Effects of Prey Movement and Prey Odor on Feeding in Garter Snakes

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With 6 figures

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Abstract and Summary

The role of prey movement in feeding behavior was investigated in 10 garter snakes (Thamnophis sirtalis) repeatedly presented with paired stationary and continuously rotating sections of earthworm (Lumbricus terrestris). Additionally, prey odor intensity and source were varied and the performance of a tongueless snake was compared to normal animals.

Experiment 1 showed that garter snakes will selectively attack rotating over nonmoving sections of earthworm across a wide range of speeds (1—20 48 rpm) with an optimum between 16 and 256 rpm. However, blocking the odor from the sections and presentation of speeds greater than 500 rpm decreased response to moving sections. Experiment 2 showed that at 22—32 rpm moving sections were selected over stationary sections when odor from both was blocked.

Experiment 3 assessed the effects of varying ambient odor conditions upon selection of artificial moving and stationary prey. Ambient earthworm odor resulted in a sustained high rate of tongue-flicking while, with no odor present, snakes showed a gradually increasing rate of tongue-flicking that declined within a few minutes.

Experiments 4 and 5 studied the effects of tongue removal upon the selection of moving and nonmoving prey. Gross changes in the feeding sequence were noted. A long-term tongueless adult fed by opening her mouth and thrashing about her cage when presented with earthworm odor and only preferred moving prey at 32 rpm; a control showed the normal stalk-and-strike sequence. The tongueless snake was less attracted to the moving earthworm at a distance than were normal snakes and the use of vision seemed less integrated rather than compensably improved.

The results are discussed in reference to the critical flicker-fusion frequency, kleptoparasitism, and escape tactics of prey.

Studies of the role of visual cues in nonvenomous snake feeding have typically been limited to investigating movement or contrast (Burghardt
1970; Czaplicki and Porter 1974; Herzog and Burghardt 1974; MacDonald 1973), and have rarely been conducted in the absence of odor from the prey tested, despite the demonstrated importance of chemosensory cues in the feeding sequence (e.g. Burghardt 1969). Exceptions to this (Burghardt 1966; Chiziar et al. 1981; Drummond 1979; and Wiedemann 1931) indicate that movement in the absence of chemical cues elicits orientation, increased tongue-flicking, and approach, but not, in the case of garter snakes, attack behavior. Previous studies have not, however, used prey or models whose movement has been strictly controlled and quantitatively varied by the experimenter; there are also few such studies on other animals (see Curio 1976).

The following experiments address themselves to assessing the role of continuous movement of prey in the feeding sequence of the garter snake. Members of this species eat earthworms, amphibians, and fish, among other small prey, that may move either slowly or quickly in nature. Prey items rotating at a constant rate in a horizontal plane were presented with stationary prey items in a simultaneous choice test situation. Odor of the same type of prey was typically introduced from a different location in the testing cage. Although only a few animals were used in each experiment, the repeated testing gave informative results. Further, as snakes have rarely been used in learning and discrimination studies (Burghardt 1977), the training procedures employed may prove useful techniques for investigating other questions.

General Methods

Subjects and Housing

10 garter snakes (Thamnophis sirtalis) were used; further details are noted in each experiment. Snout-vent lengths ranged from 24 to 75 cm. Snakes were fed earthworms (Lumbricus terestris) or earthworms and goldfish (Carassius auratus), and were deprived of food for at least five days before testing.

At least four days prior to testing, snakes were individually housed in covered 60 × 30 × 30 cm wood and Plexiglas® cages, where they lived in a 50 × 30 cm section separated by an opaque Plexiglas® divider from a 10 × 30 × 30 cm test chamber (Fig. 1). A water dish, small rock, and plastic shelter were provided in the home chamber.

During each test the divider was removed, giving the snakes access to the test stimuli. Absorbent paper (Kimpak® standard cage liners) covered the bottom of the home chamber, and a strip of newspaper covered the floor of the testing chamber.

Temperatures in the experimental room ranged between 22°C and 26°C. The light/dark cycle was controlled by natural window lighting. Testing took place in daylight between 24 June and 29 July.

Stimuli

Before sectioning, earthworms (Lumbricus terestris) were killed by scalding for 30 s in hot water. The end and clitellum sections were discarded. Sections were kept moist until use by a damp towel placed over them. When positioning worm pieces, care was taken not to touch them against any part of the test chamber. Hooks were washed thoroughly before and after each trial, and the newspaper covering the floor of the test chamber was changed between trials. Test chambers were washed with soap and water before and after each day's trials.
To provide airborne prey odor, a "wormbag" (a porous cloth sack filled with 6 or 7 earthworms) was hung over the center of the home chamber during testing. In some experiments a clean empty sack was used ("control bag").

