Journal of Herpetology, Vol. 40, No. 3, pp. 388–394, 2006

Ontogenetic Diet Change in the Arthroleptid Frog *Schoutedenella xenodactyloides*

David C. Blackburn[1,2] and Corrie S. Moreau[3]

[1]*Department of Herpetology, Museum of Comparative Zoology, Harvard University, Cambridge, Massachussetts 02138, USA; E-mail: dblackb@fas.harvard.edu*
[3]*Department of Entomology, Museum of Comparative Zoology, Harvard University, Cambridge, Massachussetts 02138, USA*

Abstract.—**Anuran amphibians are important consumers of arthropods in tropical ecosystems. Previous research has indicated that very small, terrestrial frogs, especially juveniles, largely consume small leaf litter arthropods. To date, few studies have examined diet in African anurans, and no studies exist of ontogenetic change in prey composition for any African frog. We investigated the change in diet that accompanies body size increase in the arthroleptid frog *Schoutedenella xenodactyloides* (Anura: Ranoidea) from a population located on the Mulanje Massif in Malawi, central Africa. *Schoutedenella xenodactyloides* is a miniature (< 22 mm snout–urostyle length; SUL), direct-developing frog that is often very abundant and is likely an important consumer of small leaf litter arthropods. Based on examination of stomach and intestinal contents from specimens that span the known range of posthatching body sizes, we document the taxonomic diversity of prey consumed by *S. xenodactyloides*. We present evidence that *S. xenodactyloides* exhibits a size-related ontogenetic change in the type and relative proportions of prey taxa. Small frogs (≤ 13 mm SUL) consume large numbers of collembolans and mites. As frogs attain larger body sizes; ants constitute a larger percentage of the total number of prey consumed; and collembolan and mite consumption falls below 10% of the total prey items. The prey consumed by *S. xenodactyloides* include at least 10 orders of arthropods and an unidentified mollusk. This is a greater diversity of prey items than previously found in *Schoutedenella* as well as most other arthroleptid species.**

The ranoid frog family Arthroleptidae, comprising 50 species in three genera, is restricted to sub-Saharan Africa; most species are largely terrestrial. The genus *Schoutedenella* consists of miniaturized species all of which are believed to hatch as froglets directly from terrestrial eggs (i.e., direct development). *Schoutedenella xenodactyloides* is a small (< 22 mm snout–urostyle length; SUL) arthroleptid frog found throughout much of central, eastern, and southeastern Africa. It is found in the leaf litter in moist forest habitats and grassland swamps and is often extremely abundant. The species occurs throughout the Eastern Arc Mountains in Tanzania and southern Kenya and in portions of Zimbabwe, Zambia, Malawi, and Mozambique (Channing, 2001). Several subspecies have been erected for this species based largely on coloration and pattern (Loveridge, 1942, 1953), but the validity of these taxa has not been thoroughly addressed.

Although arthroleptid frogs are typically common components of the anuran leaf litter fauna in sub-Saharan Africa, the ecology of these frogs is poorly known (for an exception, see Barbault and Rodrigues, 1979). The diet of arthroleptid frogs has received little attention even though they and other African anurans are likely important consumers of arthropods. All previous studies examining stomach and intestinal contents of arthroleptids have focused exclusively on adult diet composition; there is great variation in the composition of prey taxa found by these studies. The majority of these studies found only one to three prey taxa represented (Noble, 1924; Barbour and Loveridge, 1928, 1930; Loveridge, 1942, 1953; Toft, 1982), whereas others found many (> 12) taxa present (e.g., Inger and Marx, 1961).

