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Diet Selection and Depression of Prey Abundance by an Intensively Foraging Lizard

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ABSTRACT.—Diet of the intensively foraging Puerto Rican lizard *Ameiva exsul* included most taxa of macroorganisms found in the leaf litter and soil surface at the study site. Nevertheless, certain items, *Anolis* eggs an extreme example, were overconsumed in relation to their abundance as determined by stratified random sampling of the leaf litter and soil surface where the lizards foraged. Other food items, such as land snails, were important in the diet but underconsumed relative to their high level of abundance in the leaf litter. Millipedes and termites were the only common litter organisms encountered that were not found in diet samples. Effects of *Ameiva* predation on abundance of land snails were studied in two experiments with hardware cloth enclosures that permitted free movement of snails through the 1.3 cm × 1.3 cm mesh and entrance of *Anolis* and birds through the open tops. Adult *A. exsul* were the only predators known to be excluded. Protection from *A. exsul* was associated with increased abundance of the low mobility land snails. No consistent changes in other species were detected.

Exposure to high quality prey items or high quality patches permits selectivity in the context of a broad diet, a tenet of foraging theory (Stephens and Krebs, 1986). The probing, investigative, energetic behavior of intensive foragers (Anderson and Karasov, 1981; Regal, 1983) may bring them into contact with a great number of potential prey including some items of high quality (Huey and Pianka, 1981). Moreover, the high level of movement of intensive foragers may increase the chance of encounter with rich patches of prey.

Intensively foraging lizards obtain broad diets by searching large areas (Schoener, 1971; Regal, 1983). The Puerto Rican teiid *Ameiva exsul*, for example, has been reported to eat everything from other lizards and lizard eggs to frogs, arthropods, snails, fruit, fungi, and garbage as it probes the leaf litter and soil surface (Wolcott, 1924; Rodriguez-Ramirez, 1985; Lewis, 1986; Lewis and Saliva, 1987). Whereas emphasis sometimes has been placed on diet breadth giving the impression that such relative omnivores forage indiscriminately (Heatwole and Torres, 1967), intensive foragers avoid some potential prey types (Vitt and Cooper, 1986) and probably favor others. Activity of lizards over the spectrum of styles from sit-and-wait foraging to intensive foraging in both Brazil (Magnusson et al., 1985) and Africa (Huey and Pianka, 1981) is positively correlated with the number of termites, a patchy resource, in the diet.

Enclosure and enclosure experiments with experimentally amenable aquatic organisms indicate that predators can modify prey abundance and thus, at least potentially, mold community structure (Morin, 1984; Quammen, 1984; Vanni, 1986). Experiments with sit-and-wait

iguanids suggest that lizards using this low energy foraging mode are selective feeders that take disproportionate quantities of relatively rare items (Stamps et al., 1981) and influence the structure of arthropod communities in certain microhabitats (Pacala and Roughgarden, 1984). Intensively foraging lizards, particularly when present at high density, may similarly modify relative and absolute abundance of litter dwelling macroorganisms.

Evidence is presented here to test hypotheses that 1) *Ameiva exsul* forages selectively and that 2) foraging by *A. exsul* has a significant impact on the leaf litter community.

METHODS

The study site was an abandoned pasture invaded by weedy introduced trees, primarily *Cassia* sp. It was located on the grounds of the Center for Energy and Environment Research (Joyuda site) overlooking Mayaguez Bay 7.7 km south of the University of Puerto Rico, Mayaguez, Puerto Rico. In 1981 the site was surveyed into 41 contiguous square blocks measuring 10 m on a side. A steep bank ran through the northern tier of blocks. The population of *Ameiva exsul* inhabiting the site dug den holes in the bank from which individuals moved out to forage during the day. Patterns of size and growth of lizards at this location as determined from trapping data were described by Lewis (1986). The study of foraging reported here was restricted to 15 blocks in the eastern end of the area.

