

# Ontogenetic and seasonal variation in the diets of a Costa Rican leaf-litter herpetofauna

Steven M. Whitfield<sup>1</sup> and Maureen A. Donnelly

Florida International University, Department of Biological Sciences, UP Campus, OE 167, Miami, Florida, USA  
(Accepted 27 January 2006)

**Abstract:** Ontogenetic and seasonal variation in diet was examined for 11 species of insectivorous forest-floor frogs and lizards from a lowland wet forest in north-eastern Costa Rica. Specimens were collected systematically over an entire seasonal cycle and represented individuals of all sizes. Individual prey items were removed from stomachs of preserved specimens, measured and identified. Ontogenetic shifts in prey size were pervasive. Ontogenetic shifts in prey composition were limited to four species; these were not the species with greatest range in body size, nor the species with the broadest diets. Small prey types (ants, mites, collembolans) decreased in representation and large prey types (roaches, orthopterans, millipedes) increased in importance over ontogeny; this could be because prey selection is based primarily on prey size or because of different prey preferences among age classes. There is little evidence for size-structure in this assemblage. There is no evidence that total availability of arthropod prey varies among seasons, but some evidence that preferred prey are less common in the wet season. Diet was similar between lizards and frogs. Lizards were more likely to have empty stomachs, but also greater stomach volume, than frogs; this indicates a difference in food-gathering strategies. Our study indicates strong similarity between frogs and lizards in diet despite enormous differences in physiology and behaviour.

**Key Words:** amphibians, intraspecific variation, passive sampling, prey selection, reptiles, seasonality, size-structured assemblages, trophic ecology, tropical wet forest

## INTRODUCTION

Predator-prey relationships are a fundamental component of ecology. Advances in our understanding of behavioural aspects of prey selection (Huey & Pianka 1981, Stephens & Krebs 1986), trophic-based community structure (Chase *et al.* 2002, Pianka 1986), and energy flow in ecosystems (Beard *et al.* 2003, Magnusson *et al.* 2001) are all dependent on detailed data on trophic relationships which are lacking for most assemblages. When available, descriptive diet data are often biased by age distributions and times of year that data are collected. Too few studies of intraspecific variation in diet are currently available to determine if and when size distributions or seasonality will affect trophic relationships.

In some assemblages, body size rather than species identity may be the predominant factor determining

the outcome of interspecific interactions (Polis 1984, Werner & Gilliam 1984). In these 'size-structured assemblages', strong ontogenetic shifts in ecology or behaviour cause intraspecific variation to exceed interspecific variation (Werner & Gilliam 1984). Ontogenetic shifts in diet may emerge because of passive sampling (*sensu* Diaz & Carrascal 1990) in which prey is based exclusively upon size without regard for prey taxon, because of ontogenetic changes in foraging mode or habitat preference (Lima & Moreira 1993), or because different age classes of a species simply show preferences for different prey taxa (Lima 1998). Nonetheless, many studies of diet implicitly assume that there is little or no significant change in patterns of prey use between age classes.

Seasonality may also be a strong factor affecting intraspecific variation in diet. Long viewed as aseasonal because of the lack of drastic yearly fluctuations in temperature, humid tropical forests have increasingly been demonstrated to show strong seasonal rhythms (Leigh *et al.* 1982, Sanford *et al.* 1994). Seasonality may

<sup>1</sup> Corresponding author. Email: steven.whitfield@fiu.edu

affect diet because the relative abundance of prey types changes seasonally, or because seasonal lows in total prey populations cause reduced prey availability for the entire consumer assemblage (James 1991). While both ontogeny and seasonality may affect feeding, there is no consensus about how often, or under what conditions, effects of size or season should matter (Hodgkison & Hero 2003, James 1991, Lima & Magnusson 1998, Magnusson & da Silva 1993).

Assemblages of terrestrial amphibians and reptiles occupying leaf-litter habitat of moist tropical forests provide an ideal system for studies of trophic ecology. These assemblages feature high diversity and density of syntopic species (Lieberman 1986, Scott 1976) that show convergent patterns in diet (Caldwell & Vitt 1999, Lima *et al.* 2000). While previous studies of tropical herpetofaunas have identified ontogenetic or seasonal variation in diet (Donnelly 1991, Fleming & Hooker 1975, James 1991, Lima & Magnusson 1998), they generally have been limited in number of species examined, and are unable to test for the generality of these effects.

To better clarify intraspecific patterns of prey utilization by leaf-litter amphibians and reptiles, we ask the following questions: (1) do species show shifts in prey size with change in body size? (2) Do species show shifts in prey type with change in body size? (3) Is there evidence of seasonal limitation of food availability for members of this assemblage? (4) Are there differences in prey types utilized between seasons? (5) Are there seasonal differences in niche breadth among members of this assemblage? (6) Are there major differences in diet between syntopic lizards and frogs?

