

INFLUENCE OF MICROHABITAT ON THE TROPHIC ECOLOGY OF TWO LEPTODACTYLIDS FROM NORTHEASTERN ARGENTINA

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ABSTRACT: We analyzed trophic ecology and its relationship with environmental variables for two leptodactylid species, *Leptodactylus latinasus* and *L. bufonius* (Anura: Leptodactylidae). The two species are common around Corrientes City, Argentina, where they live in the same habitat. The main objectives were to analyze the diets and patterns of coexistence relative to the microhabitat of each species. Weekly sampling was carried out January 1997–February 2000. A randomization test and canonical correspondence analysis (CCA) were used for data analysis. In *L. latinasus*, the diet was dominated numerically by isopterans and coleopterans (25.25% and 21.21%, respectively) and volumetrically by insect larvae (37.14%). In *L. bufonius*, the alimentary contents were dominated numerically by isopterans (60.49%) and volumetrically by coleopterans (62.47%). The trophic niche breadth was wider in *L. latinasus* (6.55) than *L. bufonius* (2.44). The overlap in the trophic niche (prey proportion) was higher ($O_{jk} = 0.81$) and significantly greater than the expected mean value obtained by chance (0.27). Spatial niche overlap between the two species was low ($O_{jk} = 0.331$) and not significantly different than the mean value expected by chance (0.52). Differences in microhabitat use were observed. While *L. latinasus* showed strong preference for mud, ground with crevices, and short grass and mud, *L. bufonius* showed preferences for dry land and short grass. In addition, the presence of this species was positively correlated with temperature and rainfall variables. Niche complementarity was observed between these species; although they exhibit high overlap in food, they tended to have low overlap in microhabitat use.

Key words: Anura; *Leptodactylus bufonius*; *Leptodactylus latinasus*; Microhabitat use; Niche complementarity; Subtropical area; Trophic ecology

THE VARIATION in resources used by two sympatric amphibian species may not necessarily reflect competition. Empirical research shows that species can differ in three main categories of resource dimensions: food, habitat, and time of activity (Pianka, 1975; Schoener, 1974; Toft, 1980, 1981). The study of trophic relationships among sympatric species is crucial to understanding interspecific interactions (Duré and Kehr, 2001). Some differences in food resource use between two species may be caused by different foraging patterns and microhabitat use. Within the limitations imposed by evolutionary history, exploitation of particular prey by a species can influence the interactions of that species in a particular environment and, hence, may determine activity periods, reproductive features, and predator–prey interactions (Caldwell, 1996; Polis, 1991; Polis et al., 1989).

A first step in studying and analyzing the roles of individual species in communities is to gather detailed ecological and natural history information. Studies that proceed without a

basic knowledge of the natural history of each species run the risk of producing irrelevant results. In fact, conceptual-based questions must be assumed within the framework of the ecology of individual species if they are to be examined and interpreted appropriately (Greene, 1986; Vitt et al., 2002).

Leptodactylus latinasus and *L. bufonius* are two common species sharing habitats in northeastern Argentina. Both leptodactylid species are present virtually year-round in the study area. *Leptodactylus latinasus* is distributed in Argentina in the provinces of: Buenos Aires, Córdoba, Santa Fé, Chaco, Formosa, Entre Ríos, Corrientes, and Misiones, and it also occurs in Uruguay and southern Brazil (Ceï, 1980). The distribution of *L. bufonius* in Argentina is scattered throughout the chacoan range, southern localities in San Luis, in the north of San Juan province, in Corrientes, and north of Santa Fé provinces. It also occurs in Paraguay and Bolivia.

Both species belong to the *fuscus* group within the genus *Leptodactylus*. They exploit the same habitats for reproduction. Male *L. latinasus* call on the ground near water that is

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hidden in crevices or land depressions and will be flooded eventually. *Leptodactylus bufonius* males build cone-shaped nests that rise up from the ground. The depression fills with water, and the mud nests fall (Cei, 1980; Crump, 1995).