Fig. 1: Home and testing chamber for garter snakes

Apparatus

Two reversible, remotely controlled Minarec® electric motors were used to vary the speed of rotation of 1.3-cm sections of earthworms fastened onto hooks secured to the armatures of the motors (Fig. 2). The sections of worm were spaced 10 cm from each other and centered in the test chamber 1 cm above the floor. The side on which the moving section was presented varied from left to right for each subject according to a randomized sequence (FELLOWS 1967). The stand with the motors did not touch the table supporting the cage.

By turning on one or both motors, pieces of worm could be rotated at various speeds. The linear speed of the ends of the earthworm sections varied from 0.04 cm/s at 0.5 rev/min (rpm) to 161 cm/s at 2048 rpm. The continuous circular motion used had the advantage of being confined to one location. Irregularity or sporadicity of motion is a cue in itself (Robin-
son 1969; Herzog and Burghardt 1974; Curio 1976). To reduce vibrations, felt and rubber strips were placed under the table, under the cages, and under the stand that held the motors.

Since the sections of earthworms were rotating in a horizontal plane, from the snake’s usual perspective (a point near the floor of the cage), the movement appeared as a shortening and lengthening of the worm sections, at a rate twice that of the speed of rotation. That is, at 32 rpm a section would appear to alternately shorten to approximately .3 cm (its thickness) and grow to 1.5 cm (its length) 64 times/min. This apparent movement is not totally un-wormlike (earthworms do lengthen and shorten their bodies), although most speeds presented greatly exceeded wormlike speeds but not that of other prey (e.g., fish, frogs). This rate of apparent movement is about 2% faster than linear worm end speed at all rpms.

Maximum length of the moving section of worm was the same as the length of the stationary section. From the extreme rear of the testing chamber, a distance of 55 cm from the worm sections, the angles subtended by the moving worm sections were 1.56° maximum and 0.31° minimum; from the border of the testing chamber, 5 cm from the sections, the angles were 17.0° and 3.42°, respectively; and from a distance of 1.5 cm from the sections (53.15° and 11.42°). Attacks usually occurred after a pause bracketed between 1.5 and 5 cm.

Test Procedure

Prior to testing a snake its cage was transferred to a testing table and the top, shelter, water dish, and rock removed. A wood partition equipped with a one-way mirror placed on one end of the table separated the subjects from the experimenters. Two 15-W cool-white fluorescent lights placed on the cage side of the mirror provided illumination.

The motors were turned on prior to the habituation period, which varied in different experiments from 30 s to 40 min (long habituation periods were found to be generally unnecessary as methods were refined). The divider was then removed and behavior verbally recorded on a cassette recorder. The primary measures used were occurrence and latency of 1) orientation to either worm section (characterized by freezing with the head pointed towards a worm section), 2) entrance of the snake’s head into the test chamber, 3) prey attack, and 4) worm section chosen.

The motors were turned off immediately upon attack of either worm section; the snakes were allowed to remove and eat the piece of worm attacked. When necessary the experimenters assisted a snake in removing the worm section from the hook.

In the first experiment each snake was tested three or four times per day. In later experiments more trials were run, to a maximum of 20 per day. In all experiments trials were terminated at preset time (usually 5 min) if no openmouthed attack occurred. Trials were also terminated if a snake crawled completely under the paper lining in its home chamber.

Experiment I

After live prey is introduced in its enclosure, a garter snake will ordinarily crawl about vigorously flicking its tongue. The snake sometimes orients towards the prey, but may approach without doing so. At approximately 1.5—5.0 cm from its prey, it hesitates briefly; usually the tongue, as it flicks in and out, can be seen to touch the prey. During this hesitation the snake often follows movement of the prey with its head, and may inch slowly forwards. A sudden movement by the prey (or disturbance in the vicinity) can cause retreat at this point. Otherwise the prey is attacked and ingestion begins. Roth (1976) found a similar pause after prey model movement in the Italian bolitoglossine salamander, Hydromantes italicus.

Pilot tests showed us that the apparatus worked and snakes would select moving prey. But it was difficult to tell to what extent chemical and mecha-
mical cues were implicated in the selection of moving earthworm sections. Was a "stirring up" (Herzog and Burghardt 1974) of air or airborne chemical cues important in leading the snakes to the moving earthworm sections? Airflow in the vicinity of the moving pieces of worm was not measured. However, Eisner et al. (1976) measured airflow near an "overhead twirler" which was smaller than, but shaped identically to, a hook carrying an earthworm section. A 4.1 mm long twirler operating through a range of 75—126 rpm was found to cause a periodic (due to its two-bladed nature) airflow of up to 0.5 mm/s at a spot 2 mm outside the circle of rotation. It was decided on the basis of these measurements that the rotating earthworm sections stirred up the air sufficiently to act as a possible chemical or mechanical cue.

Experiment I was designed to determine, across a wide range of speeds, the response of snakes to moving worm sections, first with chemical cues from the prey present in the environment, and then when the odor from the worm was blocked. In both cases additional diffuse "priming" odor of prey was introduced from overhead prior to testing.

