

Differential Exploitation of Trophic Resources by Two Pseudid Frogs from Corrientes, Argentina

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The study of trophic relationships among sympatric species is critical to understanding interspecific interactions. Two species of the neobatrachian family Pseudidae, *Lysapsus limellus* and *Pseudis paradoxa*, are common in permanent ponds covered with floating vegetation (e.g., *Hydrocleys* sp.; Parodi, 1980). Both species use floating vegetation as a substrate for feeding. In Argentina, these species are largely sympatric in the provinces of Formosa, Chaco, Santa Fé, Corrientes, and Entre Ríos (24°00'S–33°00'S; and 56°00'W–62°00'W; Cei, 1980; Gallardo, 1987). *Lysapsus limellus* generally prefers thickly vegetated semipermanent or permanent ponds (Kehr and Basso, 1990), whereas *P. paradoxa* strongly prefers permanent ponds with abundant vegetation (Dixon et al., 1995; pers. obs.). In Corrientes, the two species commonly occur in the same permanent aquatic habitats. This study describes the diet and foraging patterns of *P. paradoxa* and *L. limellus* and compares them by examining the degree of trophic niche overlap.

The individuals analyzed were captured in a permanent pond located 15 km from the city of Corrientes (27°30'S, 58°45'W), province of Corrientes, Argentina. The pond was circular, with a diameter of approximately 60 m and a maximum depth of approximately 1.5 m in the pond center. Sampling took place approximately every seven days from November 1996 to May 1997. Frogs were captured by hand or a net, sometimes from a small boat. An attempt was made to sample all pond microhabitats. Specimens were immediately fixed in 10% formalin and deposited in the Centro de Ecología del Litoral (CECOAL) collection. Sex (determined by examination of gonads and external nuptial features), body length (mm), and maximum mouth width (mm) were recorded for each individual.

Prey was obtained by removing the complete ali-

TABLE 1. Types of prey in the diets of *Lysapsus limellus* and *Pseudis paradaxa*.

Prey category	<i>Pseudis paradaxa</i>				<i>Lysapsus limellus</i>				
	N	%	Volume (cm ³)	% of volume	N	%	Volume (cm ³)	% of volume	Frequency of occurrence
INSECTA									
Orthoptera	2	3.17	0.17000	7.025	3	1.37	0.07000	13.550	3
Diptera	25	39.68	0.04000	1.653	137	62.84	0.20000	40.470	36
Hymenoptera	3	4.76	0.25000	10.331	8	3.66	0.00800	1.570	8
Hymenoptera (Formic.)	1	1.58	0.00030	0.012	1	0.45	0.00010	0.019	1
Hemiptera	5	7.93	0.23000	9.504	6	2.75	0.01600	3.140	3
Larvae	3	4.76	0.02000	0.826	2	0.91	0.00100	0.190	2
Odonata	—	—	—	—	1	0.45	0.03600	7.070	1
Lepidoptera	2	3.17	0.24000	9.917	—	—	—	—	—
Coleoptera	13	20.63	0.41000	16.942	5	2.29	0.00800	1.570	3
Collembola	2	3.17	0.00007	0.003	4	1.83	0.00020	0.039	4
Homoptera	1	1.58	0.03600	1.488	7	3.21	0.02500	4.900	5
ARACHNIDA									
Araneae (spiders only)	3	4.76	0.02800	1.157	1	0.45	0.00020	0.004	1
Acari (mites)	—	—	—	—	39	17.88	0.00002	0.004	4
MOLLUSCA									
Gasteropoda	1	1.58	0.00050	0.021	—	—	—	—	—
VERTEBRATA									
Osteichthyes	—	—	—	—	4	1.83	0.14000	27.500	1
Amphibia	2	3.17	1.00000	41.322	—	—	—	—	—
TOTAL	63	100.00	2.42000	100.000	218	100.00	0.50000	100.000	—

TABLE 2. Summary of morphological data and trophic features of *Lysapsus limellus* and *Pseudis paradoxa* ($\bar{x} \pm 1$ SD).