If the leaf-litter herpetofauna does show characteristics of a size-structured assemblage, we expect that size will have as great an effect on diet as species identity, and that ontogenetic diet shifts in prey type will be a general phenomenon for members of this assemblage. If lizards and frogs select prey through passive sampling, we expect that ontogenetic shifts in prey size will be widespread, changes in prey composition will be concentrated in those species showing the greatest range in body size, and species will change diet composition to reflect seasonal changes in arthropod abundance. If prey preferences are based primarily on species identity, then species will show ontogenetic shifts in prey size with ontogeny but not prey type; and species identity will be a much stronger factor than body size in the determination of diet. If seasonal fluctuations in resource abundance cause a period of seasonal food limitation, then we expect that the proportion of individuals with empty stomachs will vary seasonally, as will mean stomach volume for individuals with stomach contents. Furthermore, if resources are limited seasonally, niche breadth should contract in the season of highest food availability, indicating increased selection for favoured prey types. By utilizing an approach

that examines a large number of syntopic species, we can test not only for intraspecific variation in diet, but use data on species-specific traits to attempt to identify broad patterns that lend species to dietary plasticity.

## STUDY SITE

The individuals examined in this study were collected at the La Selva Biological Station, Heredia Province, Costa Rica (10°26' N, 83°59' W). This site is an approximately 1600-ha, evergreen forest reserve described as a tropical wet forest, located in the Caribbean lowland region of Costa Rica at between 30 and 135 m asl (McDade & Hartshorn 1994). Annual rainfall averages about 4000 mm; rainfall peaks in July and there is a short, mild dry season from January to April (Sanford *et al.* 1994). The herpetofauna at this site comprises a total of 48 species of amphibians and 87 species of reptiles, and is very well known in comparison to other tropical wet forests (Guyer 1990, Guyer & Donnelly 2005). More detailed characteristics of the study area have been provided in previous work (McDade & Hartshorn 1994).

## METHODS

### Collection of specimens

Specimens examined in this study were collected during a 13-mo period from November 1973 to December 1974 with a combination of monthly leaf-litter quadrats, pitfall traps and opportunistic collections (Lieberman 1986). All specimens were killed upon collection, fixed with formalin, and preserved in ethanol. Specimens remain in the herpetology collections at Florida International University and at the Museum of Natural History of Los Angeles County. Data on other aspects of this collection have been reported elsewhere (Donnelly 1999, Lieberman 1986, Watling & Donnelly 2002).

### Examination of diet

For four of the most abundant species within this assemblage (the anurans *Eleutherodactylus bransfordii* and *Dendrobates pumilio*, and the lizards *Norops humilis* and *Norops limifrons*), we removed stomachs from ten individuals per month, except in cases in which ten individuals per month were not available. An additional seven species were sampled less intensively due to unavailability of specimens in some months. For these species (the anurans *Eleutherodactylus fitzingeri*, *Eleutherodactylus megacephalus*, *Gastrophryne pictiventris* and *Bufo haematiticus*, and the lizards *Lepidoblepharis*

*xanthostigma*, *Sphenomorphus cherriei* and *Ameiva festiva*), we sampled ten individuals for each month for 6 mo. Two months were chosen as representative samples of the dry season (February 1974 and March 1974), two months of the wet to dry transition (May 1974 and June 1974) and two months of the wet season (October 1974 and November 1974). Although additional species are represented in this collection, limited sample sizes for less common species make detailed analyses difficult, and qualitative diet data have been reported elsewhere (Guyer & Donnelly 2005, Lieberman 1986).

Stomachs were dissected and individual prey items were removed. Each prey item was identified to the lowest taxonomic rank possible. Arthropods were generally assigned to order, except for ants (considered separate from other Hymenoptera because of distinct differences in morphology and behaviour) and holometabolous larvae (considered separately from adults). For each prey item, we measured body length and body width with an ocular micrometer to the nearest 0.1 mm, and estimated volume using the equation for volume of a prolate spheroid:

$$Volume = \frac{4}{3}\pi \left(\frac{1}{2}length\right) \left(\frac{1}{2}width\right)^2,$$

where we defined length as the axis of greatest length of the body of the prey item, and width as the greatest axis of length perpendicular to the length axis. We follow previous workers by using volumetric data, rather than counts, as the basis of analyses (Caldwell & Vitt 1999, Donnelly 1991).

We calculated niche breadth for each species using the formula proposed by Simpson (1949):

$$B = \frac{1}{\sum_{i=1}^n p_i^2},$$

where  $p_i$  is the proportional utilization coefficient (the proportion of each prey type in a species' diet) of each prey type. Niche breadth varies from one (only one prey taxon consumed) to  $n$  (all prey taxa consumed in equal proportions).

### Analyses

To test for ontogenetic change in prey size, we used a linear regression with  $\log_{10}$ -transformed prey volume as a dependent variable and SVL (snout-vent length) as an independent variable. To test for differences in prey availability among seasons, we used logistic regression with species and season as factors and stomach condition (empty or not empty) to compare the proportion of individuals with empty stomachs between species and seasons, and we compared total volume of all stomach contents per individual between seasons with an analysis

of covariance (ANCOVA) using SVL as a covariate to control for effects of body size.

