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## Foraging and Diet of a Diurnal Predator (*Eumeces laticeps*) Feeding on Hidden Prey

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**ABSTRACT.**—The diet of *Eumeces laticeps* consists of a variety of insects and their larvae, snails, isopods, spiders, *Anolis* lizards, and even juvenile *Eumeces*. Many of the prey species occur only in leaf litter or under surface objects (“hidden prey”) during the predator’s activity period. The diet thus differs from that of visually-oriented lizards.

Various measures of prey size correlate with size of the lizards’ trophic structures. Prey types and sizes vary seasonally. Laboratory and field observations of foraging lizards indicate that both visual and chemical cues are important in locating prey. Movement of foraging skinks through leaf litter suggests that hidden prey may also be flushed from diurnal retreats. Two abundant potential prey, velvet ants (Mutillidae) and millipedes (Diplopoda), were avoided.

Prey eaten by lizards have been described in a large number of studies (Pianka, 1967, 1970a, 1973; Schoener, 1968; Vitt et al., 1981; Schoener et al., 1982; Powell and Russell, 1984; and many others). Most of these studies deal with diurnal, insectivorous lizards, whose prey are active on the surface. Such diets reflect a sampling of “available” (in this case, surface active) prey items. Some diurnal lizards, however, frequently feed on prey that are not diurnally active on the surface. For example, *Cnemidophorus* (Teiidae) often dig insect larvae from the soil as well as breaking open terrestrial castings of termites (Milstead, 1957; Pianka, 1970b; Mitchell, 1979). We refer to these as “hidden” prey, defined as prey which can be located only by searching under debris or in the soil or litter, i.e., not within the visual field of a lizard. It is important to not confuse “hidden” with “cryptic.” The latter refers to organisms camouflaged to resemble part of the environment (Edmunds, 1974).

Both foraging modes and sensory capabilities of lizards may correlate with types of prey eaten. Lizard species that actively forage feed on relatively more hidden prey than do species that are wait-and-ambush predators (Huey and

Pianka, 1981). Likewise, the variation in sensory capabilities among lizard taxa (Burghardt, 1970) suggests that species relying on chemical cues may locate hidden prey that are unavailable to visually-oriented lizards.

Skinks (Scincidae) have highly developed chemosensory capabilities. North American *Eumeces* use chemoreception to identify prey (Loop and Scoville, 1972; Burghardt, 1973), species (Cooper and Vitt, 1985, in press, a), and sex (Cooper and Vitt, 1984a, b). Male *E. laticeps* can follow trails of conspecific females (Cooper and Vitt, in press, b). This large skink (to 143 mm SVL) can eat a diversity of prey, including relatively large items. Large prey are generally attacked at the anterior end and swallowed head first (Cooper, 1981a); orientation cues appear to be visual (Cooper, 1981b). The role of chemical cues in prey acquisition remains unknown, but our observations on feeding behavior and the diet of this species suggest that chemical cues may be important for prey location and discrimination.

We here describe the diet of *E. laticeps*, and comment on the potential role of chemical cues in predation. The specific questions we address are: 1) What

types and sizes of prey are used by broad-headed skinks? 2) Do prey vary between sexes or with season? 3) Is prey use consistent with observed foraging behavior? 4) Is prey size correlated with lizard size? 5) Why are some abundant potential prey types not eaten?

#### METHODS

Sexually mature male and female *E. laticeps* were collected from April through September 1983 at Kiawah Island, Charleston Co., South Carolina. These lizards usually occupy hardwood forests in the southern part of their range. They are often abundant on barrier islands, and much less wary than on the mainland. The herpetofauna of Kiawah Island has been described by Gibbons and Coker (1978).

Lizards were noosed, captured by hand, or shot with BB rifles, immediately placed on ice, and subsequently frozen. Snout-vent length (to 1.0 mm), body mass (to 0.001 g), head length (anterior edge of tympanum to tip of snout), head width (measured at the posterior edge of the mandible), and gape (measured by opening the mouths of relaxed dead lizards with calipers until relatively strong resistance was felt) were subsequently recorded for each individual lizard. All measurements (to 0.1 mm) were taken by the same researcher.