	<i>Pseudis paradoxa</i>	<i>Lysapsus limellus</i>
Body length (mm)	39.60 (\pm 5.20)	16.90 (\pm 2.70)
Mouth width (mm)	15.10 (\pm 1.40)	5.60 (\pm 0.50)
Mean prey diversity (H' Shannon's index)	1.73 (\pm 0.24)	0.94 (\pm 0.28)
Niche breadth (Levins Index)	4.58	2.31
Foraging patterns	Generalist	Generalist
Strategy	Active forager	Active forager

mentary canal, as suggested by Schoener (1989) for individuals with few prey items. Prey were identified to the order level using the keys of Brewer and Arguello (1980) and Coronado Padilla and Marquez Delgado (1978). The number of prey items per stomach for each prey category and the individual volume of each prey item were recorded. Volume of each prey item was estimated using the formula for an ellipsoid (Dunham, 1983). All measurements were taken with a calipers to the nearest 0.01 mm. Prey were only included if at least 70% of their body was undigested. Prey diversity and niche breadth were calculated using Shannon's index (Shannon and Weaver, 1949) and the Levins' index (1968), respectively. Niche overlap was calculated using the "general overlap" (GO) measure introduced by Petraitis (1979) and discussed by Ludwig and Reynolds (1988), which is based on the probability that the utilization curve of one species could have been drawn from that of another species. Parametric and nonparametric tests were used to establish the relationship between the predator's morphology and the prey's volume (Kehr, 1994; Zar, 1996).

A total of 125 individuals were captured (*Pseudis paradoxa*: $N = 50$; *Lysapsus limellus*: $N = 75$), of which 67 had identifiable stomach or intestinal contents (*P. paradoxa*: $N = 21$; *L. limellus*: $N = 46$). The *P. paradoxa* sample consisted of 14 females and 7 males, and *L. limellus*, 29 females and 17 males. Each species contained 13 types of prey (Table 1). In *L. limellus*, the alimentary contents was dominated numerically and volumetrically by dipterans, whereas that of *P. paradoxa* was dominated numerically by dipterans but volumetrically by amphibians. The mean diversity index was greater for *P. paradoxa* ($\bar{x} = 1.73 \pm 0.24$) than *L. limellus* ($\bar{x} = 0.94 \pm 0.28$; Table 2). Values of niche breadth revealed that *P. paradoxa* had a wider trophic niche (4.58) than *L. limellus* (2.31). However, both species exhibited a positive correlation between body length and width of the mouth [*L. limellus*: $y = 0.31 + 0.14x$; $r^2 = 0.52$; ANOVA, $F = 47.5$, $P < 0.001$; $N = 46$]; [*P. paradoxa*: $y = 0.50 + 0.25x$; $r^2 = 0.85$; ANOVA, $F = 106.85$, $P < 0.001$; $N = 21$]. Mean prey volume for *L. limellus* was not correlated with mouth width ($y = -0.013 + 0.03x$; $r^2 = 0.031$; ANOVA, $F = 1.41$, $P > 0.05$; $N = 46$); however, this relationship was linear, positive, and significant for *P. paradoxa* ($y = -0.400 + 0.29x$; $r^2 = 0.25$; ANOVA, $F = 6.31$, $P < 0.05$; $N = 21$). The Petraitis niche overlap index indicated that the diet of the two species was significantly different (V

$= 25.44$; $g1 = 15$; $P = 24.99$). Although we did not find significant differences in the volumes of dipterans and coleopterans consumed by the two species, *P. paradoxa* consumed prey of greater size than did *L. limellus*, as shown by the significant difference in volume of hymenopterans (Diptera = Mann-Witney U -test = 101.50; $P = 0.81$; Coleoptera = $U = 21$; $P = 0.06$; Hymenoptera = $U = 24$; $P = 0.01$). Significant differences were not observed in the diet between the sexes in either species (*L. limellus*: $V = 12.37$, $df = 12$, $P = 21.02$; *P. paradoxa*: $V = 10.37$, $df = 12$, $P = 21.02$).

