

Feeding behavior modulation in the leopard lizard (*Gambelia wislizenii*): Effects of noxious versus innocuous prey

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Abstract

Feeding, a fundamentally rhythmic behavior in many animals, is expected to exhibit modulation with respect to prey type. Using high-speed videography (200 frames s⁻¹) and kinematic analysis, we investigated prey-processing behavior in the long-nosed leopard lizard (*Gambelia wislizenii*). The effects of two prey types were examined, innocuous immature crickets (*Acheta domesticus*) and noxious stinging hymenopterans (honeybees [*Apis mellifer*] and yellow jackets [*Vespa* sp.]). Stinging hymenopterans are processed more extensively, with higher gape-cycling frequencies, and for a greater duration than are crickets. Generalized tetrapod feeding models were used as a framework to test the hypothesis that gape profile characteristics are modulated in response to prey noxiousness. Cricket processing generally fits the models, but hymenopteran processing departs from typical model parameters. In particular, the SO phase is absent to barely detectable during hymenopteran processing. This likely represents an effect of extrinsic neural input on a centrally directed rhythmic motor pattern, possibly to avoid being stung. Differences in the capture behavior of crickets versus hymenopterans indicate that *G. wislizenii* assesses prey noxiousness before physical contact with prey and modifies its capture behavior accordingly. These results add to the growing body of evidence that sensory information can play a critical role in shaping stereotyped rhythmic behaviors in non-mammalian tetrapods.

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Introduction

The modulation of feeding behavior as a function of prey or food type is a widespread phenomenon among vertebrates (Liem, 1979; Thexton et al., 1980; Throckmorton, 1980; Sanderson, 1988; Anderson, 1993; Herrel et al., 1996; Deban, 1997; Valdez and Nishikawa, 1997; Tomlinson, 2000), and many investigations have focused on

prey processing in the oral cavity (Lauder, 1983; Wainwright, 1989; Wainwright and Turingan, 1993; Friel and Wainwright, 1998; Herrel and De Vree, 1999; Hiiemae and Palmer, 1999). Food processing is a cyclical behavior that is directed, at its most basic level, by central pattern generators (Dellow and Lund, 1971; Thexton, 1974, 1976; see discussion on lizards in Herrel et al., 2001). Pattern generators are in turn influenced by peripheral receptor input as well as information from higher centers (Grillner, 1981). Sensory information clearly modulates food-processing cycles in mammals (Thexton et al., 1980), and it appears to play a similar role in lizards (Throckmorton, 1978, 1980; Herrel et al., 1996).

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Based on the premise that intraoral transport cycles among a diversity of animal groups share an ancestral mechanism, Bramble and Wake (1985) developed a generalized model of tetrapod feeding based on data from several non-mammalian taxa. In the model, the gape cycle is divided into five distinct phases: slow open I and II (SO-I and SO-II), fast open (FO), fast close (FC), and slow close-power stroke (SC-PS). The model incorporates processing cycles, a subcategory of intraoral transport cycles, which facilitate the mechanical reduction of food (Bramble and Wake, 1985; Schwenk, 2000a). Others have proposed modified versions of the model, particularly with respect to the SO phases and their recognition based on gape profiles (Reilly and Lauder, 1990; McBrayer and Reilly, 2002). Such models provide a useful baseline hypothesis with which to examine and compare variation in feeding behavior due, for example, to phylogenetic distinctions, feeding stages, and, in particular, prey-type effects that represent sensory modulation of motor patterns.

The effects of prey type on feeding behavior have been examined in several lizard taxa (Bels and Baltus, 1988; Urbani and Bels, 1995; Delheusy and Bels, 1999; Herrel and De Vree, 1999; Herrel et al., 1999; Smith et al., 1999). Previous studies usually have employed only commercially available prey that may or may not be representative of natural foods (but see O'Connell and Formanowicz, 1998). Nevertheless, they have been illuminating with respect to the effects of prey characteristics (e.g., size, shape, hardness, activity level) on feeding behavior. Delheusy and Bels (1999) and Herrel et al. (1999) demonstrated that, although some kinematic variables differ with prey type in lizards, the general form of the gape cycle is consistent across prey types (i.e., all phases are present).

