removed and the result of the presentation (ingestion or refusal) was recorded. The prey in the experiments were so small that prey size never thwarted ingestion. Prey that were offered dead were first killed by freezing and were thawed for 20 min prior to presentation. On any presentation day only a single prey was offered to each snake. The one exception (experiment 4) is indicated in the text.

The P values given below refer to the probability of the observed outcome and all worse cases as evaluated by the Fisher exact test, two tails (Sokal & Rolf 1969, p. 593).

Field Observations

The occurrence of prey and natural diet at the collecting site have not been studied extensively, but the following notes may facilitate an ecological interpretation of the experiments. To date 63 prey items have been recovered from 26 *T. sirtalis*. Three amphibians (18 *Ambystoma gracile*, 18 *Hyla regilla* and 25 *Rana aurora*) accounted for 97% of the prey items. Two individual cyprinid fish accounted for the remaining proportion of items. Although only one of the prey species (*H. regilla*) used in the experiments has actually been found in the natural diet, some of the prey species, or close relatives, used in the tests are probably encountered by *T. sirtalis* at the collection site. A close relative of one species is known to be present (*Taricha granulosa*) and four species, or close relatives, are probably present (*Ariolimax columbianus*, *Batrachoseps attenuatus*, *Bufo boreas* and *Ensatina eschscholtzi*). Two species, however, are not native to California (*Gambusia affinis* and *Lumbricus terrestris*), and two species are certainly not present although they are native to California (*Hyla cadaverina* and *Xantusia vigilis*).

Experiment 1. The Effect of Prey Movement

This experiment was designed to test whether prey movement is an important stimulus in eliciting attack in naive snakes and whether experience with live, moving fish increases the tendency to attack dead, motionless fish.

Methods

Live fish, as well as dead fish, were presented by simply placing them on the dry substrate of the cage. This mode of presentation was employed so that the movement of live fish

could never completely thwart feeding. Live fish in even a small volume of water can elude *T. sirtalis* for hours or days. Although flopping fish are encountered only in special cirumstances in nature (e.g. in drying ponds or when a fish escapes from a snake after the snake has moved onto land), even naïve snakes are very responsive to the stimuli they present.

Two experimental groups were repeatedly offered dead and live fish (*Gambusia affinis*). Each group was offered live fish on four occasions and dead fish on four occasions (Fig. 1). One group (A) received live fish as the first food and dead fish as the second food. The other group (B) was offered dead fish as the first food and live fish as the second food. The sequence of presentations was otherwise identical for both groups. Each group was composed of 18 snakes. Six snakes were taken from each of the same three litters to form each group. Three litters were distributed across the two experimental groups in order to control for any intrinsic differences among litters.

A control group (C) of 20 snakes (two litters) received a sequence of dead fish on the same schedule as the experimental groups except that only six presentations were accomplished. All snakes in all groups were tested at the same age, and none of the snakes received food prior to the tests.

Results

Naïve, 14-day-old snakes were more prone to eat live fish than dead fish (Fig. 1). The group (A) presented with live fish showed significantly more attacks than the two groups presented with dead fish ($P < 0.001$). The scores of the two groups (B and C) presented with dead fish are not statistically different ($P = 0.28$) and so their scores were combined for the preceding test.

Snakes that experienced a live fish at age 15 days showed a marked increase in the tendency
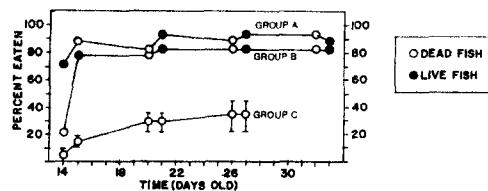

Fig. 1. The effect of prey movement on the tendency to attack fish (experiment 1). The symbols for the control group (C) indicate the mean of two litters ($N = 9$ and 11). The separate scores for these two litters are shown by the bars at the ends of the vertical lines.

to eat a dead fish when tested at age 20 days. At this age the score of group B is significantly greater than the score of the control group (C) ($P = 0.008$) even though the proportion of snakes that ate dead fish increased slightly in the control group.

The proportion of snakes eating fish approached an asymptote in each of the three groups, but in each case the asymptote was less than 100%. This was because some snakes in each group refused fish throughout the experiment.

