

INSTITUTO NACIONAL DE PESQUISAS DA AMAZÔNIA (INPA)
FUNDAÇÃO UNIVERSIDADE DO AMAZONAS (FUA)

EFFECTS OF PREY SIZE AND
FORAGING MODE ON THE
ONTOGENETIC CHANGE IN THE
FEEDING NICHE OF *COLOSTETHUS*
STEPHENI (ANURA:
DENDROBATIDAE)

Albertina P. Lima

VEDADO EMPRÉSTIMO

Dissertação apresentada ao Programa de Pós-Graduação em Biologia Tropical e Recursos Naturais do Convênio INPA/FUA como parte dos requisitos para obtenção do título de **Mestre em Ciências Biológicas**, área de concentração Ecologia.

Supervisor: William E. Magnusson

Manaus - Amazonas

1992

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Colostethus stepheni



Postmetamorphic $\pm 6.0\text{mm}$



Adult $\pm 14.0\text{mm}$

Effects of Prey Size and Foraging Mode on the
Ontogenetic Change in Feeding Niche of
Colostethus stepheni (Anura: Dendrobatidae)

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Key words: ontogenetic change, diet, electivity, prey size, prey types, C. stepheni, frog, foraging behavior, availability of prey.

Synopsis

Aspects of the diet, electivity for prey types independent of electivity for prey size, foraging mode and their relationships with the size of Colostethus stepheni (Dendrobatidae) were studied in Reserva Florestal Adolfo Ducke, Central Amazônia, Brasil.

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ABSTRACT

The feeding niche of Colostethus stepheni changes during ontogeny. Small individuals eat small arthropods that are principally mites and collembolans, and larger frogs eat bigger prey of other types. The shift in prey types is not a passive effect of selection for bigger prey. There is a strong relationship between electivity for prey types and frog size, independent of electivity for prey size.

Four indices of general activity during foraging (number of movements, velocity, total area utilized and percent of time moving), which are associated with electivity for prey types in adult frogs and lizards, did not predict the ontogenetic change in the diet of C. stepheni. Apparently, the behavioral changes that cause the ontogenetic change in C. stepheni are more subtle than shifts in general activity during foraging.

Studies of niche partitioning in communities of anurans that do not take into consideration ontogenetic changes in diet and seasonal changes in the size structures of populations present a partial and possibly erroneous picture of the potential interactions among species.

INTRODUCTION

The degree of specialization in types and sizes of prey changes with the body size of a predator and this can be the result of many factors. Among fish, ontogenetic shifts have been related to changes in the habitat use (Griffiths, 1975; Ross, 1978; Grossman, 1980; Stoner and Livingston, 1984). In reptiles, ontogenetic shifts may be associated with changes in habitat use (Schoener and Gorman, 1968; Clark and Gibbons, 1969; Mushinsky et al., 1982). However, ontogenetic changes in the diets of lizards are usually related to ontogenetic changes in prey size. This causes shifts in prey types because the distribution of arthropod sizes varies depending on the taxon (Rose, 1976; Dominguez and Salvador, 1990). Ontogenetic shifts in prey types and sizes also occur in postmetamorphic amphibians and it has been suggested that the shift in prey types is a result of the change in prey size (Pengilley, 1971; Labanick, 1976; Christian, 1982; Donnelly, 1991; Wiggins, 1992).

Studies of the mechanisms that lead to differences in sizes and types of prey have compared species and used only adult animals. In lizards and anurans, the mechanisms are related to morphology and foraging mode. In general, species that forage actively eat small prey that live in aggregations, that are slow-moving, are often chitinous, and often have chemical defenses (e.g. ants, termites, mites). Species that are sedentary foragers

eat prey of larger size that are normally solitary such as orthopterans, beetles and spiders (Huey and Pianka, 1981; Toft, 1981 and 1985; ; Strüssmann, 1984; Magnusson et al., 1985; Pough and Taigen, 1989; Perry et al., 1990).

In general, animals that do not chew their food are limited to eating prey that fit in their mouths. Species of lizards and frogs are adapted to efficiently capture prey that are proportional to the size of their jaws (Pianka, 1983; Pough et al. 1989). Postmetamorphic anurans also do not chew their prey. Consequently, the ontogenetic change in body size allows larger individuals to eat larger prey. This can cause a shift in prey types simply because the mean sizes of individuals differ among arthropod orders (Schoener and Jansen, 1968; Domínguez and Salvador, 1990).

Few species of anurans eat mites, despite the fact that mites are among the most common soil and litter arthropods in most regions of the world (Simon and Toft, 1991). These authors suggest that mites are not lucrative prey for most anurans because they are small (in general < 1.0 mm). Larger prey have a smaller surface-to-volume ratio, and therefore, a smaller proportion of chitin. Chitin takes more time to digest than other components of arthropods. Therefore, mites are lucrative prey only for small frogs, that cannot eat bigger prey. The fact that the proportion of mites is inversely proportionally to the size of the frogs supports this hypothesis. Colostethus species are small

and in general are specialists on ants and mites (Simon and Toft, 1991)

There are no studies of anurans or reptiles that determined whether the ontogenetic change in prey types is a consequence of the ontogenetic shift in prey size or results from a change in foraging behavior.

In Central Amazônia, Colostethus stepheni (Martins, 1989) forages for arthropods in the leaf litter during the day. Their tadpoles complete development in terrestrial nests (Junca, 1989; obs. pers.). Adults have snout-urostyle lengths of 14.0 to 17.5 mm but recently metamorphosed juveniles leave the nests at lengths of less than 6 mm. Individuals of all sizes forage in the same microhabitat and, as they are not disturbed by the presence of humans, can be followed easily and their foraging behavior recorded.

This study investigates the following questions:

1 - Is there an ontogenetic change in the types and sizes of prey in the diet of C. stepheni?

2 - If there is an ontogenetic change, is the shift in electivity for prey types independent of electivity for prey size?

3 - Are the shifts in the sizes and types of prey associated with changes in foraging activity?

METHODS

Study area:

This study was conducted in a 10000 ha tropical rainforest reserve, Reserva Florestal Adolfo Ducke (RFAD), located 25km northeast of Manaus, Amazonas, Brasil (Lat. 03°08'S; Long. 60°04'W). The RFAD is covered by "terra firme" primary tropical rainforest, which is not subjected to seasonal flooding (Guillaumet, 1987). The study was done along six trails in an undisturbed part of the RFAD. Three of these trails follow the margins of shallow forest streams, one along 500m of a stream about 3.5m wide, and two others of 1000m and 1200m, along two tributaries about 1.3m wide. The other three trails are 1000m, 1183m and 1350m long and run perpendicular to the streams.

