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Trophic Ecology of a Tropical Anuran Assemblage

By

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ABSTRACT I examined the diets of 867 anurans of 58 species from Cuzco Amazónico, Peru. A total of 6393 prey items in 62 prey categories was identified from the 610 anurans (70%) with prey in their gastrointestinal tracts—4316 (77%) from the stomach, 2077 from the intestines. Anuran species differ greatly in average number of prey per individual and the relative size of prey consumed. Bufonids, microhylids, and dendrobatids eat large numbers of relatively small prey (a high percentage of ants). Most hylids eat a few large prey, and leptodactylids are intermediate in number and size of prey eaten. Larger hylid species eat primarily orthopterans, roaches, and moths, whereas smaller hylids eat primarily spiders, beetles, and larvae. Most leptodactylids have large niche breadths and eat a great diversity of prey. Beetles, orthopterans, and millipedes are important prey items volumetrically, and ants and beetles are most important numerically. Most morphological variation (corrected for size) among species (71%) was accounted for by two principal component axes and seems to be associated with phylogeny, and to a lesser extent, diet. The two hylids that differ most from other members of their family, *Sphaenorhynchus lacteus* (differs in diet), and *Phyllomedusa atelopoides* (differs in microhabitat and diet) differ in morphology as well. Microhylids and dendrobatids have narrower heads and shorter jaws than hylids or leptodactylids. Maximum, and to a lesser extent, minimum prey size is correlated with frog size, but different families exhibit different relationships. Head shape is important in the number and size of prey consumed regardless of overall size; anurans with narrower heads and shorter jaws eat more, and smaller prey items. Most diet overlaps are low and terrestrial species have lower diet overlap values than arboreal species. The anurans exhibit guild structure in their diet. The terrestrial species are distributed in two distinctive feeding guilds—an ant/termite guild and a larger-prey guild. The arboreal community has only one ant specialist; many of the other species of hylids do not include ants in their diets.

Key words: Feeding ecology, Resource partitioning, Tropical anurans, Diet, Stomach contents, Peru.

RESUMEN Se examinó las dietas de 867 anuros de 58 especies del Cuzco Amazónico, Perú. Un total de 6393 partes de presas se identificaron en los 610 anuros (70%) con presas en sus aparatos gastrointestinales; 4316 (77%) en el estómago y 2077 en los intestinos. Las porciones de presas halladas se clasificaron en 62 categorías. Diferentes especies de anuros varían en el número medio de presas por individuo y en el tamaño relativo de las presas consumidas. Los bufónidos, microhílicos y dendrobátidos comen una gran cantidad de presas relativamente pequeñas (un porcentaje alto de hormigas). La mayoría de los hílicos comen unas pocas presas grandes y los leptodactílicos son intermedios en el número y tamaño de presas que consumen. Las especies más grandes de hílicos comen fundamentalmente ortópteros, cucarachas y polillas, mientras que hílicos más pequeños comen principalmente arañas, escarabajos y larvas. La mayoría de los leptodactílicos tienen nichos amplios y comen una gran diversidad de presas. Los escarabajos, ortópteros y milpies son los más importantes volumétricamente, mientras que las hormigas y los escarabajos son los más importantes numéricamente. La mayoría de la variación morfológica (corregida por tamaño) entre las especies (71%) se debe a dos componentes axiales principales, y parece estar asociada con filogenia y, en menor grado, con dieta. Los dos hílicos que se diferencian más de los otros miembros de la familia, *Sphaenorhynchus lacteus* (difiere en dieta) y *Phyllomedusa atelopoides* (difiere en microhabitat y dieta) difieren también en morfología. Los microhílicos y dendrobátidos tienen cabezas más estrechas y mandíbulas más cortas que los hílicos o leptodactílicos. El tamaño máximo y, en menor grado, el tamaño mínimo de la presa está correlacionado con el tamaño del anuro; sin embargo diferentes familias exhiben diferentes relaciones. La forma de la cabeza es importante en el número y tamaño de las presas consumidas, sin importar el tamaño total del anuro; los anuros con cabezas estrechas y mandíbulas cortas comen mayor cantidad de presas de menor tamaño. La mayoría de las dietas presentan poca superimposición, siendo la misma menor en especies terrestres que en especies arbóreas. Los anuros exhiben estructura de gremio en su dieta. Las especies terrestres se distribuyen en dos gremios distintivos de alimentación—un gremio de hormigas/termitas y uno de presas más grandes. La comunidad arbórea tiene sólo un especialista que consume hormigas; muchas de las otras especies de hílicos no incluyen hormigas en sus dietas.