Ontogenetic diet change in prey type in postmetamorphic anuran amphibians has been investigated in a number of species, mostly in the Neotropics (Donnelly, 1991; Lima and Moreira, 1993; Giaretta et al., 1998; Lima, 1998; Van Sluys et al., 2001) but also in temperate North America (Flowers and Graves, 1995), Europe (Tyler, 1958) and Japan (Hirai, 2002). Because of the often significant difference between the diets of adults and small juveniles, these studies have revealed that understanding ontogenetic changes in prey type is necessary to accurately assess the interactions of an anuran species with other taxa in the faunal community (e.g., Lima and Moreira, 1993; Lima, 1998). Size-related differences in diet have been examined in African anurans in two previous studies, but neither examined ontogenetic changes in prey consumption (Lescure, 1971; Luiselli et al., 2004). In general, few studies exist of the diet composition of African frogs, and none examines ontogenetic change in prey type (e.g., Inger and Marx, 1961; Lescure, 1971; Barbault, 1974; Toft, 1982; Eniang et al., 2003; Luiselli et al., 2004).

Our aims in this study are twofold. First, we document the diet composition of *S. xenodactyloides* across the range of posthatching body sizes to determine the taxonomic range of prey consumed. Second, we investigate whether changes in the type and relative proportions of prey occur during ontogeny (i.e, with increasing body size). This is the first study of ontogenetic change in prey composition of an African frog.

Materials and Methods

All specimens were collected under low-lying vegetation (generally less than 15 cm high) near the swimming hole upstream from the Ruo River Gorge

[2]Corresponding Author.

Hydroelectric Station on the Mulanje Massif in southern Malawi on 17 January 2005 (elevation approximately 1000 m). Both juveniles and adults of *S. xenodactyloides* were extremely abundant. All specimens were collected during the day between 1000 and 1400 h and were active in the leaf litter (average temperature in the shade: 23°C).

All specimens were preserved in 10% neutral-buffered formalin overnight and then stored in 70% ethanol. Specimens are deposited in the Museum of Comparative Zoology (MCZ) at Harvard University. SUL, measured from the snout tip to the most caudal tip of the urostyle, was measured to the nearest 0.1 mm under a dissecting microscope using digital calipers. These specimens were collected primarily for use in a study of posthatching skeletal development and as such data on foraging behavior, and the relative abundance of prey in the leaf litter were not collected. The 26 specimens examined, all of which contained prey items, range from 5.8 mm SUL to adult size (males: 14.9–15.4 mm; females: 16.2–16.9 mm). The mean SUL of adults of this population collected in January 2005 are as follows: males, 15.2 ± 0.4 mm (MCZ 137001, 137003, 137014); females, 16.7 ± 0.9 mm (MCZ 137000, 137004–013, 137015, 137034–037, 137074). Sex and maturity of adult specimens were determined via examination of gonads and other secondary sexual structures. Adult males exhibit distended gular skin, darkly pigmented testes, and an hypertrophied third finger, lined with small spines, that is typical of most mature male arthroleptid frogs. Adult females studied exhibit large ova (1.3–1.6 mm) and well-developed fat bodies.

The stomach and intestine were removed and preserved in 70% ethanol. The alimentary tract of each specimen was dissected under a dissecting microscope and the contents were examined to determine the prey taxa present and number of specimens thereof. If specimens were disarticulated, we established the minimum number of individuals present. For instance, we counted four ants present in a *S. xenodactyloides* specimen that contained three head capsules, one mesothorax, and four gasters. In some cases, it was difficult to identify the gut contents to the level of order; these are listed as ''unidentified'' arthropods or mollusks.

Statistical analysis, including correlation coefficients (Pearson's *r*), was performed using SPSS version 11.0.4 (SPSS Inc., Chicago, IL). Significance was assessed based on $\alpha = 0.05$.

Results

All 26 specimens examined contained prey in the stomach or intestine. The number of prey present ranges from 1–59. The number of prey consumed exhibits a significant negative trend in that larger specimens contain fewer prey ($r = -0.48$, $P = 0.007$; Fig. 1A). Ten arthropod orders and one unidentified mollusk are represented in the prey consumed by these specimens with springtails (Collembola), ants (Hymenoptera: Formicidae), and mites (Chelicerata: Acari) constituting the majority of prey items (Table 1). The majority of other identifiable prey items are coleopteran larvae and adults; other prey taxa are represented by only one or two specimens.