Methods

Subjects: Two male and one female adult laboratory-raised Thamnophis s. sirtalis familiar with the apparatus and procedures were tested.

Procedure: The snakes were allowed simultaneously choices between nonmoving earthworm sections and sections rotating at 1, 16, 32, 256, 512, 1024, and 2048 rpm. One snake was given the tests in ascending followed by descending order; the remaining two snakes were given the tests in descending followed by ascending order. The sequences were then repeated with an addition: transparent 0.25-l drinking glasses (6 cm diameter) were inverted over the test sections. Thus, each snake was tested twice on each stimulus condition.

When worm sections were uncovered, approach usually resulted in attacks. When glasses were in place only two open-mouthed attacks occurred, although the snakes oriented to and approached the sections of worm. Therefore, the covered worm section selected was considered to be the one whose glass was first touched by the snout or tongue of the snake. Latency was scored as time from divider removal until one of the glasses was contacted (covered) or until attack occurred (uncovered). Because of the small number of tests at each speed, in some analyses the slowest (1—32 rpm) and fastest (256—2048 rpm) speeds were grouped ("slow" and "fast", respectively).

Results

Selection of worm sections: With uncovered worms there was a strong preference for moving sections at slow speeds and no significant pattern at fast speeds. With the covered worms there was no preference at slow speeds, but a significant preference for the stationary prey when the other worm piece was rotating at fast speeds (Table 1).

At each of the 7 speeds (Fig. 3) the snakes selected moving sections less frequently when glasses were in place (p < 0.02, Wilcoxon matched-pairs signed-rank test, two-tailed). Moreover, the shapes of the curves were remarkably similar. In each condition selection of moving sections was less frequent
Table 1: Frequency of selection of moving (M) and stationary (S) worm sections when covered and uncovered by glasses (Experiment 1)

<table>
<thead>
<tr>
<th>Stimuli</th>
<th>Moving prey speed</th>
<th></th>
<th></th>
<th></th>
<th></th>
<th></th>
</tr>
</thead>
<tbody>
<tr>
<td></td>
<td>slow</td>
<td>slow</td>
<td>slow</td>
<td>fast</td>
<td>fast</td>
<td>fast</td>
</tr>
<tr>
<td></td>
<td>M</td>
<td>S</td>
<td>p*</td>
<td>M</td>
<td>S</td>
<td>p*</td>
</tr>
<tr>
<td>Uncovered worm</td>
<td>15</td>
<td>1</td>
<td>&lt;.005</td>
<td>10</td>
<td>14</td>
<td>N.S.</td>
</tr>
<tr>
<td>Odor-blocked worm</td>
<td>9</td>
<td>6</td>
<td>N.S.</td>
<td>2</td>
<td>13</td>
<td>&lt;.025</td>
</tr>
</tbody>
</table>

p* = combined two-tailed binomial tests for each snake (see Table 2).

at fast speeds than at slow speeds with “no selection” counted (normal, $G_{adj} = 15.62$, df = 2, $p < .001$; blocked, $G_{adj} = 9.30$, df = 2, $p < .01$). Blocking the odor reduced selection from 93.2% to 71.4% ($G_{adj} = 9.00$, df = 1, $p < .01$).

Speeds ranging from 16 to 256 rpm were particularly effective for uncovered prey. Snakes generally followed the typical approach and attack sequence except when moving prey were rotating rapidly (256 rpm or faster). In these cases the snake sometimes oriented to the moving worm section as soon as the divider was removed or when the head first turned in the general direction of the worm sections. The snake would then crawl rapidly into the test chamber and attack the moving section without pausing. They would even crawl over the stationary section of worm if it were encountered on the way to the moving one. At slow speeds of rotation, stationary worm sections were usually attacked if they were encountered upon approach to the moving section. These quick attacks at high rotation speeds probably did not allow time for the typical contact of the prey prior to the strike. This could not be determined with any certainty, however, without detailed film analysis.

Latency of response: Total latencies for trials when glasses were present averaged 75.4 s compared to 93.7 s for trials without glasses. Although different measures of preference were used in normal and blocked conditions, the mean latencies at each speed were not significantly different ($t_{dep} = 1.09$, df = 6) and the data were pooled for subsequent analyses.
The lowest combined average latencies occurred at 32 and 256 rpm (Fig. 4). Trials during which the snake did not respond to either stimulus were omitted. Subject differences were great with this measure, especially for one snake (51b) who had long latencies at all speeds and did not respond 64.3% of the time in the blocked condition. A two-way ANOVA on mean subject latencies at each speed was not significant for rpm (F = .88, df = 6, 12), but was highly significant for subject effects (F = 8.07, df = 2, 12, p < .01). A more restricted test using only latencies of response to moving stimuli was not possible due to the low number of responses to moving stimuli at higher speeds and the opposite at lower speeds, confounding comparisons.

