

Prey Handling Behavior of *Eumeces gilberti* with Comments on Headfirst Ingestion in Squamates

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ABSTRACT.—Captive Gilbert's skinks (*Eumeces gilberti*) almost always swallowed prey that were relatively difficult to ingest (crickets) headfirst, regardless of whether they initially grasped the anterior or posterior half of the prey. Skinks took longer to handle (subdue and swallow) crickets attacked posteriorly than those attacked anteriorly. The skinks tended to swallow prey that were relatively easy to ingest (mealworms) headfirst also. However, for these prey, site of attack influenced direction of ingestion: mealworms attacked anteriorly were more likely to be swallowed headfirst than those attacked posteriorly. Nevertheless, the tendency to ingest mealworms headfirst was not completely dependent on site of attack. Neither site of attack nor direction of ingestion influenced handling time of mealworms. Failure to find an advantage for the headfirst ingestion of easily-swallowed prey may represent true lack of such an advantage, the behavior being maintained through phylogenetic inertia or generalization of a response to prey that are more difficult to swallow.

Many snakes and at least some lizards tend to swallow prey headfirst (Diefenbach and Emslie, 1971; Loop and Bailey, 1972; Loop, 1974; Klein and Loop, 1975; Greene, 1976; Cooper, 1981a), a behavior generally regarded as an adaptation to reduce the resistance offered by the appendages and body covering of the prey (Diefenbach and Emslie, 1971; Greene, 1976). Furthermore, for a number of snakes (Loop and Bailey, 1972) and the Bengal monitor, *Varanus bengalensis* (Loop, 1974), the probability of headfirst ingestion increases with increasing prey size, thus apparently tracking the degree of difficulty of ingestion.

Two observations, however, suggest that this view of headfirst ingestion as a direct adaptation may not be correct. First, headfirst ingestion by some squamates is at least partially dependent on initial attack of the prey's anterior end (Diefenbach and Emslie, 1971; Cooper, 1981a), raising the possibility that headfirst ingestion is a by-product of selection for anterior attack. Second, the one investigation that looked for a reduction in swallowing time associated with headfirst ingestion, taking prey size into account, failed to find one (Loop, 1974).

Here, we examine the adaptive significance of headfirst ingestion in Gilbert's

skinks (*Eumeces gilberti*) by putting together in one study the kinds of observations made for different species in previous investigations. In particular, we look for an association between direction of ingestion and initial site of attack, and a reduction in subduing and swallowing time associated with headfirst ingestion and anterior attack. These associations are examined for prey that differ in ingestion difficulty. In addition, we give a brief analysis of headfirst ingestion as a behavioral homology. Our results favor a less strictly adaptationist view of headfirst ingestion than is current in the literature.

METHODS AND MATERIALS

Our subjects were eight adult, wild-caught *Eumeces gilberti* (four males and two females from Monterey Co., CA and a male and female from San Diego Co., CA), housed 1-3 to a terrarium in the Museum of Vertebrate Zoology and maintained on a diet of live crickets and mealworms. The skinks ranged from 73-95 mm SVL.

Skinks were fed and observed between 1000-1830 PDT at 2-4 day intervals from 30 April-9 July 1983. Each terrarium was provided with a heat lamp and exposed to the natural Berkeley photoperiod. Ambient temperature, measured away from the lamp and about 1 cm above the sub-

strate, ranged from 25–31°C, which is within the normal activity range of this species (Brattstrom, 1965).

Cardboard barriers served to isolate skinks during feeding trials. Four types of prey were presented: (1) live mealworms (*Tenebrio*); (2) live crickets (*Gryllus*); (3) crickets freshly killed by momentary immersion in boiling water; and (4) freshly killed crickets placed in opaque glass vials with their posterior ends protruding. The last category was designed to force skinks to attack the posterior ends of dead crickets. Mealworms averaged 2.98 ± 0.27 (SD) mm in greatest width and 22.04 ± 2.24 mm in length; crickets averaged 5.27 ± 0.37 mm in greatest width and 22.39 ± 1.91 mm in length. Mean relative prey width (greatest prey width/skink head width) was 0.26 for mealworms and 0.47 for crickets.