Measures of foraging mode:

Observations of the foraging mode of the animals were made in the same area between February 1991 and April 1992. I followed 32 juveniles and 14 adults (5 males and 9 females) for a period of 30 minutes each. Frogs were followed in different hours throughout the day (Fig. 1). The distribution of the animals

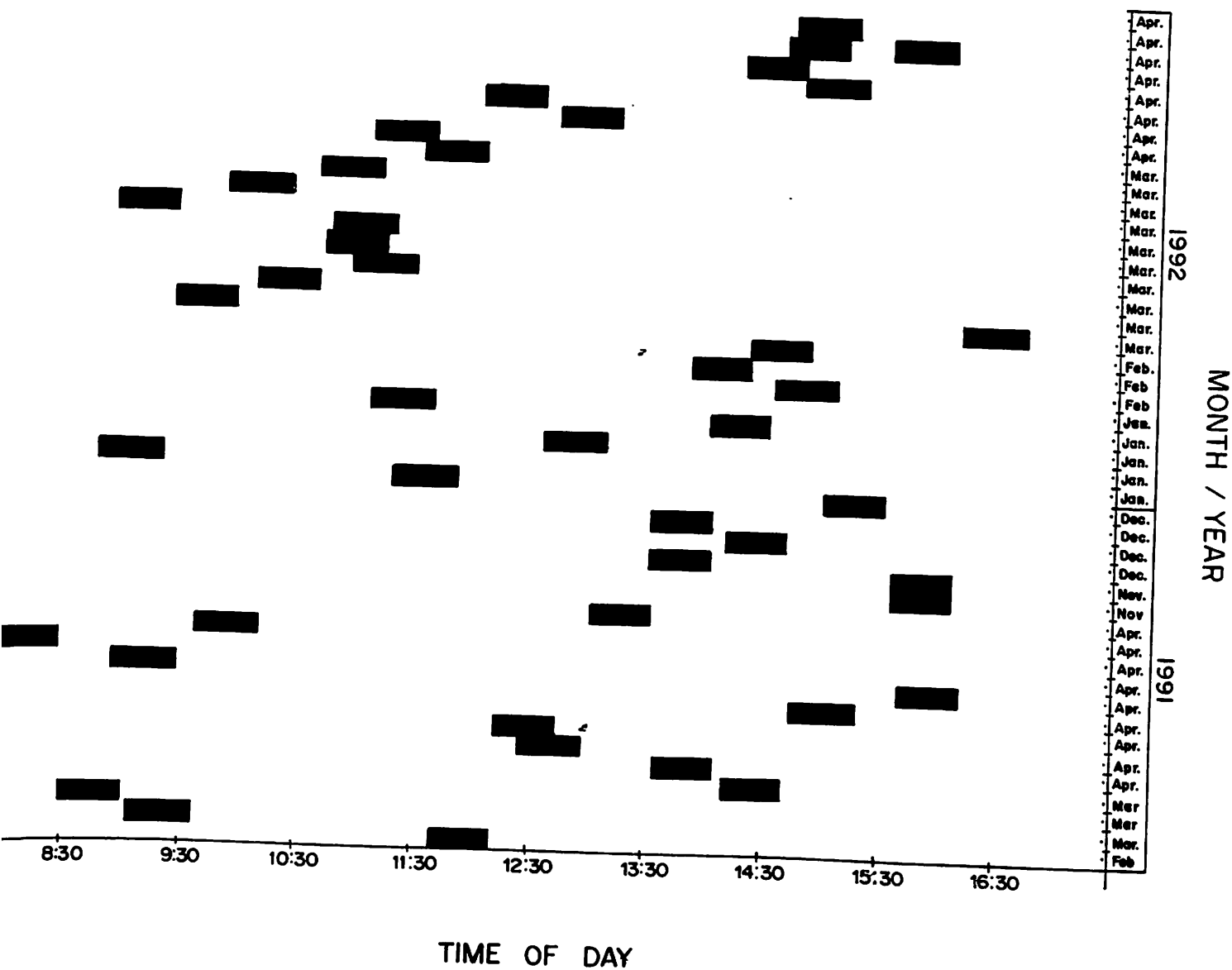


FIGURE 1- Times each frog was followed to establish ativity of foraging.

among sizes was as follows: <6.5mm, 5 animals; 6.6-7.5mm, 9; 7.6-8.5mm, 7; 8.6-9.5mm, 2; 9.6-10.5mm, 3; 11.6-12.5mm, 3; 12.6-13.5mm, 1; 13.6-14.5mm, 2; 14.6-15.5mm, 1; >15.6mm, 13.

The frogs were watched from a distance of 1-5m and I used binoculars when necessary. For each minute of observation, I noted the number of movements, the total distance moved, and the duration of each movement. A movement was recorded only if it resulted in displacement of the body. At the end of the observation period, the total distances moved in the two longest perpendicular axes were registered. Those observations were used to create five indices of activity of foraging: number of movements/30min; velocity when moving (cm/s); total distance moved in 30 min; time moving in 30 min, and total area used (the product of the two longest perpendicular axes in cm, transformed to their natural logarithms to reduce the effects of extremely high values). The time in movement was recorded with digital chronometers accurate to 0.01 seconds. At the end of the observation period the animals were captured and killed for analyses of diet. Analyses in which I evaluate the relationships between indices of foraging behavior and mean size prey are based only on the diets these individuals.

Food availability

Prey availability was estimated from samples of litter and soil to a depth of 5cm collected with a 6.4x6.6cm soil corer. Samples were collected each month from February 1991 to March 1992 (except September and October 1991). The arthropods were extracted in Berlese funnels for 8 days and identified to order or family. The samples were collected in different points along each trail in each month. I collected 84 samples in the rainy season of 1991; five samples for each trail in February - March and two samples for each trail in April - May. In June, July and August of 1991 (dry season) I collected 60 samples in the same sites as in the rainy season. In the remainder of the months (November and December of 1991, January, February and March of 1992) I collected two samples along each trail in each month.

Prey Consumption

The 443 frogs that were used for analyses of the ontogenetic change in the diet and electivity were collected during 2-3 day periods each month from April 1988 to October 1989 (except June and July 1989) between 0800 and 1700h. I walked all trails and captured every frog within one meter of the center of the trail. The animals were killed immediately and fixed in 10% formalin. Their snout-urostyle lengths were measured with Vernier callipers

after preservation.

For analyses of diet, I used only items in the stomach. They were sorted into prey categories (generally orders or family). Prey categories that contributed less than 15% (mass) of the diet of all size categories were grouped as "other arthropods" or "holometabolous larvae". Sizes of prey were measured under a dissecting microscope with a gridded eyepiece. In the case of disarticulated items, the original size of the prey was estimated by comparison with a reference collection. Masses of the preserved animals were determined on a digital balance accurate to 0.0001g. I estimated the masses of animals that were lighter than the limit of reading of the balance by grouping 10 to 100 preserved arthropods of similar size from the same taxon, weighing them and then, calculating the mean mass.

Statistical analyses

Electivities were calculated from Jacobs (1974):

$$D = (R_k - P_k) / [(R_k + P_k) - (2 \cdot R_k \cdot P_k)]$$

where R_k is the proportion of prey k in the stomach contents and P_k is the proportion of prey k in the environment. D varies from +1, for complete selection or preference of prey k , through 0, when prey k is taken in the same proportion as found in the environment, to -1 when prey k is absent in the diet but present

in the environment.

Statistical analyses were done with the "SYSTAT" computer program (Wilkinson, 1990). Proportions were transformed to "arcsin" before being submitted to analysis of variance.

The original data for each individual had high variance, were not multivariate normal, and could not be transformed to conform to the assumptions of the analyses. Therefore, I used the mean of the variables registered for frogs within intervals of body length of 0.5mm (diet) or 1.0mm (electivity and foraging behavior). Thus, the degrees of freedom are associated with the number of size categories and not the total number of individuals.

To reduce the dimensionality of the data on diet and prey availability, I used the first principal component of a principal components analysis (Wilkinson, 1990). The first principal component was chosen a priori because it summarizes the greater part of the variation in the original data. The other components could be correlated with the dependent variables, but in that case it would be necessary to correct the probabilities for the number (6) of tests made. This increases the probability of a type II error. In an exploratory study with the aim of generating hypothesis it is interesting to investigate all the components. However, as I had an a priori hypothesis, I considered it better to use only the component that reflects the greatest part of the variation in the diet so as to preserve the validity of the statistical tests.