Experiment 2. Responses to Tadpoles and Fish During a Mixed Presentation Schedule

This experiment was designed to test the feeding responses of naïve snakes exposed to a mixed presentation of two prey species.

Methods

Two groups of naïve snakes were repeatedly exposed to both tadpoles (*H. regilla*) and fish (*G. affinis*) for a 5- to 6-week period. Two presentations of one prey were alternated with two presentations of the other prey. The snakes were offered one prey on two successive days (a dead prey on one day and a live prey on the next day) and then, after an interval of 1 to 6 days, they were offered the other prey on two successive days.

Group A (11 snakes from one litter) began the sequence with fish as the first two presentations (Fig. 2). These snakes were 15 days old at the first presentation on 19 August. Group B (45 snakes from four other litters) began the sequence with tadpoles as the first two presentations (Fig. 3). These snakes were of various ages at the first presentation on 12 August (10 days, 10; 12 days, 8; 14 days, 13; 15 days, 14).

Results

Two striking results are apparent in this experiment. First, snakes ate tadpoles on nearly every occasion. The tendency to eat tadpoles appeared to be unaffected by the absolute age of naïve snakes (in the range 10 to 15 days), by whether the tadpoles were live or dead, or the prey type at the first exposure to prey, Second, the proportion of snakes eating fish did not reach 100% in either group, as in experiment 1. This was because some snakes in both groups consistently refused both live and dead fish. Thus some snakes ate only tadpoles while other snakes ate both tadpoles and fish.

Other apparent trends in the data should probably not be taken seriously because of the loose design of this experiment (e.g. the heterogeneity of ages in one group and the failure to control for any intrinsic litter effects by distributing littermates across both treatment groups). For example, the seeming difference between groups in the tendency to eat fish is probably not significant in light of the defects in design just mentioned. The data also suggest that the snakes were more prone to eat tadpoles than fish, but the design does not allow an unambiguous test of this trend.

Experiment 3. Chemoreceptive Response to Frogs and Fish when Snakes Are Raised on Frogs or Fish

This experiment was designed to test whether chemoreceptive responses to fish and frogs could be modified by exclusive diets of fish or frogs.

Methods

One group (12 snakes from one litter) was raised with fish (*G. affinis*) as the only food, and the other group (19 snakes from two other litters) was raised with frogs (*H. regilla* and *H. cadaverina*) as the only food. The fish-raised group was offered fish on 14 occasions with the first presentation at age 10 days and
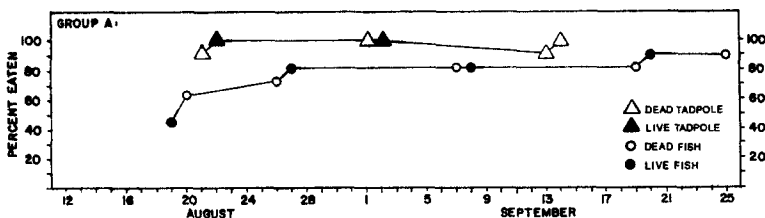

Fig. 2. Responses to tadpoles and fish during a mixed presentation schedule with fish as the first food (experiment 2). The upper line connects the group's scores for tadpoles, and the lower line connects the same group's score for fish.

the last at 5 days before the test day. On five of these occasions live fish were presented and on all others dead fish were offered. Fish were eaten in 88% of all presentations. This group was 64 days old on the test day. The frog-raised group was offered frogs on 10 occasions with the first presentation at age 10 days and the last at 5 days before the test day. On two occasions live frogs were offered; dead frogs were offered on all other occasions. *H. regilla* was offered on nine occasions and dead *H. cadaverina* on one occasion. Frogs were eaten in 98% of all presentations. The snakes in this group were all 53 days old on the test day. Both groups tested on the same day.

For tests of chemoreceptive response, odiferous cotton swabs were prepared the following way. Ten frozen individuals of each prey species (*H. regilla* and *G. affinis*) were thawed for 20 min, placed in two glass beakers, and covered with a volume of tap water equal to the prey volume. Cotton-tipped swabs (Tomac cotton-tipped applicators, medium tip, 15·5 cm long) were swirled in the water among the prey until saturated. Sixty-two swabs were prepared for each of the two prey species. Control swabs were prepared by saturating the tips with tap water. The swabs were kept in large test tubes. immersed in crushed ice, until used in the chemoreception tests the same morning.