For each trial we placed a single prey with a single skink and observed the lizard's behavior from a distance of about 0.5 m. The skinks did not seem to be disturbed by our presence. The following variables were recorded: (1) the number of unsuccessful open-mouthed strikes at the prey; (2) site of attack—the site on the prey's body (anterior or posterior half) initially grasped successfully in the skink's jaws; (3) whether the skink pressed the prey to the substrate by orienting the snout downwards; (4) whether the skink shook the prey in its jaws; (5) direction of ingestion (head- or tailfirst); and (6) handling time—elapsed time (nearest sec) from the moment the prey was successfully grasped to mouth closure.

We also observed other lizards (*Gerrhonotus coeruleus*, *Xantusia henshawi*, *Anolis carolinensis* and *Sceloporus occidentalis*) feeding on mealworms and crickets, and recorded site of attack and direction of ingestion. Experimental conditions were as for *E. gilberti*.

Because feeding trials for a particular skink are not independent, using individual trials as replicates from which to infer tendencies for the sample as a whole is not valid (Hurlbert, 1984). Therefore, except where otherwise noted, we used individual skinks rather than individual feeding

trials as data points. For example, in performing *t*-tests on percentages of prey swallowed headfirst, individual skinks are the replicates and overall means are the averages of the percentages for the individual animals, not the individual feeding trials. In comparisons of different prey categories (e.g., mealworms vs. live crickets; items ingested head- vs. tailfirst), paired *t*-tests were used, with data for an individual animal's response to the two prey categories constituting a pair.

Percentage data approximate a normal distribution only when the subsample size, in this case number of feeding trials for a given skink, is about five or more (C. McCulloch, pers. comm.), and this was the minimum number of feeding trials in a given prey type category deemed necessary to include a particular skink in a *t*-test involving percentages. When *t*-tests failed to reject an hypothesis, a binomial sign test was used if employing such a test increased the sample size (i.e., number of skinks). All tests are one-tailed.

RESULTS

Handling Time, Unsuccessful Strikes, Pressing, and Shaking.—Compared to mealworms, live crickets took longer for the skinks to subdue and swallow ($\bar{x}_c = 71$ sec, $\bar{x}_m = 13$, $t = 3.35$, $N = 8$, $P < 0.01$), were struck at unsuccessfully with greater frequency ($\bar{x}_c = 0.67$ unsuccessful strikes/prey, $\bar{x}_m = 0.05$; Wilcoxon's signed-ranks test: $T_s = 4.5$, $N = 8$, $P < 0.04$), were pressed in a greater proportion of the trials ($\bar{x}_c = 0.80$, $\bar{x}_m = 0.05$, $t = 9.42$, $N = 4$, $P < 0.002$), and were shaken in a greater proportion of the trials ($\bar{x}_c = 0.39$, $\bar{x}_m = 0.10$, $t = 4.56$, $N = 4$, $P < 0.01$).

Direction of Ingestion and Site of Attack.—Two mealworms were ingested middlefirst; all other prey were ingested either head- or tailfirst. Skinks tended to ingest both mealworms and crickets headfirst (Table 1; using 50% ingested headfirst as the null hypothesis: mealworms— $t = 7.61$, $N = 7$, $P < 0.001$; live crickets— $t = 14.25$, $N = 5$, $P < 0.0001$; dead crickets—sign test, $N = 7$, $P < 0.01$). This tendency was stronger for live crickets than for live mealworms ($t = 4.51$, $N = 4$, $P < 0.02$).

TABLE 1. Percentages of prey ingested headfirst by eight *Eumeces gilberti*. Sample sizes in parentheses.

Lizard #	Live mealworms	Live crickets	Dead crickets
1	90.0 (10)	100.0 (8)	100.0 (6)
2	80.0 (10)	88.9 (9)	100.0 (8)
3	77.4 (31)	100.0 (3)	—
4	66.7 (21)	100.0 (4)	100.0 (3)
5	80.0 (10)	100.0 (7)	100.0 (7)
6	63.6 (11)	85.7 (7)	100.0 (8)
7	72.7 (11)	100.0 (1)	100.0 (6)
8	100.0 (4)	100.0 (6)	100.0 (7)
Mean	78.8 (8)	96.8 (8)	100.0 (7)

TABLE 2. Percentages of prey attacked anteriorly by eight *Eumeces gilberti*. Sample sizes in parentheses.