The main objectives of this study were: (1) to classify and quantify the prey consumed by both species, (2) to calculate the niche width and diversity of the diet of *L. latinasus* and *L. bufonius*, and (3) to establish the relationship between microhabitat, diet, and foraging strategy used by the two species.

MATERIALS AND METHODS

Study Area

The study area is located approximately 15 km east of Corrientes City (27° 30' S, 58° 45' W); it is characterized by many temporary, semi-permanent, and permanent ponds. Biogeographically, the area belongs to the Chaqueño Domain, Oriental District Chaqueño (Cabrera and Willink, 1980; Carnevali, 1994). The mean annual precipitation is 1500 mm, and the mean annual temperature is 23 C. The predominant vegetation of the study area is the forest, with herbaceous strata composed of gramineous, numerous cacti and terrestrial bromeliads.

Data Analysis and Analytical Procedure

Diet was analyzed by the two general categories of size and taxon. Weekly sampling was carried out January 1997–February 2000. We captured frogs by hand, using visual encounters surveys (Crump and Scott, 1994). Specimens were immediately fixed in 10% formalin and deposited in the Centro de Ecología del Litoral (CECOAL-CONICET).

Microhabitat categories recorded for individual frogs were: short grass (<10 cm high) inside forest in dry place, short grass (<10 cm high) in places with mud, places with mud alone, crevice land (either in dry or muddy places), and dry land. We also recorded rainfall by month, temperature, and month and year when the animals were captured.

Sex (detected by examination of gonads and external nuptial features), body length (mm), and maximum mouth width (mm) were recorded for each individual. Diets were analyzed by removing the complete alimentary

canal, as recommended by Schoener (1989), for individuals with few prey items. Prey were only included that had at least 70% of their body undigested. All measurements were taken with calipers to the nearest 0.01 mm. Prey were determined to order using keys of Brewer and Arguello (1980) and Coronado Padilla and Marquez Delgado (1978). The individual volume of each prey item and the number of prey items per stomach for each prey category were recorded. Volume of each prey item was estimated using the formula for an ellipsoid,

$$V = 4/3\pi(1/2L)(1/2W)^2$$

where V is volume, L is length, and W is width (Dunham, 1983). The diversity index used was the Shannon index (H') (Shannon and Weaver, 1949),

$$H' = -\sum_{j=1}^s p_j \ln p_j$$

where p_i is the proportion of the resource (prey item) in the diet, \ln = natural logarithm, and s = total number of species (prey). The niche breadth was calculated using the index of Levins (Levins, 1968),

$$Nb = \left(\sum p_{ij}^2 \right)^{-1}$$

where p_{ij} represents the probability of finding the item i in the sample j .

We calculated dietary overlaps in two ways by considering the food proportions and the volume of each prey with the formula (Pianka, 1973):

$$O_{jk} = \frac{\sum_{i=1}^n P_{ij}P_{ik}}{\sqrt{\sum_{i=1}^n P_{ij}^2 \sum_{i=1}^n P_{ik}^2}}$$

where P_{ij} and P_{ik} are the proportions of utilization of the i_{th} food resource by the j_{th} and k_{th} species, respectively. The overlap values vary from 0–1. Overlap values of 1.0 indicate identical diets or food volume, whereas overlap values of 0 indicate no similarity in diets or food volume. To determine whether measured overlap values differed from what would be expected based on a random sampling of the species data, we performed a randomization analysis through the EcoSim software (Gotelli and Entsminger, 2003). EcoSim performs

Monte Carlo randomizations to create “pseudo-communities” (Pianka, 1986), and then statistically compares the patterns in these randomized communities with those in the real data matrix. In this analysis (randomization algorithms RA3; Winemiller and Pianka, 1990), “scrambled zeros”, and all values of the original matrix were randomized 1000 times, and the niche breadth was retained for each species. In other words, the algorithms retained the amount of specialization for each species (Gotelli and Entsminger, 2003).