Approximately 60 *A. exsul* foraged in the 15 block area where diet analysis and enclosure studies were carried out (Lewis, 1983). Local density was thus about 400/ha which is high

for teiids (Turner, 1977; Stamps, 1983). Individuals of this species have relatively small ($<700 \text{ m}^2$), overlapping home ranges and move actively while foraging (Lewis and Saliva, 1987).

The abundance of macroorganisms in the leaf litter and soil surface was estimated from a stratified random sample taken during September 1982. Five 0.25 m^2 quadrats were placed in each of the blocks by means of random coordinates giving a total of 75 quadrats in the 15 blocks. Litter samples were sorted by hand at the site. With the exception of ants, termites, and isopods all vertebrates and macroinvertebrates in the leaf litter and soil surface of each quadrat were counted; ants, termites, and isopods were scored as present or absent. Total number of individuals in each taxon for the 15 block area was calculated with standard error (Cochran, 1963).

Diet of *Ameiva exsul* was determined by analysis of stomach-flush samples (Legler and Sullivan, 1979) and feces eliminated during the process of stomach flushing for 47 lizards trapped with drift fence and funnel traps near a concentration of den holes in the bank. Lizards trapped at the den holes foraged over the 15 block area where litter samples were gathered. Animals were removed from traps within seconds of capture to avoid escapes, and stomachs were pumped immediately to avoid food loss through digestion. Diet samples were preserved in alcohol and subsequently teased apart and analyzed under a dissecting microscope.

Forty-four stomach-flush samples and 18 feces samples were collected in late July and August 1982. Three stomach-flush samples and three feces samples were collected in October 1982. All samples were from the rainy season. July, August, September, and October are climatically similar in Mayaguez. Average temperatures are 26.3°C , 26.4°C , 26.4°C , and 26.0°C while average precipitation is 24.38 cm, 25.60 cm, 27.96 cm, and 20.59 cm (Calvesbert, 1970).

Differences between stomach and feces samples in frequency of important foods were analyzed with Yates corrected χ^2 -contingency-tests (Campbell, 1974). Electivity for a food category was calculated as Ivlev's index $[(r_i - p_i)/(r_i + p_i)]$ where r_i = relative abundance of prey item i in the gut and p_i = relative abundance of prey item i in the habitat (Jacobs, 1974; Strauss, 1979). Ivlev's index is scaled from -1 to $+1$ with zero indicating neutral preference.

The impact of *Ameiva* predation on land snails inhabiting the leaf litter was studied in two enclosure experiments carried out in the 15 block area where litter and diet samples were taken. The first ran from January to September 1982, to coincide with litter samples and diet analysis; the second ran from May to October 1983. Square

hardware cloth enclosures measuring 0.5 m on a side and 15 cm high were placed by means of random coordinates in blocks where lizards were seen foraging. No more than three enclosures were placed in any block with totals of 18 in the first experiment and 20 in the second. Each enclosure was paired with an adjacent control area. Different control designs, described in the results, distinguished the experiments.

The enclosures were open on top to allow entry of *Anolis* lizards, birds, and mammals. Anoles were observed perching on the wire of the enclosures; ground feeding birds and mammals, such as introduced mongoose and rodents, were not observed at the site. Hatchling *A. exsul* were small enough to pass through the mesh of the hardware cloth. They were, however, observed to be deflected by it while foraging. Adult *A. exsul* were the only predators known to be excluded. When its foraging course was deflected by the wire, a lizard would round the corner of the enclosure and continue more or less on its original course. While I cannot eliminate the possibility that predation by non-excluded predators was reduced by the enclosures, the low profile of the enclosures should minimize this effect.

Prey organisms could move freely through the $1.3 \text{ cm} \times 1.3 \text{ cm}$ mesh. Highly mobile species, such as millipedes and most insects, were expected to diffuse through the enclosures at such rates that differences in population density between enclosures and controls resulting from predation by *Ameiva* would not be great. Larger differences in density were expected for the abundant, less mobile land snails which the lizards had been observed to eat. At the end of the experimental period numbers of organisms in each enclosure and control were counted and analyzed by means of paired-sample t -tests (Roscoe, 1975). A one-tailed test was used as the enclosure was expected to contain more organisms of each taxon than the control.

