

Feeding ecology of *Elachistocleis bicolor* in a riparian locality of the middle Paraná River

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Elachistocleis bicolor is a poorly known South American microhylid frog. Although it has been claimed to be an ant specialist, there have been no detailed studies of ontogenetic diet change and prey selectivity in this species. We analysed the diet of 114 individuals of this frog through the post-metamorphic ontogeny. We also studied the anurans' morphometric relationships to prey size, and compared diet with prey availability, estimating predation tactics. All prey categories were consumed out of proportion relative to their availability in the environment. The results suggest that the three stages of *E. bicolor* are selective foragers with a strong preference for ants, although the prey spectrum includes other taxa. The diet of subadults was more similar to that of juveniles, and had the widest diet overlap. Juveniles ate smaller prey, and this could be reducing food competition with older stages. Although the three stages are selective ant foragers, as frogs grow up, there is a partial and gradual change in prey category captured.

Key words: Anura, diet specialization, Formicidae, ontogenetic diet change, Microhylidae, prey availability

INTRODUCTION

Empirical evidence suggests that feeding relationships within anuran assemblages vary seasonally while population structure changes as juveniles are recruited and individuals grow (see Toft et al., 1982; Moreira & Lima, 1991). For many amphibians, little is known about intraspecific variability in food and foraging (Duellman & Trueb, 1986). Also, feeding strategies of this group vary when prey differing in quality and abundance, either temporally or spatially, are available (Krebs, 1978).

Ecologists have viewed diets of a particular species as being influenced by interactions with competing species at the local level (Connell, 1983). Furthermore, examination of ontogenetic diet change is necessary before community structure can be analysed on the basis of food utilization (Hirai, 2002). In Argentinian Mesopotamia, only one study of anurans has taken ontogenetic diet change into consideration (Lajmanovich, 1996).

Foraging selectivity is usually defined as any significant deviation in predator diet compared to prey samples taken from the predator's environment (Stephens & Krebs, 1986). Many factors contribute to selectivity but prey body size is often a major determinant (Krebs, 1978; Stephens & Krebs, 1986). *Elachistocleis bicolor* has been described as a termitophagous (Gallardo & Varela de Olmedo, 1992) and myrmecophagous (López, 2003) specialist, like other species of the family (Langone, 1994; Kwet & Di Bernardo, 1999; Hirai & Matsui, 2000; Solé et al., 2002). However, trophic selectivity of *E. bicolor* has never been determined by comparing diet with prey availability, and all studies have been carried out only on adults. *Elachistocleis bicolor* has a history of systematic confusion with *E. ovalis* since 1841 (Lavilla et al., 2003). Langone (1994), Kwet & Di Bernardo (1999) and Solé et al.

(2002) followed Klappenbach & Langone (1992) in considering the specimens in their works as *E. ovalis*. Following the current operative framework proposed by Lavilla et al. (2003) – that the populations occupying the southern portion of the generic range must be considered *E. bicolor* – the populations studied in the three cited diet works would belong to *E. bicolor*.

In this study we examined post-metamorphic ontogenetic diet change of *E. bicolor* in a population inhabiting the floodplain of the Middle Paraná River in Argentina, considering prey availability in order to evaluate trophic selectivity.

MATERIALS AND METHODS

This study was conducted at the Reserva Universitaria El Pozo (31°37'S, 60°41'W) in the floodplain of the Paraná River, near Santa Fe city (Santa Fe Province, Argentina). The area includes tall grass wetlands and hydrophilous forests.