Palabras claves: Ecología de alimentación, Partición de recursos, Anuros tropicales, Dieta, Contenido estomacal, Perú.

INTRODUCTION

Few studies have dealt with the resource utilization of anuran communities (Das, 1992; Duellman, 1978; Inger and Marx, 1961; Piñero and Durant, 1993; Toft 1980a,b, 1982). Many herpetologists consider frogs to be feeding generalists, but more detailed studies have revealed the existence of several feeding guilds. At two neotropical locations (Panama, Peru), leaf-litter frogs could be categorized as either ant-specialists or non-ant (fewer, larger prey) specialists, with a few generalists in between (Toft, 1980a,b). In an Amazonian leaf-litter vertebrate community (8 species of frogs and 2 of lizards), distinct feeding guilds with significant differences in types and sizes of prey taken by different species were discovered (Vitt and Caldwell, 1994).

Anurans are most diverse in the Neotropical Realm, particularly in the Amazonian region of South America (Duellman, 1988). There are more than twice as many anuran species in South America than in sub-Saharan Africa, even though the areas are comparable in size (Duellman, 1993). Tropical Asian forests exhibit lower densities of frogs and are similarly depauperate in anuran species compared with neotropical regions (Heyer and Berven, 1973; Scott, 1976; Inger, 1980). With the continuing destruction of the rainforests (Gentry, 1990; Ehrlich and Wilson, 1991), research on the complex interactions and resource dependencies within these speciose communities is urgently needed. As the number of species increases, the potential number of interactions increases exponentially. Therefore, study of a tropical rainforest in which the number of vertebrate species is in the hundreds and the number of invertebrate species is often an order of magnitude greater is a daunting task. There is only one published study of a complete food-web for a tropical forest; many scientists required more than three decades to compile information on trophic interactions at the El Verde Field Station in Puerto Rico (Reagan and Waide, 1996). More often, researchers must examine parts of the whole community to complete a study in a reasonable amount of time. And in many cases food webs are compartmentalized, and focusing on one level makes sense biologically.

Bird communities are probably the most thoroughly examined system in terms of resource partitioning. A survey of the recent literature on patterns of resource use (145 papers mostly from the 1980's and early 1990's) found bird communities to be the most commonly examined assemblages; 52% utilized vertebrates and only 2 studies (1.3%) examined anuran communities (MacNally, 1995). Furthermore, only 6% investigated systems of greater than 35 species, and over 50% examined communities of fewer than six species. The idea that niche differences or overlap among species are closely related to the probability and intensity of interspecific competition has been per-

sistent in community ecology. Wiens (1989) expanded on Schoener's (1982) survey of papers on patterns of change in niche overlap through time in communities studied over several seasons or years. Overlap generally decreases in periods of relative resource scarcity, possibly an indication of interspecific competition. The dogma of competition being the major organizing force in communities (review of field experiments in Schoener, 1983) has now been replaced with an expectation that other factors such as predation, disease, abiotic factors, and even symbiotic factors can play major roles in structuring communities (Strong et al., 1984). Most observational and experimental studies of species interactions among birds and other taxa focus on a small set of species that are ecologically or taxonomically similar. It is assumed that competition is likely to be the most intense among such taxa. This study examines a diverse and speciose assemblage of anurans.

The orientation of this study is taxonomic; I examined the diets of the anurans at Cuzco Amazónico, Peru. The anuran fauna is only a portion of the diverse community of organisms found at this tropical-rainforest locality; these frogs certainly had to compete with many other predators, including lizards, birds, mammals, and spiders for their invertebrate prey. Some members of this anuran community may rarely interact, live in different microhabitats, and certainly share prey with members of distant taxonomic groups. I review past studies of anuran diets and feeding behavior, and what approaches have been used. Predator-prey size relationships are also examined; I compare overall size and head dimensions with prey size. The community ecology of this anuran assemblage is analyzed in terms of dietary similarities, and I perform a cluster analysis based on diet to determine what factors influence dietary composition.