![Graph](image)

*Fig. 4: Mean total and chamber latencies for combined normal and odor blocked prey conditions for three garter snakes tested at each speed and condition (Experiment 1).*

An alternate latency measure, the time from entry into the test chamber until attack or contact with the glass, indicated that the snakes spent a longer time in the vicinity of the earthworm sections at fast than at slow speeds before attack or contact with the glass. This latency measure was less variable than the total latency. A two-way ANOVA on the mean subject latencies at each speed showed a marginal effect of speed (F = 2.43, df = 6, 12, .05 < p < .10) and no subject effect (F = 2.02, df = 2, 12). Thus, while mean (and median) response latencies differed markedly across speeds, the great variability precluded strong statistical effects with the conditions that prevailed (but see Expt. 4). Test chamber latencies, however, were less affected by subject differences.

There also was an inverse relationship between percentage of moving prey taken and mean latency of response over all subjects. While the correlation with total latency was not significant (r = - .57), the correlation with chamber latency was (r = - .89, p = .01), confirming the greater reliability of the latter measure.
Discussion

The occurrence of two attacks to the covered worm sections indicates that attacks can occur independently of odor from, or tongue contact with, the prey itself. These attacks only occurred to the moving sections, indicating that movement, in the presence of appropriate ambient chemical cues, can elicit attack independently of chemical cues from the prey itself in experienced adult garter snakes. However, such attacks were the exception rather than the rule. Usually the snakes encountered the glass as they approached the worm section and began circling it with the snout pushed against the glass.

The reduced preference for the moving worm sections across all speeds when the sections were covered indicates that tongue contact and/or "fanning" of odor by the moving worm are facilitating factors when sections are uncovered. The 1 and 16 rpm speeds were not particularly effective in eliciting approach. But greater movement did attract the snakes; the failure to demonstrate a preference for moving worm sections when they were covered seems due to the small number of trials at each of a wide range of speeds and the fact that at 1024 and 2048 rpm the snakes apparently ignored covered rotating sections. At these speeds worm sections were rotating so fast that to humans they did not appear to be moving and certainly were beyond the critical flicker-fusion frequency (CFF) for reptiles (Jennsen and Swenson 1974).

The increased choices of uncovered stationary prey when the uncovered moving prey were rotating at fast speeds could have been an active avoidance of fast moving prey after being attracted to the test chamber by distal cues (e.g., wafting odors) and prior conditioning. The shapes of the total latency curves in Fig. 4 are compatible with Schneirla's (1965) approach/withdrawal theory, although the ontogeny of this effect has not been studied.

Experiment II

In Experiment I some of the speeds presented were either too slow or too fast to attract the snakes to the covered worm sections without the additional cue of odor from the sections themselves. Experiment II tested the response of the snakes to covered worm sections that were rotating at speeds known to be highly effective when odors from the worm sections were blocked. By repeated testing of individual snakes at a given rotation speed, the pooling over speeds needed in Experiment I was avoided. In addition, covered and uncovered trials were interspersed.

Method

Subjects: Three Thamnophis s. sirtalis were used, two from the previous experiment, and another that was laboratory-reared and experimentally naive.

Procedure: The snakes were presented with earthworm sections moving at 22 or 32 rpm, paired with stationary sections. Besides being counterbalanced for side preferences as in Experiment I, sections were covered or uncovered with glasses in a balanced fashion (Fircles...
1967). Each snake was given up to 20 trials daily. Tests were conducted until preference (as measured in Experiment I) for moving or stationary worm sections was demonstrated for either the uncovered or covered condition ($p < 0.025$, two-tailed binomial test). At this point the color sequence was replaced by one that consisted mainly of the condition that had not reached significance (3:1). It was not necessary to run more than 27 trials or “little experiments” (see Cole 1962) for results to reach the predetermined level of significance for preference to moving sections in the glass condition.

Results

All three snakes chose the moving worm more often than the non-moving worm in both the covered and uncovered conditions (Table 2), although the uncovered condition for the naive snake did not reach traditional significance. Results for the snake tested at 32 rpm were significant in the minimum number of trials; that is, this snake never chose the stationary section. This could be due to individual differences or to the speed presented to this snake, which may have elicited a stronger or more reliable preference than did 22 rpm. The seeming contrast with covered worms in Experiment I may be an experience effect.

*Table 2: Frequency of selection of moving (M) and stationary (S) worm sections. (Experiment 2)*

<table>
<thead>
<tr>
<th>Worm Section</th>
<th># 22 (22 RPM)</th>
<th># 91b (32 RPM)</th>
<th># 26 (Naive) (22 RPM)</th>
<th>Combined * *</th>
</tr>
</thead>
<tbody>
<tr>
<td>Condition:</td>
<td>M</td>
<td>S</td>
<td>p*</td>
<td>M</td>
</tr>
<tr>
<td>Odor-blocked</td>
<td>9</td>
<td>1</td>
<td>.022</td>
<td>7</td>
</tr>
<tr>
<td>Normal</td>
<td>7</td>
<td>0</td>
<td>.016</td>
<td>7</td>
</tr>
</tbody>
</table>


Subject mean total latencies were short for all snakes, and did not differ for responses to covered and uncovered worm sections (uncovered $\bar{x} = 27.8''$, covered $\bar{x} = 31.3''$). Subject mean test chamber latencies were also similar (uncovered $\bar{x} = 4.45''$, covered $\bar{x} = 3.50''$).