For analyses of prey composition, we grouped several uncommon prey taxa (Gastropoda, Lepidoptera, Onychophora, Pseudoscorpiones and 'unknown') into a single category 'other'. In order to weigh the relative effects of species and size on prey composition, we used a crossed two-factor analysis of similarity (ANOSIM), with species and size class as factors. We used Bray-Curtis dissimilarity matrices as a basis for our ANOSIM analyses. To create discrete categories from continuous data, we pooled individuals into 10-mm size classes for analyses for all species. To weigh the relative effects of species and season, we used a crossed two-factor ANOSIM using SVL and season as factors. We then used non-metric multidimensional scaling (nMDS) as an accompanying graphic representation of differences among species and size categories. These procedures test for an overall effect of body size on diet regardless of species identity, but do not test for ontogenetic shifts within a single species. To test for ontogenetic change in prey composition for each species, we used Mantel tests with Spearman's coefficients to test for correlations between two distance matrices. One matrix included Bray-Curtis dissimilarity for all species combinations and the other included the absolute value of the difference in SVL between each pair of individuals. These procedures provide a strong test of ontogenetic shifts in diet composition, but do not indicate which prey taxa are used most heavily by different size classes. We used non-parametric Kendall's rank correlations to test for a relationship between proportion of each prey type in the diet and snout-vent length for all species which were determined to show significant ontogenetic shifts in prey composition.

### RESULTS

We sampled 6078 individual prey items from 693 individuals representing 11 species (Table 1). Twenty-four prey categories were represented (Acari, Annelida, Araneae, Blattodea, Chilopoda, Coleoptera, Collembola, Diplopoda, Diptera, Formicidae, Gastropoda, Hemiptera, Homoptera, Hymenoptera, Isopoda, Isoptera, larvae, Lepidoptera, Onychophora, Opiliones, Orthoptera, Pseudoscorpiones, Thysanoptera and Vertebrata). The most common prey types based on volumetric data included Orthoptera, Blattodea, Isopoda, Formicidae, larvae and Araneae. Mean ( $\pm$  SE) prey volume per taxon ranged from  $0.117 \pm 0.059 \text{ mm}^3$  for Thysanoptera to  $461 \pm 313 \text{ mm}^3$  for Vertebrata, and there were strong differences among prey taxa in mean volume (Kruskal-Wallis  $\chi^2 = 2605$ ,  $df = 25$ ,  $P < 0.001$ ) and variance in volume (Levene's test,  $F_{24,6051} = 117$ ,  $P < 0.001$ ). When excluding prey types representing less than

**Table 1.** Number of specimens and prey items sampled for 16 species of leaf litter frogs and lizards.

Species	Number of specimens	Number of prey items	Volumetric niche breadth
Frogs			
Leptodactylidae			
<i>Eleutherodactylus bransfordii</i> Cope 1886	130	370	5.79
<i>Eleutherodactylus fitzingeri</i> O. Schmidt 1857	48	67	4.45
<i>Eleutherodactylus megacephalus</i> Cope 1875	46	75	3.92
Bufonidae			
<i>Bufo haematiticus</i> Cope 1862	36	501	1.85
Microhylidae			
<i>Gastrophryne pictiventris</i> Cope 1885	46	730	2.91
Dendrobatidae			
<i>Dendrobates pumilio</i> O. Schmidt 1857	124	3660	2.58
Lizards			
Polychrotidae			
<i>Norops humilis</i> Peters 1863	119	166	6.00
<i>Norops limifrons</i> Cope 1862	105	130	4.89
Gekkonidae			
<i>Lepidoblepharis xanthostigma</i> Noble 1916	47	121	4.58
Scincidae			
<i>Sphenomorphus cherriei</i> Cope 1893	49	159	4.05
Teiidae			
<i>Ameiva festiva</i> Lichtenstein & von Martens 1856	38	99	2.89
Total	693	6078	

five individuals, mean log prey volume was positively correlated with standard deviation of prey volume (Pearson's correlation coefficient = 0.802,  $P < 0.001$ ), indicating that larger prey types are also more variable in size.

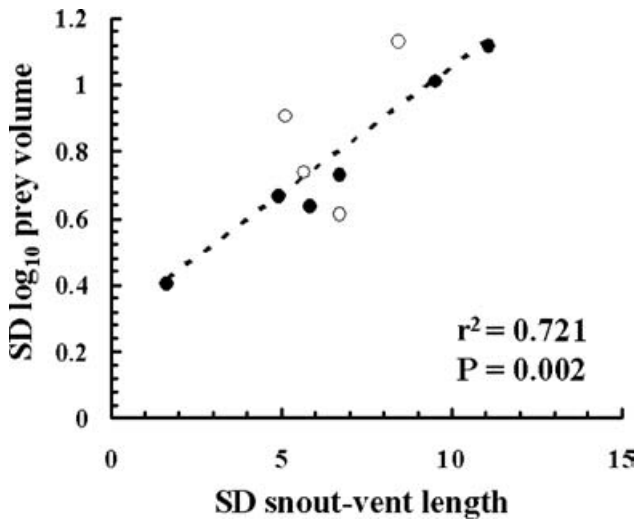
All species showed ontogenetic shifts in mean prey size except *Dendrobates pumilio* (Table 2). Species with greater variation in body size showed greater variation in prey size (Figure 1) and *Dendrobates pumilio* has the lowest variation in body size of the species examined here. Results of ANOSIM indicated differences in prey composition by both species (Global  $R = 0.408$ ,  $P < 0.001$ ) and by size class (Global  $R = 0.032$ ,  $P = 0.019$ ), yet species showed a much more profound effect. Non-metric MDS showed strong grouping by species, but not by size class

(Figure 2). Three species of myrmecophagous frogs (*Bufo haematiticus*, *Gastrophryne pictiventris* and *Dendrobates pumilio*) were separated from a larger guild of 'generalists' including the remaining species of frogs and lizards (Figure 2).