The literature is filled with anecdotal reports of anuran diets. Rarely have data been collected with the specific purpose of examining diet as an evolutionary trait (e.g., Caldwell, 1996; Toft, 1995), or to determine dietary differences among species in assemblages of more than three species. Currently, the biology of feeding in lower vertebrates is an active research field; thus studies on dietary and feeding behavior of anurans are increasing. Most studies on amphibians focus on either kinematic studies of prey capture (e.g., Beneski et al., 1995; Deban and Nishikawa, 1992; Maglia and Pyles, 1995; Miller and Larsen, 1990; Nishikawa and Cannatella, 1991) or investigation of the neural pathways involved in feeding behavior (e.g., Cobas and Arbib, 1992; Lauder and Shaffer, 1988; Nishikawa and Roth, 1991; Roth et al., 1990). The goal of such studies is to identify behavioral transitions during phylogenesis and to elucidate their neurological bases.

Feeding mechanisms in anurans range from the completely aquatic pipids, which lack tongues and use hydraulic flow for prey transport (Avilia and Frye, 1978; Sokol, 1969), to the neobatrachian pattern of tongue flipping (i.e., rotated over the mandible during feeding). Until recently, only the genus *Bufo*, a relatively derived taxon of neobatrachian frogs, has been the subject of detailed kinematic studies (Gans and Gorniak, 1982a,b). Nishikawa and colleagues expanded these studies to two archaeobatrachians, *Ascaphus truei* (Nishikawa and Cannatella, 1991) and *Discoglossus pictus* (Nishikawa and Roth, 1991), and two neobatrachians, *Hemisus marmoratum* (Ritter and Nishikawa, 1995) and *Pachymedusa dacnicolor* (Gray and Nishikawa, 1995). Studies have shown that *Rana pipiens* (Anderson, 1993) and *Bufo japonicus* (Kuramoto and Aratani, 1994) can change their feeding behavior in response to different kinds of prey.

Primitive frogs (such as *Ascaphus*) lunge at prey and have broadly attached tongues, which are barely moveable, whereas many advanced frogs have evolved a highly protrusible or even projectile tongue. A flipping tongue also is absent in at least two species from more derived lineages, *Telmatobius* (Leptodactylidae) and *Cyclorana* (Hylidae) (Regal and Gans, 1976). *Rhinophrynus* has a unique feeding mechanism in which the tongue is stiffened hydrostatically and protruded from the mouth (Trueb and Gans, 1983). Studies of anuran tongue morphology (Magimel-Pelonnier, 1924; Regal and Gans, 1976; K. Nishikawa, pers. comm.) demonstrate the diversity and potential for evolutionary convergence in this trophic structure (Cannatella et al., 1993). Although in this study I focus on head dimensions and general feeding behavior in relation to diet, the tongue, vomerine dentition, and even eyes probably also play a role in prey capture. It has been demonstrated that the forelimbs can assist in prey capture in anurans, especially arboreal groups (Gray et al., 1997).

Nearly all adult amphibians are carnivorous; the majority feed on invertebrates, mostly insects. The two documented exceptions are *Rana hexadactyla* from India, which consumes insects in the juvenile stage and primarily aquatic macrophytes as adults (Das and Coe, 1994), and *Hyla truncata*, which includes fruit in its diet (da Silva et al., 1989). Whereas anurans are generally regarded as opportunistic feeders (Duellman and Trueb, 1986; Larsen, 1992; Stebbins and Cohen, 1995), results of field and laboratory studies reveal that some species are selective in their feeding. Prey of most species, particularly of rare and tropical species, is still unknown. Examples of prey specialization include *Tornierella* (Hyperoliidae) feeding on land snails (Drewes and Roth, 1981), *Discodeles guppyi* and *Rana cancrivora* (Ranidae) on crabs (Elliot and Karunakaran, 1974; Premo and Atomowidjojo, 1987) and *Thoropa miliaria* (Leptodactylidae) on marine invertebrates (Sazima, 1972).