RESULTS

C. stepheni eats a diversity of prey types (appendix). However, only five categories (Collembola, Acarina, Isoptera, Formicidae and holometabolous larvae) represented more than 15% of the diet in all size classes. The "others" category includes all other arthropods.

I could determine the sex of individuals only when they were greater than 14.0mm. In the months of November, December and January when 87% of individuals in the population were adult (Moreira and Lima, 1991). I used the proportion of the total mass (transformed to arcsin) represented by three prey categories (Formicidae, Isoptera and other arthropods) found in stomachs during these three months to test for the effect of sex on the diet. There was no significant difference between the diets of the sexes (Tab. 1). I could not use the six prey categories (Collembolas, Isoptera, Formicidae, Acarina, holometabolous larvae and other arthropods) because the samples were too small and adults eat few Acarina and Collembolas.

The proportions of Acarina (Fig. 2A) and Collembola (Fig. 2B) in the diet decrease, and the proportions of Isoptera (Fig.

Table 1 - Sumary statistics for the MANOVA of the independent variable "sex" on the dependent variables: Isoptera (Isop), Formicidae (Form) e outros artrópodos (Outr).

Univariate F Test of the effect of sex

	Gl	SQ	MQ	F	P
Isop	1	0.789	0.789	2.054	0.164
error	26	9.987	0.384		
Form	1	0.079	0.079	0.268	0.609
error	26	7.643	0.294		
Outr	1	0.856	0.856	4.718	0.039
error	26	4.718	0.181		

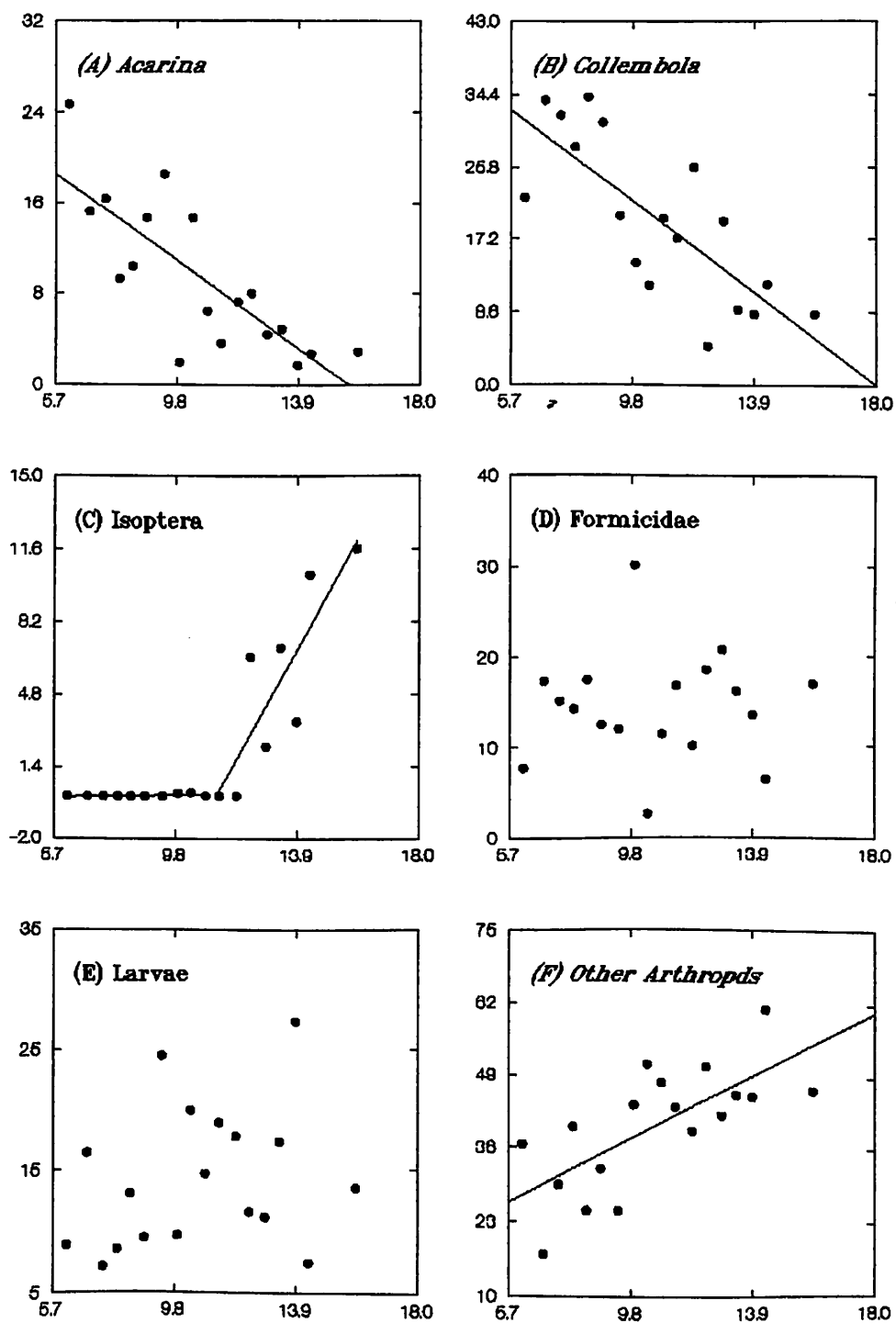
Multivariate Test Statistics for the effects of sex

	gl	F	P
"Wilks' Lambda"=0.790	24	2.122	0.124
"Pillai Trace"=0.210	24	2.122	0.124
"Hotelling-Lawley Trace"=0.265	24	2.122	0.124

Figure 2. Mean proportions of the total mass of stomach contents for each prey type in relation to the mean length of the frogs. For animals <14mm, each point represents means within each interval of 0.5mm in frog length. The last point in each graph represents means for frogs larger than 14mm.

There are significant relationships between the mean length of C. stepheni (ML) and the following prey types: Acarina (AC) [AC=29.1-1.86ML, $r^2=0.62$, $F_{1,16}=26.147$, $P=0.000$]; Collembola (C) [C=47.6-2.6ML, $r^2=0.59$, $F_{1,16}=23.6$, $P=0.000$]; Isoptera (I) [I= 28.4-2.5ML, $r^2=0.71$, $F_{1,16}=15.0$, $P=0.008$]; and other arthropods (OA) [OA=5.9-0.35ML, $R^2=0.30$, $F_{1,16}=6.9$, $P=0.018$]. The relationship for termites was calculated for animals with ML>11.2mm because smaller individuals did not eat prey from this category. There was no significant relationship between the mean length of frogs and the proportions of ants ($r^2=0.001$, $F_{1,16}=0.019$, $P=0.891$) or holometabolous larvae ($r^2=0.070$, $F_{1,16}=1.21$, $P=0.288$) in the diet.

PROPORTION OF TOTAL MASS OF STOMACH CONTENTS (%)



2C) and "other arthropods" (Fig. 2F) increase, with increasing frog size. There was no significant relationship between the proportions of Formicidae or holometabolous larvae in the diet and frog size (Fig. 2D and E).

The categories of prey do not represent independent information because they are highly correlated. To reduce the dimensionality of the diet represented by the six prey types (Acarina, Collembola, Isoptera, Formicidae, holometabolous larvae and other arthropods) I used principal components analysis. The first principal component explained 47.6% of the total variation in diet. Acarina, Collembola, Isoptera and other arthropods had high loadings on this component (Tab. 2), indicating that it retains much of the information inherent in the original variables.