Full stomachs were removed, weighed, emptied, and reweighed. Stomach content mass was calculated by subtraction. The largest prey item in each stomach was individually weighed. Insects were identified to at least familial level, other invertebrates to at least ordinal level, and vertebrates to generic level. Prey items were spread evenly on a gridded petri dish. The proportional contribution of each prey type (taxon) was estimated by this procedure and the number of individuals of each prey type was recorded. Actual mass of each prey type was estimated by multiplying its proportional contribution by the stomach content mass.

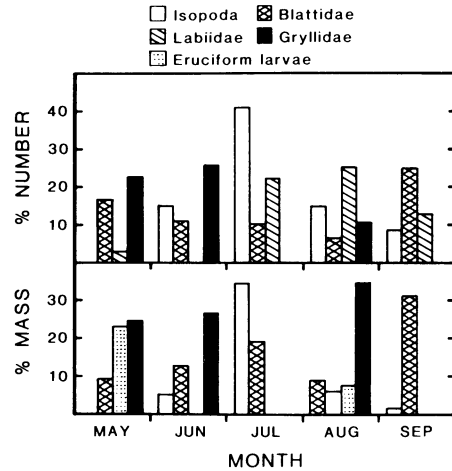


FIG. 1. Seasonal variation in prey utilization by adult male and female *Eumeces laticeps*. The percent utilization (prey category/total prey) in numbers of the five most commonly eaten prey by month is shown in the upper figure and the percent utilization of prey mass of the five most commonly used items is shown below.

Diversities ( $H'$ ) of prey types by number and mass (Shannon and Weaver, 1949), and percent overlaps ( $D$ ) in prey between sexes (Schoener, 1970) were calculated.

We recorded many field observations of foraging resulting in prey capture. Although observations were not quantified, those bearing directly on the interpretation of diet are summarized.

#### RESULTS

*Summary of the Diet.*—The diet of *E. laticeps* consists of a variety of invertebrates and vertebrates including insects, snails, isopods, spiders, and lizards (including juvenile *E. laticeps*) (Table 1). Most apparent are many prey that are not diurnally surface active. At least half of the prey taxa can only be located by searching underneath surface items. For example, we were able to collect isopods, earwigs, and camel crickets (Gryllidae) only by raking through leaf litter and turning logs. Although no plant material was found in the stomach samples, we have observed

TABLE 1. Composition of the diet of *Eumeces laticeps*. Prey number, proportion of the total sample, mass of each prey type, and the proportion of the total prey mass contributed by a particular prey type are given. Sexes were pooled for this summary. Frequency refers to the number of lizard stomachs containing a particular prey item. Asterisks indicate prey items generally not available on the surface during the day.

Prey type	# prey	% total # prey	Mass of prey	% total mass prey	Frequency
<b>Orthoptera</b>					
Acrididae	2	1.0	1.334	3.1	2
*Blattidae	25	12.4	5.790	13.6	22
*Gryllidae	20	10.0	8.689	20.4	15
Tettigoniidae	2	1.0	0.746	1.8	1
<b>Coleoptera</b>					
Carabidae	1	0.5	0.290	0.7	1
*Larvae	1	0.5	0.105	0.2	1
Cerambycidae	7	3.5	1.769	4.2	5
Elateridae	7	3.5	1.329	3.1	5
*Larvae	1	0.5	0.107	0.3	1
*Erotylidae	3	1.5	0.209	0.5	1
Meloidae	2	1.0	0.414	1.0	1
*Passalidae	1	0.5	0.211	0.5	1
*Larvae	1	0.5	0.286	0.7	1
Phengodidae					
*Larvae	4	2.0	1.866	4.4	2
Scarabaeidae					
*Larvae	2	1.0	0.219	0.5	2
*Staphylinidae	1	0.5	0.211	0.5	1
Tenebrionidae	5	2.5	0.599	1.4	3
<b>Dermoptera</b>					
*Labiidae	31	15.4	1.649	3.9	10
<b>Hemiptera</b>					
Pyrrhocoridae	1	0.5	0.120	0.3	1
<b>Homoptera</b>					
Cicadidae	1	0.5	0.867	2.0	1
<b>Lepidoptera</b>					
Unidentified	1	0.5	0.078	0.2	1
Eruciform larvae	6	3.0	3.677	8.6	4
*Arctiidae	6	3.0	1.361	3.2	2
<b>Diptera</b>					
Asilidae	2	1.0	0.173	0.4	2
Syrphidae					
*Larvae	1	0.5	0.272	0.6	1
<b>Hymenoptera</b>					
Formicidae	5	2.5	*0.154	0.4	3
Siricidae	1	0.5	0.211	0.5	1
<b>Other Invertebrates</b>					
*Amphipoda	1	0.5	0.141	0.3	1
Aranaea	3	1.5	0.865	2.0	4
*Isopoda	41	20.4	4.006	9.4	12
*Opiliones	7	3.5	1.120	2.6	4
*Pulmonata	3	1.5	0.091	0.2	1