Discussion

Our findings in Experiments I and II, which demonstrate a reliable preference for moving stimuli even when devoid of prey odor are similar to those of Drummond (1979) for amphibious predation in the water snake, Nerodia s. sipedon. Drummond found that prey models devoid of prey odor directed and elicited attack both in and out of the water, even when diffuse odor of prey was absent. Motionless models were attacked less frequently than moving models, and orientation to, and attacks of, models were more frequent when prey odor was present in the testing environment. But in addition to different experimental conditions there also seem to be some species differences. On
the basis of prey chemical tests BURGHARDT (1968) suggested that newborn
N. sipedon rely more upon non-chemical cues than do newborn garter snakes.
CZAPLIK and PORTER (1974) further characterized N. sipedon as probably
being more reliant upon visual cues than terrestrial garter snakes. DRUMMOND
(1979, 1980) takes issue with CZAPLIK and PORTER, arguing that some
Thamnophis are extremely visual, particularly in aquatic foraging.

T. sirtalis has rarely been shown to attack earthworms without prior
tongue contact. One exception is the single adult studied by BURGHARDT and
PRUITT (1975) from which the tongue had been removed. This animal fed in
an unusual manner and may still have been responding to chemical cues via
olfaction or the vomeronasal organ (see Experiments IV and V below). The
isolation of chemical cues effected here ruled out the possibility of any chemi-
cal cue from the sections that were struck at.

Prey movement can thus attract garter snakes and direct them to the
vicinity of their prey when there is prey odor present in the environment. As
striking distance is approached, some cue from the prey seems to be important
in eliciting attack.

Experiment III

In the previous two experiments a few attacks occurred when glasses
covered the earthworm sections. This happened only to the moving sections,
suggesting, as did the extremely rapid attacks noted in preliminary inves-
tigations, that movement sometimes elicits attack without prior tongue contact
with the prey if diffuse prey odor is in the environment. In this experiment
snakes were tested both in the presence and the absence of diffuse prey odor,
enabling us to determine whether, for garter snakes with extensive feeding
experience, movement of prey is sufficient to elicit attack. We also predicted
that ambient worm odor would lead to higher rates of tongue flicking.

Methods

Subjects: Four adult females, two Thamnophis s. sirtalis collected in East Tennessee
and two T. s. semifasciata collected in Cook County, Illinois were tested. Snout-vent lengths
ranged from 39 to 65 cm. All four snakes were naive to our experimental situation.

Procedure: The snakes were given two series of seven trials. Two were first tested with
a wormbag in place and the remaining two were first tested with a control bag free of prey
odor. Conditions were reversed for the second series of 7 trials. The critical results concern
the first two trials in each series in which 1.5-cm sections of unscented plastic realistic earth-
worm fishing lures were presented. The usual 1.5-cm sections of Lumbricus were presented
for the remaining five trials.

Tongue-flicks were counted and recorded every min during each trial. Each time the
tongue was extended, oscillated up and down, and retracted was counted as one tongue-flick.

Each trial was divided into four periods: a 3-min baseline, with no wormbag or control
bag present and with the divider in place; a 3-min habituation period, with a wormbag or
control bag in place but the divider still down; a 4-min period with the divider raised but
both motors off (period A); and a 4-min period with both motors rotating at 32 rpm (period
B). Trials were terminated upon completion of period B when the plastic nightcrawler was
used. When the real earthworm sections were used trials were terminated upon attack to one
of the worm sections.
Results

Rate of tongue-flicking (plastic worms): Mean subject tongue flick rates (TFR) over the four periods differed in both the control bag (F = 13.28, df = 3, 9, p < .005) and wormbag (F = 6.79, df = 3, 9, p < .01) trials (Fig. 5). Rate of tongue-flicking increased when the wormbag was added. There was also a slight corresponding increase for each subject when the control bag was added across the entire habituation period. All snakes had higher mean TFR in the wormbag habituation period than in the control bag habituation period. Only with the wormbag was there a substantial increase comparing the minute prior with the minute following the presentation of the bag.

![Graph showing tongue-flick rates for four garter snakes tested two times each in control and wormbag conditions (Experiment 3)](image)

*Fig. 3*: Mean subject tongue-flick rates for four garter snakes tested two times each in control and wormbag conditions (Experiment 3)

When a new section of the cage was opened to exploration (period A), tongue-flicks of the control animals quickly increased to about the level of the animals with the wormbag. When the motors were turned on (period B), there was no difference in tongue-flick rates for the first 2 min, but in the last 2 min of period B the rate of tongue-flicking by the wormbag animals remained constant, while the rate of tongue-flicking by the control animals decreased.