There was a significant linear relationship between "diet" (1st principal component) and the size of C. stepheni (Fig. 3). Frog size explained 83% of the variation in "diet", indicating a strong ontogenetic change in prey taken.

There was a significant linear relationship between the size of C. stepheni and the mean size of prey eaten (Fig. 4). However, the change in the mean size of the prey eaten might result in a change in prey types simply because size distributions differ among arthropod types. The types of prey that represented the

Table 2. The loadings for the first principal components for diet and size specific electivity.

COMPONENT	LOADINGS	
	"Diet"	"Electivity"
Collembola	-0.901	-0.929
Isoptera	0.809	0.815
Formicidae	0.069	0.507
Acarina	-0.775	-0.743
Larvae	0.099	0.797
Orther arthropods	0.882	0.958

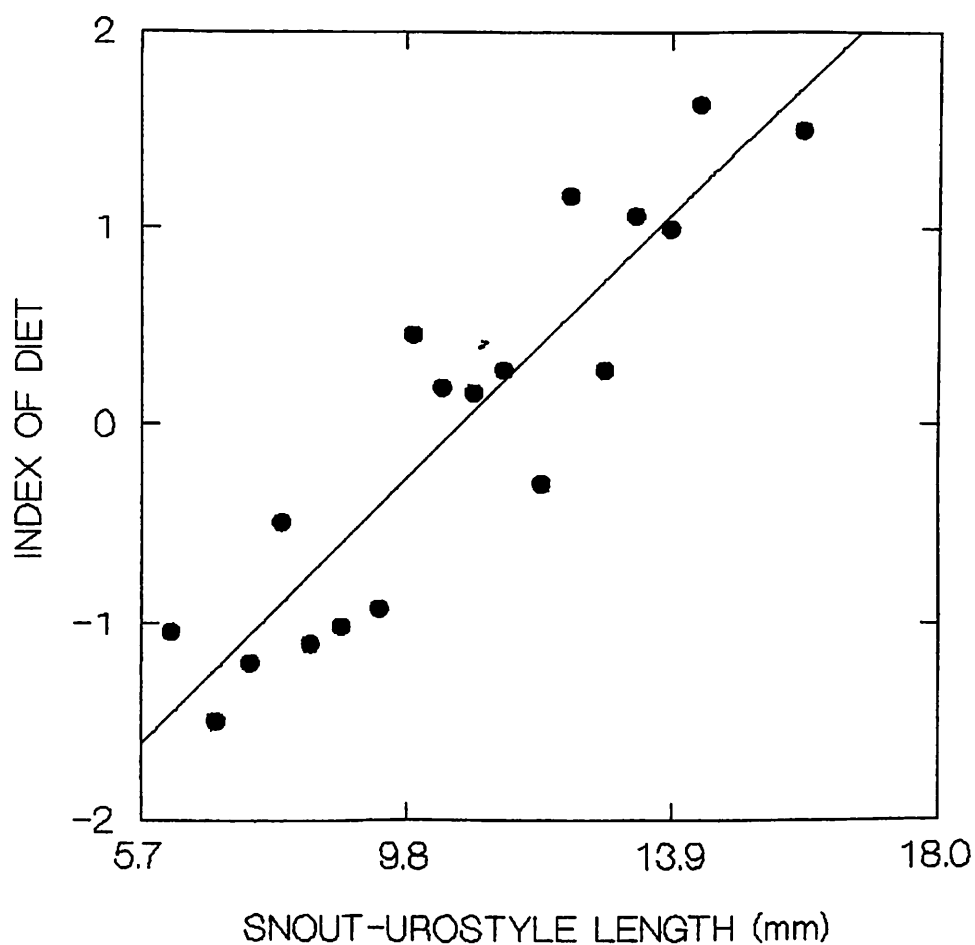


FIGURE 3- Relationship between "diet" (D) (1st principal component, which summarizes the variation in the proportions of Acarina, Collembola, Isoptera, Formicidae, holometabolous larvae and other arthropods in the diet) and mean size (MS) of C. stepheni ($D = -3.5 + 0.3MS$, $r^2 = 0.83$, $F_{1,16} = 77.59$, $P = 0.000$). For animals <14mm, each point represents the means within 0.5mm intervals of frog length. The last point on the graph represents means for frogs >14mm.

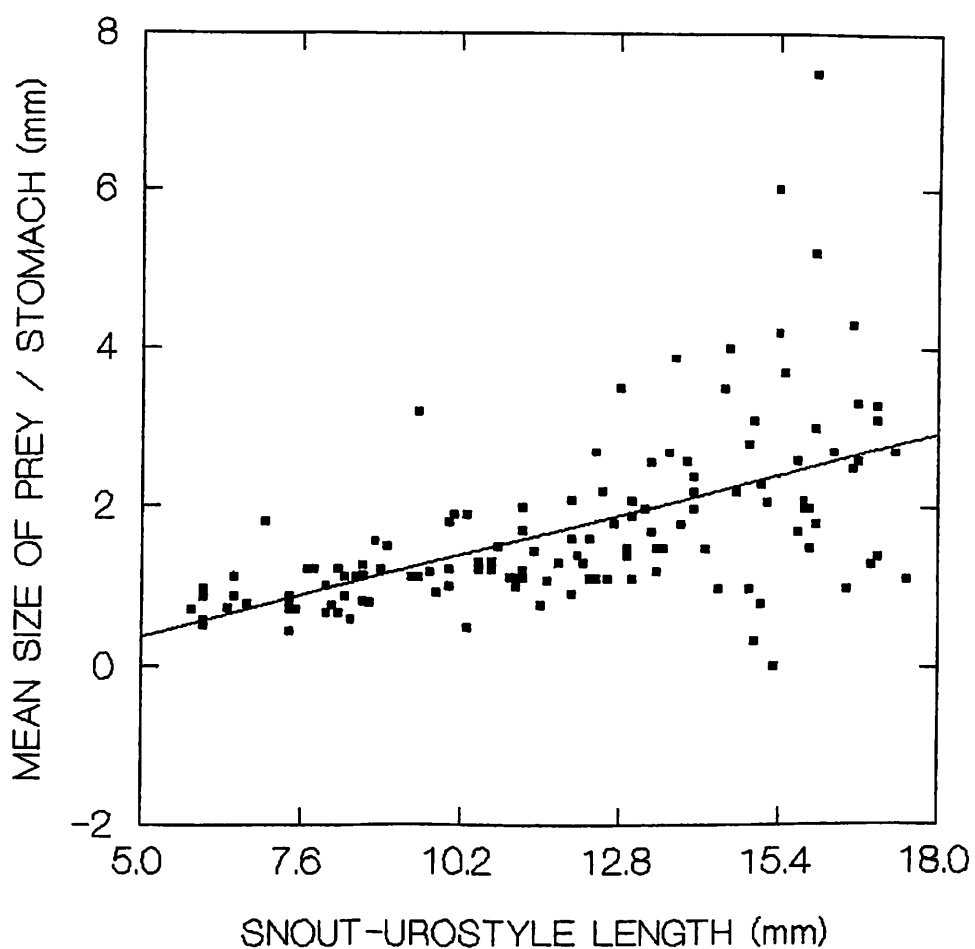


FIGURE 4- Relationship between mean size of the prey (SPM) in the stomach contents and the length of the frogs (LF) in mm. [$SPM = -0.6 + 0.2LF$, $F_{1,128} = 60.88$, $r^2 = 0.32$, $P = 0.000$].