Frogs and arthropods were sampled by placing 27 wet pitfall traps (plastic cups 100 mm in diameter and 150 mm deep) (Corn, 1994) flush with the ground at about 15 m intervals on the hydrophilous forest floor, at a distance of approximately 4–5 m from the nearest flooded zone. This trap size allowed us to sample only *E. bicolor* frogs and arthropods, avoiding the capture of non-target animals. Since *E. bicolor* is an abundant microhylid in the riparian environments of the Paraná River, there is no indication that our sampling affected this frog population. As *E. bicolor* is a fossorial frog difficult to collect by hand, pitfall traps are an appropriate method for sampling them. Traps were set for two days once a month from August 2002 to July 2003. Specimens were preserved in 10% formalin (ASIH, HL & SSAR, 2001) and deposited in the

amphibian collection of the Instituto Nacional de Limnología (Santa Fe, Argentina). Invertebrates were preserved in ethylene glycol and then classified and quantified to estimate prey availability. Although there is no unbiased method to assess relative abundance of ground-dwelling invertebrates, we assume that this technique provided a good approximation of environmental prey availability because all prey taxa identified in the frogs' diet were also recorded in the traps.

The following body measurements were taken on each individual with a digital calliper (precision 0.01 mm): snout–vent length (SVL); mouth width (MW), maximum measurement at the angles of jaws; and femur length (FL), from mid-vent to knee when leg held as a Z with femur at right angles to vertebral column. We classified the frogs into three categories, adults (A), subadults (S) and juveniles (J), by applying a quantitative dissimilarity index, “Mean Character Difference Distance” (Kovach, 1999), to the morphometric data. Adults were also separated from subadults based on sexual maturity.

In order to determine the frogs' diet, their digestive tracts were extracted and contents analysed under a stereoscopic dissecting microscope. Each prey was measured using a calibrated ocular micrometer and identified to the highest possible taxonomic category. We counted as individuals only prey that still evidenced key structures for identification (heads, elytra, jaws, and the like). Volume for each order of prey item was estimated using the formula for an ellipsoid: $V = \frac{3}{4} \pi (L/2) (W/2)^2$. For each taxon, frequency of occurrence was calculated according to the formula of Lescure (1971). Mean trophic diversity (H^*) also was calculated. To determine the trophic diversity (H) and the accumulated trophic diversity (H_k), we followed Hurtubia's criteria (1973). We used H_k to estimate the minimum sample of digestive tracts to be analysed in order to evaluate sample representativity. Most published works on feeding use prey number (N), volume (V), or occurrence frequency (FO) separately to analyse frog diet. In this work, we calculated values of the relative importance index (IRI) (Pinkas et al., 1971) that combine the three measurements mentioned above to determine each prey category's contribution to the diet. As this index gives an adimensional value, we transformed quantitative results into percentages (IRI%) to allow easier comparisons. Levins' index (1968) was applied to determine trophic niche breadth (Nb). We applied a correlation test and simple linear regression to relate anuran morphometric variables and prey size.

To compare dietary composition of the three ontogenetic stages we used Pianka's (1974) symmetric overlap index (O), which ranges from 1 (total overlap) to 0 (no overlap). The index was calculated on the basis of the IRI instead of N because, as it combines N, FO and V, it provides more information about the frogs' diet (López, 2003). In addition, prey number, volume, lengths and trophic diversity of tract contents of the three stages were compared by Kruskal–Wallis tests and Dunn's Multiple Comparisons post-tests. Pianka's (1974) overlap index was also used to compare the frogs' diet with prey availability in the environment. This analysis was run with the

diet of frogs collected in March 2003 (the month with the maximum number of captures) when we estimated potential prey availability. Also, to elucidate dietary preferences, we calculated Jacobs' electivity index (D) (Jacobs, 1974) for the more important prey items. This index runs from +1 (complete preference) through 0 (no selection at all) to –1 (complete avoidance).

RESULTS

We analysed the diet of 30 adults, 36 subadults and 48 juveniles of *E. bicolor*. Fifty-nine percent of 114 frogs analysed were captured in March. February, April and May also had important rates of capture (15%, 10% and 12% respectively). In June only two frogs (less than 2% of captures), one adult and one subadult, fell into the traps. A single adult fell in July and another in October (less than 1% each). In the other four months no captures were recorded.