Consumption of springtails, ants, and mites changes with increasing SUL. For ease of discussion, specimens of *S. xenodactyloides* are placed into three size categories: 5.0–9.0 mm SUL, 9.1–13.0 mm SUL, and 13.1–17.0 mm SUL (Table 1). Specimens in the largest size category are all sexually mature adults. As *S. xenodactyloides* attains larger body sizes, it consumes fewer springtails ($r = -0.49$, $P = 0.006$; Fig. 1B) and mites ($r = -0.62$, $P < 0.001$; Fig. 1C) and more ants ($r = 0.74$, $P < 0.001$; Fig. 1D). Springtails occur in 70% of the specimens of the smallest size category and represent as much as 85% of the total prey consumed by a particular individual. No springtail was found in any of six adult specimens. Of the prey items consumed by the two smallest categories, mites constitute approximately 30% of the prey consumed and were found in 18 of the 20 individuals. A single mite was found in three adults; mites constitute only 6% of the total prey items consumed by this largest size category.

At least seven genera of ants are consumed by *S. xenodactyloides* at this locality. Thirty-seven of the 118 ants are identified to genus: *Anochetus* (7), *Crematogaster* (3), *Oligomyrmex* (12), *Pyramica* (9), *Solenopsis* (3), *Strumigenys* (2), and *Tapinoma* (1). In general, these are all small ants found in leaf litter. Ants were found in nearly all specimens (24 of 26), and there is a positive correlation between body size and the number of ants consumed relative to other prey items (Fig. 1D). With increasing body size, ants comprise a larger proportion of the total prey items consumed. Ants represent only 8.3% of the total prey items found in the smallest size category. Ants constitute 0–80% of the prey consumed by specimens in the 9.1–13.0 mm category and represent 48.4% of the total prey consumed by this group. Ants comprise the majority (50–90%) of the total prey items consumed by each adult.

Discussion

The diet of *S. xenodactyloides* is largely consistent with those of other small terrestrial anurans that inhabit leaf litter. Ants, coleoptera, and mites have all been found previously to play an important role in the diet of small leaf litter anurans (e.g., Barbault, 1974; Donnelly, 1991; Toft, 1980; Simon and Toft, 1991). Although springtails have been reported less often (Simon and Toft, 1991; Lima and Moreira, 1993), this may be because very small juvenile stages are not frequently examined in studies of diet.

Previous dietary studies of arthroleptid frogs have found that termites, beetles, ants, and orthopterans, such as crickets and roaches, are the most common prey (Table 2). Aside from these prey, several studies have found arthroleptids to consume a wide range of taxa including mollusks, myriapods, earwigs, earthworms, and even another anuran (Noble, 1924; Inger and Marx, 1961; Barbault, 1974). Only two previous studies have noted mites in the diet of arthroleptid species. Barbault (1974) found that mites constituted a very small percentage (0.5%) of the total prey items consumed by *Arthroleptis poecilonotus*. The study by Inger and Marx (1961) of *Arthroleptis stenodactylus* also reported mites and is the only previous study of arthroleptid diet to find springtails. However, these resumably represent very few of the total prey