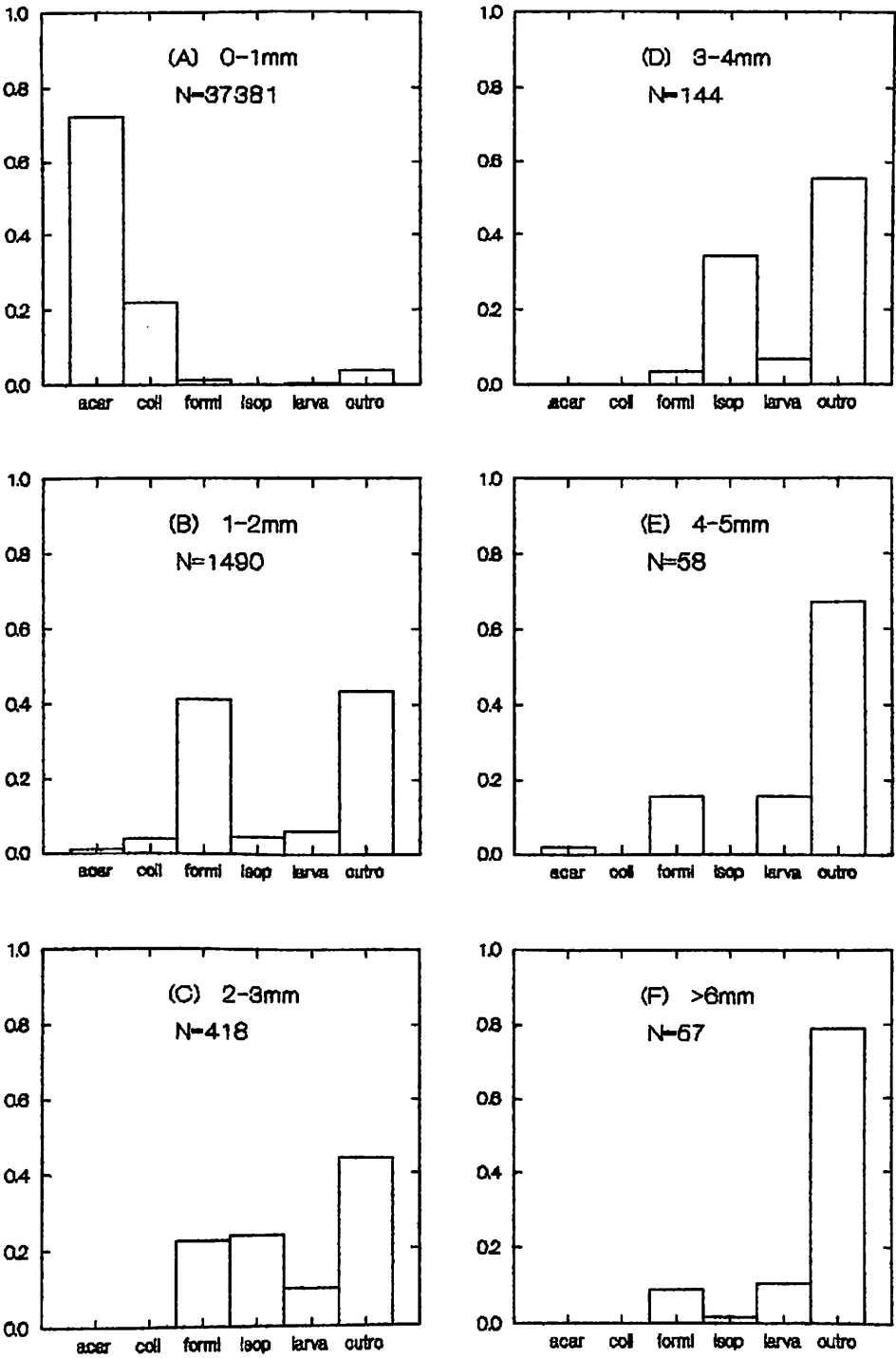
greatest proportions of prey available in the size class <1.0 mm were Acarina and Collembola (Fig. 5A); Formicidae in the class 1-2 mm (Fig. 5B); Isoptera in the class 3-4 mm (Fig. 5D); and other arthropods in the classes >4 mm (Fig. 5 E and F).

To determine if the electivity of C. stepheni for prey types changes with frog size independently of the electivity for prey size, I created size-specific indices of electivities for each class of frog size (Fig. 6). For these indices, I used only prey in the stomach that was within ± 1 sd of the mean prey size for frogs in that size class, and prey in the leaf-litter samples that were also within ± 1 sd of the mean prey size for frogs in that size class. I assume that prey in these size classes were easily captured and swallowed by the frogs and, therefore, prey size will have little influence on the choice of the frog in comparison with electivity for prey types.

The strongest pattern in electivity was the negative electivity for Acarina in comparison with the other arthropod groups (Fig. 6). The size-specific electivities for Acarina (Fig. 6A) and Collembola (Fig. 6B) decrease, and the size-specific electivities for Isoptera (Fig. 6C), Formicidae (Fig. 6D), holometabolous larvae (Fig. 6E) and other arthropods (Fig. 6F) increase with frog size. There was no significant relationship between size-specific electivity for ants and frog size.

FIGURE 5- The proportion of the total number of individuals in each category of size represented by each type of arthropod in the samples of food availability (Acar=Acarina, Coll=Collembola, Isop=Isoptera, Formi=Formicidae, Larva=holometabolous larvae, and outro=other arthropods)