Considering the type and proportion of prey in the diets, both species could be considered generalists (Toft, 1981). Toft (1981) suggested that a series of intermediate possibilities exists between the two extreme strategies of sit-and-wait forager and active forager. From the morphological features of these frogs, and the type and number of prey consumed, *L. limellus* would be classified nearer to the extreme of active foraging. *Pseudis paradoxa*, however, consumed larger, but fewer, prey and has a robust body with a large mouth. Therefore, we also consider it to be an active foraging species, although not to the degree of *L. limellus*.

We originally hypothesized that *P. paradoxa* and *L. limellus* exploit the same microhabitats and consume the same types of prey because they were observed feeding from the leaves of floating aquatic plants (pers. obs.). Nevertheless, significant differences were observed in diet composition as reflected by differences in the proportion and size of items consumed. The difference in body size observed between the species seems sufficient to explain the difference in prey volume, as the smaller mouth width would prevent smaller individuals from consuming large prey (Schoener, 1979; Dickman, 1988). However, prey size selection is not independent of prey type selection because different types of prey have different sizes (Pimentel Lima, 1998). *Pseudis paradoxa* consumed three prey categories that were not eaten by *L. limellus* (lepidopterans, gastropods, and amphibians) all of which reach relatively large dimensions. However, large numbers of *Acari* were present in the diet of *L. limellus*. Although these small arthropods are available in large numbers, they are difficult to digest (Simon and Toft, 1991). We hypothesize that for *P. paradoxa* the selection of this prey type would not be profitable owing to the cost-benefit ratio; they would need to consume large quantities of *Acari* to obtain sufficient energy (Krebs and Davies, 1978; Dickman, 1988). The proportionately high number of dipterans in the diet of *P. paradoxa*, even though they formed the lowest volume, is suspected to be a result of the abundance of these insects in the sampled area. *Lysapsus limellus* also ate a large number of dipterans, significantly more than *P. paradoxa*. Niche breadth was larger for *P. paradoxa* than for *L. limellus*. *Pseudis paradoxa* consumed a broad variety of prey, whereas *L. limellus* ate predominantly dipterans. As mouth width increased, *P. paradoxa* consumed larger prey; this relationship was not observed in *L. limellus*. In summary, these two species are associated in the same habitats. However, the differences observed in the prey volumes would favor the coexistence of both aquatic species in an effective way.

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Terrestrial Habitat Use by Adult California Tiger Salamanders

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Although most aquatic-breeding amphibians spend much of their lives away from water, relatively little is known about terrestrial habitat requirements or movements for most species. Recent discussions of strategies to conserve amphibians have emphasized the importance of maintaining adequate buffers of suitable terrestrial habitat adjacent to aquatic breeding areas (Semlitsch, 1998). Unfortunately, available data are often insufficient to determine terrestrial habitat requirements and buffer widths with any confidence. For example, Dodd (1996) surveyed the published data on terrestrial movement by North American salamanders and frogs and found that most reports were based on incidental observations of a few unmarked individuals away from water.

The California tiger salamander, *Ambystoma californiense*, is considered a species of special concern by the state of California, and recently the U.S. Fish and Wildlife Service listed the remaining populations in Santa Barbara County as endangered (U.S. Fish and Wildlife Service, 2000). Although this salamander currently lacks formal protection throughout most of its range, recent development and management plans have included efforts to set aside sufficient habitat to maintain viable populations (S. Meyers, pers. comm.). Much is known about the aquatic habitat requirements of *A. californiense* (Fisher and Shaffer, 1996), and aspects of its adult life history and demography have been described elsewhere (Barry and Shaffer, 1994; Loredo and VanVuren, 1996; Trenham et al., 2000). In comparison, essential terrestrial habitats and buffer requirements are relatively poorly understood.

Loredo et al. (1996) visually tracked the nocturnal emigration of adult and newly metamorphosed *A. californiense* from the pond edge until they were no longer visible on the surface. They found that adults almost always settled in mammal burrows and that dis-

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