The test swabs were presented to each snake in the same sequence; control, *Hyla, Gambusia, Hyla, Gambusia,* control. Forty-five minutes elapsed between presentations to each snake. Each swab was used once and discarded.

At each test presentation the cotton tip of the test swab was held 1 cm in front of the snake's snout. If the snake failed to protrude the tongue, the cotton tip was touched lightly to the snake's snout. Once the tongue touched the cotton tip, the swab was held stationary

for the next 60 s. During this interval the number of tongue flicks that touched the cotton swab was counted to yield a tongue flick rate (tongue flicks per min). Sometimes the snake attempted to attack the swab with an open-mouth lunge. In these cases the swab was quickly moved away to prevent the snake from ensnaring its teeth on the cotton tip. The time to attack was timed to within 0·1 s with a stop watch starting from the first tongue flick that touched the cotton tip. The number of tongue flicks preceding attack was also recorded. These data were then used to calculate the tongue flick rate preceding attack.

Observation of *Thamnophis* tongue flicking under stroboscopic lighting showed that the tongue oscillates vertically after each protrusion as Ulinski (1972) described for *Constrictor constrictor*. In this paper the term 'tongue flick' refers to a bout of vertical oscillations bounded by tongue protrusion and retraction, i.e. a 'tongue flick cluster' in Ulinski's terminology.

Standard deviations of tongue flick rates for different swab types were very unequal and correlated with means ($r = 0.95$, $N = 12$). A logarithmic transformation, base 10, of individual tongue flick rates was used to give more homogeneous variances for the analyses of variance in Table I.

Results

Different feeding history had no effect on response to frogs. There was no difference between the two groups in tongue-flick rate (Table I) or in proportion of attack responses (Table II) to frog odour. Similarly there was no difference between groups in responses to the tap water control. In contrast, the fish-raised group showed faster tongue flick rates toward the fish swabs than the frog-raised group and a
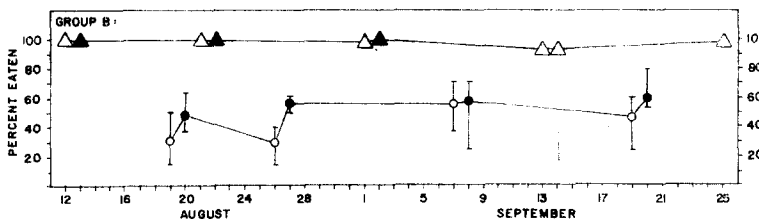

Fig. 3. Responses to tadpoles and fish during a mixed presentation schedule with tadpoles as the first food (experiment 2). Symbols as in Fig. 2. Symbols indicate mean scores and vertical lines indicate the range in scores of the four litters comprising the group.

higher proportion of fish-raised snakes attacked fish swabs.

Experiment 4. Responses to Novel Prey when Feeding Histories Differ

This experiment was designed to test whether feeding history affects the tendency to eat novel prey.

Methods

Three groups of snakes were raised from birth on different prey (frogs only, fish only, fish and tadpoles only) for a period of 4 to 5 months. The frog group (18 snakes from two litters) received three species of anurans (*H. regilla, H. cadaverina, Bufo boreas*). The fish group (51 snakes from five litters) was offered three species of fish (*G. affinis, Notropis dorsalis, Pimephales notatus*). The fish–tadpole group (136 snakes from 16 litters) received the same three species of fish as the fish group and six species of anuran tadpoles (*H. regilla, H. cadaverina, Rana aurora, R. catesbiana, R. muscosa* and *B. boreas*). The snakes in each group received their first food at the age of 10 to 18 days and were then fed twice each week. Some of the snakes in these groups were used in experiments 1 to 3.

Each group was offered novel prey during a test period lasting 7 weeks. The first test day (6 January) differed from the subsequent test days in two respects (Table III). On this day two prey species (a dead *B. boreas* and a dead *G. affinis*) were presented to each snake by placing the two prey in the cage simultaneously. On all other days only one prey species was presented. In addition, the presentations represented novel prey for only some groups. Thus *G. affinis* was novel prey only for the frog group, and *B. boreas* was novel prey only for the fish and fish–tadpole groups. On all other days novel prey were presented to all three groups.