Lizard #	Live mealworms	Live crickets	Dead crickets
1	77.8 (9)	25.0 (8)	100.0 (4)
2	75.0 (8)	50.0 (6)	100.0 (2)
3	56.7 (30)	100.0 (2)	—
4	70.0 (20)	100.0 (2)	100.0 (1)
5	75.0 (8)	60.0 (5)	100.0 (3)
6	57.1 (7)	40.0 (5)	50.0 (2)
7	72.7 (11)	0.0 (1)	100.0 (3)
8	100.0 (3)	80.0 (5)	33.3 (3)
Mean	73.0 (8)	56.9 (8)	83.3 (7)

Skinks tended to attack the anterior half of mealworms ($t = 5.82$, $N = 7$, $P < 0.001$), showed a non-significant trend in this direction for dead crickets (excluding posterior presentations, sign test, $N = 6$, $0.10 < P < 0.11$), and no detectable tendency for live crickets ($t = 0.11$, $N = 5$, $P > 0.45$; sign test, $N = 7$, $P = 0.5$; Table 2; sample sizes in Table 2 are lower than in Table 1 because attacks on the prey's middle are not included—this also accounts for discrepancies in size-adjusted handling times reported in Table 4).

Despite numerous posterior attacks (some forced by posterior presentation), skinks always ingested dead crickets headfirst, and in all but two instances ingested live crickets headfirst.

To test for an association between site of attack and direction of ingestion of mealworms we examined ingestion directions for anterior and posterior attacks separately. There was a strong tendency for mealworms attacked anteriorly to be swallowed headfirst (again using 50% headfirst as the null hypothesis: $t = 41.02$, $N = 6$, $P < 0.0001$) and an almost significant tendency for mealworms attacked posteriorly to be swallowed tailfirst (sign test, $N = 4$, $P < 0.063$). By comparing the proportion of posterior attacks resulting in tailfirst ingestion with the proportion of anterior attacks resulting in headfirst ingestion we determined that the association of anterior attacks with headfirst ingestion was stronger than that of posterior attacks with tailfirst ingestion (sign test, $N = 5$, $P < 0.04$).

Lizards of four other species in three families also tended to attack the anterior half of prey and ingest them headfirst (Table 3). These data are in the form of non-independent feeding trials and are thus not necessarily indicative of species-wide tendencies.

Relationships of Direction of Ingestion and Site of Attack to Handling Time.—The mean size-adjusted handling time (i.e., handling time/prey width) was shorter for live crickets attacked anteriorly than those attacked posteriorly. Neither site of attack nor direction of ingestion significantly affected size-adjusted handling time in any other case (Table 4). However, when data for each skink were tested separately (and individual feeding trials were the data points), size-adjusted handling times were longer for the two live crickets swallowed tailfirst than for live crickets swallowed headfirst (skink 2: $t = 4.55$, $N = 9$, $P < 0.005$; skink 6: $t = 2.27$, $N = 7$, $P < 0.05$). The two crickets that were swallowed tailfirst were both attacked posteriorly; when only crickets attacked posteriorly were considered, the effect of direction of ingestion was non-significant (skink 2: $t = 4.91$, $N = 3$, $0.05 < P < 0.1$; skink 6: $t = 0.85$, $N = 3$, $0.2 < P < 0.3$), though for both skinks the size-adjusted handling time for the cricket swallowed tailfirst was greater than for any of the crickets swallowed headfirst.

DISCUSSION

Crickets were more difficult for Gilbert's skinks (*Eumeces gilberti*) to capture, subdue,

TABLE 3. Frequencies of anterior attack and headfirst ingestion for lizards in the families Anguillidae (*Gerrhonotus*), Xantusiidae (*Xantusia*), and Iguanidae (*Anolis* and *Sceloporus*).

Species (# individuals)	Prey	Site of attack anterior/posterior	Direction of ingestion headfirst/tailfirst
<i>Gerrhonotus coeruleus</i> (1)	crickets	9/6	12/4
<i>Xantusia henshawi</i> (2)	mealworms	4/2	5/2
<i>Anolis carolinensis</i> (1)	crickets and mealworms	17/4	20/4
<i>Sceloporus occidentalis</i> (6)	crickets and mealworms	14/8	20/3
Totals		44/20	57/13

and swallow than were mealworms. Compared to mealworms, crickets took longer for the skinks to subdue and swallow, and were more frequently struck at unsuccessfully, shaken, pressed to the substrate, and swallowed headfirst. These differences are probably due to the crickets' greater speed and size, and relatively larger legs.