Relationships between microhabitat and diet and foraging strategy by the two species were tested through a canonical correspondence analysis (CCA; Ter Braak, 1986, 1987). The CCA is a multivariate direct gradient analysis method derived from correspondence analysis, but has been modified to allow environmental data to be incorporated into the analysis. It is calculated using the reciprocal averaging form of correspondence analysis. However, at each cycle of the averaging process, a multiple regression is performed of the sample scores on the environmental variables. New site scores are calculated based on this regression, and then the process is repeated and continued until the scores stabilize. The result is that the axes of the final ordination, rather than simply reflecting the dimensions of the greatest variability in the species data, are restricted to linear combinations of the environmental variables and the species data. The CCA test was performed using MVSP software (Kovach, 1999). All data were transformed to natural logarithms (Ln) before tests were run.

Parametric tests were used to establish the relationship between the morphology of the predator and the volume of the prey (Kehr, 1994; Zar, 1996). When assumptions of normality were broken, the data were natural logarithms (Ln) transformed. All means are presented as mean \pm standard deviation.

RESULTS

Leptodactylus latinasus Diet

Seventy individuals (males = 43, females = 27) were captured January 1997–February 2000 (Fig. 1). All individuals had identifiable stomach or intestinal contents. The diet consisted of 15 types of prey (Table 1) and

was dominated numerically by isopterans and coleopterans (25.25% and 21.21%, respectively) and volumetrically by insect larvae (37.14%). Coleopterans were the most frequently represented prey in 28 individuals (40% of adults).

Prey diversity was 2.14. Niche breadth was 6.55. The difference between the body length and mouth width between the sexes was not significant (t -Student Test [body length] = -1.41 , $df = 68$, $P = 0.16$; t -Student Test [width mouth] = -0.32 , $df = 68$, $P = 0.75$). The mean body length of males ($n = 43$) was 27.7 ± 2.2 mm and for females ($n = 27$) was 28.5 ± 2.4 mm. The mean mouth width of males ($n = 43$) was 8.2 ± 1.4 mm and for females ($n = 27$) was 8.3 ± 1.4 mm.

A positive and significant correlation existed between Ln body length (independent variable) and Ln mouth width (dependent variable) ($\text{Ln } y = -2.779 + 1.464 \text{ Ln } x$; $n = 70$; $r = 0.66$; $F_{(1,68)} = 54.49$; $P < 0.001$). Mean prey volume for was not correlated with Ln mouth width ($r = 0.09$; $n = 70$; $F_{(1,68)} = 0.67$; $P = 0.41$). Prey number/stomach was not correlated with Ln body length ($r = -0.21$; $n = 70$; $F_{(1,68)} = 3.19$; $P = 0.08$).

The individuals analyzed were captured mainly in areas with short grass (<10 cm) and muddy ground. This species also prefers to stay inside loamy cracks, especially during winter when rains are infrequent.

Leptodactylus bufonius Diet

Twenty individuals were captured January 1997–February 2000 (Fig. 1). All had identifiable stomach or intestinal contents. The diet consisted of seven types of prey (Table 1). The alimentary contents were dominated numerically by isopterans (60.49%) and volumetrically by coleopterans (62.47%).