Many herpetologists separate the arthropod prey of frogs into two groups: (1) ants and other small, chitinous, slow-moving prey, and (2) all other prey (Toft, 1981). Specialization on ants or termites has occurred in most members of the Bufonidae and Microhylidae, many derived species of leptodactylids, as well as in dendrobatid genera such as *Dendrobates*, *Minyobates*, and *Epipedobates*. A narrower head and reduction in dentition is common, but not ubiquitous, among ant-eating frogs; well-developed dentition may not be necessary for consuming this type of prey. Other groups of frogs, such as *Pyxicephalus* (Ranidae), *Megophrys montana* (Pelobatidae), *Ceratophrys* (Leptodactylidae), and *Hemiphractus* (Hylidae), are able to eat large prey in relation to their body size. Whereas these frogs are in four different families, they all possess a large gape and numerous teeth, in many species teeth are modified into recurved fanglike structures. Many frogs, such as most ranids, are more generalized predators; they ingest both large and small prey. In a review of herpetological resource-partitioning studies, Toft (1985) found that frogs tend to partition food type more consistently than salamanders and lizards, but not as strongly as snakes.

Traditionally, anuran dietary studies have emphasized taxonomic groups as the most important resource dimension. Often, prey size also was recorded, but unfortunately, measurement of prey size has not been standardized across studies. Two of the most broadly comparative studies used two different measurements for prey size, volume, and length (Inger and Marx, 1961; Toft, 1981). Prey behavior has been considered an important feeding cue. Freed (1980) found that although mosquitoes were common in the habitat of *Hyla cinerea*, they were not found in stomachs of wild-caught individuals. A laboratory experiment revealed that prey behavior rather than taxon or size cued feeding behavior in this species. Mosquitoes had slower, more deliberate movements, whereas flies (Diptera) displayed more and quicker movements, which elicited feeding behavior in *Hyla cinerea*.

Resource availabilities are not easily measured in the field. Different techniques can yield very different results. Péfaur and Duellman (1980) collected all insects that they could find and only collected 10% of species that were in the stomachs of frogs at the same sites. Resources also can vary in time and space, and actual availabilities also depend on the behavior and sensory modalities of the frogs. In this study, I use community-wide utilization to estimate the prey-resource spectrum available to all frogs. Many ecologists (e.g., Winemiller and Pianka, 1990; L. Vitt, pers. comm.) think this method is superior to more direct methods of estimation of prey availabilities to a speciose taxon. If a particular prey item was not consumed by any of the frogs examined in the community, it probably is not part of the prey spectrum consumed by anurans at that location.

This study adds to our limited knowledge of tropical anuran communities. It is the most detailed look at such a species-rich community of frogs. Anuran dietary information was published for Santa Cecilia (Duellman, 1978), but the analysis was not so detailed. Duellman (1993) noted that of all the ecological parameters of anuran communities, diet was the least known aspect. This comprehensive analysis of a single anuran assemblage in tropical Peru takes advantage of an extensive collection from one site in the Neotropics. I examine resource utilization of all species, and use null models and clustering algorithms to elucidate the trophic structure of this assemblage of frogs. Anuran larvae at Cuzco Amazónico could be separated in several ecomorphological guilds based mostly on oral morphology (Wild, 1996), and I compare the guilds of adult and larval stages. I also analyze the morphological relationships between predator and prey, taking size and phylogenetic aspects into account.

A correlative relationship between predator and prey body size was demonstrated for most major groups of vertebrates (Hespenheide, 1973). Both intra- and interspecifically, prey and predator body size covary with ordinary least-squares slopes of between 0.7 and 1.2 (e.g., Inger and Marx, 1961; Toft, 1980a), thereby suggesting a general pattern of body-size relationships. This holds true whether mean or maximum prey size is considered. Morphological features of related function often are correlated, and many are correlated with body size. Therefore, correlation is not the best measure to determine if a particular trophic structure is directly limiting prey size. An allometric model can generate specific predictions of the necessary value of the scaling relationship between trophic morphology and body size for the trophic structure to be limiting the prey size taken (Emerson et al., 1994). Geometric similarity is used most often as a null model, because it is based on Euclidean geometry and entails no a priori biological assumptions (Emerson and Bramble, 1993).

Prey size was related not only to body size (a classic measurement used in food-niche separation studies; e.g., Schoener, 1968; Simberloff, 1983), but also to aspects of trophic morphology. Regression analyses between prey size and frog size (and gape dimensions) were performed. Predator trophic morphology should scale with geometric similarity to predator mass for maximum prey size to be strictly a function of predator body size (Emerson et al., 1994). This assumes selection for maintenance of functional equivalence with increases in predator body size. Differences in relative head width often are obvious in tropical anurans, and differences in head shape may correspond to differences in prey size.