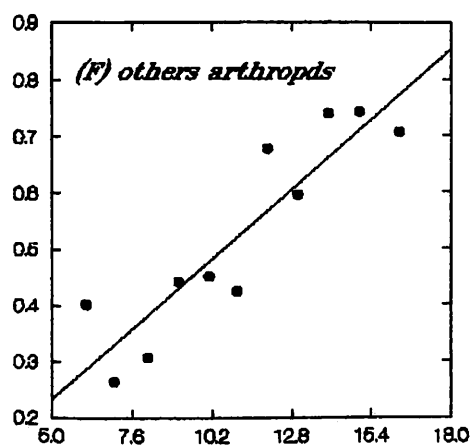
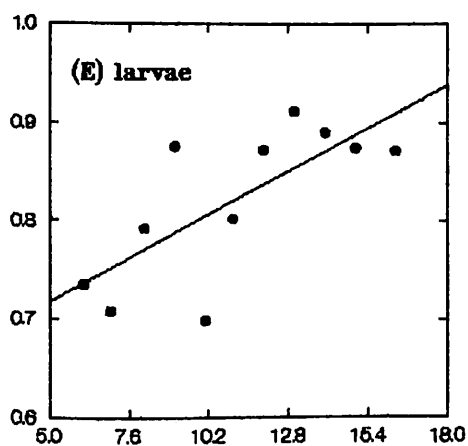
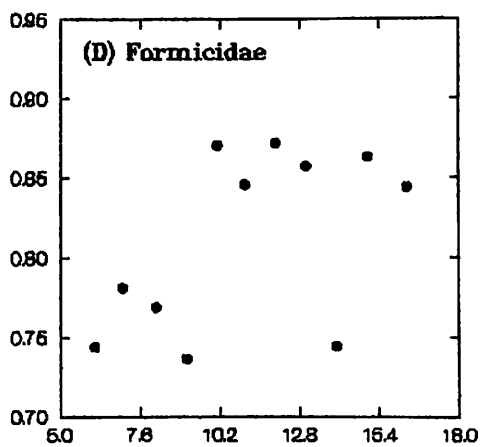
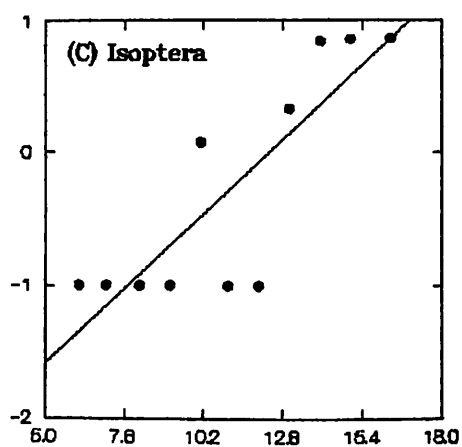
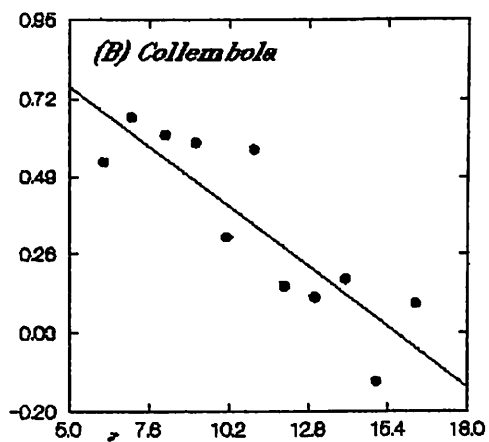
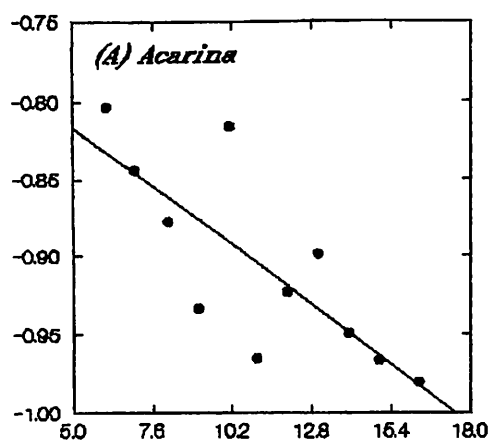
PROPORTIONS OF EACH PREY TYPE IN EACH SIZE CLASS



TYPE OF PREY

FIGURE 6- Relationship between electivities for each prey type in the diet and mean length of the frogs. Each point represents means for frogs in intervals of 1.0mm. There were significant relationships between the mean length of C. stepheni (ML) and the electivities for the following prey types: Acarina (AC)[AC= $-0.74-0.015ML$, $F_{1,9}=14.383$, $r^2=0.615$, $P=0.004$]; Collembola (C)[C= $1.096-0.068ML$, $F_{1,9}=26.501$, $r^2=0.746$, $P=0.001$]; Isoptera (I)[I= $-2.675+0.217ML$, $F_{1,9}=20.642$, $r^2=0.696$, $P=0.001$]; holometabolous larvae (HL) [HL= $0.632+0.017ML$, $F_{1,9}=10.156$, $r^2=0.530$, $P=0.011$] and other arthropods (OA)[OA= $-0.0005+0.048ML$, $F_{1,9}=39.531$, $r^2=0.815$, $P=0.000$]. There was no significant relationship for Formicidae ($r^2=0.282$, $F_{1,9}=3.536$, $P=0.093$).

INDEX OF ELECTIVITY



SNOUT-UROSTYLE LENGTH (mm)

However, the size-specific electivities for each category of prey do not represent independent information because they are highly correlated. To reduce the dimensionality of electivity represented by the electivities for the six prey types (Acarina, Collembola, Isoptera, Formicidae, holometabolous larvae and other arthropods), I used principal components analysis. The first principal component explained 64% of the variation in total electivity. The electivities of the six prey types had high loadings for this component (Tab. 2), indicating that it retains much of the information inherent in the original variables.

There was a significant linear relationship between the "general electivity" based on the size-specific electivities for each diet category (1st principal component) and the mean size of C. stepheni (Fig. 7). The size of C. stepheni is associated with 94% of the variation in the "general electivity" indicating a strong ontogenetic change in the choice of prey types independent of electivities for prey sizes.

The structure of the population of C. stepheni changes throughout the year (Moreira and Lima, 1991) but the sample of arthropod availability was based on pooled samples for the whole year. To confirm that ontogenetic differences occur within the same season, I compared the electivities of small C. stepheni (6.5 - 7.5 mm) with those of larger C. stepheni (14.5 - 15.5 mm) within a three-month period (Feb, Mar. and Apr.). I did not have sufficient samples to compare the other size classes within

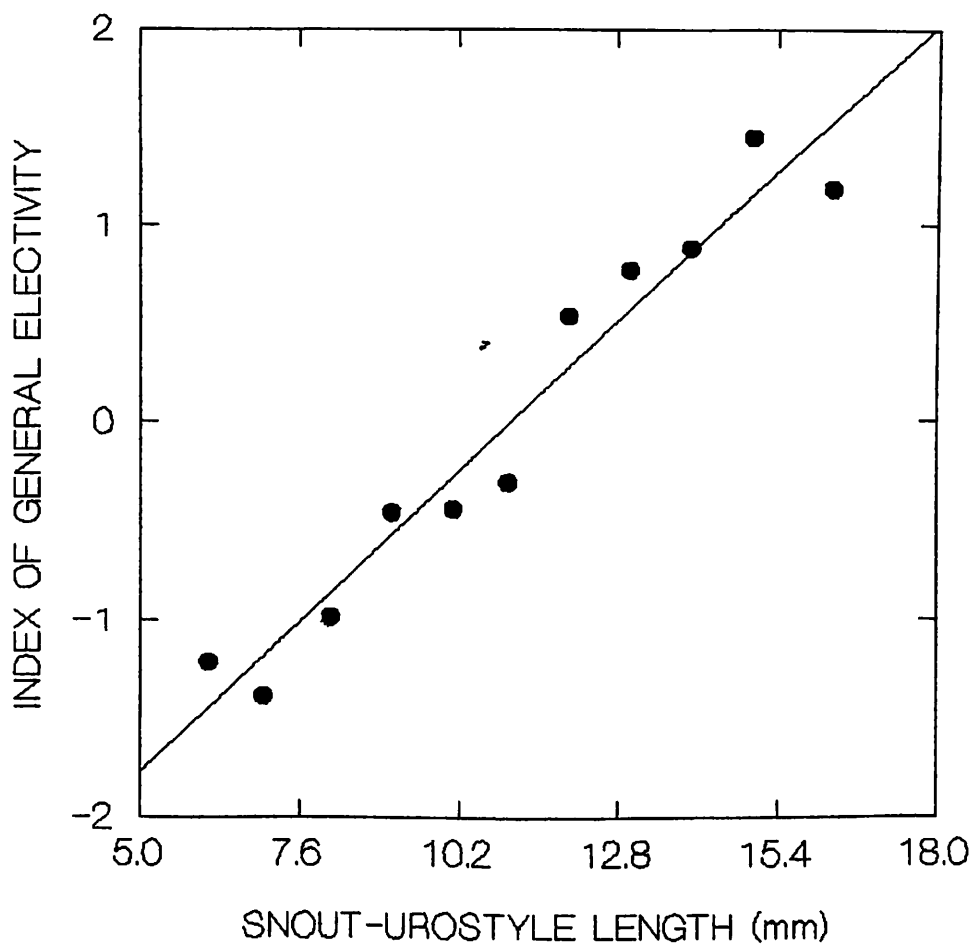


FIGURE 7- Relationship between "general electivity" (GE) (1st principal component summarizing the variation in electivity for Acarina, Collembola, Isoptera, Formicidae, holometabolous larvae and other arthropods) and mean size (MS) of C. stepheni ($GE = -3.229 + 0.292MS$, $F_{1,9} = 153.570$, $r^2 = 0.945$, $P = 0.000$). Each point represents means within intervals of 1.0mm in frog snout-urostyle length.

seasons. I calculated an "general electivity" based on the coefficients from first principal component described above. Analysis of variance showed significant difference between the "general electivities" of the two size classes ($F_{1,28}=39.6$, $P=0.000$). Variation in electivities among different size classes therefore does not appear to be due to an effect of seasonality on prey availability.