Coleopterans were present in eight individuals (40% of stomachs analyzed) and were the prey most frequently represented. Prey diversity was 1.26, and niche breadth was 2.44. The difference in body length and mouth width between the sexes was not significant (t -Student Test [body length] = 0.121 , $df = 18$, $P = 0.452$; t -Student Test [mouth width] = 1.27 , $df = 18$, $P = 0.11$). The mean body length of males ($n = 12$) was 44.2 ± 4.2 mm and for females ($n = 8$) was 43.8 ± 6.9 mm. The mean mouth width of males ($n = 12$) was

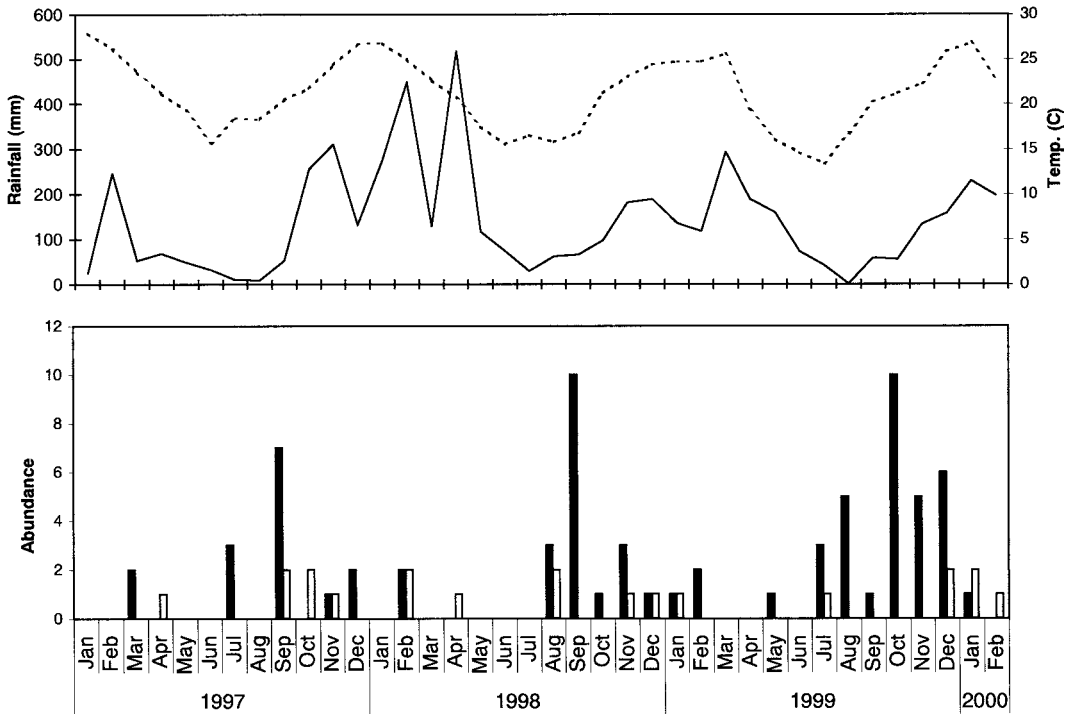


FIG. 1.—Abundance of *Leptodactylus latinasus* (black bar) and *L. bufonius* (white bar) from Corrientes, Argentina, from January 1997–February 2000. The upper figure represents rainfall (mm) (solid line) and temperature (C) (broken line) for the study period.

14.6 \pm 1.9 mm and for females ($n = 8$) was 13.5 \pm 1.9 mm.

There was a positive and significant correlation between Ln body length (independent variable) and Ln width of the mouth (dependent variable) ($\text{Ln } y = -0.828 + 0.92 \text{ Ln } x$; $n = 20$; $r = 0.79$; $F_{(1, 18)} = 29.72$; $P < 0.001$). Mean prey volume was not correlated with Ln mouth width ($r = 0.22$; $n = 20$; $F_{(1, 18)} = 0.97$, $P = 0.33$). Furthermore, Ln body length was not correlated with number of prey/stomach ($r = 0.35$; $n = 20$; $F_{(1, 18)} = 2.57$, $P = 0.12$). All individuals were captured in short grass and on dry land.

Comparison Between Diets of Two Species

The trophic niche overlap (prey proportion) between the species was high ($O_{jk} = 0.81$). Randomizations with all data produced a significant difference between measured (observed) overlaps and simulated (expected) overlaps using diet proportion (P [observed \leq expected] = 1.00, and P [observed $>$ expected] = 0.001). Therefore, the observed

mean (0.81) was greater than the expected mean value by chance alone (0.27 ± 0.17).