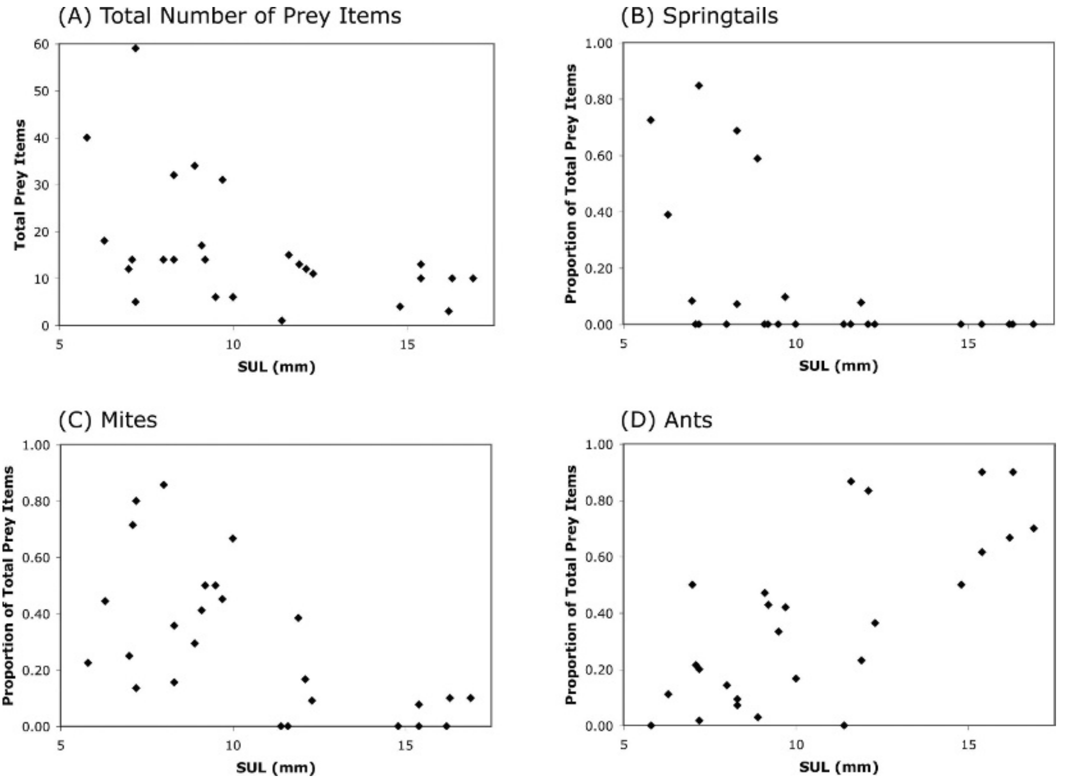

FIG. 1. Ontogenetic diet change in *Schoutedenella xenodactyloides*. Results are plotted against snout–urostyle length. (A) Total number of prey items; proportion of total prey items represented by (B) springtails (Collembola), (C) mites (Acari), and (D) ants (Formicidae).

items found as Inger and Marx (1961) do not report the number of specimens found of either taxon.

Ants are a typical component of arthroleptid diet (Table 2), as they are in many other anuran taxa (e.g., Barbault, 1974; Toft, 1980; Donnelly, 1991; Eniang et al., 2003). Although ants are often among the most abundant prey items, several studies of arthroleptid diet have either not found ants or found that they represent only a small percentage of the total prey consumed (Noble, 1924; Barbour and Loveridge, 1928, 1930; Loveridge, 1942). Interestingly, one study of *A. stenodactylus* found ants to constitute the majority of prey items, whereas no ants were found in two others (Table 2). It remains to be seen whether this discrepancy is a function of differences in season, locality, body size, or actual differences in the ecology of these populations. Of the five ant genera identified by Barbault (1974) in his study of *A. poecilonotus*, only two (*Crematogaster* and *Strumigenys*) were found in our study of *S. xenodactyloides*. We did not find the two genera most frequently found by Barbault, *Pheidole* and *Tetramorium*, but both occur at this locality since they were found among the prey items consumed by a sympatric *Bufo* sp. juvenile.

Very small juveniles of two taxa sympatric with *S. xenodactyloides* were collected at the same time as the specimens examined in this study. In a specimen of *Bufo* sp. (8.5 mm SUL), six ants (*Pheidole* and *Tetramorium*) and one beetle were found. A specimen of *A. stenodactylus* (9.1 mm SUL) contained one coleopteran larva, one fly, two unidentified ants, one wasp, and one unidentified arthropod. Given the many springtails and mites, especially the latter, consumed by small *S. xenodactyloides*, it is notable that springtails and mites were not found in either of these two small juveniles of other sympatric species. A similar proportion of ants found in *Bufo* sp. is not found in similarly sized *S. xenodactyloides*. In fact, the relative proportion of ants exceeded 80% in only four of the *S. xenodactyloides* specimens examined, two of which were adults. Although these are interesting differences, further research incorporating more specimens of other sympatric species is obviously needed.