The long-nosed leopard lizard, *Gambelia wislizenii* (Iguania, Crotaphytidae), of the western North American deserts (Stebbins, 1985; McGuire, 1996), frequently consumes stinging hymenopterans in nature. Combined data from the literature ($N = 328$ lizards) show that 30% of *G. wislizenii* specimens had recently eaten hymenopterans (Pack, 1922; McCoy, 1967; Milstead and Tinkle, 1969; Tanner and Krogh, 1974; Parker and Pianka, 1976; Mitchell, 1984; Lappin, 1999). Stinging hymenopterans consumed by *G. wislizenii*, as identified from museum specimens and specimens stomach-flushed in the field ($N = 110$ lizards), include a variety of apid, andrenid, and halictid bees, as well as sphecid and vespid wasps (Lappin, 1999).

Here, we compare the prey-processing kinematics and prey-capture behavior of *G. wislizenii* feeding on innocuous (immature crickets) versus noxious (stinging hymenopterans) prey. Our goals were: (1) to assess the behavioral effects of prey noxiousness on prey processing and prey capture in a non-mammalian tetrapod; (2) to test whether behavioral modulation materializes as

deviations from generalized tetrapod feeding models developed using innocuous prey; and (3) to address the need for comparative feeding studies focused on natural behaviors (e.g., using natural prey that have driven ecomorphological evolution) to investigate the role of sensory integration in neuro-motor modulation.

Materials and methods

Specimens

Eleven adult *G. wislizenii* were used in the feeding trials. This species is sexually dimorphic with females attaining greater body and head size than males (Lappin and Swinney, 1999), which was reflected by our sample of specimens (mean \pm SE: females – SVL = 113.2 ± 4.0 mm, head length = 27.7 ± 1.4 mm, $N = 7$; males – SVL = 90.2 ± 2.4 mm, head length = 22.4 ± 0.8 mm, $N = 4$). Specimens were collected in the Mojave and Great Basin Deserts from May through August, 1998 and 1999, and maintained in aquaria on a 12h:12h L:D cycle with fine gravel substrate, refugia, and basking rocks heated by incandescent lights. Lizards normally were fed live crickets dusted with calcium carbonate and a vitamin supplement 4 times/week, but were fasted for 48 h prior to feeding trials, which we conducted within 90 days of specimen collection. Given that all of the *G. wislizenii* in the sample were adults, and the high incidence of hymenopteran prey in the diet of this species, we assumed that all of the experimental specimens had previous experience preying upon stinging hymenopterans.

Immature crickets (*Acheta domesticus*) served as innocuous prey, and stinging hymenopterans represented noxious prey. Although *A. domesticus* is not sympatric with *G. wislizenii*, it is similar to other orthopteran prey common in this lizard's diet in terms of its size, integument hardness (Lappin, unpub. data), and by virtue of being innocuous. Hymenopterans used were honeybees (*Apis mellifera*) and yellow jackets (*Vespula sp.*). The immature crickets were slightly larger than the hymenopterans (total length: cricket = 17.7 ± 0.1 mm, honeybee = 11.8 ± 0.1 mm, yellow jacket = 13.4 ± 0.2 mm). Hymenopterans were wild-collected immediately prior to trials, held on ice in individual 20 ml glass vials ventilated by holes drilled into the plastic caps, and warmed to $\sim 30^\circ\text{C}$ immediately prior to use in a trial.

Videography

Video sequences were recorded at 200 frames^{-1} on S-VHS tapes with a HSC 250X2 Plus high-speed camera (J.C. Labs, Inc.). Lizards were allowed to feed

unrestrained in a glass aquarium (51 cm L × 32 cm H × 26 cm D) with a screen lid and fine gravel substrate. A 150 W incandescent lamp on the screen lid provided heat and lighting. Prey items were introduced singly through a trapdoor in the lid of the cage. For each lizard, the order of presentation of prey types was switched during each trial sequence (i.e., each day trials were run). Videotapes were reviewed for quality and time-coded using a Panasonic AG-DS555 VCR. Analog video output was analyzed using NIH Image v1.62 on a Power Macintosh 8600/200.