Table I. Chemoreceptive Responses to Odiferous Swabs

Log_{10} tongue flick rate (flicks per min)

Subjects		Test sequence					
		Control	Frog	Fish	Frog	Fish	Control
Raised on fish ($N = 12$)	Mean SD	0·31 (0·34)	1·54 (0·71)	1·34 (0·79)	1·44 (0·87)	1·24 (0·72)	0·27* (0·37)
Raised on frogs ($N = 19$)	Mean SD	0·30 (0·34)	1·83 (0·32)	0·37 (0·48)	1·64 (0·68)	0·26 (0·50)	0·20 (0·26)
One way analyses of variance	$F(1, 29) =$	0·004 NS	2·41 NS	17·98 **	0·48 NS	18·69 **	0·45 NS

*One snake attacked the control swab without first flicking its tongue. This snake was deleted from the calculations giving a sample size of 11 rather than 12.
**$P < 0.01$.

Table II. No. of Attack Responses to Odiferous Swabs

Subjects	Control	Frog	Fish	Frog	Fish	Control
			Test sequence			
Raised on fish $N = 12$	0	9	8	7	7	0*
Raised on frogs $N = 19$	0	16	1	13	1	0
Fisher exact test	NS	NS	**	NS	**	NS

* One snake attacked the control swab without first flicking its tongue. This snake was deleted from tabulation and calculation in this column.
**$P < 0.01$.

Table III. Responses to Novel Prey when Feeding Histories Differ. The Proportion of Snakes that Ingested Prey is Shown in Each Cell

Test date	Prey	Feeding history			Prey type	χ^2
		Frogs	Fish	Fish and tadpoles		
6/1	*Bufo boreas*†	18/18	50/51	30/32	Toad	1·93 NS
6/1	*Gambusia affinis*†	1/18	48/51	24/32	Fish	52·52**
13/1	*Lumbricus terrestris*	11/18	39/51	96/136	Annelid	1·61 NS
17–27/1	*Xantusia vigilis*	0/17	0/51	3/131	Lizard	NS
30/1	*Ariolimax californicus*†	0/17	1/51	10/127	Slug	3·50 NS
3/2	*Tarica torosa*†	12/17	14/19	26/27	Salamander	6·26*
10/2	*Ensatina eschscholtzi*	17/17	19/30	42/55	Salamander	8·11*
17/2	*Batrachoseps attenuatus*†	16/17	40/51	92/121	Salamander	2·87 NS

†Indicates that prey were offered dead.
*$P < 0.05$.   **$P < 0.01$.

Some test prey were small enough to be ingested whole, but other prey had to be cut into small pieces in order to be ingested. Thus *G. affinis*, small *Xantusia vigilis*, and recently transformed *B. boreas* were presented whole. Small pieces (1 to 3×10 mm) of the other test prey were offered (*Ariolimax californicus, Lumbricus terrestris* and the salamanders *Batrachoseps attenuatus, Ensatina eschscholtzi* and *Taricha torosa*). Small transverse sections of the tail were used in the case of the three salamander species. Because supplies of some prey were limited, it was not possible to test all the snakes in each group.

The snakes were offered dead *G. affinis* as a maintenance food between test days. Generally *Gambusia* were offered on Thursdays and test species on Mondays or Fridays. In retrospect *Gambusia* was a poor choice as a maintenance food, since many snakes in the frog group refused this food throughout the test period. As a consequence, hunger probably varied substantially between the three groups and should be considered an uncontrolled variable in this experiment.

Results

The responses to the first presentation of each novel prey are reported in Table III. Feeding history had no effect on responses to some prey (*Bufo, Lumbricus, Ariolimax, Xantusia Batrachoseps*), had a small effect on responses to two salamanders (*Taricha* and *Ensatina*) and had a dramatic effect on response to fish (*Gambusia*). In the case of fish, snakes which had never encountered this prey tended to ignore *Gambusia*. Since, in general, groups showed a

large proportion of attacks to novel prey, a general phenomenon of imprinting is ruled out by this experiment.

Discussion

The present study has demonstrated that feeding responses to particular prey can be changed by experience. Feeding responses to other prey were unaffected by experience in the laboratory and perhaps are not modified by experience in nature. In previous studies with *Thamnophis* enhancement and inhibition of feeding responses have been demonstrated, whereas stability of response despite differences in feeding history has not been reported.