Trophic niche overlap by prey volume was low ($O_{jk} = 0.35$). Randomizations with all data produced no difference between measured (observed) overlaps and simulated (expected) overlaps using diet volume (P [observed \leq expected] = 0.81, and P [observed $>$ expected] = 0.18). The observed mean (0.35) was similar to that expected by chance (0.22 ± 0.20).

Comparison of Microhabitats

The spatial niche overlap between the two species was low ($O_{jk} = 0.33$). Randomizations with all data produced no significant difference between measured (observed) overlaps and simulated (expected) overlaps using microhabitats (P [observed \leq expected] = 0.18, and P [observed $>$ expected] = 0.82). Thus, the observed mean (0.331) was similar to that expected by chance (0.52 ± 0.22).

Leptodactylus bufonius was more frequently encountered in short grass (<10 cm high)

TABLE 1.—Types of prey in the diets of *Leptodactylus latinasus* ($n = 70$) and *Leptodactylus bufonius* ($n = 20$) from northeastern Argentina.

Prey category	<i>Leptodactylus latinasus</i>					<i>Leptodactylus bufonius</i>				
	<i>n</i>	%	Volume (cm ³)	% of volume	Frequency of occurrence	<i>n</i>	%	Volume (cm ³)	% of volume	Frequency of occurrence
INSECTA										
Coleoptera	42	21.21	0.2496	14.09	28	14	17.28	1.102	62.47	8
Hemiptera	3	1.51	0.0395	2.23	2	—	—	—	—	—
Hymenoptera (ants)	28	14.14	0.0665	3.75	18	6	7.40	0.075	4.25	5
Hymenoptera (no ants)	1	0.50	0.00016	0.009	1	6	7.40	0.249	14.11	3
Diptera	18	9.09	0.0263	1.48	12	—	—	—	—	—
Isoptera	50	25.25	0.1467	8.28	6	49	60.49	0.180	10.20	4
Homoptera	13	6.56	0.0218	1.23	10	3	3.70	0.017	0.96	2
Mantodea	2	1.01	0.0122	0.68	2	—	—	—	—	—
Trichoptera	1	0.50	0.0011	0.062	1	—	—	—	—	—
Orthoptera	2	1.01	0.2850	16.09	2	—	—	—	—	—
Collembola	7	3.53	0.0020	0.11	4	—	—	—	—	—
Lepidoptera	2	1.01	0.0995	5.61	2	2	2.46	0.136	7.70	2
Larvae	14	7.07	0.6578	37.14	12	1	1.23	0.005	0.28	1
ARACHNIDA										
Araneae (spiders only)	10	5.55	0.1630	9.20	10	—	—	—	—	—
Acari (mites)	4	2.02	0.0000014	0.00008	2	—	—	—	—	—
TOTAL	197	100.00	1.771	100.00	—	81	100.00	1.764	100.00	—

inside the forest in dry places and on dry land. In contrast, *L. latinasus* preferred short grass near ponds, with mud and with ground crevices. *Leptodactylus bufonius* generally preferred relatively dry land.

Correlations Between Prey and Microhabitats

The CCA indicated high correlations between the variable scores (prey items) and case scores (two species) relative to environmental variables. The first two axes of the CCA accounted for 56% of the variation in the variable scores and case scores relative to the environmental variables. A biplot of environmental variables and CCA variable scores on the first two ordination axes indicated that lepidopterans and isopterans were associated with dry land, while hemipterans, hymenopterans, and coleopterans were correlated with short grass (Fig. 2). The larvae, homopterans and spiders were associated mainly with mud, crevice land, and month. Mites, trichopterans, collembolans, orthopterans and ants were associated with short grass and mud.