Attacks (plastic worms): Three attacks occurred to the moving plastic worm sections during period B; once with the wormbag present and twice (by one animal) when the control bag was in place and no worm odor had been introduced. But as these attacks occurred during the second series of trials after the snake had attacked and eaten a number of earthworm sections in the test chamber, a conditioned response is a likely explanation. Under both con-
trol bag and wormbag conditions, attack occurred only three times in 128 min of exposure to plastic earthworm models, occurred only to moving models, and in all instances the sections were immediately released.

Discussion

In garter snakes, attacks generally do not occur to moving prey in the absence of chemical cues, nor to diffuse chemical cues in the absence of visually-perceived movement of prey. This suggests that a chemical cue on or very near the prey is typically involved in the actual elicitation of attack, but that with experience garter snakes may occasionally attack moving objects. This is in agreement with findings by Sheffield et al. (1968), who demonstrated that attack-eliciting components of water-based prey extracts are non-volatile.

Burghardt (1980) reported that earthworm volatiles alone were only marginally effective in increasing TF rates, and discussed the inconsistency with data from experiments, similar to those reported here, where introduction of diffuse chemical cues from prey leads to an increase in the rate of tongue-flicking. Nevertheless, such cues seem to be effective in alerting the snake to the presence of prey and in initiating appetitive searching. While opening a new section of the home cage to exploration did not cause a higher rate of tongue-flicking in the wormbag group than in the control bag group, the wormbag animals maintained this rate in the presence of “prey” movement while the tongue-flick rate of the control bag group began to decrease. This suggests that prey movement alone is not sufficient to maintain a high level of interest in foraging snakes. General visual cues from prey have been shown to interact with chemical cues in an additive manner (Chiszar et al. 1981) and it could be that the various visual cues are also additive.

Snakes placed in an unfamiliar environment show rates of tongue-flicking that are higher than for snakes that are returned to their home cages after comparable handling (Chiszar and Carter 1975; Chiszar et al. 1976). For garter snakes, the presence of food odors in the unfamiliar environment results in an even greater rate of tongue-flicking (Chiszar et al. 1976). Rate of tongue-flicking is also positively correlated with general activity in garter snakes (Burghardt and Abeshaaen, unpubl.; Kubie and Halpern 1975).

Experiment IV

Newborn garter snakes show almost total suppression of feeding following tongue removal, but experienced snakes will resume feeding (Burghardt and Pruitt 1975). An intact vomeronasal (Jacobson’s) organ is apparently essential for courtship, feeding, and prey trailing in male garter snakes as shown by surgical manipulation (Kubie and Halpern 1979; Halpern and Frumin 1979).

Given the importance of the tongue-Jacobson’s organ system in the feeding of garter snakes, how would a snake with impaired functioning of this system respond to moving worm sections? The tongueless adult T. s. sirtalis used by Burghardt and Pruitt (1975) was still available for testing. Its
performance was compared to that of a normal snake. While data from only one experimental subject are, at best, suggestive, ethical considerations deterred us from further surgery.

Methods

Subjects: Two snakes naive to the apparatus were tested; they were an adult female *T. s. coinermus* from northwestern Oregon and the adult female *T. s. sirtalis* used by Burkhardt and Pruitt (1975). The tongue of this snake had been severed at a point 19 mm below the fork several years previously. This snake became very aggressive after surgery and remained so. The prey attack behavior of this snake was unlike that of all other snakes tested. Rather than approaching prey, pausing, and then lunging and seizing it, as normal snakes did, this snake approached the general prey location, opened its mouth, and thrashed about until her jaws encountered the prey.

Procedure: Both snakes were presented with stationary earthworm sections paired with moving sections at 0.5, 4, 32, 256 and 2048 rpm. After an initial trial at 32 rpm the order of speeds was random, with the restriction that all speeds were presented before any speed was repeated. The snakes were tested a maximum of 20 trials daily, or until latencies for two consecutive trials exceeded 90 s each. Because of the tongueless snake's bizarre feeding behavior she was tested for several additional days (a total of 75 trials). The wormbag was in place throughout.

Results

Combining attacks over all speeds, the normal snake attacked the moving prey in preference to the stationary (39 : 20, p < 0.025, binomial test, two-tailed); the tongueless snake showed no preference for moving prey items (40 : 35). These results were confirmed with an rpm \times response G-test (normal,

![Figure 6: Mean total response latencies to moving or stationary prey choice for a normal garter snake (n = 11 or 12 at each speed) and a tongueless garter snake (n = 15 at each speed)]
$G_{adj} = 10.51$, df = 4, $p < .05$; tongueless, $G_{adj} = 7.06$, df = 4, $0.10 < p < .20$). However, at 32 rpm both snakes chose moving prey over stationary prey (11:1, normal; 12:3, tongueless; both $p < 0.05$, binomial test, two-tailed). Additionally, the normal snake significantly selected moving earthworm sections at 256 rpm (10:2, $p < .05$) and showed decreased latencies at both 32 and 256 rpm (Fig. 6). The tongueless snake showed no decreased mean latency at 32 rpm, the speed at which it preferred moving sections of worm. Total latencies for the tongueless snake were longer than latencies for the control at both 32 and 256 rpm ($p < .01$, Mann-Whitney U test, two-tailed). Test chamber latencies were similar at all speeds.