Four species showed significant evidence of ontogenetic variation in prey composition: the ant-eating frog *Bufo haematiticus*, the generalist frogs *Eleutherodactylus bransfordii* and *E. fitzingeri*, and the generalist lizard *Norops humilis* (Table 2). There was no significant change in niche breadth with body size (ANCOVA,  $F_{1,11} = 0.158$ ,  $R^2 = 0.346$ ,  $P = 0.692$ ). When all species were pooled, negative correlations were found for small prey items (Acari, Collembola and Formicidae); but positive correlations were found for larger prey types

**Table 2.** Results of linear regression for change in mean prey size and for Mantel tests for change in prey composition with ontogeny.

Species	df	Size			Composition	
		F	P	R <sup>2</sup>	Spearman's $r_m$	P
<i>Eleutherodactylus bransfordii</i>	1,99	70.8	< 0.001	0.417	0.113	0.029
<i>Eleutherodactylus fitzingeri</i>	1,29	25.4	< 0.001	0.448	0.193	< 0.001
<i>Eleutherodactylus megacephalus</i>	1,31	55.2	< 0.001	0.640	0.090	0.055
<i>Bufo haematiticus</i>	1,32	9.53	0.004	0.205	0.221	0.037
<i>Gastrophryne pictiventris</i>	1,38	28.5	< 0.001	0.428	0.032	0.337
<i>Dendrobates pumilio</i>	1,121	2.36	0.127	0.019	0.017	0.338
<i>Norops humilis</i>	1,79	24.6	< 0.001	0.298	0.060	0.011
<i>Norops limifrons</i>	1,66	13.7	< 0.001	0.172	0.023	0.244
<i>Lepidoblepharis xanthostigma</i>	1,34	7.04	0.012	0.172	0.057	0.116
<i>Sphenomorphus cherriei</i>	1,31	16.8	< 0.001	0.583	0.015	0.372
<i>Ameiva festiva</i>	1,20	22.5	< 0.001	0.529	0.080	0.182



**Figure 1.** The relationship between standard deviation of log-transformed prey size and standard deviation in consumer body size. Closed circles indicate species with no ontogenetic change in prey composition; open circles represent species with significant ontogenetic shifts in prey composition. Ontogenetic shifts in prey composition are not concentrated in species showing the greatest variation in body size or prey size. One outlier was excluded from this analysis.

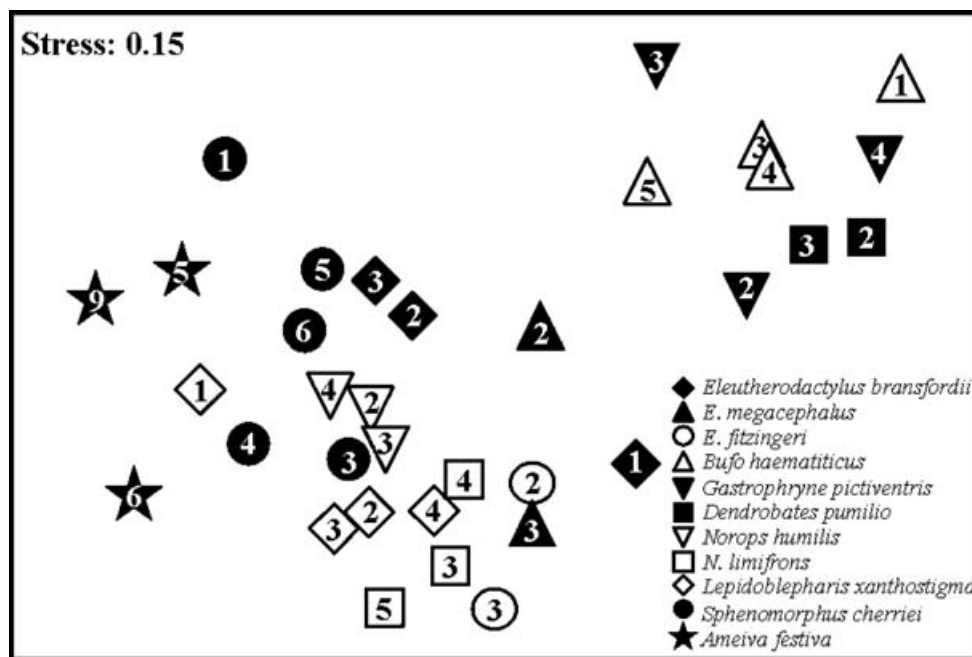
(Blattodea, Orthoptera and Araneae; Table 3). For species that had ontogenetic shifts in prey composition according to Mantel tests, correlations were generally negative for small prey types and positive for large prey types (Table 3). The species that showed significant ontogenetic shifts in prey composition were not the species characterized by

**Table 3.** Significant results of rank correlations for individual prey taxa, both for all individuals pooled regardless of species identity, and for individual species which demonstrated significant ontogenetic shifts in the results of Mantel tests.