We identified 3527 prey items (65.66% in stomachs and 34.34% in intestines) belonging to 45 taxonomic categories (Table 1). Most categories were found only in stomachs (51.22%) or in both parts of digestive tracts (42.68%). Some were found only in intestines (6.1%). Plant materials and minerals were also frequently found in digestive tracts. Approximately half of adults and subadults (14 out of 30 and 16 out of 36 respectively) had parasites (helminths) in their intestines while juveniles were almost free of parasites (only five out of 48).

For the three stages of *E. bicolor*, ants were the principal component of diet (IRI% values: A=96.65%; S=99.86%; J=99.06%). Adults mainly ate ants of genera (in order of importance) *Pheidole* and *Paratrechina*; subadults, of genera *Paratrechina*, *Solenopsis* and *Pheidole*; and juveniles, of genera *Solenopsis*, *Pheidole* and *Strumigenys* (Fig. 1). Subadults ate a larger number of preys than adults ($P < 0.05$), but there was no difference between juveniles and the two older groups. Food volume per individual was bigger in subadults than in juveniles ($P < 0.001$) and adults ($P < 0.05$). No difference was found between adults and juveniles. Trophic spectrum (number of categories) was bigger in smaller frogs (A: 22, S: 29 and J: 31). The analysis of entire digestive tract contents showed that mean trophic diversity was bigger in juveniles than in adults ($P < 0.001$) and subadults ($P < 0.01$). No difference was found between adults and subadults ($P > 0.05$). Analysing only stomach contents, we found a different pattern. Although mean trophic diversity was still bigger in juveniles than in adults ($P < 0.001$), there was no difference between juveniles and subadults; the difference between adults and subadults was statistically significant ($P < 0.05$; Table 1). Also, analysing only stomach contents, mean trophic diversity value decreased because of the underestimating of diet (in adults, a decrease of 16.13%, in subadults 5% and in juveniles 20.53%) (Table 1). There was a statistically significant relationship between prey size and both frog SVL and MW (Spearman correlations, $r = 0.31$, $P < 0.00093$ and $r = 0.25$, $P < 0.008$ respectively). However, no difference in prey size between adults and subadults was found ($P > 0.05$),

Table 1. Comparison of diet composition between the three stages of *E. bicolor* and prey availability in the environment. The number of frogs analysed is given in parentheses. H*: mean trophic diversity; DT: entire digestive tract; ST: stomach; Nb: trophic niche breadth; N: number of prey; V: volume of prey; IRI%: percentage relative importance index; n.i.: not identified.