Analyses

We predicted that noxious prey would generally elicit more urgent and/or deliberate prey-processing behavior. To test this, we performed two separate kinematic analyses. The first consisted of count and duration variables for a general comparison of prey-processing behavior. In the second analysis, we digitized gape angle profiles (defined by jaw tips and quadrate-articular jaw joint) to calculate excursions, velocities, and durations of specific phases of the gape cycle. These variables were used to examine prey-processing behavior in light of generalized tetrapod feeding models.

Ninety-seven feeding sequences (2–14 per individual among 7 F and 4 M) gave a view of the gape cycles suitable for determining the following count and duration variables: (1) total number of prey-processing cycles; (2) prey-processing duration (onset of prey processing to onset of pharyngeal packing); and (3–5) duration of first, second, and third prey-processing cycles. To account for individual effects, individual means for these variables were calculated for each prey type. Two-way ANOVAs were performed on the means with prey type and sex as factors. *P*-values were subjected to sequential Bonferroni tests.

Twenty-three feeding sequences (2–6 per individual among 5 F and 3 M) provided a good lateral profile for digitization of prey-processing gape cycles. From the first five prey-processing cycles in each sequence, we calculated: (1) duration of SO phase; (2) duration of FO phase; (3) maximum angular velocity during FO phase; (4) duration of FC phase; (5) maximum angular velocity during FC phase; (6) duration of SC-PS phase; and (7) peak gape angle. The gape cycle phases were delineated by inflections in the gape profile (Bramble and Wake, 1985).

Studies of lizard feeding kinematics have typically found that processing cycles are kinematically similar to intraoral transport cycles and should be considered a subset thereof (Schwenk and Throckmorton, 1989; Bels et al., 1994; Schwenk, 2000b; but see Delheusy and Bels, 1999). We found this to be the case with *G. wislizenii* and, therefore, did not distinguish between them.

The seven gape cycle phase variables were analyzed separately. For each prey-processing cycle (first five

cycles), the mean of each variable was calculated for each individual for each prey type. Because more than one observation was made per individual (i.e., five cycles per feeding bout), we used a nested model ANOVA including prey type, sex, and prey type × sex (fixed effects) and individual(sex) and prey type × individual (sex) (random effects). *P*-values were subjected to sequential Bonferroni tests.

With respect to prey-capture behavior, we tested the hypothesis that the capture of hymenopterans would be more urgently followed by prey processing than when crickets are captured. Whereas crickets were always captured from the substrate, bees and wasps sometimes were caught in flight. Because a lizard's ability to capture a noxious prey item in some deliberate manner is likely to be compromised when that prey item is flying, we also predicted that the onset of hymenopteran processing would be more rapid for aerial than for terrestrial captures. We tested these predictions by comparing the delay between prey capture and the onset of prey processing among cricket, terrestrial hymenopteran, and aerial hymenopteran capture events using descriptive statistics and ANOVA with post hoc pairwise comparisons (Fisher's PLSD). Statistical analyses were performed using StatVIEW version 5 for Windows and SuperAnova version 1.1 for Mac OS.

Results

Prey-processing behavior

Compared to when crickets were processed, hymenopterans elicited about three times more prey-processing cycles, a considerably greater prey-processing duration, and far shorter gape cycle durations (Tables 1 and 2). Significant effects of the factor 'sex' and interaction for the 'duration of the third gape cycle' reflect its greater duration in males when they processed innocuous prey.

A clear SO phase was typically present during cricket-processing cycles (Table 1, Fig. 1). However, during hymenopteran processing, an average of 15% of the first five cycles had no distinguishable SO phase. For the cycles that did have an SO phase, it was considerably truncated compared to when crickets were processed (Tables 1 and 2, Fig. 1). Males had slightly greater SO phase durations than females when processing both prey types. When processing hymenopterans, both the duration and velocity of fast mouth opening (FO) were significantly greater than when crickets were processed (Tables 1 and 2). FO duration is greater for males than for females across prey types (significant sex effect). FC velocities were greater and FC durations were shorter with hymenopteran prey in females (significant