It is difficult to interpret the prey composition of *S. xenodactyloides* found in our study in the light of previous studies of the diet of *Schoutedenella*. Barbour and Loveridge (1928) examined stomach contents of specimens assigned to *Schoutedenella sylvatica* (MCZ 13168–72) and *S. xenodactylus* (MCZ 13173–210). Most of their specimens, however, are misidentified; MCZ 13168–72 are referrable to *S. xenodactylus*, whereas MCZ 13170–210 represent both *S. xenodactylus* and *S. xenodactyloides* (Table 2). Barbour and Loveridge (1928) did not indicate

TABLE 1. Dietary analysis of 26 specimens of *Schoutedenella xenodactyloides*, which span the entire post-hatching size range for this population. Data are separated into three frog size categories: 5.0–9.0 mm snout–urostyle length (SUL; 10 specimens), 9.1–13.0 mm SUL (10 specimens), and 13.1–17.0 mm SUL (six specimens). Results are presented as the number of prey items of each taxon (also expressed as the percent of the total sample represented by this number) and the frequency at which each taxon was found (also expressed as the percent of specimens in which the taxon occured).

	Number			Frequency		
Prey Item	5.0–9.0 mm	9.1–13.0 mm	13.1–17.0 mm	5.0–9.0 mm	9.1–13.0 mm	13.1–17.0 mm
ARTHROPODA						
Insecta						
Coleoptera						
larva	7 (2.9%)	4 (3.2%)	1 (2.0%)	5 (50%)	4 (40%)	1 (17%)
adult		2 (1.6%)	3 (6.0%)		2 (20%)	3 (50%)
Collembola	130 (53.7%)	4 (3.2%)		7 (70%)	2 (20%)	
Crustacea	1 (0.4%)	1 (0.8%)		1 (10%)	1 (10%)	
Diptera	1 (0.4%)	1 (0.8%)		1 (10%)	1 (10%)	
Hemiptera		1 (0.8%)	1 (2.0%)		1 (10%)	1 (17%)
Hymenoptera						
Formicidae	20 (8.3%)	61 (48.4%)	37 (74.0%)	9 (90%)	9 (90%)	6 (100%)
'wasps'		1 (0.8%)	1 (2.0%)		1 (10%)	1 (17%)
Orthoptera			1 (2.0%)			1 (17%)
Thysanoptera		1 (0.8%)			1 (10%)	
unidentified						
juvenile	2 (0.8%)	1 (0.8%)	3 (6.0%)	2 (20%)	1 (10%)	2 (33%)
adult	5 (2.1%)	3 (2.4%)		2 (20%)	3 (30%)	
Chelicerata						
Acari	74 (30.6%)	43 (34.1%)	3 (6.0%)	10 (100%)	8 (80%)	3 (50%)
Araneae		1 (0.8%)			1 (10%)	
unidentified		2 (1.6%)			2 (20%)	
MOLLUSCA						
unidentified	2 (0.8%)			1 (10%)		
Totals:	242 (100%)	126 (100%)	50 (100%)	—	—	—

which prey items were found in which specimens of the MCZ 13170–210 series; thus, the prey taxa listed by them, ants in one specimen and amphipod crustaceans in two others, may have come from either species. Toft (1982) found that 85% of total prey items consumed by *S. sylvatica* were termites, whereas only 10% were ants. Although ants are abundant year round, comparisons between our study and Toft's should be made with caution because both studies are based on material from very narrow time frames in different seasons (this study: rainy season; Toft [1982]: dry season). Since we have no knowledge of the relative abundance of prey taxa in the leaf litter at these different localities, it is impossible to know whether the electivity for the prey items consumed differs between these two *Schoutedenella* species.