A biplot with the species preferences (defined here as their microhabitat of highest abundance) on the environmental variables also showed a clustered distribution in ordination space, revealing strong preferences for

particular microhabitat (Fig. 3). *Leptodactylus bufonius* preferred dry land, short grass, and correlated positively with temperature and rainfall variables (Figs. 1, 3). In contrast, *L. latinasus* preferred mud, crevice land, short grass and mud, and were correlated with months (Figs. 1, 3). A few *L. latinasus* preferred dry land and short grass.

DISCUSSION

We initially hypothesized that *L. latinasus* and *L. bufonius* exploit the same habitats and consume the same types of prey because they were observed feeding together in the same habitat. We found, however, that *L. latinasus* had a wider trophic niche (Levin's index: 6.55) than *L. bufonius* (Levin's index: 2.44), and the former consumed eight prey categories that were not eaten by the latter species (hemipterans, dipterans, mantodeans, trichopterans, Orthopterans, collembolans, spiders, and mites). *Leptodactylus latinasus* has a body length and mouth width significantly smaller than *L. bufonius*. However, the lack of correlation between the volume of prey and the width of the mouths of predators suggests that both species look for small and medium-sized prey. Although isopterans were the most frequent food item for both species, they

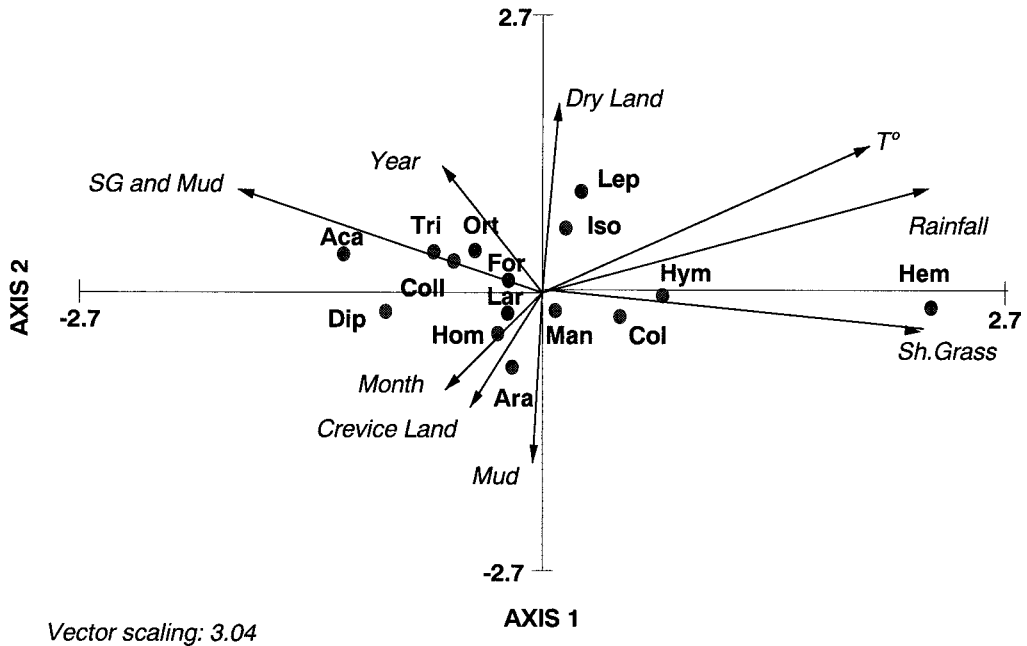


FIG. 2.—Biplot of canonical correspondence analysis results for prey item. Points are prey items eaten by the two amphibian species, *Leptodactylus bufonius* and *L. latinasus*. Names of Prey: Aca.: Acari; Ara.: Aranae; Col.: Coleoptera; Coll.: Collembola; Dip.: Diptera; For.: Formicidae; Hem.: Hemiptera; Hom.: Homoptera; Hym.: Hymenoptera (not ants); Iso.: Isoptera; Lar.: Larvae; Lep.: Lepidoptera; Man.: Mantodea; Ort.: Orthoptera, and Tri.: Trichoptera. Arrows represent environmental variable scores (arrowhead position) and direction of environmental gradients.