Table 1. Descriptive statistics for kinematic variables that describe prey-processing behavior and phases of prey-processing gape cycles in *Gambelia wislizenii* grouped by prey type and sex

	Females		Males	
	Cricket	Hymenopteran	Cricket	Hymenopteran
<i>Count/Duration variables</i>				
Total number of cycles	4.92 ± 0.46	14.61 ± 0.53	5.33 ± 0.86	14.46 ± 1.85
Prey-processing duration (ms)	877 ± 146	1794 ± 167	1322 ± 238	1753 ± 242
Duration 1st cycle (ms)	183 ± 22	66 ± 13	188 ± 17	70 ± 5
Duration 2nd cycle (ms)	196 ± 27	58 ± 8	229 ± 14	70 ± 12
Duration 3rd cycle (ms)	157 ± 16	81 ± 12	568 ± 114	127 ± 28
<i>Phases of gape cycle</i>				
SO duration (ms)	139 ± 7	15 ± 2	193 ± 9	18 ± 4
FO duration (ms)	11 ± 1	19 ± 1	12 ± 1	22 ± 1
FO velocity (deg/s)	1559 ± 100	2483 ± 89	1803 ± 125	2793 ± 95
FC duration (ms)	22 ± 1	19 ± 1	21 ± 1	21 ± 1
FC velocity (deg/s)	1711 ± 105	2344 ± 108	1647 ± 119	2971 ± 208
SC-PS duration (ms)	19 ± 2	26 ± 4	23 ± 2	28 ± 3
Gape angle (deg)	25.7 ± 1.7	32.7 ± 3.0	27.6 ± 2.4	37.4 ± 2.0

Values are mean ± 1 SE.

prey-type effect and interaction). SC-PS duration was greater during hymenopteran processing (significant prey-type effect). Peak prey-processing gape angles were greater with hymenopterans than with crickets, and males exhibited greater gape angles than females during hymenopteran processing (significant interaction).

Prey-capture behavior

Gambelia wislizenii captures crickets by rushing them with the mouth open, tongue extended, and typically no pause before they are seized. Stinging hymenopterans, when captured from the substrate, are examined, some-

times circled, and most often deliberately prehended by the thorax. When captured in flight, however, *G. wislizenii* leaps into the air after the stinging insect with no apparent control over its initial prehension. We found that the delay between prey capture and the onset of prey processing differed significantly between crickets (467 ± 60 ms) and either terrestrial (174 ± 37 ms) or aerial (24 ± 2 ms) hymenopteran captures (ANOVA: $F_{2,91} = 6.56$, $P = 0.002$; Fisher's PLSD: cricket/terrestrial hymenopteran – $P = 0.0019$; cricket/aerial hymenopteran – $P = 0.0355$). Although terrestrial and aerial hymenopteran captures did not differ significantly ($P = 0.4855$), the delay to the onset of prey processing

Table 2. Results of two-way ANOVA of variables that describe prey-processing behavior (df = 1, 18 for main effects) and nested two-way ANOVA (fixed effects) of variables that describe phases of prey-processing gape cycles in *G. wislizenii*

	Prey type		Sex		Prey type × Sex	
	F-ratio	P	F-ratio	P	F-ratio	P
<i>Count/Duration variables</i>						
Total number of cycles	114.73	<0.01****	0.02	0.99	0.10	0.75
Prey-processing duration (ms)	12.10	<0.01****	1.09	0.31	1.58	0.22
Duration 1st cycle (ms)	39.80	<0.01****	0.05	0.82	0.00	0.96
Duration 2nd cycle (ms)	53.72	<0.01****	1.24	0.28	0.29	0.59
Duration 3rd cycle (ms)	37.28	<0.01****	29.58	<0.01****	19.40	<0.01****
<i>Phases of gape cycle</i>						
SO duration (ms)	218.71	<0.01****	2.74	0.14	2.53	0.16
FO duration (ms)	61.49	<0.01****	13.21	0.01*	0.75	0.41
FO velocity (deg/s)	47.83	<0.01****	2.02	0.20	0.06	0.82
FC duration (ms)	9.27	0.02***	0.72	0.42	8.17	0.02*
FC velocity (deg/s)	35.63	<0.01****	0.69	0.43	4.49	0.07
SC-PS duration (ms)	7.88	0.03***	0.26	0.62	2.14	0.19
Gape angle (deg)	83.69	<0.01****	0.84	0.39	18.15	<0.01***

* $P < 0.05$; *** $P < 0.05$, sequential Bonferroni test; **** $P < 0.01$, sequential Bonferroni test.