The skinks tended to ingest crickets headfirst, regardless of whether they initially grasped the anterior or posterior half of the prey. Headfirst ingestion, by minimizing the resistance offered by the prey's appendages, should ease swallowing, as has been suggested for a variety of snakes (Diefenbach and Emslie, 1971; Loop and Bailey, 1972; Greene, 1976) and the skink *Eumeces laticeps* (Cooper, 1981a). Consequently, this behavior should reduce time and energy costs of swallowing, and extend the range of ingestible prey. The last is of doubtful importance to our study because the skinks were probably capable of swallowing the prey we used either head- or tailfirst, as evidenced by the modest handling times recorded and the fact that two crickets were ingested tailfirst. Minimizing handling time might be important because this period may represent time taken away from other activities, and may also be a time of increased susceptibility of the predator to its own predators. For the sample of skinks as a whole, we were unable to demonstrate a difference in size-adjusted handling times for tail- vs. headfirst-ingested crickets (Table 4). However, it seems likely that a larger sample of tailfirst ingestions would uncover a real difference, since the size-adjusted handling time for each of the two crickets swallowed tailfirst was greater than for any of

the crickets swallowed headfirst by the particular skink involved. We did not measure energy costs; however, for the skink *Chalcides ocellatus*, energy and time costs of subduing and swallowing crickets are highly correlated, at least for a given lizard body temperature. Furthermore, the energy costs are a small fraction of energy gained from the prey and may not be ecologically significant (Pough and Andrews, 1985).

The skinks also showed a tendency, albeit not statistically significant, to attack the anterior half of dead crickets (Table 2). Our impression is that, at least for certain individual skinks, this is a real tendency. In the posterior presentation tests we had to substitute an opaque vial when the skinks tried to grasp the anterior ends of the crickets by biting at the clear vial we initially used. Cooper (1981a, b) demonstrated an anterior attack tendency in *Eumeces laticeps* and hypothesized that this was advantageous (1) as a means of avoiding the prey's defenses (e.g., jaws) and (2) if the prey is to be swallowed headfirst, to minimize pre-ingestion maneuvering. The latter should reduce both handling time and opportunities for the prey to escape. Our data show that anterior attack is associated with reduced handling time of live crickets (Table 4). Skinks that attacked live crickets posteriorly would often hold on to them for long periods before swallowing them. Shifts in grip to the cricket's head did not occur until the prey was either forced into a corner or pressed vigorously to the substrate. Such behavior is presumably advantageous since crickets attacked posteriorly remain mobile and might escape if the skink attempted to

TABLE 4. Mean size-adjusted handling times (handling time in sec/prey width in mm) for prey attacked anteriorly vs. posteriorly and ingested head- vs. tailfirst by *Eumeces gilberti*. *P*-values are results of paired *t*-tests.

Prey	Site of attack ($\bar{x} \pm SD$)				Dir. of ingest. ($\bar{x} \pm SD$)			
	Anterior	Posterior	N	<i>P</i>	Headfirst	Tailfirst	N	<i>P</i>
Mealworms	4.34 \pm 1.96	4.87 \pm 2.56	7	0.11	4.33 \pm 1.96	4.54 \pm 2.59	7	0.34
Live crickets	10.10 \pm 5.81	20.14 \pm 13.1	5	0.02	7.55 \pm 0.23	18.73 \pm 3.54	2	0.07
Dead crickets	12.91 \pm 8.61	12.82 \pm 4.11	7	0.49	11.46 \pm 6.86	—	7	—

change its grip prematurely. Thus anterior attack directed at immobile (in this case, dead) prey can be explained by the difficulties skinks have with mobile prey. The lack of a tendency to attack live crickets anteriorly is probably a result of the preys' rapid movements, which make it difficult to attack them at any specific site.

The skinks also tended to attack mealworms anteriorly and swallow them headfirst (Tables 1 and 2). Here, as has been demonstrated for the rat snake *Elaphe climacophora* (Diefenbach and Emslie, 1971) and the skink *Eumeces laticeps* (Cooper, 1981a) feeding on adult and neonate mice, respectively, site of attack influenced the subsequent direction of ingestion: mealworms attacked anteriorly were usually ingested headfirst while those attacked posteriorly were usually ingested tailfirst. However, because the association between anterior attack and headfirst ingestion was stronger than that between posterior attack and tailfirst ingestion, the tendency to ingest prey headfirst was partially independent of site of attack. In other words, if attack sites were random (half anterior, half posterior) the skinks would still swallow more than half their mealworm prey headfirst.