Species	Prey taxon	Kendall's $\tau$	P
All species pooled			
	Acari	-0.24	< 0.001
	Araneae	0.12	0.005
	Blattodea	0.11	0.007
	Collembola	-0.20	< 0.001
	Formicidae	-0.17	< 0.001
	Orthoptera	0.14	< 0.001
<i>Eleutherodactylus bransfordii</i>			
	Acari	-0.33	< 0.001
	Collembola	-0.33	< 0.001
	Formicidae	-0.20	0.008
<i>E. fitzingeri</i>			
	Diptera	-0.36	0.019
	Orthoptera	0.31	0.041
<i>Bufo haematiticus</i>			
	Acari	-0.24	0.043
<i>Norops humilis</i>			
	Diptera	-0.26	0.004
	Diplopoda	-0.23	0.014

greatest variation in size over ontogeny (Figure 1), nor were they always species with the widest dietary niche breadth (Table 1).

Species varied widely in the season in which proportion of empty stomachs was the highest, but more species showed highest proportion of empty stomachs in the wet season (Table 4). Proportion of individuals with empty



**Figure 2.** MDS plot of effects of species and size on diet composition. Numbers indicate 10-mm size classes. Groupings are based upon species identity, but not upon size class.

**Table 4.** Seasonal differences in prey availability. Proportion of individuals with empty stomachs is given. Proportion of empty stomachs varied by species, but not by season.

Species	Percentage of empty stomachs			
	Dry	Transition	Wet	Total
<i>Eleutherodactylus bransfordii</i>	17.5	25.0	28.0	22.3
<i>Eleutherodactylus fitzingeri</i>	40.0	40.0	27.8	13.3
<i>Eleutherodactylus megacephalus</i>	26.3	0	31.3	25.4
<i>Bufo haematiticus</i>	10.5	5.6	37.5	2.8
<i>Gastrophryne pictiventris</i>	10.0	18.8	0	10.9
<i>Dendrobates pumilio</i>	0	0	2.0	0.8
<i>Norops humilis</i>	27.5	50.0	24.0	31.9
<i>Norops limifrons</i>	42.5	11.1	28.3	31.4
<i>Lepidoblepharis xanthostigma</i>	10.0	21.1	37.5	19.1
<i>Sphenomorphus cherriei</i>	25.0	22.0	12.5	20.4
<i>Ameiva festiva</i>	27.8	33.3	40.0	36.8

stomachs was significantly affected by species ( $\chi^2 = 72.8$ ,  $df = 10$ ,  $P < 0.001$ ), but not by season ( $\chi^2 = 1.61$ ,  $df = 2$ ,  $P = 0.464$ ); there was no interaction between species and season ( $\chi^2 = 30.1$ ,  $df = 20$ ,  $P = 0.069$ ). Only one species demonstrated a significant difference in total volume of stomach contents between seasons: *Dendrobates pumilio* showed highest stomach volume in the dry-to-wet transition, intermediate volumes in the wet season, and low stomach volume in the dry season ( $F_{2,49} = 7.30$ ,  $P = 0.002$ ). These results were supported by examination of the counts of stomach contents between seasons ( $F_{2,49} = 10.3$ ,  $P < 0.001$ ). Niche breadth did not vary significantly among seasons (Friedman Test,  $\chi^2 = 4.91$ ,  $df = 2$ ,  $P = 0.086$ ). The ANOSIM results indicated that there is no significant effect of season on prey composition (Global R = 0.022,  $P = 0.073$ ), but because ANOSIM is an exceptionally conservative test (Clarke & Gorley 2001), we suggest that this P-value is suggestive of weak shifts in seasonal prey composition.

The total proportion of individuals with empty stomachs varied strongly between species (range from 0.009 for *Dendrobates pumilio* to 0.354 for *Eleutherodactylus fitzingeri*). Lizards as a group showed a greater proportion of empty stomachs than did frogs ( $t_9 = -2.80$ ,  $P = 0.021$ ). However, when controlling for snout-vent length, lizards showed greater average stomach volume than did frogs both when empty stomachs were included in the analysis (ANCOVA,  $F_{1,766} = 23.8$ ,  $P < 0.001$ ) and when empty stomachs were excluded (ANCOVA,  $F_{1,605} = 49.3$ ,  $P < 0.001$ ). These results were maintained even when ant-eating frogs that generally show low percentages of empty stomachs were excluded from the analyses (ANCOVA,  $F_{1,408} = 39.7$ ,  $P < 0.001$ ).

## DISCUSSION

The prey taxa represented in the diets of the studied species are similar in composition to those reported for

other assemblages of terrestrial tropical amphibians and reptiles (Caldwell & Vitt 1999, Lima 1998, Lima & Magnusson 1998, Lima *et al.* 2000). Prey type was associated with prey size, and prey volumes ranged over five orders of magnitude. As in similar studies, common small prey items included ants, mites, and collembolans; mid-range prey items included opiliones, larvae, beetles and spiders; and common large prey items included isopods, millipedes, orthopterans and roaches.

## Diet ontogeny

All species increased in their use of large prey with ontogeny except for *Dendrobates pumilio*, a species characterized by specialization on small ants and mites, as well as the lowest variation in adult size of the species examined here. The strength of the relationship between variation in mean prey size and variation in body size suggests that ontogenetic shifts in prey size are likely a general phenomenon among members of terrestrial amphibian and reptile species that do show large differences in size between metamorphosis or hatching and maximum size (Figure 1).