RESULTS

Diet Selection.—Land snails were overwhelmingly the most abundant macroscopic organisms counted in the leaf litter at Joyuda. Millipedes, insects, and arachnids were the next most abundant groups. Vertebrates, represented by *Anolis* eggs, were least abundant (Table 1).

The broad diet of *A. exsul* included snails, six orders of insects, other arthropods, earthworms, and *Anolis* eggs (Table 2). Insects and *Anolis* eggs had higher frequencies in feces than in stomachs (Yates corrected $\chi^2 = 11.623$, $df = 1$, $P < 0.05$, insects; Yates corrected $\chi^2 = 3.84$, $df = 1$, $P < 0.05$, *Anolis* eggs). Snails, on the other hand, had nominally higher frequencies in stomachs

TABLE 1. Total abundance of macroscopic organisms in the leaf litter at Joyuda for the 15 blocks where diet was studied. Numbers are based on a stratified random sample with 5 quadrat samples, each 0.25 m², taken from each block. Frequency gives proportion of the 75 quadrats where at least one of the organisms was counted. No attempt was made to count individual ants, termites, or isopods; only frequency of occurrence is given (the number of samples in which at least one unit of the particular food was found).

Species	Abundance	Standard error	Frequency
Snails			
<i>Subulina octona</i>	10,740	1930	0.533
<i>Alcadia striata</i>	3780	600	0.400
<i>Bulimulus guadelupensis</i>	900	330	0.120
Insects			
Scarabaeidae	240	180	0.026
Carabidae	320	150	0.053
Formicidae	—	—	0.480
Isoptera	—	—	0.160
Other arthropods			
Diplopoda	2580	930	0.187
Arachnida	400	170	0.067
Isopoda	—	—	0.187
Vertebrates			
<i>Anolis</i> eggs	80	79	0.013

than in feces, but the difference was statistically insignificant (Yates corrected $\chi^2 = 2.832$, df = 1, $P > 0.05$).

Insects were 2.4 times more numerous than snails in the diet, yet snails were 28 times more numerous than insects in the litter. While *A. exsul* will occasionally snap at insects in the air (Lewis, 1986), the relative excess of insects in the diet was not simply a consequence of feeding in microhabitats excluded by the quadrat sampling. With the exception of flies the insects in the diet were typical of those found in the leaf litter and soil surface. Snails were only three times more numerous than *Anolis* eggs in the diet yet snails were 200 times more numerous than *Anolis* eggs in the litter. Neither millipedes, large and abundant, nor termites were found in the diet samples. Plant matter may have been ingested incidentally; there was no evidence in diet samples of the fruits or seeds known to be consumed at other sites.

Ivlev's index allowed organisms from the litter at Joyuda to be ranked by electivity in the diet of *A. exsul*: annelids > *Anolis* eggs = insects > arachnids > snails > diplopods (Table 3).

Exclosure Experiments.—In the first exclosure experiment each control area was located at a

corner of its exclosure on the extended diagonal. Control areas were completely open. Significantly larger average numbers of the snail *Subulina octona* were found in the exclosures than in the paired controls when scored after 8 months (Table 4). A second snail, *Alcadia striata*, was marginally more abundant in the exclosures. Snails were distributed throughout the exclosures and not clustered along the wire. The relatively common millipedes and other less common organisms were evenly distributed between exclosures and controls. Leaf litter was not weighed. Shannon and Simpson diversity indices for exclosures and controls were similar (Krebs, 1985).

In the second experiment each control was located beside its exclosure. One side of the exclosure was extended enclosing the control on two sides. Six of the 20 exclosures in the second experiment were destroyed by cows. The remaining 14 exclosures were scored after 5 months to preclude additional losses. Fewer kinds of organisms were found in the second experiment, but patterns of abundance paralleled those of the first experiment even though each control area was half enclosed. More *S. octona* were again found in the exclosures than in the controls (Table 4). The numbers were strikingly similar to those in the first experiment, but they did not attain the same level of significance. Millipedes were more common in the controls than in the exclosures. Other rarer organisms and leaf litter itself were evenly distributed between exclosures and controls. Shannon and Simpson diversity indices for exclosures and controls were similar.