Neither site of attack nor direction of ingestion significantly influenced handling time of mealworms (Table 4). Seven skinks exhibited both posterior attack and tailfirst ingestion of mealworms, thus a strong effect of site of attack and direction of ingestion on handling time is not likely to have been masked by small sample size. This suggests that anterior attack and headfirst ingestion are selectively neutral in dealing with mealworms or similar slow-moving and easily-swallowed prey.

Dipteran larvae make up a part of the diet of wild *E. gilberti* (Stebbins, 1954), suggesting that our results are relevant to animals in nature.

We suggest that the adaptive tendencies for anterior attack and headfirst ingestion of prey that are difficult to subdue and swallow have been carried over to prey for which these behaviors confer no advantage. That is, the skinks follow a rule for all prey specifying "attack the anterior half and swallow headfirst." Finer tuning of behavior to characteristics of the prey may be unnecessary if the inappropriate behavior carries no cost, which is supported by our finding that anterior attack and headfirst ingestion have neither positive nor negative effects on handling time of mealworms (Table 4).

An examination of Loop's (1974) data for *Varanus bengalensis* supports this interpretation of headfirst ingestion when the prey is relatively easy to swallow. *V. bengalensis* exhibited a strong tendency to swallow mice headfirst even though there was no apparent increase in ingestion time associated with tailfirst ingestion. However, ingestion time for the largest item (in terms of prey diameter relative to lizard head width) swallowed tailfirst was unusually long. Loop dismissed this observation as aberrant and concluded that some advantage, as yet undetected, other than decreased ingestion time must accrue from headfirst ingestion by *V. bengalensis*. We suggest that for most of the relative prey sizes in this study headfirst ingestion is a neutral trait, but that for relatively large prey—e.g., the observation he dismissed—it significantly reduces handling time.

Loop (1974) also suggested that head-

first ingestion might be a behavioral homology for snakes and varanids, which are sometimes considered to be closely related (Camp, 1923; McDowell and Bogert, 1954). Homology, in the sense of similarity resulting from inheritance through a common ancestor, obviously requires that the trait be inherited. If headfirst ingestion is innate, as stated by Klein and Loop (1975), it meets this criterion. However, if the behavior is learned, as suggested by the observation that some naive snakes attempt to swallow mice tailfirst before eventually locating the head and swallowing them headfirst (Greene, 1976), the issue is clouded since an inherited tendency to learn to ingest prey headfirst might or might not be involved. In any case, even if headfirst ingestion is a homologous behavior in *Varanus* and snakes, this does not imply that the behavior arose in their immediate common ancestor as a means of dealing with large prey, for the behavior characterizes a much more inclusive group. Many squamates other than varanids and snakes show a tendency to ingest prey headfirst (Tables 1 and 3; Cooper, 1981a), though not necessarily independent of site of attack (which is generally anterior—another possible homology). Our data for *E. gilberti* do show a tendency towards headfirst ingestion independent of attack site, and anecdotal evidence suggests this is true for a wide variety of vertebrates, including owls (Bolles, 1890), many mammals (Ewer, 1968), pike (Tinbergen, 1972), and gars (A. R. McCune, pers. comm.). Assuming that headfirst ingestion is homologous among these animals, the taxonomic distribution of the trait would lead one to conclude that it originated at least as early as the most recent common ancestor of actinopterygians and tetrapods, though expressed only in those forms that ingest prey whole.

The ubiquity of headfirst ingestion in vertebrates may reflect a universal advantage for the behavior; however, our data suggest rather that, at least for certain prey of certain predators, it currently does not confer a selective advantage. If the behavior is innate, it is conceivable that a ten-

dency to ingest prey headfirst would be retained even after a dietary shift to more easily-swallowed prey rendered the behavior neutral for *all* natural prey. In any case, the assumption that the tendency to ingest prey headfirst *must* always be selectively advantageous is questionable; we would like to emphasize that less strictly adaptationist hypotheses for this behavior are not only plausible but also favored by available data.

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