While ontogenetic shifts in prey size were widespread, only four species showed evidence of ontogenetic change in diet composition. These individual species decreased in proportion of small prey types (ants, mites, collembolans and flies) and increased in proportion of large prey types (beetles, spiders and orthopterans). These general results are supported by correlations between body size and prey type when all species are pooled, signs of correlation coefficients in species that did not show significant ontogenetic shifts with Mantel tests, and by signs of non-significant correlation coefficients for individual prey taxa for species that did show significant ontogenetic shifts with Mantel tests. The species that did show ontogenetic shifts in prey composition were not the species showing the greatest variation in body size (Figure 1), nor were they the species with the widest dietary niche breadth. While critical conditions necessary for size-structure and passive sampling are found in this assemblage (widespread ontogenetic shifts in prey size, association between prey type and prey size), we find no evidence for either size-structure or passive sampling. Species-specific preferences in prey types thus appear to be more important than passive response to the most common prey of a given size, supporting trends detected elsewhere (Lima 1998).

Only one system to our knowledge has documented significant ontogenetic shifts in prey composition for all members of a similar assemblage, that of leaf-litter anurans in Central Amazonia (Lima 1998, Lima & Magnusson 1998). The discrepancy between the frequency of ontogenetic shifts in their study and ours

may be attributed to differences in size distributions between the species examined in these studies. The central Amazonian species conformed more closely to a single size class than do the species examined in this study. Additionally, prey taxa in the Central Amazonian studies were lumped into categories higher than orders, increasing power for determination of significant correlations. Both the central Amazonian studies and ours suggest that ontogenetic shifts in ecology can be common in assemblages that are not size-structured due to species-specific and age-specific patterns of prey preference. Additional studies that relate compositional assessments of diet to environmental availability of prey (Hodgkison & Hero 2003, Lima & Moreira 1993) will be necessary to provide more complete assessments of prey preference.

### Diet seasonality

We found no evidence of a seasonal trend in food limitation for any species as indicated by proportion of individuals with empty stomachs. Previous studies at this site have demonstrated that some leaf-litter vertebrate populations are directly limited by arthropod availability (Guyer 1988a, b), but these studies were unable to determine if the intensity of food limitation is either seasonal or relatively constant throughout the year. Studies have demonstrated that arthropod density fluctuates seasonally (Lieberman & Dock 1982, Wolda 1979), but that fluctuations are independent among arthropod taxa.

While we use presence or absence of food in the stomach as an indication of prey availability, other factors may also strongly affect presence of food in the stomach. Reproductive activities such as territorial defence, courtship or parental investment may also reduce time spent in foraging activities (Townsend 1986, Woolbright & Stewart 1987); and thus could also explain patterns in proportion of empty stomachs among seasons. Reproductive phenology of the species in this assemblage is variable, but for many species, reproduction peaks at the end of the dry season (Donnelly 1989, 1999; Watling & Donnelly 2002, Watling *et al.* 2005). Because we detected no strong patterns in seasonality of empty stomachs for most species, our data do not broadly support the hypothesis that reproductive activities are a predominant determinant of presence of food in the stomachs. The one species that did show seasonal differences in stomach volume, *Dendrobates pumilio*, plausibly reduces foraging during the wet season in order to allocate more time to elaborate mating behaviours and intensive parental care (Prohl & Hödl 1999). We conclude that there is no seasonal variation in the total availability of arthropod prey for amphibians and reptiles at La Selva.

There was only a mild effect of season on diet composition. The lack of strong differences in prey composition between seasons is not surprising for La Selva, a consistently wet forest with milder seasonality than that of many Neotropical sites which have been previously examined. Trophic niche overlap values between members of this assemblage are lowest in the dry season and peak in the wet season, with guild structure being strongest in the dry season and weakest in the wet season (S. M. Whitfield & M. A. Donnelly unpubl. data). Both of these patterns suggest seasonal shifts in diet consistent with the hypothesis that food is most limiting during the wet season. This appears to conflict with the data presented in this study, yet the two analyses are based largely upon the same data set. We suggest that this disparity can be resolved if total availability of arthropod prey is not limiting seasonally, but preferred arthropod types become seasonally less abundant. As preferred arthropod types decrease in frequency, individuals may increase consumption of less-favoured prey types. Such a pattern would be consistent with the data presented here and capable of producing seasonal shifts in prey composition.

Seasonal patterns in diet have been examined for elements of several other tropical herpetofaunas. Studies of feeding patterns show that species generally shift in prey composition seasonally (e.g. James 1991, Toft 1981, but see Magnusson & da Silva 1993, Teixeira-Filho *et al.* 2003), indicating that diet in amphibians and reptiles may track fluctuations in abundances of arthropod prey. There is less evidence that total prey availability varies seasonally, yet either the wet season (Fleming & Hooker 1975) or dry season (Hodgkison & Hero 2003, Miranda & Andrade 2003) may serve as the season of greatest prey limitation. Clearly, the response of arthropods, amphibians and reptiles to rainfall seasonality is complex and varies among precipitation regimes and a suite of other biotic and abiotic factors. Additional studies of herpetofaunal response to tropical seasonality are critical to gaining a basic understanding of population dynamics of these organisms in tropical habitats.