Correlations between skull characteristics and diet have been recognized in many vertebrate taxa (Gans, 1952; Jones, 1997; Radinsky, 1981). A biomechanical model re-

lating prey characteristics and feeding behavior of frogs to morphological variables of the jaws and skull revealed a form-function correlation between diet and skull shape (Emerson, 1985). These data are preliminary, but indicate that frogs that eat relatively small, slow prey have relatively short jaws and a symmetrical feeding cycle, in which equal amounts of time are spent catching and bringing the prey into the mouth. Frogs that eat relatively large, slow prey have relatively long jaws and an asymmetrical feeding cycle, in which time of prey capture is less than the time to bring prey into the mouth. Morphological differences between small-prey specialists and larger-prey specialists are examined herein. Anurans that specialize on small prey should have relatively narrow heads, and frogs specializing on large prey should have disproportionately wide heads and long jaws relative to their body length.

There is no standard protocol for analyzing ecological patterns of diverse communities. This should be expected because each system and study is unique. There are many patterns of interest, and different hypotheses require different sets of methods for analysis. The amount of overlap in diet can be an indication of potential competition or interactions involving food resources. By definition, the occurrence of competition depends on limitation of common resources in the environment. Investigation of prey resources in tropical ecosystems (especially in the arboreal microhabitat) is difficult and rarely attempted. Estimates of total numbers of soil insects range from 25,000/m² in a Trinidad forest (Strickland, 1945) to 92,000/m² in a forest site in the Solomon Islands (Greenslade and Greenslade, 1967). A few anuran dietary studies have examined arthropod abundances in samples of leaf litter (Donnelly, 1991; Lieberman, 1986; Toft, 1980a,b). A common hypothesis that tropical insect populations fluctuate less than temperate ones has been refuted in several studies (Bigger, 1976; Wolda, 1978). Anuran diets may fluctuate with seasonal abundances of prey, and the dietary differences reported herein may reflect these changes.

Nearest-neighbor and cluster analyses allow the complex phenomena of diet to be simplified and represented graphically. The observed community was compared to computer-generated "null-communities" to determine whether there is structure in the data, or the frogs simply utilized prey resources randomly. The hybrid technique of merging null models with ranked niche neighbors was developed by Winemiller and Pianka (1990), and subsequently, was used several times by Vitt and colleagues (Vitt and Caldwell, 1994; Vitt and Zani, 1996). Inger and Colwell (1977) pioneered the ranked nearest-neighbor technique. If niches of species in a community are areas or volumes in resource space (Hutchinson, 1957), then each

niche will have a first, second, ..., *i*th nearest neighbor. In general, overlap will be greatest with the first nearest neighbor, less with the second, and so on, with distant neighbors having little or no overlap. I assumed that nearest neighbors overlap most in niche space; it is possible that a nearest neighbor may have more niche overlap with a third, more distant taxon. Examination of the distribution of ranked overlaps and their variance provides information about community structure. Are frogs using prey types in a random fashion (compared to all stomach contents combined), or are most species utilizing a few, important prey categories? Does each species exploit its own prey category, or are species separated into several distinct dietary guilds, with each feeding on a common prey resource?

Null models have become more popular among ecologists in the last 20 years (Strong et al., 1984; Gotelli and Graves, 1996), but there have been controversies when null models have been used to address specific mechanisms and patterns in community ecology (Harvey et al., 1983). A typical null model generates communities or community patterns expected to occur in the absence of a particular mechanism. Patterns in these "pseudo-communities" then are compared statistically to patterns in the real community. Deviations from the null model can be compared to the predictions of ecological theory. Null models differ from mathematical models in that they require empirical data for analysis, and are designed to test patterns in real data sets (or to compare among mathematical models); mathematical models can be constructed for heuristic purposes or for comparison with other models (Roughgarden, 1983).

The hybrid technique of Winemiller and Pianka (1990) has considerable potential for analyzing patterns of resource utilization in diverse and speciose natural assemblages. This technique only deals with consumers and resource categories and cannot deal with complex issues (e.g., stability) addressed by food-web theory (Paine, 1988; Pimm, 1982; Wilbur, 1997). Although I describe the diet on a species-by-species basis, I also attempt to determine if there are properties of the assemblage beyond the mere collection of species.