**Discussion**

The differences in the performances of the two snakes seemed to be due to the peculiar feeding behavior of the tongueless *T. s. siralis*. Not only was the normal sequence of stalk and attack not evident in this snake, but the preference for moving earthworm sections was affected. Although the control subject was a different subspecies than the tongueless snake, her behavior was very similar to that of the other *Thamnophis sirtalis* used in the prior experiments.

**Experiment V**

The wormbag provided a strong competing source of the same prey odor as provided by the earthworm sections. Experiment III demonstrated that this played a role in the initial responses of snakes to a non-odiferous prey object. Would the absence of the wormbag lead to a different pattern of response by the snakes used in Experiment IV?

**Methods**

*Subjects:* The tongueless *T. s. sirtalis* and the *T. s. concinnus* from Experiment 4 were used.

*Procedure:* The two snakes were presented with stationary and moving (32 rpm) sections, first with the control bag present (5 trials), and then with the wormbag present (5 trials for the experimental, 4 for the normal). Each snake received all trials on the same day.

**Results**

All snakes attacked and ate a worm piece on every trial. There was no preference for the moving stimulus by the tongueless snake (5:5) but a clear preference for moving by the normal (8:1, $p = .04$, binomial test, two-tailed). Both latency measures were shorter for the normal snake when the wormbag was in place than when the control bag was in place (Table 3) although only the total latency difference was significant ($p < .02$, Mann-Whitney U test), confirming the result for 32 rpm in Experiment IV. Interestingly, however,
Table 3: Mean combined attack latencies to moving (32 rpm) and stationary prey (Experiment 5)

<table>
<thead>
<tr>
<th>Snake</th>
<th>Test chamber latency (s)</th>
<th>Total latency (s)</th>
<th>Control bag</th>
<th>Wormbag</th>
<th>Control bag</th>
<th>Wormbag</th>
</tr>
</thead>
<tbody>
<tr>
<td></td>
<td></td>
<td></td>
<td>Test chamber latency (s)</td>
<td>Total latency (s)</td>
<td>Control bag</td>
<td>Wormbag</td>
</tr>
<tr>
<td>Tongueless</td>
<td>4.8</td>
<td>38.8</td>
<td>28.6</td>
<td>66.0</td>
<td></td>
<td></td>
</tr>
<tr>
<td>Normal</td>
<td>23.0</td>
<td>4.5</td>
<td>28.8</td>
<td>16.0</td>
<td></td>
<td></td>
</tr>
</tbody>
</table>

the tongueless animal had shorter chamber latencies when the control bag was in place (p < 0.025, U test).

Odor of prey releases appetitive behavior of searching (crawling around while flicking the tongue) in normal snakes. In the tongueless *sirtalis* odor of prey caused it to thrash about with open mouth. Once aroused (via the wormbag) the normal snake was able to readily locate the moving prey despite a strong competing source of the same odor. Thus the time spent in the chamber was significantly less in the wormbag than in the control bag condition (p < .05, U test). The tongueless snake seemed unable to do this. Instead, its feeding strategy was to cover the most possible territory with open mouth. In this way the tongueless subject spent more time away from the test chamber but once there its frantic behavior encountered the worm more quickly than did the normal snake.

Discussion

Olfaction may alert garter snakes to the presence of prey (BURGHARDT 1969, 1970). This can occur during normal breathing without any active behavior on the part of the snake. Once the snake is alerted, tongue protrusion brings the tongue-vomeronasal organ system into use; this system is important in the following of airborne and surface odors to their source (review in BURGHARDT 1980). Since normal transfer of particles to the vomeronasal organ was disrupted in the tongueless snake, the abnormal feeding behavior may have been the best alternative method of finding prey in face of decreased ability to locate prey by chemical means. The dependence of the garter snake upon chemical means of locating prey is evident in the tongueless snake by the disruption of its normal feeding pattern; it seemed less rather than more able than normal snakes to utilize visual cues in locating prey. Nonetheless this snake did show a plasticity in her behavior not found in neonate snakes deprived of their tongues (BURGHARDT and PRUITT 1975). Temporarily blinded neonate garter snakes will locate and attack prey objects in close proximity (BURGHARDT and HESS 1968).