In this study of *S. xenodactyloides*, we have found that the consumption of mites, springtails, and ants changes significantly with increasing body size. Mites and springtails are known to be important components of the diet of very small frogs. Recently metamorphosed frogs of some species consume large quantities of springtails (e.g., Tyler, 1958; Lima and Moreira, 1993), whereas mites figure largely in the diets of small juveniles of various anurans (e.g., Donnelly, 1991; Simon and Toft, 1991; Lima and Moreira, 1993; Van Sluys et al., 2001). Lima and Moreira (1993) found that ontogenetic change in mite, and springtail consumption in the dendrobatid *Colostethus stepheni* is caused by an ontogenetic change in electivity for prey type that is independent of electivity for prey size. In a separate study, Lima and Magnusson (2000) demonstrated that ontogenetic changes in diet are not always sufficiently explained by changes in foraging mode. Similar to the results presented here, Lima and Magnusson's (1998) study of seven Brazilian frog species found that as body size increases mites and springtails represent proportionally less of the total mass of prey items, whereas the proportion of ants increases. The ontogenetic changes in prey consumption in *S. xenodactyloides* may be caused by a change in electivity of prey type or possibly some difference in foraging mode, but it is not possible to test these hypotheses with the currently available data. Because most prey items in our analysis are disarticulated, ontogenetic change in the size of prey consumed cannot be analyzed. However, it is clear that changes in body size in *S. xenodactyloides* are associated with significant change in both prey type (e.g., springtails) and relative proportions of certain prey types consumed (e.g., mites and ants).

In direct-developing anurans, growth prior to hatching is limited by the amount of yolk with which each egg is provisioned. This necessarily

TABLE 2. Summary of studies of diet in arthroleptid frogs including this study. In several studies, the number of specimens examined is unknown; in these cases, the maximum number of specimens collected is the upperbound of specimens examined. If numerical data or relatively quantities were provided by the authors, the prey taxa are ordered by their predominance in the diet. If known, the country and month(s) in which the specimens were collected are noted. The results of our study of *Schoutedenella xenodactyloides* are summarized in the same three body size categories that are used in the text.