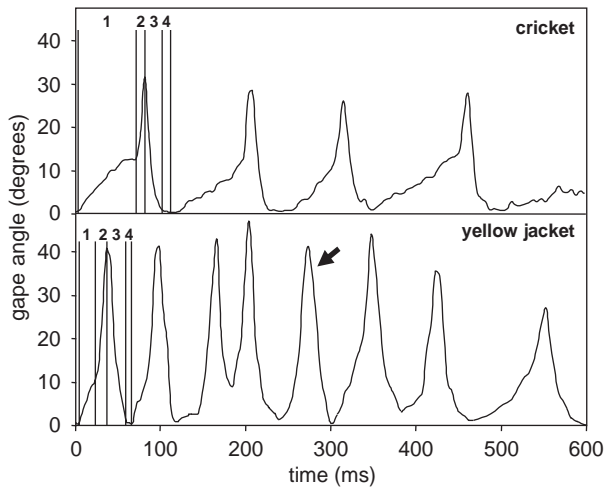


Fig. 1. Gape cycle profiles of a *G. wislizenii* processing a cricket (top panel) and a yellow jacket (bottom panel). Gape cycle phases are numbered (SO = 1, FO = 2, FC = 3, SC-PS = 4) following Bramble and Wake (1985). Arrow in lower panel indicates a gape cycle lacking an SO phase definable by a gape angle inflection. The presence of gape cycle doublets during hymenopteran processing indicates that the lizard sometimes did not fully adduct its jaws between prey-processing cycles. This probably reflects feedback controlled modulation in response to numerous prey characteristics, including ones that change as prey are processed, such as the contraction frequency of wing muscles (i.e., ‘buzzing frequency’) and the dimensions of rigid body parts (e.g., thorax).

for the four aerial captures we observed averaged only 14% that of terrestrial captures.

Discussion

Prey-type effects on prey-processing behavior

The number of prey-processing cycles and prey-processing duration are greater when *G. wislizenii* eat stinging hymenopterans compared to crickets. Further, processing cycle frequency (number of cycles/processing duration) is greater when *G. wislizenii* dispatches hymenopterans. All of this translates into noxious prey being processed more extensively, hastily, and for a longer time than innocuous prey. This pattern is analogous to the greater number of attacks and longer attack duration observed when Texas spotted whiptails (*Cnemidophorus gularis*) prey upon scorpions (a natural prey) versus crickets (O’Connell and Formanowicz, 1998). Although the two behaviors are fundamentally different (intraoral processing by *G. wislizenii* versus repeated attacks by *C. gularis*), they share the function of incapacitating noxious prey. The rapid immobilization of hymenopterans should help lizards avoid being stung. However, the behavioral modification to do so may incur an added cost in terms of foraging efficiency.

Gape cycle duration averaged over 3-fold shorter when hymenopterans were processed, which is due primarily to a reduced or absent SO phase. The greatly truncated SO phase during hymenopteran processing may reduce the risk of being stung by decreasing the time during which the tongue is fitted to the insect. Greater fast phase (FO and FC) velocities and the attainment of greater gape angles during hymenopteran processing may reduce the risk of being stung by providing the prey with less response time and more clearance, respectively. The longer SC-PS phase during hymenopteran processing may relate to incapacitating noxious prey, for example, by fracturing a hard yellow jacket thorax (see below). We hypothesize that these examples of behavioral modulation associated with dispatching noxious prey likely represent the effects of sensory input, primarily visual and tactile, on a central motor program.