	Adults (n=30)			Subadults (n=36)			Juveniles (n=48)			Environment
	N	V	IRI%	N	V	IRI%	N	V	IRI%	N
Arachnida										
Acari	2	0.16	0.05	2	0.07	0.01	17	0.61	0.43	483
Araneae	2	0.34	0.11	2	0.65	-	1	0.47	-	54
Opilionidae	-	-	-	-	-	-	-	-	-	2
Pseudoscorpionidae	-	-	-	-	-	-	-	-	-	1
Crustacea										
Isopoda	-	-	-	1	0.16	-	2	3.81	0.02	277
Miriapoda										
Chilopoda	1	12.56	0.12	1	5.66	0.01	-	-	-	6
Insecta										
Larvae n.i.	4	3.95	0.08	1	0.47	-	2	0.20	0.01	-
Suctoria	-	-	-	-	-	-	-	-	-	1
Ephemeroptera	-	-	-	-	-	-	-	-	-	1
Hemiptera	-	-	-	-	-	-	-	-	-	6
Orthoptera	-	-	-	-	-	-	-	-	-	9
Larvae of Lepidoptera	-	-	-	-	-	-	-	-	-	11
Thysanoptera	-	-	-	-	-	-	-	-	-	25
Blattaria	-	-	-	-	-	-	-	-	-	8
Protura	-	-	-	-	-	-	-	-	-	20
Coleoptera	-	-	-	-	-	-	1	2.29	0.01	95
Larvae of Coleoptera	-	-	-	-	-	-	4	15.47	0.09	9
Bruchidae	1	-	0.01	-	-	-	1	0.29	-	-
Carabidae	-	-	-	1	0.47	-	-	-	-	-
Staphylinidae	-	-	-	2	12.57	0.05	2	5.29	0.02	-
Collembola	1	-	0.01	5	3.38	0.03	13	0.64	0.07	8901
Entomobryidae	1	0.47	0.01	-	-	-	2	0.10	0.01	-
Poduridae	1	-	0.01	3	0.07	0.02	12	0.44	0.17	-
Sminthuridae	-	-	-	1	0.06	-	7	0.66	0.08	-
Diptera	1	0.91	0.02	1	0.13	-	2	1.14	-	139
Larvae of Diptera	-	-	-	-	-	-	1	0.91	-	30
Larvae of Chironomidae	-	-	-	-	-	-	1	2.09	0.01	-
Homoptera	-	-	-	-	-	-	-	-	-	72
Aphidae	1	0.24	0.01	2	0.12	0.01	-	-	-	-
Larvae of Aphidae	-	-	-	-	-	-	-	-	-	2
Hymenoptera	8	18.18	2.62	1	-	-	1	-	-	36
Formicidae	60	18.01	17.48	82	25.62	2.35	112	1.70	5.75	786
<i>Brachymyrmex</i> sp.	88	81.94	3.32	1	1.57	-	10	5.89	0.16	-
<i>Camponotus</i> sp.	1	2.94	0.04	-	-	-	8	16.39	0.43	-
<i>Paratrechina</i> sp.	196	237.79	15.75	443	528.73	35.64	48	31.93	1.30	-
Unidentified Myrmicinae	-	-	-	1	0.16	-	-	-	-	-
<i>Acromyrmex</i> sp.	7	53.09	4.52	7	19.30	0.17	7	10.93	0.20	-
<i>Crematogaster</i> sp.	-	-	-	25	14.94	0.07	-	-	-	-
<i>Crematogaster quadriforme</i>	-	-	-	11	5.12	0.06	-	-	-	-
<i>Cyphomyrmex</i> sp.	-	-	-	1	0.47	-	1	1.14	0.01	-
<i>Elasmopheidole</i> sp.	-	-	-	-	-	-	18	1.76	0.15	-
<i>Mycetarotes</i> sp.	-	-	-	-	-	-	1	1.57	0.01	-
<i>Pheidole</i> sp.	22	30.18	2.87	3	11.16	0.02	-	-	-	-
<i>Pheidole bergi</i>	147	183.17	27.61	328	433.13	24.59	219	176.76	19.20	-
<i>Pheidole fimbriata</i>	105	155.46	19.93	193	200.31	4.96	139	87.00	8.82	-
<i>Solenopsis</i> sp.	43	35.52	3.01	482	209.30	31.80	439	266.95	55.20	-
<i>Strumigenys</i> sp.	2	0.57	0.10	3	1.55	0.04	90	41.64	5.89	-
Unidentified Ponerinae	-	-	-	1	3.72	0.01	-	-	-	-
<i>Ectatomma</i> sp.	22	116.57	2.33	-	-	-	-	-	-	-
<i>Cryptopone</i> sp.	-	-	-	6	22.84	0.14	38	44.75	1.96	-
<i>Pseudomyrmex</i> sp.	-	-	-	2	3.14	0.01	-	-	-	-
Total	716	952.05	100	1612	1504.84	100	1199	722.83	100	
Minimum sample		20			17			12		
H*		DT: 0.31 ST: 0.24			DT: 0.6 ST: 0.57			DT: 1.02 ST: 0.81		
Nb		2.9			1.33			0.72		