TABLE 1. Continued.

Prey type	# prey	% total # prey	Mass of prey	% total mass prey	Frequency
Vertebrates					
<i>Anolis</i>	2	1.0	1.508	3.5	2
<i>Eumeces</i>	1	0.5	0.652	1.5	1
<i>Eumeces</i> tail	1	0.5	0.158	0.4	1
*Lizard eggs	2	1.0	1.013	2.4	1
Unidentified Material	—	—	0.247	0.6	1
Totals	201	100.2	42.537	99.9	
Prey diversity (H'):	Numbers 1.217		Mass 1.246		

*E. laticeps* feeding on muscadine grapes which were on the ground.

Seasonal use patterns for the five most common prey types (sexes pooled) are shown in Fig. 1. Prey diversities (sexes pooled) also varied seasonally (Fig. 2). The high yearly summary  $H'$  values compared to monthly  $H'$  values (Fig. 2) suggest that temporal availability of prey types significantly affects the diet. Prey overlap between sexes varied considerably through the season. If the small September sample is omitted,  $H'$  for prey numbers is negatively correlated with prey overlap between sexes ( $r_s = -1.0$ ,  $P < 0.05$ ,  $N = 4$ ) indicating that prey use by sexes diverges as more prey types become available.

Both mean and maximum prey mass were weakly but significantly correlated with lizard head size (Table 2), suggesting that this is one determinant of prey size, even though the lizards are capable of eating larger prey. Regression analyses using SVL and body mass as independent variables yielded extremely low coefficients of determination ( $R^2$ ).

Although prey size varies considerably among individual lizards, there are no significant differences between sexes in total prey mass, mean prey mass, maximum prey mass, or number of prey in four of five months (May–August, all  $P_s > 0.10$ ). During three months (May–July), sampled males were significantly larger than females in all measurements (all  $P_s < 0.03$ ). During Septem-

ber, when total prey mass, mean prey mass, and maximum prey mass differed between sexes (all  $P_s < 0.043$ ), there were no significant size differences between sexes (all  $P_s > 0.05$ ) in our samples. Seasonal variation in mean and maximum prey mass was also evident (Fig. 3) and these variables were significantly correlated ( $r_s = 1.0$ ,  $P < 0.05$ ,  $N = 5$ ).

When size and diet data are pooled for the entire sampling period by sex, significant sexual differences characterize all variables except numbers of prey eaten (Table 3). Males were larger than females, and generally ate larger prey items. The disparity between results of the pooled and monthly analyses may owe to the relatively small samples in the latter. In general the monthly differences in prey size are in the same direction as that of the pooled data comparison.

*Predatory Behavior.*—Broad-headed skinks are active foragers, moving over the leaf litter (primarily *Quercus*) looking from side to side and often flicking the tongue. They often stop, push the head into the litter, and emerge with prey. The lizard often burrows into the litter and emerges several minutes later at another point.

Skinks were often observed foraging in and from trees. They generally forage only on the trunks or large limbs, and descend from perches to pursue prey. Here visual cues constituted the primary basis for prey attack. Long-term

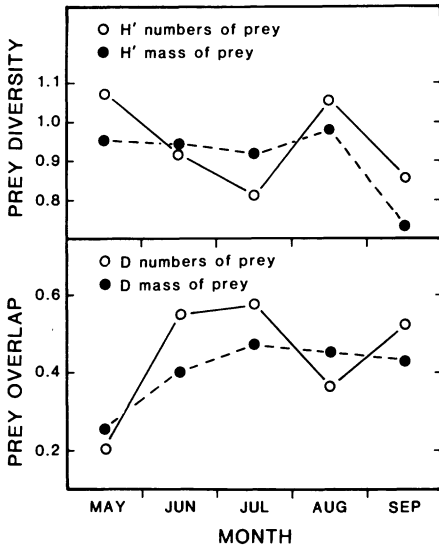


FIG. 2. Seasonal variation in diversities (H') of prey used by *Eumeces laticeps* (upper figure; sexes pooled) and seasonal variation in prey overlap between sexes of *Eumeces laticeps* (lower figure).