DISCUSSION

Although *A. exsul* consumes a wide variety of foods, it feeds selectively from the array of acceptable prey items available in the leaf litter. Certain rarer foods are disproportionately represented in the diet. Moreover, the exclosure experiments associate predation by *A. exsul* with depression of land snails.

Although some prey types in the diet were not found in the litter samples from the 15 blocks described in this study, representatives of all the invertebrate taxa appearing in the diet, including annelids, were found at low density in litter samples taken at the same time from the adjacent 26 blocks (Lewis, unpubl. data). Thus, I believe that the absence of some prey organisms from litter samples was due to low density of such prey and consequent sampling error rather than escape of prey from the litter samples or changes in abundance of prey between times when stomachs were flushed and prey sampled. The lizards probably locate preferred prey more efficiently than does quadrat sam-

TABLE 2. Analysis of stomach-flush and feces samples from *Ameiva exsul* at Joyuda, PR. The results are expressed as frequencies (the number of samples in which at least one unit of the particular food was found) and as number of prey in all samples. A total of 47 stomachs was pumped. Only 22 stomachs contained food, but 32 lizards yielded either food from the stomach and/or feces samples.

Food type	Frequency				Number	
	Stomachs	Feces	Combined	% combined	# prey	% prey
Snails						
Total snails	7	2	9	20.1	18	17.6
<i>Subulina octona</i>	4	1	5	11.6	7	6.9
<i>Alcadia striata</i>	1	0	1	2.6	1	1.0
<i>Bulimulus guadelupensis</i>	1	1	2	4.7	7	6.9
Unident. snail	3	0	3	7.0	3	2.9
Insects						
Total insects	9	19	27	62.8	53	52.0
Formicidae	5	2	7	16.3	10	9.8
Dermaptera	1	2	3	7.0	3	2.9
Diptera	1	3	4	9.3	4	3.9
Gryllidae	2	0	2	4.7	2	2.0
Blattidae	1	1	2	4.7	2	2.0
Scarabaeidae	0	3	3	7.0	3	2.9
Other Coleoptera	2	4	6	14.0	7	6.9
Lepidoptera larva	2	5	7	14.0	7	6.9
Insect eggs	1	1	2	4.7	2	2.0
Unident. insect	2	9	11	25.6	13	12.7
Other arthropod						
Spider	1	2	3	7.0	5	4.9
Mite	1	1	2	4.7	2	2.0
Isopod	1	0	1	2.6	1	1.0
Amphipod	1	0	1	2.6	1	1.0
Other invertebrate						
Annelid	1	1	2	4.7	2	2.0
Vertebrate						
<i>Anolis</i> egg	0	5	5	11.6	6	5.9
Other						
Unident. animal	3	2	5	11.6	10	9.8
Plant matter	1	3	4	9.3	4	3.9
Sample size	22	21	43		102	

pling. Supplementary sampling methods, such as the Tanglefoot traps (Dunham, 1983; Pacala and Roughgarden, 1984) or sweep samples (Stamps et al., 1981) might provide a rough check on the validity of the litter samples for highly mobile prey. The insect traps would need to be operated in a manner that would not cause them to capture nocturnal insects, which are unavailable to the strictly diurnal lizards.

Stomach pump samples and feces samples may be biased in different directions. Short residence times in stomachs and indigestibility of chitin and leathery eggshell may cause insects and *Anolis* eggs to be relatively more frequent in feces samples than in stomach samples. Dissolution or fragmentation of snail shells during digestion and lack of persistent hard parts other than the radula may reduce detectability of snails

in the feces samples. Short residence times in the stomach could lower the apparent consumption of snails.