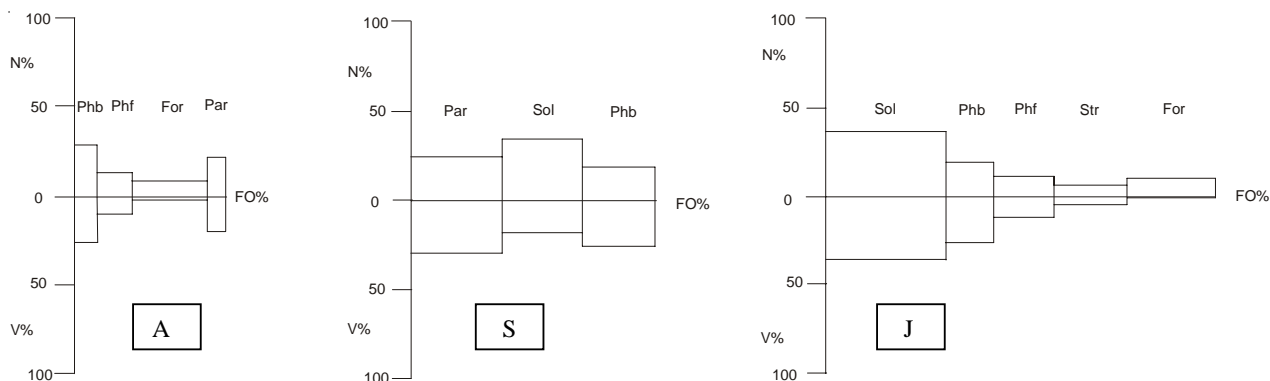


Fig. 1. Graphical representation of prey relative importance index (IRI) for adults (A), subadults (S) and juveniles (J). Each one of the three components of the IRI (FO%, N% and V%) is represented on an axis. Phb=*Pheidole bergi*; Phf=*Pheidole fimbriata*; For=Formicidae n.i.; Par=*Paratrechina* sp.; Sol=*Solenopsis* sp.; Str=*Strumigenys* sp.

but both ate bigger prey than juveniles ($P < 0.05$ and $P < 0.01$ respectively).

Adult diet overlapped more with subadults ($O = 0.65$) than with juveniles ($O = 0.4$), but subadults had a greater overlap with juveniles ($O = 0.72$). Subadults had the greatest general overlap ($O = 0.685$) of the three stage categories, followed by juveniles ($O = 0.56$) and adults ($O = 0.525$).

Overlap of the diet of all frogs with prey availability was minimal ($O = 0.1$). Juveniles had the greatest overlap ($O = 0.12$), while adults and subadults had the same overlap ($O = 0.09$). Frogs tended to eat all prey taxa in different proportions from those in the surrounding environment. Jacobs' index showed that all three stages of *E. bicolor* prefer ants ($D = 0.99$). Other selectively caught prey items were non-formicid hymenopterans ($D = 0.67$) and millipedes ($D = 0.24$) in adults and coleopteran larvae ($D = 0.59$) in juveniles. Subadults did not have a preference for other arthropods. The remaining prey categories had different avoidance values. Ants and non-formicid hymenopterans were more frequent in the diet than in the environment, whereas collembolans, mites and isopods were under-represented in digestive tracts (Fig. 2).

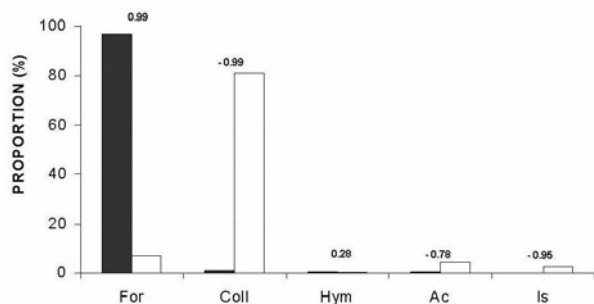


Fig. 2. Relationship between prey availability (open bars) and diet composition (shaded bars). Electivity index values (D) are shown atop each pair of bars. For=Formicidae; Coll=Collembola; Hym=non-Formicidae Hymenoptera; Ac=Acari; Is=Isopoda.