The analysis of electivities must be evaluated with care, because the proportions of the types of prey change between the months and this causes significant variation in the index of availability based on the first principal component ($F_{11,206}=2.909$, $P=0.001$). However, the first principal component explained only 13.4% of the monthly variation in the types of prey and there is no relationship between it and the mean ($r^2=0.139$, $F_{1,8}=1,295$, $P=0.288$) or median ($r^2=0.032$, $F_{1,8}=0.261$, $P=0.63$) of frog sizes in corresponding months. Although the monthly mean sizes of frogs are based on samples from the two years before the samples of availability were collected, the pattern of recruitment of C. stepheni, seems to repeat among years (Moreira and Lima, 1991; Allmon, 1991 [this author used the name Colostethus sp.]) and my casual observations in 1990, 1991 and 1992 did not indicate changes in the period of juvenile recruitment.

There was no significant relationship between the indices of

foraging behavior (number of movements, total distance moved, velocity while moving , total area used and time moving) and the mean size of C. stepheni (Fig. 8). The four indices also could not predict the ontogenetic variation in the "general electivity" (1st principal component) (Tab. 3). There was a strong correlation between the indices "total area utilized" and "total distance moved" (Pearson $r=0.86$, $n=45$). Therefore, in the analyses involving activity of foraging and diet, I used only the indice "total area used".

There was no significant relationship between any of the four indices of foraging and the mean size of prey (number of movements - $r^2=0.006$, $F_{1,8}=0.046$, $P=0.836$; time moving - $r^2=0.014$, $F_{1,8}=0.116$, $P=0.743$; velocity while moving - $r^2=0.029$, $F_{1,8}=0.239$, $P=0.638$; total area used - $r^2=0.010$, $F_{1,8}=0.083$, $P=0.781$) and the four indices in concert could not predict the mean size of the prey (Tab. 4). The tests for significant relationships between frog size and electivity (Fig. 6) and frog size and prey size (Fig. 3) have more degrees of freedom in the residual than the tests for the significance of the indices of foraging behavior (Tab. 3 and 4). However, frog size and prey size remain significant even when entered into the analyses with the indices of foraging behavior (Tab. 5 and 6), indicating that frog size is the major determinant of electivity independent of behavioral changes and the loss of degrees of freedom in the multiple regression.

FIGURE 8- Indices of foraging behavior in relation to mean size of C. stepheni. Each graph represents one index of foraging: A - number of movements per 30min ($F_{1,8}=0.669$, $r^2=0.077$, $P=0.437$); B - total area utilized ($\ln(\text{cm}^2)$) ($F_{1,8}=0.020$, $r^2=0.003$, $P=0.890$) ; C - Velocity when moving ($\mu\text{cm/s}$) ($F_{1,8}=0.341$, $r^2=0.041$, $P=0.576$) and D - time moving ($F_{1,8}=0.063$, $r^2=0.008$, $P=0.809$); E - total distance moved in 30 min (cm) ($F_{1,8}=0.081$, $r^2=0.010$, $P=0.783$). Each point represents the means within each interval of 1.0 mm in frog length.

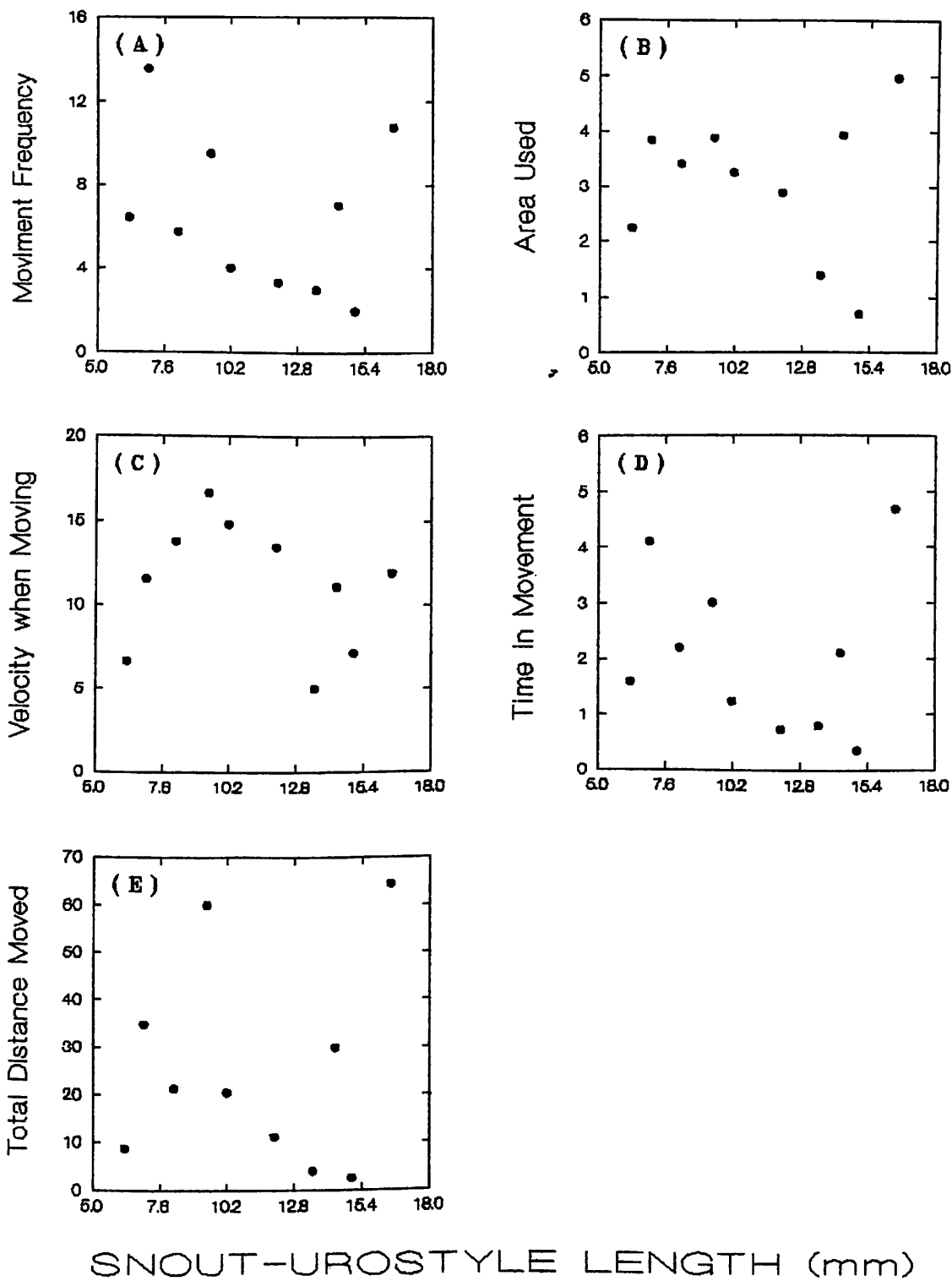


Table 3 - Summary statistics for the regression of the dependent variable "general electivity" on the independent variables: number of movements per 30min (NM), total area used [$\ln(\text{cm}^2)$] (TAU), time moving (PTM) and velocity when moving cm/s (V).