represented a larger proportion of the diet in *L. bufonius*. Coleopterans were also important in the diet of *L. latinasus*. Volumetrically, in *L. latinasus*, insect larvae were very important, whereas in *L. bufonius* coleopterans were important. *Leptodactylus bufonius* shows a clear tendency to eat clumped prey (isoptera), whereas *L. latinasus* consumes clumped prey (isoptera) and relatively mobile prey (coleopterans).

Considering the type and prey proportion, *L. latinasus* appears to be a generalist with a foraging strategy that can be considered intermediate of a sit-and-wait and an actively foraging predator. A typical sit-and-wait predator has a low metabolic rate, the prey are active, the encounter rate with prey is low, niche breadth is wide, and the sensory mode is visual (Perry and Pianka, 1997). This species also selected some sedentary prey (insect larvae), and, for that, the predator would change from sit-and-wait behavior to actively foraging. Most reviews of foraging strategy have emphasized that active foragers search for their prey (e.g., Bell, 1991; Owen, 1980).

Similar behavior is observed with isoptera because the predator (as active) needs to encounter the colony. After that, the predator can act as a sit-and-wait predator. Under this situation, the frequency of prey passing within capture range of the frog likely is correlated with the frequency of feeding. The feeding behavior of *L. latinasus* is variable because this species is common in many microhabitats. The spatial niche of *L. latinasus* is wide, and the prey diversity is great.

Leptodactylus bufonius is a predator whose foraging pattern is also identified as generalist, although less so than *L. latinasus*. The proportionately higher number of termites in the *L. bufonius* diet resulted in a low diversity index and in a narrower niche breadth. The foraging strategy can be considered intermediate of a sit-and-wait and active predator, similar to the behavior of *L. latinasus*.

Niche breadth of prey proportion for the two species was significantly overlapping ($O_{jk} = 0.81$), indicating a similarity between the diets. The traditional interpretation of this pattern has been that a significantly large