DISCUSSION

This study revealed that *E. bicolor* from Argentinian riparian localities of the Middle Paraná River feed predominantly on ants. Considering the low similarity between the proportions of *E. bicolor* diet items and environmental prey availability, we infer that this microhylid is a very selective forager. The marked overrepresentation of ants in *E. bicolor*'s diet suggests that this frog is a myrmecophagous predator. This agrees with the results of other dietary studies of *E. bicolor* (López, 2003), although Gallardo & Varela de Olmedo (1992) describe *E. bicolor* as a termitophagous specialist and observe that termites and ants are a similar "ecological and morphological prey kind" because of their morphological and behavioural similitudes. *E. bicolor* is probably limited to capturing these ecomorphological prey, and termitophagy or myrmecophagy would result from the relative environmental abundance of these two prey items. It is important to note that no termite was found in our arthropod samples.

Some traits of *E. bicolor* have been interpreted as defence mechanisms against ant attacks while they are eating them. For example, the transversal fold posterior to the eyes can extend ahead, covering them, while the skin releases a viscous secretion (Langone, 1994). It has also been proposed that some microhylids search ant trails by olfaction and that once a trail is located they tend to pick up ants as they pass by (Duellman & Trueb, 1986).

In many herpetological dietary studies, only stomachs of frogs are analysed (e.g. Caldwell & Vitt, 1999; Guix, 1993; Cogalniceanu et al., 2000), but Peltzer et al. (2000) demonstrated that recording only stomach contents generates an underestimation of anuran diet. Here we found that working with entire digestive tracts led us to a more complete description of *E. bicolor*'s diet because of the inclusion of prey categories found only in the intestines. Proportions of taxa would also have changed, leading to a different trophic diversity value. We conclude that it is important to analyse entire digestive tracts whenever possible.

Comparisons of prey number per digestive tract between the three stages could be affected by high standard

deviations of values. Subadults, which showed the greatest number and volume of prey per tract, included a couple of frogs that ate disproportionately more than the others (231 and 134 preys items each). The relationship between anuran morphometry and prey size has been demonstrated in many species (Zug & Zug, 1979; Toft, 1980; Parmelee, 1999; Peltzer & Lajmanovich, 1999); *E. bicolor* is not an exception to this rule and bigger specimens ate larger prey. A noticeable difference in diet among the three stages of *E. bicolor* is that each of them shows a marked preference for specific genera of ants. Moreover, adults and juveniles also capture other prey besides ants proportionally more than their availability in the environment. Also, the decrease of mean trophic diversity and reduction of trophic spectrum from juveniles to adults indicates a progressive dietary specialization throughout ontogeny, although niche breadth increased from juveniles to adults. As frogs grow up, there is a partial and gradual change in prey categories captured. That is why neighbouring stages have a greater diet overlap. Finally, as was expected, dietary similarity with other stages was greatest for subadults and lower between adults and juveniles.

According to our results, parasite infection seems to happen during the subadult stage. The consequences of this infection are an important and unknown issue, but this subject is not treated here.

Finally, it is interesting to note that Caldwell (1996) revealed the inclusion of a high percentage of Formicidae in the diet of toxic frog species of the family Dendrobatidae. Myrmecophagy is common in *Elachistocleis* genera (Langone, 1994; Kwet & Di Bernardo, 1999; Hirai & Matsui, 2000; Solé et al., 2002) and has also been mentioned in other genera of the subfamily Microhylinae (Schülter & Salas, 1999; Hirai & Matsui, 2000). To understand myrmecophagy and its relationships with toxicity in this subfamily, more studies are needed in many species within different phylogenetic lineages.

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