### Comparison of diet between frogs and lizards

There were no major differences in diet between frogs and lizards in prey composition. However, there were considerable differences in the proportion of empty stomachs and mean prey volumes between frogs and lizards. Lizards were more likely to have empty stomachs than frogs, but lizards of comparable body size had greater stomach volume than did frogs, even given the greater proportion of empty stomachs in lizards. A contrasting pattern was detected in northern Amazonia, in which frogs had greater stomach volume than lizards (Caldwell & Vitt 1999). These authors suggested a

fundamental disparity in food-gathering strategies between frogs and lizards: because frogs are limited in activity by ambient moisture, selection may have favoured larger gut capacity to allow prolonged gaps in foraging when moisture is limiting. It is plausible that this response to moisture limitation operates in the drier and more seasonal northern Amazonian site, but that in the consistently wet forests in the Caribbean lowlands of Costa Rica, moisture is less of a selective pressure affecting foraging possibilities. Alternatively, it is possible that lizards, which are more often heliothermic than frogs, have greater rates of digestion than do frogs.

We have examined interspecific variation in diet in a large sample of leaf-litter amphibians and reptiles. Our data show that ontogeny is a strong determinant of several aspects of diet (prey size, prey taxa for some species) and show that seasonality is a much less powerful determinant of diet. Because species identity is a much stronger factor than size class in the determination of diet, we find no support for the hypotheses that this assemblage is size-structured with respect to diet or that species select prey through passive sampling. Our study emphasizes that a complex of factors, including species identity, size and prey availability influence dietary patterns. Finally, a general finding of this study is the overwhelming similarity in prey use between anurans and lizards despite enormous differences in physiology, behaviour and evolutionary history.

## ACKNOWLEDGEMENTS

The specimens examined in this study were originally collected by C. F. Dock, C. S. Lieb, J. J. Talbot, and R. W. VanDevender for a project funded by NSF grant BMS 7301619A01 to J. M. Savage, I. R. Straughan, T. Philippi, M. Harvey, D. Kizirian, T. Ugarte, J. Watling, A. Catenazzi, R. Saporito, K. Ruiz, R. von May, M. Warren, K. Bell and two anonymous reviewers provided helpful comments on this manuscript. J. Savage and R. Feeney provided specimens from the Los Angeles County Museum on loan. This work was completed as partial fulfillment for the degree of M.S. in Biology from Florida International University.

## LITERATURE CITED

BEARD, K. H., ESCHTRUTH, A. K., VOGT, K. A., VOGT, D. J. & SCATENA, F. N. 2003. The effects of the frog *Eleutherodactylus coqui* on invertebrates and ecosystem processes at two scales in the Luquillo Experimental Forest, Puerto Rico. *Journal of Tropical Ecology* 19:607–617.

CALDWELL, J. P. & VITT, L. J. 1999. Dietary asymmetry in leaf litter frogs and lizards in a transitional northern Amazonian rain forest. *Oikos* 84:383–397.

CHASE, J. M., ABRAMS, P. A., GROVER, J. P., DEIHL, S., CHESSON, P., HOLT, R. D., RICHARDS, S. A., NISBET, R. M. & CASE, T. J. 2002. The interaction between predation and competition: a review and synthesis. *Ecology Letters* 5:302–315.

CLARKE, K. R. & GORLEY, R. N. 2001. *Primer v5: User Manual/Tutorial*. Primer-E, Ltd., Plymouth. 91 pp.

DIAZ, J. A. & CARRASCAL, L. M. 1990. Prey size and food selection of *Psammodrammus algirus* (Lacertidae) in central Spain. *Journal of Herpetology* 24:342–347.

DONNELLY, M. A. 1989. Reproductive phenology and age structure of *Dendrobates pumilio* in northeastern Costa Rica. *Journal of Herpetology* 23:362–367.

DONNELLY, M. A. 1991. Feeding patterns of the Strawberry Poison Frog, *Dendrobates pumilio* (Anura: Dendrobatidae). *Copeia* 1991:723–730.

DONNELLY, M. A. 1999. Reproductive phenology of *Eleutherodactylus brodfordii* in northeastern Costa Rica. *Journal of Herpetology* 33:624–631.

FLEMING, T. H. & HOOKER, R. S. 1975. *Anolis cupreus*: the response of a lizard to tropical seasonality. *Ecology* 56:1243–1261.

GUYER, C. 1988a. Food supplementation in a tropical mainland anole, *Norops humilis*: demographic effects. *Ecology* 69:350–361.

GUYER, C. 1988b. Food supplementation in a tropical mainland anole, *Norops humilis*: effects on individuals. *Ecology* 69:362–369.

GUYER, C. 1990. The herpetofauna of La Selva, Costa Rica. Pp. 371–385 in Gentry, A. H. (ed). *Four neotropical forests*. Yale University Press, New Haven.

GUYER, C. & DONNELLY, M. A. 2005. *Amphibians and reptiles of La Selva, Costa Rica, and the Caribbean Slope*. University of California Press, Berkeley. 420 pp.

HODGKISON, S. & HERO, J.-M. 2003. Seasonal, sexual and ontogenetic variations in the diet of the 'declining' frogs *Litoria nanotis*, *Litoria rheocola* and *Nyctimystes dayi*. *Wildlife Research* 30:345–354.

HUEY, R. B. & PIANKA, E. R. 1981. Ecological consequences of foraging mode. *Ecology* 62:991–999.

JAMES, C. D. 1991. Temporal variation in diets and trophic partitioning by coexisting lizards (*Ctenotus*: Scincidae) in central Australia. *Oecologia* 85:553–361.

LEIGH, E. G., RAND, A. S. & WINDSOR, D. M. 1982. *The ecology of a tropical forest: seasonal rhythms and long-term changes*. Smithsonian Institution Press, Washington, DC. 468 pp.