Species	# Specimens	Country	Month(s)	Diet	Author
Arthroleptis adolfifriederici	1	Dem. Rep. Congo	unknown	Coleoptera (unidentified larvae and adult curculionid) > Myriapoda	Barbour and Loveridge (1930)
*Arthroleptis affinis**	8	Tanzania	Sept–Dec	Orthoptera > Lepidoptera = Araneae > Formicidae = Crustacea	Barbour and Loveridge (1928)
Arthroleptis poecilonotus	1	Dem. Rep. Congo	July, Oct	Formicidae > ?Coleoptera larva	Noble (1924)
Arthroleptis poecilonotus	151	Ivory Coast	Mar–Nov	Formicidae > Isoptera > Coleoptera > Araneae > Dermaptera > Myriapoda > Mollusca > Acari > Hemiptera	Barbault (1974)
Arthroleptis stenodactylus	10	Tanzania	Sept–Dec	Orthoptera > Coleoptera > Myriapoda > Araneae = Mollusca	Barbour and Loveridge (1928)
Arthroleptis stenodactylus	215	Dem. Rep. Congo	Jan–Mar, Nov	Formicidae > Isoptera > Orthoptera > Coleoptera > Araneae > Oligochaeta > Lepidoptera > Myriapoda > Hemiptera > Isopoda > Diptera > Amphibia	Inger and Marx (1961)
Arthroleptis stenodactylus	unknown (< 33)	Kenya & Tanzania	Mar–Apr, June–July	Formicidae, Coleoptera	Loveridge (1942)
Arthroleptis stenodactylus	unknown (< 44)	Malawi	Mar, Aug, Oct, Dec	Orthoptera	Loveridge (1953)
Arthroleptis variabilis	17	Dem. Rep. Congo	Feb–July, Sept–Nov	Isoptera > Formicidae > Mollusca (*Helixarion*) = Lepidoptera > Orthoptera > Araneae > Myriopoda = Coleoptera	Noble (1924)
Cardioglossa gracilis	1	Dem. Rep. Congo	Sept	Formicidae	Noble (1924)
Cardioglossa leucomystax	3	Dem. Rep. Congo	Feb–Mar, June, Sept	Isoptera	Noble (1924)
Cardioglossa leucomystax	2	Gabon	Oct–Nov	Isoptera > 'miscellaneous arthropods' > Formicidae	Toft (1982)
Schoutedenella sylvatica	17	Gabon	Oct–Nov	Isoptera > Formicidae > 'miscellaneous arthropods' > Orthoptera	Toft (1982)
*Schoutedenella xenodactylus**	1	Tanzania	Sept	Orthoptera	Barbour and Loveridge (1928)
Schoutedenella xenodactylus and *Schoutedenella xenodactyloides**	3	Tanzania	Sept–Dec	Formicidae, Crustacea (Amphipoda)	Barbour and Loveridge (1928)
S. xenodactyloides (5.0–9.0 mm)	10	Malawi	Jan	Collembola > Acari > Formicidae > Coleoptera (larvae) > Mollusca > Crustacea = Diptera	This study
S. xenodactyloides (9.1–13.0 mm)	10	Malawi	Jan	Formicidae > Acari > Coleoptera (larvae) = Collembola > Coleoptera (adult) > Crustacea = Diptera = Hemiptera = 'wasps' = Thysanoptera = Araneae	This study
S. xenodactyloides (13.1–17.0 mm)	3	Malawi	Jan	Formicidae > Coleoptera (adult) = Acari > Coleoptera (larvae) = Hemiptera = 'wasps' = Orthoptera	This study

*Species redetermined by DCB through examination of specimens.

means that hatchling froglets will be very small. Previous studies have not observed springtails as a component of arthroleptid diet and only a few have found mites to play even a minor role in diet. However, based on the small size of hatchling froglets, we predict that future work on ontogenetic diet change in arthroleptids will find that very small juveniles rely heavily on small arthropods such as springtails and mites.

Studies of prey consumption based on only a single ontogenetic stage can be very misinformed. As we have found in *S. xenodactyloides*, the taxonomic composition and relative proportions of prey taxa in the diet are markedly different between small juveniles and adults. Future work on arthroleptid diet composition should focus on common species such as *A. stenodactylus* to determine whether differences observed by previous studies are the result of seasonal and ontogenetic changes, differences in habitat, or population-level differences in electivities for certain prey items. Further study of the role of small arthropods, such as mites and springtails, in the diet of terrestrial anurans is important for better understanding trophic relationships in African ecosystems.

Acknowledgments.—We thank N. Gawani and L. Mazibuko (Museums of Malawi—Blantyre) and B. Zimkus (MCZ—Harvard) for assistance in fieldwork and logistics in Malawi. Fieldwork was funded by a Putnam Expeditionary Grant (to DCB) from the Museum of Comparative Zoology (Harvard). We acknowledge C. Feldman (Utah State University) for encouraging one of us (CSM) to be interested in the diets of reptiles and amphibians. We thank J. Hanken and W. B. Jennings for providing valuable comments on this manuscript.

Literature Cited

Barbault, R. 1974. La régime alimentaire des amphibiens de la savane de Lamto. Bulletin de l'Institute français d'Afrique noire. Série A, Sciences naturelles 36:952–972.

Barbault, R., and M. T. Rodrigues. 1979. Observations sur la reproduction et la dynamique des populations de quelques anoures tropicaux. III. *Arthroleptis poecilonotus*. Tropical Ecology 20:64–77.