In evaluating the effects of prey noxiousness on feeding behavior, it is necessary to consider the influences of other prey characteristics, such as size and hardness. Among iguanians, larger prey generally elicit longer total prey transport/processing durations because the number of gape cycles and gape cycle duration correlate positively with prey size (Bels and Baltus, 1988 on *Anolis*; Herrel et al., 1996 on *Agama*). In contrast, in *G. wislizenii*, the number of gape cycles and prey-processing duration is greater for the slightly smaller prey (hymenopterans) across the sexes, likely reflecting an overriding effect of prey noxiousness. Processing duration is greater for the smaller males (i.e., prey relatively larger due to smaller heads of males) across prey types, corroborating the results of previous studies. Herrel et al. (1996) showed that the duration of all gape cycle phases increased with prey size, and maximum gape angle has been positively correlated with prey size in iguanian and scleroglossan lizards (Herrel and De Vree, 1999; Delheusy and Bels, 1999). Greater FO duration and maximum gape angle in male *G. wislizenii* across prey types is likely an analogous size effect. However, our results that FO duration and maximum gape angle are far greater during hymenopteran processing (smaller prey) across the sexes further indicate a strong effect of prey noxiousness on feeding behavior.

Hardness is another prey characteristic expected to influence feeding behavior. Somewhat counter-intuitively, Herrel et al. (1996) found in *Agama* that crickets of similar size but greater hardness than grasshoppers elicited shorter gape cycles (i.e., expectation would be longer cycles to process harder prey). We also found shorter cycle durations when *G. wislizenii* processed the relatively harder hymenopterans (crushing forces measured using a piezoelectric force transducer [Type 9203, Kistler Inc., Switzerland] fitted with the lower jaw of a *G. wislizenii* [Lappin, unpub. data]: immature

crickets = 2.0 ± 0.2 N; bees/yellow jackets = 3.3 ± 0.3 N). However, this is a result of SO phase truncation, which we propose is related to avoiding stings. In *Agama*, the SC-PS phase did not change as a function of prey hardness (Herrel et al., 1996). In contrast, we found a longer SC-PS phase in *G. wislizenii* when the harder hymenopterans were processed, perhaps due to more time being required to generate the bite forces to fracture a hymenopteran integument. However, to determine whether this is an effect of prey hardness or noxiousness or both will require further study using additional prey taxa (e.g., coleopterans).

How noxious is noxious?

On a few occasions, we observed *G. wislizenii* being stung in the mouth when feeding on hymenopterans. When this occurred, the lizard would process and ingest the hymenopteran and then extensively lick the site of the sting. If a honeybee's sting became embedded in the oral cavity (usually in the epithelium of the dental arcade), then the licking motions would continue until it was dislodged. Hymenopterans do not appear to be hazardous to *G. wislizenii* in the sense that they are incapacitating or significantly interfere with the ability to feed normally. However, stings were obviously uncomfortable enough that lizards would not feed on additional hymenopterans during a given trial sequence after being stung. During trials on a day after being stung, lizards would again eat hymenopterans. Notably, even when not suffering a sting, lizards always consumed far fewer hymenopterans (usually 1 or 2 and never more than 5) than crickets (up to 15) during a trial sequence, which perhaps reflected a risk-assessment response.

Deviations from tetrapod feeding models

Bramble and Wake's (1985) generalized model of prey transport/processing is based on data from a number of tetrapods, including salamanders, turtles, and lizards. In developing the model, prey usually were standardized to minimize possibly confounding variables while still developing a model applicable to a variety of taxa and amenable to testing. Our results on prey processing by *G. wislizenii* fit the general architecture of the Bramble and Wake model, with two exceptions. First, although the SO phase is typical and often extended during cricket-processing cycles, it is absent or highly truncated during hymenopteran-processing cycles. Gape cycles missing the SO phase are not entirely unusual during prey processing by generalized lepidosaurs (Schwenk, 2000b), but its absence or extreme truncation being typical during prey processing is unusual. As mentioned above, SO phase elimination or truncation by *G. wislizenii* during hymenopteran processing may be a

response that shortens the gape cycle to avoid stings. In the thorny devil (*Moloch horridus*), a highly specialized ant-eating lizard that does not process its prey, transport cycles are extremely brief due to an absence of the SO phase (Meyers and Herrel, 2005). The similar patterns of SO elimination/truncation in these two lizard taxa demonstrate the plasticity of the SO phase, both in terms of behavioral modulation (*Gambelia*) and evolutionary specialization (*Moloch*).