General Discussion

Altogether these experiments demonstrate that prey movement is a potent cue in attracting garter snakes and is enhanced by the presence of ambient prey odor. Further, snakes show considerable learning in the test environment
and “expectations” engendered by prior experience need to be taken into account. This finding, in retrospect, was foreshadowed by the increased responses to control cotton swabs following prey odor treated swabs in neonate garter snakes of several species (Burghardt 1969).

Prey rotating around 32 rpm (16—256) were optimally effective for both normal and a tongueless snake. Prey rotating at higher speeds (> 512 rpm) were almost totally ignored, especially when covered and wafting odors were eliminated. How do these results compare with the visual critical flicker-fusion frequency (CFF)? Reptiles have been little studied, but one recent study indicates that 7 highly visual Anolis species had a range of 26—42 for the CFF as measured in a standard rotating drum optokinetic apparatus (Jenisse and Swenson 1974). In the present test situation, assuming the snakes viewed the prey from the horizontal plane (as they did most of the time) it has already been pointed out that the lengthen-shorten rate was twice the speed of rotation. Although Thamnophis seem quite visual for snakes, they should not be as sensitive as a diurnal, bright-environment lizard. If we estimate their CFF as 30, then only the 1024 and 2048 rpm speeds exceed their resolution. Since no covered prey exceeding 512 rpm were chosen but some were at 512 rpm, the CFF for T. sirtalis can be estimated to lie between 17 and 34. Standard optokinetic drum experiments would be usefully run on snakes, particularly natricines with differing apparent reliance on vision.

Prey movement is a particularly potent cue in combination with ambient prey odor, shown especially clearly in Nerodia sipedon by Drummond (1979). This effect may be related to a frequent observation when groups of garter snakes are maintained together in captivity and a more than sufficient number of earthworms are distributed in an enclosure. When one snake grabs a worm others rush towards it and attempt to attack the worm hanging from the first snake’s jaws, ignoring all the other, usually quiescent, prey. The snake with the worm attempts to elude his pursuers by racing away with its head held high in a distinctive posture. This also occurs in the field (Drummond, pers. comm.). While this complex “grab running” response deserves careful comparative consideration (Schleidt, pers. comm.), its proximate mechanism may very well be evolutionarily derived from the prey movement/prey odor effects demonstrated here. Drummond (pers. comm.) in our laboratory has documented such kleptoparasitism in juvenile Thamnophis sirtalis and T. elegans, as well as in Nerodia sipedon during their first meal. Thus it is not an ontogenetically derived phenomenon.

While the movement speeds employed in this study seem too fast for the natural locomotion of earthworms, several points need to be made. First, we have replicated the phenomenon with small minnows. Quickly moving fish and frogs are natural items in the diet of T. sirtalis. Second, unlike some snakes (e.g. Oxybelis aeneus) that cease an overt predatory sequence when a strike is unsuccessful, Thamnophis will quickly orient to, follow, and repeatedly re-attack prey, even chasing it for short distances. Prey movement is very important in triggering these subsequent attacks. Even a bitten but unsecured worm will squirm rapidly. Third, Dial and Fitzpatrick (1983) have shown that
mammal and snake predators attack or handle a rapidly twitching autotomized lizard tail (up to and exceeding 300 vibrations per min) in preference to a nonmoving tail or the larger, slower moving owner. This separated tail phenomenon also occurs in salamanders and worms, which are a part of many garter snake diets including \textit{T. sirtalis}. Thus preferences for rapidly moving prey, needed by predators for their capture, have also been exploited by some prey to aid their escape, showing once again that predatory behavior can not be understood without equal attention to the prey.

\textbf{Zusammenfassung}

Die Rolle der Beutebewegung im Freßverhalten wurde untersucht an zehn Strumpfbandnattern (\textit{Thamnophis sirtalis}), die wiederholt mit je zwei Regenwurnstücken gereizt wurden, wovon eines jeweils stillstand, während das andere sich ununterbrochen um sich selbst drehte. Außerdem wurde das Vorhandensein und die Herkunft des Beuteduftes variiert und das Verhalten einer zungenlosen Schlange mit dem normaler Tiere verglichen.

Experiment I zeigte, daß Strumpfbandnattern vorzugsweise rotierende Regenwurmstücke angriffen, und zwar in einem weiten Geschwindigkeitsbereich (1 bis 2048 rpm) mit einem Optimum zwischen 16 und 256 rpm. Duftlosmachen eines Stückes und Erhöhung der Rotationsgeschwindigkeit auf über 500 rpm verminderte jedoch die Antwort. Experiment II zeigte, daß immer duftlose Stücke, die sich mit einer Geschwindigkeit von 22 bis 32 rpm drehten, gegenüber stillstehenden bevorzugt wurden.

Experiment III bestimmte die Auswirkung unterschiedlicher Duftbedingungen in der Umgebung auf die Auswahl bewegungsfreier oder künstlich bewegter Beute. Bei Regenwurmgeruch in der Umgebung zeigte sich eine anhaltend höhere Zügelrate als ohne Duft.


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