Feeding on a particular prey sometimes enhances subsequent responses to that prey. Fuchs & Burghardt (1971) reported a progressive increase in chemoreceptive response to redworms (*Eisenia foetida*) in *T. sirtalis* feeding on this prey. The same effect was demonstrated using fish (*Poecilia reticulata*) as prey. In the present report, we found that a feeding experience with live fish enhances subsequent responsiveness to dead, motionless fish (experiment 1). This result may have been a consequence of enhanced chemoreceptive response of the kind reported by Fuchs & Burghardt (1971). Apparently *T. sirtalis* associate chemosensory cues with prey movement during the first experience with live fish, and in subsequent encounters chemoreception alone is sufficient to elicit attack.

It has been shown that feeding on some prey can inhibit subsequent response to that prey. Burghardt et al. (1973) were able to produce an aversion to earthworms (*Lumbricus terrestris*)

in *T. sirtalis* by injecting the snakes with saline or lithium chloride after an earthworm meal. Such avoidance conditioning may occur in nature as a consequence of the natural defences of prey, but the effect of natural anti-predator behaviours has not been studied even in the laboratory. Burghardt (1969), however, found that *T. sirtalus* tend to avoid slugs after a single feeding attempt.

Some prey are avidly attacked by naïve snakes on first exposure as well as on subsequent exposures. Thus experience with frogs and tadpoles had no effect on the probability of subsequent attack in *T. sirtalis* (experiments 2 and 3). Nearly 100% of the snakes attacked these prey on the first and all subsequent exposures, regardless of whether the prey were dead or alive, and regardless of absolute age of the snakes.

Thus experience with a particular prey may facilitate subsequent responses, inhibit subsequent responses or fail to change an already maximal response depending on the type of prey.

Feeding experience with one prey can inhibit responses to other prey, but this is not always the case. Fuchs & Burghardt (1971) found that chemoreceptive responses to redworms (*E. foetida*) decreased progressively during feeding experience with fish (*P. reticulata*). Similarly, inhibition of responses to fish occurred during feeding experience with redworms. In contrast, feeding experience with fish apparently does not inhibit responses to anurans (experiments 2, 3 and 4).

Responses to some prey are apparently stable over long periods in spite of experience with other prey. *T. sirtalis* that experienced only fish during the first 2 months of life were just as prone to attack frog extracts as snakes raised on only frogs for a comparable period (experiment 3). This effect was not due to a basic inability to discriminate between fish and frogs, since frog-reared snakes did discriminate between these two prey.

Food imprinting is the extreme case of inhibition of feeding responses to some prey as a consequence of experience with other prey. The defining characteristics are irreversible inhibition as a consequence of early experience. Food imprinting is certainly not a general phenomenon in *T. sirtalis* and may not occur at all. Fuchs & Burghardt (1971) found that inhibitions to certain prey could be quickly reversed. Furthermore, restricted early experi-

ence did not eliminate feeding responses to novel prey in the present study.

From the standpoints of feeding ontogeny and natural feeding ecology we know more about *T. sirtalis* than any other snake. Nevertheless, there is a considerable gap between our knowledge of laboratory behaviour and field ecology. It is still difficult to assess the significance of experience in the natural feeding economy of this species. We know, for example, that *T. sirtalis* shows geographic variation in natural diet (Fitch 1965). We do not know what proportions of this dietary variation can be ascribed to prey availability, local genotypic adaptation in feeding behaviour, experience and other causes. It may be most useful to approach this question on a prey-by-prey basis. For example, responses to some prey (frogs and tadpoles) seem immune to modification by experience. If this result holds in the face of additional laboratory perturbations, then geographic variation in diet, with respect to these prey, must be a consequence of differences in prey availability or snake genotypes.

An ecological or evolutionary interpretation of responses which can be modified by experience is more difficult. Why are responses to some prey affected by experience, while responses to other prey are not? We will probably have to wait for detailed studies relating the natural diets of local populations to laboratory behaviour before we can put relative modifiability of behaviour into an ecological perspective. In particular, we need to know how prey availabilities vary in time and space and how these variations affect the natural diets of individuals and populations.

Acknowledgments

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