LIEBERMAN, S. S. 1986. Ecology of the leaf litter herpetofauna of a neotropical rain forest: La Selva, Costa Rica. *Acta Zoologica Mexicana* (ns) 15:1–72.

LIEBERMAN, S. S. & DOCK, C. F. 1982. Analysis of the leaf litter arthropod fauna of a lowland tropical evergreen forest sites (La Selva, Costa Rica). *Revista Biología Tropical* 30:27–34.

LIMA, A. P. 1998. The effects of size on the diets of six sympatric species of postmetamorphic litter anurans in Central Amazonia. *Journal of Herpetology* 32:392–399.

LIMA, A. P. & MAGNUSSON, W. E. 1998. Partitioning seasonal time: interactions among size, foraging activity, and diet in leaf-litter frogs. *Oecologia* 116:259–266.

LIMA, A. P. & MOREIRA, G. 1993. Effects of prey size and foraging mode on the ontogenetic change in feeding niche of *Colostethus stepheni* (Anura: Dendrobatidae). *Oecologia* 95:93–102.

- LIMA, A. P., MAGNUSSON, W. E. & WILLIAMS, D. G. 2000 Differences in diet among frogs and lizards coexisting in subtropical forests of Australia. *Journal of Herpetology* 34:40–46.
- MAGNUSSON, W. E. & DA SILVA, E. V. 1993. Relative effects of size, season, and species on the diets of some Amazonian savanna lizards. *Journal of Herpetology* 27:380–385.
- MAGNUSSON, W. E., LIMA, A. P., FARIA, A. S., VICTORIA, R. L. & MARTINELLI, L. A. 2001. Size and carbon acquisition in lizards from Amazonian savanna: evidence from isotope analysis. *Ecology* 82:1772–1780.
- McDADE, L. A. & HARTSHORN, G. S. 1994. La Selva Biological Station. Pp. 6–14 in McDade, L., Bawa, K. S., HESPENHEIDE, H. A. & HARTSHORN, G. S. (eds). *La Selva: ecology and natural history of a neotropical rainforest*. University of Chicago Press, Chicago.
- MIRANDA, J. P. & ANDRADE, G. V. 2003. Seasonality in diet, perch use, and reproduction of the gecko *Gonatodes humeralis* from eastern Brazilian Amazon. *Journal of Herpetology* 37:433–438.
- PIANKA, E. R. 1986. *Ecology and natural history of desert lizards*. Princeton University Press, Princeton. 208 pp.
- POLIS, G. A. 1984. Age structure component of niche width and intra-specific resource partitioning: can age groups function as ecological species? *Ecology* 123:541–564.
- PROHL, K. & HÖDL, W. 1999. Parental investment, potential reproductive rates, and mating system in the strawberry dart-poison frog, *Dendrobates pumilio*. *Behavioral Ecology and Sociobiology* 46:215–220.
- SANFORD, R. L., PAABY, P., LUVALL, J. C. & PHILLIPS, E. 1994. Climate, geomorphology, and aquatic systems. Pp. 19–33 in McDade, L., Bawa, K. S., HESPENHEIDE, H. A. & HARTSHORN, G. S. (eds). *La Selva: ecology and natural history of a neotropical rainforest*. University of Chicago Press, Chicago.
- SCOTT, N. J. 1976. The abundance and diversity of the herpetofaunas of tropical forest litter. *Biotropica* 8:41–58.
- SIMPSON, G. 1949. Measurement of diversity. *Nature* 163:688.
- STEPHENS, D. W. & KREBS, J. R. 1986. *Foraging theory*. Princeton University Press, Princeton. 262 pp.
- TEIXEIRA-FILHO, P. F., ROCHA, C. F. D. & RIBAS, S. C. 2003. Relative feeding specialization may depress ontogenetic, seasonal, and sexual variations in diet: the endemic lizard *Cnemidophorus littoralis* (Teiidae). *Brazilian Journal of Biology* 63:321–328.
- TOFT, C. A. 1981. Feeding ecology of Panamanian litter anurans: patterns in diet and foraging mode. *Journal of Herpetology* 15:139–144.
- TOWNSEND, D. S. 1986. The costs of male parental care and its evolution in a neotropical frog. *Behavioral Ecology and Sociobiology* 19:187–195.
- WATLING, J. I. & DONNELLY, M. A. 2002. Seasonal patterns of reproduction and abundance of leaf litter frogs in a Central American rainforest. *Journal of Zoology* 258:269–276.
- WATLING, J. I., WADDLE, H., KIZIRIAN, D. & DONNELLY, M. A. 2005. Reproductive phenology of three lizard species in Costa Rica, with comments on seasonal reproduction of Neotropical lizards. *Journal of Herpetology* 39:341–348.
- WERNER, E. E. & GILLIAM, J. F. 1984. The ontogenetic niche and species interactions in size-structured populations. *Annual Review of Ecology and Systematics* 15:393–425.
- WOLDA, H. 1979. Seasonal fluctuations in abundance of tropical insects. *American Naturalist* 112:1017–1045.
- WOOLBRIGHT, L. L. & STEWART, M. M. 1987. Foraging success of the tropical frog, *Eleutherodactylus coqui*: the cost of calling. *Copeia* 1987:69–75.