The second departure from the Bramble and Wake model is that the SO phase is rarely divisible into SO I and SO II phases based on angular gape profiles. For both iguanians and scleroglossans, many authors have reported that the SO phase is separable into SO I and SO II phases during prey processing (Smith, 1984; Schwenk and Bell, 1988; Bels and Baltus, 1989; Schwenk and Throckmorton, 1989; Bell, 1990; Bels, 1990; Kraklau, 1991; Wainwright et al., 1991; Bels and Delheusy, 1992; Herrel et al., 1996; Delheusy and Bels, 1999; Herrel and De Vree, 1999). However, the SO I and SO II phases sometimes merge into one phase with no distinct plateau in the gape profile that characterizes the SO II phase (Schwenk, 2000b). We found this to be the case for *G. wislizenii*. A merged SO phase also has been reported in *Sphenodon* (Gorniak et al., 1982) and some iguanians (Delheusy and Bels, 1992; So et al., 1992). In an examination of the transport kinematics of one iguanian and six scleroglossan lizard taxa, McBrayer and Reilly (2002) reported that the SO II phase is rare in five species and entirely absent in two (scleroglossans). These observations are consistent with a modified version of the Bramble and Wake model in which the SO-II phase is not distinguished (Reilly and Lauder, 1990). Herrel and De Vree (1999) indicated that examining tongue movements is crucial to separating the SO I and SO II phases, which may not be possible based on gape profiles. The primary function of the SO II phase, fitting the tongue to the food bolus (Bramble and Wake, 1985), may not be obligatorily linked to a detectable inflection or plateau in the gape profile.

Prey-capture behavior

Typically, invertebrates possessing envenomation mechanisms are aposematically marked or colored. Therefore, if including noxious arthropods in the diet, a visual predator has an opportunity to recognize prey noxiousness prior to an attempted capture. The approach behavior of *G. wislizenii* to hymenopterans prior to physical contact with them suggests visual assessment of prey noxiousness, perhaps via aposematic color patterns. The relatively rapid onset of prey processing following the capture of hymenopterans may reflect the integration of various sensory information (e.g., visual, olfactory, textural). Although beyond

the scope of this study, the relative roles that various cues may play in modulating prey-capture and prey-processing behavior could be tested with artificial modification of prey items (e.g., painting, scenting, removing wings).

Comparison to noxious prey dispatch in other lizards

Other lizards, such as spiny lizards (*Sceloporus*) and zebra-tailed lizards (*Callisaurus*) consume stinging hymenopterans in nature (pers. obs., AKL). We have observed these lizards to typically shake hymenopterans vigorously, reminiscent of *Cnemidophorus* preying upon scorpions as described by O'Connell and Formanowicz (1998). Further, *Sceloporus* and *Callisaurus* often push a hymenopteran's abdomen into the substrate (pers. obs., AKL and MG), analogous to grasshopper mice dealing with the chemical defense of bombardier beetles (Eisner, 1966). When *G. wislizenii* ate hymenopterans, shaking rarely occurred, and prey were never pushed into the substrate. It is likely that this is a size effect, as adult *G. wislizenii* can fit most hymenopteran prey completely within the oral cavity for incapacitation via processing, whereas this is not possible for many smaller lizards. Study of neonate *G. wislizenii* feeding on hymenopterans could demonstrate an important size effect if alternative behaviors are used, such as those observed in smaller sympatric *Sceloporus* and *Callisaurus*.

Conclusion

A variety of prey characteristics (e.g., size, noxiousness, hardness, texture, movement patterns) provide potential sources of sensory information to modulate feeding behavior. As suggested by Schwenk (2000b), further experimental studies are needed to separate the effects of such characteristics on prey-processing behavior. In designing experiments, we urge researchers to consider what constitute natural prey. Information garnered prior to prey capture (e.g., visual, olfactory, vomeronasal, auditory) may provide for sensory modulation originating in higher centers. Experiments in which prey characteristics are manipulated to mimic those of other prey types are a means to explore the role of such external signals.

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