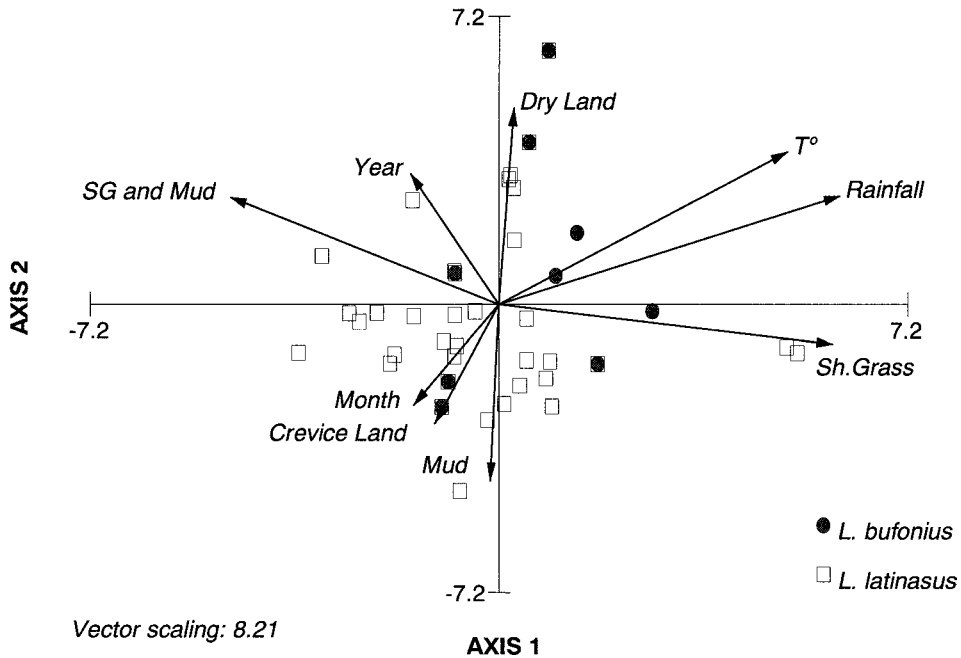


FIG. 3.—Biplot of canonical correspondence analysis results for the amphibian species *Leptodactylus bufonius* and *L. latinasus*. Points are individuals of both species that can be interpreted as preferences based on abundance. Arrows represent environmental variable scores (arrowhead position) and direction of environmental gradients.

overlap indicates shared resource utilization and a lack of competition (Gotelli and Graves, 1996). However, it is also possible that high overlap implies the potential for strong competition that has not yet led to divergence in resource use (Connell, 1980; Sale, 1974). Either scenario is possible, and additional data on resource availability and species interactions are necessary. We suggest that competitive interactions between species are infrequent because trophic resources in the area appear to be sufficient to satisfy demand and because the species generally use different microhabitats. Additionally, trophic niche overlap for prey volume was low ($O_{jk} = 0.35$) and not significant. The spatial niche overlap between the two species was also low ($O_{jk} = 0.331$) and not significant. In summary, we suggest that these species exhibit niche complementarity: they display high overlap in diet but low overlap in microhabitat. Recently, Cunha and Vieira (2004) remarked the importance of space use in the organism's ecological niche affirming that differentiation in space use might counteract complete overlap in diet. With space as the most important niche dimen-

sion, analysis of space use patterns becomes a central requisite to study species coexistence.

RESUMEN

En este trabajo analizamos la influencia del microhabitat sobre la ecología trófica de dos especies de anfibios, *Leptodactylus latinasus* y *L. bufonius* (Anura: Leptodactylidae). Estas dos especies son comunes en el área estudiada y se las halla compartiendo el mismo hábitat. El objetivo principal fue analizar las dietas y registrar la superposición de sus nichos tróficos y espacial. Los muestreos fueron realizados de manera semanal entre los años 1997 y 2000. El análisis de la información fue realizado mediante un test aleatorio ("Randomization Test") y el Análisis Canónico de Correspondencia (CCA). La superposición de nichos fue observada mediante el índice de Pianka y la amplitud del nicho a través del índice de Levins. En la dieta de *L. latinasus*, los isópteros y los coleópteros fueron los que dominaron numéricamente (25.25% y 21.21%, respectivamente), mientras que volumétricamente fueron las larvas de insectos (37.14%). En *L. bufonius*, los isópteros dominaron

numéricamente (60,49%), mientras que volumetricamente los más importantes fueron los coleópteros (62,47%). El nicho trófico fue más amplio en *L. latinasus* (Índice de Levins: 6,55) con relación al de *L. bufonius* (Índice de Levins: 2,44). El solapamiento del nicho trófico (proporción de las presa) entre las dos especies fue elevado (Ojk [Índice de Pianka] = 0,81) y significativamente mayor que el valor esperado obtenido por un test aleatorio "Randomization Test" (0,27). El solapamiento de las dos especies en el nicho espacio (microhabitat) fue bajo (Ojk = 0,331) sin registrarse una diferencia significativa con respecto al valor teórico calculado por un test aleatorio (0,52). Mientras los individuos de *L. latinasus* mostraron una marcada preferencia por áreas caracterizadas por: barro, suelo agrietado, pasto corto con barro, los de *L. bufonius* tuvieron preferencia por zonas con tierra seca y pasto corto. En síntesis, en este estudio fue comprobada una complementariedad de los nichos: mientras ambas especies exhiben una elevada superposición en el nicho trófico, sin embargo se observó un bajo solapamiento en los microhabitats utilizados.

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