Overall regression

	GL	SQ	MQ	F	P
Regression	5	4.667	1.167	1.116	0.442
Residual	4	5.226	1.045		

Independent contribution of the variables (Partial regressions).

	Coef	T	P
Constant	1.706	1.474	0.201
NM	-0.519	-1.742	0.142
TAU	0.226	0.310	0.769
PTM	0.982	1.054	0.340
V	-0.086	-0.583	0.585

Table 4 - Summary statistics for the regression of the dependent variable mean size of prey on the independent variables: number of movements per 30min (NM), total area used [$\ln(\text{cm}^2)$] (TAU), time moving (PTM), velocity when moving cm/s (V).

Overall regression

	GL	SQ	MQ	F	P
Regression	5	2.035	0.509	0.968	0.499
Residual	4	2.629	0.526		

Independent contribution of the variables (Partial regressions).

	Coef	T	P
Constant	2.408	2.931	0.033
NM	-0.343	-1.623	0.166
TAU	0.245	0.472	0.657
PTM	0.780	1.179	0.291
V	-0.079	-0.749	0.487

Table 5 - Summary statistics for the regression of the dependent variable "general electivity" on the independent variables: number of movements per 30min (NM), total area used [$\ln(\text{cm}^2)$] (TAU), time moving (PTM), velocity when moving cm/s (V) and mean length of the frogs (MLF).

Overall regression

	GL	SQ	MQ	F	P
Regression	5	9.756	1.951	57.016	0.001
Residual	4	0.137	0.034		

Independent contribution of the variables (Partial regressions).

	Coef	T	P
Constant	-2.970	-6.796	0.002
NM	0.042	0.594	0.585
TAU	-0.072	-0.532	0.623
PTM	-0.169	-0.872	0.433
V	0.000	0.004	0.997
MLF	0.297	12.194	0.000

Table 6 - Summary statistics for the regression of the dependent variable mean size of prey on the independent variable: number of movements per 30min (NM), total area used [$\ln(\text{cm}^2)$] (TAU), time moving (PTM), velocity when moving cm/s (V) and mean length of the frogs (MLF).

Overall regression

	GL	SQ	MQ	F	P
Regression	5	4.567	0.913	37.545	0.002
Residual	4	0.097	0.024		

Independent contribution of the variables (Partial regressions).

	Coef	T	P
Constant	-0.891	-2.418	0.073
NM	0.053	0.882	0.428
TAU	0.035	0.306	0.775
PTM	-0.032	-0.195	0.855
V	-0.018	-0.758	0.490
MLF	0.210	10.201	0.001

Discussion

Ontogenetic change in the types and sizes of prey in the diet is common in postmetamorphic anurans (Pengilley, 1971; Labanick, 1976; Christian, 1982; Strüssmann et al., 1984; Woolbright and Stewart, 1987; Donnelly, 1991). The mechanisms that result in this ontogenetic change have not been studied, but many of the differences in the sizes and types of prey among adult anurans of different species are associated with foraging mode (Toft, 1981 and 1985; Strüssmann et al., 1984; Woolbright and Stewart, 1987; Pough and Taigen 1989; Ovaska, 1991).

Foraging mode is not the only mechanism that could lead to differences in types or sizes of prey. For predators of arthropods, ontogenetic changes in electivity for prey types might simply be caused by changes in the electivity for prey size, because the mean size of individuals differs among arthropod orders (Schoener and Jansen, 1968; Dominguez and Salvador, 1990). The smallest arthropods in the leaf litter at Reserva Ducke are collembolans and acarina, intermediate sizes are dominated by Formicidae and Isoptera and the largest arthropods are from other taxa.

Colostethus stepheni shows a strong ontogenetic change in the type and size of its prey. Part of this change is probably due to a change in electivity for prey size. However, after

controlling for the effect of electivity for prey size on the electivity for prey type, there remained a significant relationship between electivity for prey type and the size of frogs. This indicates that C. stepheni, in Reserve Ducke, shows ontogenetic change in electivity for prey types, independent of the ontogenetic change in electivity for prey size.

A large proportion of the diet of small Colostethus stepheni consists of mites. This is, expected for a small anuran that lives in tropical-forest litter (Simon and Toft, 1991). However, C. stepheni of all sizes have negative electivity for mites. Simon and Toft (1991) suggest that mites are hard to digest in comparison with bigger prey, and optimal foraging theory (Schoener, 1979), suggests that bigger frogs should select bigger prey. However, the negative electivity for mites in C. stepheni is not only because of their small size. Electivity for mites is also negative in comparison with other prey types that are of similar size (eg. collembolas).

Mites are apparently prey of low nutritive value, but constitute a large proportion of the diet of several species of small anurans (Lieberman, 1986; Donnelly, 1991; Simon and Toft, 1991; this study). This is probably because they are the most common arthropods in the soil and litter in most places in the world (Simon and Toft, 1991). The only place where anurans apparently have positive electivity for mites is Panguana, Peru

(Simon and Toft, 1991). However, in that study, mites were estimated as only 4% of the litter-arthropod fauna. This is an order of magnitude less than the proportion of mites in Central Amazonia (this study) and in other places in the world (Simon and Toft, 1991). Other studies will be necessary to determine the cause of the anomolous situation in Panguana.

Four indices that have been used to quantify foraging mode in anurans and lizards (number of movements, total area used, time moving and velocity when moving) were not associated with the ontogenetic change in electivity for sizes or types of prey in C. stepheni. These indices, which can predict the diet of adult frogs and lizards, reflect the general activity while foraging. Apparently, the behavioral changes that cause the ontogenetic change in the types and sizes of arthropods in the diet of C. stepheni are subtler than shifts in general activity during foraging.

The relationships among the species in a community can depend on the age structure of the populations. For this reason, descriptions of niches in communities based only on adults could yield erroneous predictions (Christian, 1982; Werner and Gilliam, 1984). The food niches of C. stepheni change with the age structure of the population and it is likely that juveniles are important components in the communities in which the species occurs (Moreira and Lima, 1991). Eleutherodactylus coqui

(Woolbright and Stewart, 1987), E. johnstonei (Ovaska, 1991) and Dendrobates pumilio (Donnelly, 1991) also show ontogenetic changes in their food niches. These species also occur in diurnal leaf-litter anuran assemblages, though E. coqui and E. johnstonei are not exclusively diurnal. Descriptions of niche partitioning in communities of diurnal leaf-litter frogs in the neotropics and Africa are based mainly on the studies of Toft (1980a, 1981, 1982). She concluded that the species use different sizes and types of prey, but her studies were based only on adults. Studies that take into consideration ontogenetic changes in diet and seasonal changes in the structure of populations will be necessary to evaluate completely the realized overlap among diets of the species in these communities.

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