Barbour, T., and A. Loveridge. 1928. A comparative study of the herpetological faunae of the Uluguru and Usambara Mountains, Tanganyika Territory with descriptions of new species. Memoirs of the Museum of Comparative Zoology 50:87–265.

———. 1930. Reptiles and amphibians from the Central African Lake Region. *In* Report of the Harvard-African Expedition upon the African Republic of Liberia and the Belgian Congo, pp. 786–796. Harvard University Press, Cambridge, MA.

Channing, A. 2001. Amphibians of Central and Southern Africa. Cornell University Press, Ithaca, NY.

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

Eniang, E. A., R. King, J. Lea, D. Capizzi, and L. Luiselli. 2003. Trophic niches of four sympatric rainforest anurans from southern Nigeria: does resource partitioning play a role in structuring the community? Revue d'Écologie (La Terre et la Vie) 58:321–335.

Flowers, M. A., and B. M. Graves. 1995. Prey selectivity and size-specific diet changes in *Bufo cognatus* and *B. woodhousii* during early postmetamorphic ontogeny. Journal of Herpetology 29: 608–612.

Giaretta, A. A., M. S. Araújo, H. F. de Medeiros, and K. G. Facure. 1998. Food habits and ontogenetic diet shifts of the litter dwelling frog *Proceratophrys boiei* (Wied). Revista brasileira de zoologia 15: 385–388.

Hirai, T. 2002. Ontogenetic change in the diet of the pond frog, *Rana nigromaculata*. Ecological Research 17:639–644.

Inger, R., and H. Marx. 1961. The food of amphibians. exploration du Parc National de l'Upemba 64:1–86.

Lescure, J. 1971. L'alimentation du crapaud *Bufo regularis* Reuss et de la grenouille *Dicroglossus occipitalis* (Günther) au Sénégal. Bulletin de l'Institute français d'Afrique noire. Série A, Sciences naturelles 33:446–466.

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

Lima, A. P., and W. E. Magnusson. 2000. Does foraging activity change with ontogeny? An assessment for six sympatric species of postmetamorphic litter anurans in central Amazonia. Journal of Herpetology 34:192–2000.

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

Loveridge, A. 1942. Scientific results of a fourth expedition to forested areas in East and Central Africa. V. Amphibians. Bulletin of the Museum of Comparative Zoology 91:377–436.

———. 1953. Zoological results of a fifth expedition to East Africa. IV. Amphibians from Nyasaland and Tete. Bulletin of the Museum of Comparative Zoology 110:325–406.

Luiselli, L., L. Bikokoro, E. Odegbune, S. M. Wariboko, L. Rugiero, G. C. Akani, and E. Politano. 2004. Feeding relationships between sympatric Afrotropical tree frogs (genus *Hyperolius*): the effects of predator body size and season. Animal Biology 54:293–302.

Noble, G. K. 1924. Contributions to the herpetology of the Belgian Congo based on the collection of the American Museum Congo Expedition, 1905–191. Part III. Amphibia. Bulletin of the American Museum of Natural History 49:147–347.

Simon, M. P., and C. A. Toft. 1991. Diet specialization in small vertebrates: mite-eating in frogs. Oikos 61:263–278.

Toft, C. A. 1980. Feeding ecology of thirteen syntopic species of anurans in a seasonal tropical environment. Oecologia 45:131–141.

———. 1982. Community structure of litter anurans in a tropical forest, Makokou, Gabon: a preliminary analysis in the minor dry season. Revue d'Écologie (La Terre et la Vie) 36:223–232.

Tyler, M. J. 1958. On the diet and feeding habits of the Edible Frog (*Rana esculenta* Linnaeus). Proceedings of the Zoological Society of London 131: 583–595.

Van Sluys, M., C. F. D. Rocha, and M. B. Souza. 2001. Diet, reproduction, and density of the leptodactylid litter frog *Zachaenus parvulus* in an Atlantic rain forest of southeastern Brazil. Journal of Herpetology 35:322–325.

Accepted: 4 May 2006.