captives maintained on crickets (Gryllidae) immediately attacked them based on visual cues alone. After all live crickets had been eaten, the lizards often searched the cage while frequently tongue-flicking. If they located a freshly killed cricket, they repeatedly tongue-flicked it and then ate it. This behavior is similar to the grape-eating behavior described above.

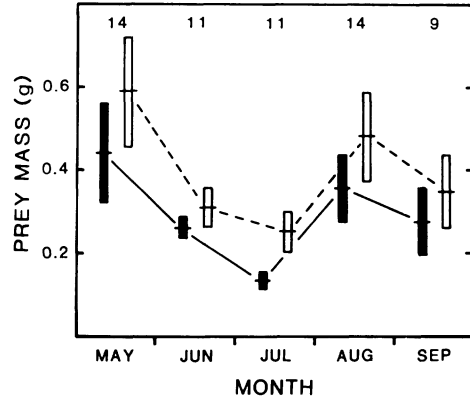


FIG. 3. Seasonal variation in mean (solid bars) and maximum (open bars) prey size for *Eumeces laticeps*. Means  $\pm$  1 SE are indicated, with number of lizard stomachs sampled per month indicated across the top of the figure. Sexes are combined (see text).

DISCUSSION

*Prey Types and Sizes.*—*Eumeces laticeps*, like many other lizard species, feeds on a wide variety of prey items. Prey size and type data probably reflect the available spectra in the microhabitats where *E. laticeps* forages. The notable difference between the diet of this species and that of many other lizards studied is the high frequency of prey types not active on the surface (hidden prey). Thus, *E. laticeps* forages in microhabitats that

TABLE 2. Regression statistics relating prey characteristics to morphological variables in *Eumeces laticeps*. HW is head width and HL is head length. In all comparisons except total prey mass  $\times$  HW and  $\times$  HL,  $R^2$  values for regressions on log transformed data were lower than reported below. The total prey mass  $\times$  HW and  $\times$  HL (log transformed) were similar in  $R^2$  values (within 0.002).

Regression	Slope	Intercept	$R^2$	F value (df)	P
# prey $\times$ HW	-0.086	5.055	0.014	0.81 (1,57)	0.372
Total prey mass $\times$ HW	-0.036	0.062	0.120	7.80 (1,57)	0.007*
$\bar{x}$ prey mass $\times$ HW	0.027	-0.194	0.206	14.57 (1,56)	<0.001*
Max. prey mass $\times$ HW	0.032	-0.172	0.206	14.56 (1,56)	<0.001*
# prey $\times$ HL	-0.087	5.474	0.015	0.89 (1,57)	0.350
Total prey mass $\times$ HL	0.031	0.017	0.094	5.91 (1,56)	0.018*
$\bar{x}$ prey mass $\times$ HL	0.026	-0.283	0.196	13.67 (1,56)	<0.001*
Max. prey mass $\times$ HL	0.029	-0.253	0.183	12.54 (1,56)	<0.001*
# prey $\times$ gape	-0.054	4.734	0.005	0.24 (1,53)	0.626
Total prey mass $\times$ gape	0.037	-0.131	0.118	7.09 (1,53)	0.010*
$\bar{x}$ prey mass $\times$ gape	0.025	-0.262	0.145	8.84 (1,52)	0.005*
Max. prey mass $\times$ gape	0.031	-0.285	0.163	10.14 (1,52)	0.003*

TABLE 3. Means ( $\pm$ SE with sample size in parentheses) of morphological characters and diet characteristics for *Eumeces laticeps*. Data are pooled for April–Sept. 1983.