The absence of termites from the diet samples was unexpected given the importance of termites to other intensive foragers (Pianka, 1970; Huey and Pianka, 1981; Magnusson et al., 1985) and the presence of termites (*Nasutitermes costalis*) on the site. Covered termite trailways descended to the ground on the surface of tree trunks, dead branches on the ground contained termites, and two of the typically elevated nests nearly touched the ground in the area of the study. When trailways or nests were damaged, anoles fed immediately on the exposed termites. This species of termite should be acceptable to *A. exsul*. According to Wolcott (1950) the termites leave trailways and nests at night

TABLE 3. Diet electivity for *Ameiva exsul* at Joyuda. Ants, termites, isopods, amphipods, and plant matter are excluded as these items were not enumerated in the leaf litter but were scored as present or absent. Abundance of prey in the habitat is based on 75 quadrat samples; abundance of prey in the diet is based on 43 stomach pump or feces samples.

Organism	Number in habitat	(p)	Number in diet	(r)	Ivlev's index
		Proportion in habitat		Proportion in diet	
Snails	15,420	0.810	18	0.237	-0.547
Insects	560	0.029	43	0.566	0.903
Arachnids	400	0.021	7	0.092	0.628
Diplopods	2580	0.136	0	0.000	-1.000
Annelids	0	0.000	2	0.026	1.000
Anolis egg	80	0.004	6	0.079	0.904
Totals	19,040	1.000	76	1.000	

TABLE 4. Results of two enclosure experiments at Joyuda. A one-tailed hypothesis, that enclosure contains more potential prey organisms than control, was tested by paired-sample *t*-test. Only positive values of the statistic *t* could lead to rejection of the null hypothesis. Ants, termites, and isopods were not scored.

Experiment 1 (18 enclosure-control pairs, placed Jan 1982, scored Sep 1982)						
Organism	Total individuals	Ave./ enclosure	Ave./ control	Paired <i>t</i>	One-tailed <i>P</i>	df
Snails						
<i>Subulina octona</i>	370	11.94	8.61	1.87	$P < 0.05$	17
<i>Alcadia striata</i>	22	1.00	0.22	1.37	$0.05 < P < 0.10$	17
<i>Bulimulus guadelupensis</i>	1	0.06	0.00	1.00	$0.10 < P < 0.20$	17
Slugs	1	0.00	0.06	-1.00		
Arthropods						
Insects	14	0.44	0.33	0.44	$P > 0.30$	17
Diplopods	42	1.17	1.17	0.00		
Chilopods	2	0.11	0.00	1.00	$0.10 < P < 0.20$	17
Other						
Annelids	4	0.11	0.11	0.00		
Anolis eggs	2	0.06	0.06	0.00		
Diversity						
Shannon index		0.78	0.70			
Simpson index		1.53	1.47			
Experiment 2 (14 enclosure-control pairs, placed May 1983, scored Oct 1983)						
Organism	Total individuals	Ave./ enclosure	Ave./ control	Paired <i>t</i>	One-tailed <i>P</i>	df
Snails						
<i>Subulina octona</i>	279	11.42	8.50	1.51	$0.05 < P < 0.10$	13
<i>Alcadia striata</i>	7	0.14	0.36	-0.56		
Arthropods						
Diplopods	25	0.43	1.36	-2.25		
Chilopods	1	0.00	0.07	-1.00		
Material	Total mass	Ave./ enclosure	Ave./ control	Paired <i>t</i>	Two-tailed <i>P</i>	df
Litter (g)	2777	103.4	110.2	-0.85	$P > 0.50$	12
Diversity						
Shannon index		0.17	0.37			
Simpson index		1.10	1.13			

to seek new sources of dead wood. During the day when *A. exsul* is active, the termites do not expose themselves. Perhaps protection afforded by nests and covered trailways is sufficient to minimize predation.

Diplopods, unconsumed by *A. exsul*, were also absent from the diet of a skink (Vitt and Cooper, 1986). Millipedes secrete potent toxic substances (Blum, 1981), and foraging lizards may generally avoid them.