Variable	Males	Females	Sexes pooled
<b>Lizard</b>			
SVL (mm)	110 $\pm$ 2.3 (34)	94 $\pm$ 2.9 (28)	103 $\pm$ 2.1 (62)
Body mass (g)	39.0 $\pm$ 2.25 (34)	24.2 $\pm$ 1.55 (28)	32.3 $\pm$ 1.69 (62)
Head width (mm)	21.6 $\pm$ 0.78 (32)	14.5 $\pm$ 0.36 (27)	18.4 $\pm$ 0.64 (59)
Head length (mm)	26.1 $\pm$ 0.82 (32)	19.1 $\pm$ 0.41 (27)	22.9 $\pm$ 0.66 (59)
Gape (mm)	25.6 $\pm$ 0.80 (28)	19.7 $\pm$ 0.51 (27)	22.7 $\pm$ 0.62 (55)
<b>Prey</b>			
Total prey mass (g)	0.850 $\pm$ 0.094 (34)	0.562 $\pm$ 0.087 (28)	0.720 $\pm$ 0.068 (62)
*Mean prey mass (g)	0.403 $\pm$ 0.064 (33)	0.204 $\pm$ 0.023 (27)	0.313 $\pm$ 0.039 (60)
Max. prey mass (g)	0.540 $\pm$ 0.073 (33)	0.269 $\pm$ 0.026 (27)	0.418 $\pm$ 0.045 (60)
# prey/stomach	3.0 $\pm$ 0.47 (36)	3.6 $\pm$ 0.81 (28)	3.3 $\pm$ 0.44 (64)

\* Mean of mean masses of all items within an individual stomach.

most visually-oriented lizards do not use.

Correlations between prey size and head and body size, and sexual differences in prey size, are weak, and thus it is doubtful that size partitioning of prey is the underlying cause of sexual size dimorphism (see Schoener, 1967). These skinks can eat prey much larger than the average size eaten (Cooper, 1981a). If resource partitioning determines body size then average prey size should be near the maximum possible to ingest; this is not the case (Table 3, Fig. 3). Sexual selection more likely accounts for sexual differences in morphology (Vitt and Cooper, 1985). Thus sexual differences in prey size are at least partially a consequence of head size differences.

The relatively low overlap between sexes in prey use ( $\bar{x}$  monthly overlap in prey numbers =  $0.4376 \pm 0.0698$ ;  $\bar{x}$  monthly overlap in prey mass =  $0.3968 \pm 0.0376$ ) suggests that males and females may forage in different microhabitats, or at different times, or have different sensory capabilities for prey identification. Because males use large trees trunks and logs as perches, particularly during the breeding season, prey differences between sexes may reflect microhabitat use. The high proportion of diurnally hidden prey in the diets of both males and females argues against

significant temporal differences in foraging behavior. Possible differential sensitivities to prey odors by sex remain unknown.

Lizards, including juvenile *Eumeces*, are sometimes eaten (Table 1), and captive adults readily feed on conspecific juveniles. Hamilton and Pollack (1961) found lizards in four of eleven *E. laticeps*; one contained three lizards, all but one being *Eumeces*.

*Unpalatable Prey.*—Two invertebrates which were very common in the habitats where we sampled skinks were absent from the diets: millipedes (Diplopoda) and female velvet ants (Hymenoptera: Mutillidae). Each possess defense mechanisms which might account for their absence in *E. laticeps* stomachs.

Millipedes produce toxins, including quinones and cyanide compounds that are released through the exoskeleton upon disturbance (Blum, 1981). Skinks held in the laboratory without food refused to eat millipedes.

Mutillids possess a number of anti-predator adaptations including a long stinger, quinone secretions, large biting mandibles, and an unusually hard exoskeleton (Schmidt and Blum, 1977). Most lizards (see citations above) feed on other stinging hymenopterans and *E. laticeps* has been observed to eat numerous *Polistes* (Vespidae) with no ap-



parent ill effects (McIlhenny, 1937), suggesting that the wasp's sting alone is ineffective. Mutillids may be avoided owing to a combination of factors.

Our observations and data on feeding ecology of *E. laticeps* suggests some basic differences from typical visually-oriented lizards. These differences correlate with expected differences between widely foraging and sit-and-wait foraging lizards (Huey and Pianka, 1981). Finally, it is clear that feeding mechanisms in lizards like *E. laticeps* are much more complex than previously believed, involving several sensory systems and complex behaviors.

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