Predation should depress the abundance of preferred foods more severely than abundance of less preferred foods according to foraging theory (Stephens and Krebs, 1986). An unanticipated aspect of the exclosure experiments is that they show depression of a prey type, land snails, with low electivity in the lizard's diet. This pattern of prey depression is seen because exclosures were designed specifically to detect changes in snail abundance not because preferred prey did not experience depression. The first exclosure experiment was terminated at the time the litter and diet samples were taken; thus, the low electivity of snails was not known when the experiment was run. It is likely that prey types of higher electivity were also depressed, but due to the rareness or greater mobility of such prey the small exclosures did not allow detection of treatment effects. Excluding *A. exsul* from larger areas may reveal treatment effects for the more mobile prey types.

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NOTES

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An Evaluation of Stomach Flushing Techniques for Crocodilians

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Among the options available for obtaining dietary data, stomach flushing techniques have been widely used as alternatives to killing study organisms to obtain their stomach contents. These techniques are especially useful for dietary analyses of protected species, or for investigators who wish to obtain dietary information from marked populations or monitor diets of individuals. Flushing techniques have been used in crocodilian diet analyses (Taylor et al., 1978; Webb et al., 1982; Ayarzagüena, 1983), but have not been rigorously evaluated. If a stomach flushing technique is not 100% effective, measurement errors may be introduced into analyses of diet composition. Counts of prey items, prey size estimates, and estimated importance of prey categories could all be affected.

The spectacled caiman, *Caiman crocodilus*, is probably the most abundant crocodilian in the world (Groombridge, 1982), and in the Venezuelan llanos populations are managed as a renewable natural resource (Rivero-Blanco, 1985). The availability of both living and dead animals make it a good species to use for evaluating dietary techniques. Caimans are primarily fish eaters in the llanos, but also consume other vertebrates, insects, crabs, and snails. During a dietary study of caimans at Hato Piñero, a private ranch and biological research station in the state of Cojedes, Venezuela, I tested three stomach flushing methods for use on crocodilians: The scoop and pump method (Taylor et al., 1978), the garden hose method (Ayarzagüena, 1983), and a modification of Ayarzagüena's (1983) technique that employs the hose in combination with Heimlich maneuvers. The Heimlich maneuver is a first-aid technique used to dislodge obstructions in the air passageways of a choking person.

Here I describe the hose with Heimlich maneuvers method and present the results of a comparison of the three techniques in terms of their effectiveness in removing stomach contents.

Between 4 November 1985 and 17 March 1986, 46 *C. crocodilus* ranging 135-1086 mm SVL were randomly subjected to one of the three methods and subsequently killed for verification of any remaining stomach contents. There was no significant difference in mean size among caimans subjected to the three methods (F -ratio = 0.050, $df = 2,43$, $P > 0.95$). Five individuals used to test the scoop and pump technique and six caimans flushed with the hose and Heimlich maneuvers method had stones and debris in their stomachs, but no food. One individual with a completely empty stomach was excluded from further analyses. Following preservation in 70% ethanol, the contents removed by flushing and any contents remaining in the subject's stomach were separately weighed to the nearest 0.1 g on a triple beam balance while still moist.

Dietary analyses usually include measures of prey size, number of prey categories, and which prey category or taxon was dominant in terms of volume or mass. To evaluate the biases of stomach flushing techniques on these determinations, I analyzed the stomach contents removed by flushing and then reanalyzed them using the data from both the flushed items and contents remaining in the stomachs. The effectiveness of each method was evaluated according to whether or not caimans were completely flushed, and if the number of prey categories, the number of prey items, the rank (by volume) of prey categories, or the prey size estimates changed after any remaining stomach contents were included.

The scoop and pump method, described by Taylor et al. (1978) and Webb et al. (1982), was tested on 16 caimans. This method employed a scoop for large items that was inserted into the animal's stomach while water was poured into the caiman until it was full. Items were then pulled out with the scoop. The pump is a plastic tube that also was inserted into the stomach. Water was poured into the tube and the crocodilian was squeezed until stomach contents entered the tube and could be poured out.