The anurans used in this study were collected at the Reserva Cuzco Amazónico, at an elevation of 200 m above sea level in Amazonian Peru. Duellman and Koechlin (1991) gave a detailed description of the preserve, and Duellman and Salas (1991) provided an annotated checklist of the amphibians and reptiles of the area. Cuzco Amazónico is a privately maintained preserve of 10,000

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MATERIALS AND METHODS

ha on an alluvial plain on the north bank of the Río Madre de Dios. It is about 15 km ENE of Puerto Maldonado, Departamento Madre de Dios, southern Peru (12°35' S, 69°05' W; Fig. 1). The vegetation was classified as Humid Tropical Forest under the Holdridge system (Tosi, 1960). With the exception of the steep banks of the river, the terrain is generally flat with a total relief no more than 5 m.

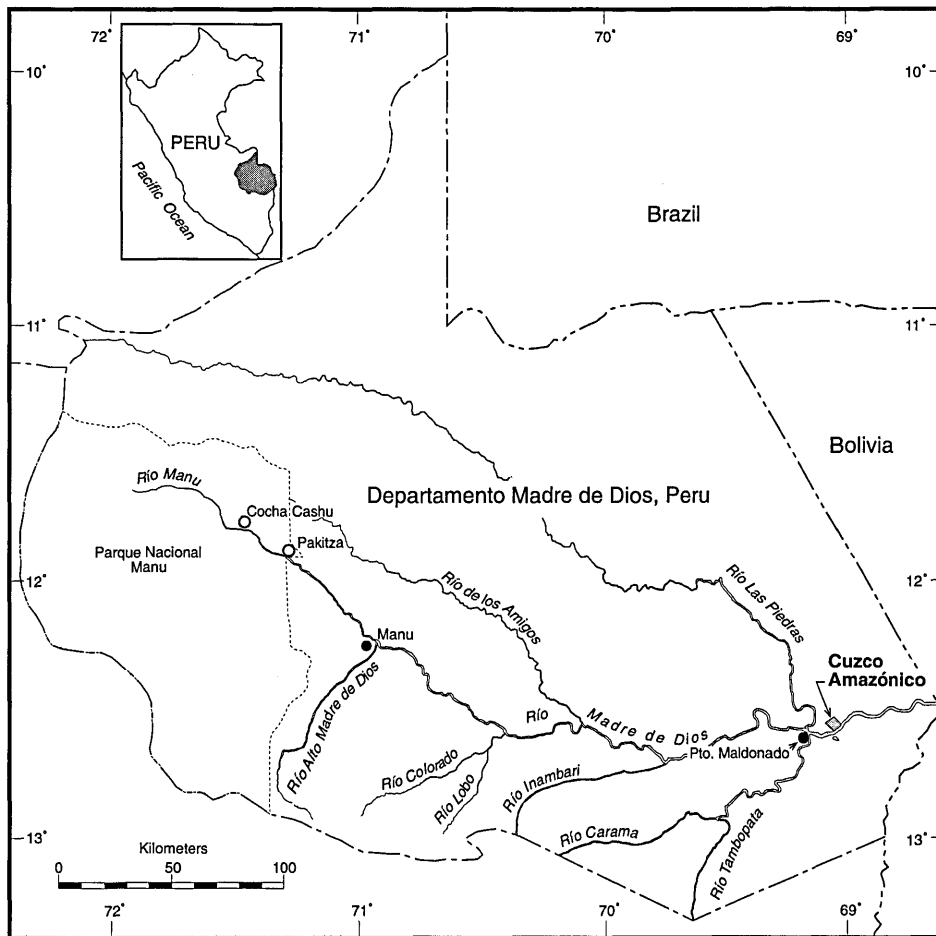


Fig. 1. Map of Departamento de Madre de Dios, Peru, showing the location of the Reserva Cuzco Amazónico. Based on *Mapo Físico Político, Departamento de Madre de Dios, Atlas del Perú*, Instituto Geográfico Nacional, Lima, 1989.

Total annual rainfall at Puerto Maldonado is 1836–3418 mm (\bar{x} = 2387). The rainy season extends from October through March; the heaviest rainfall generally is in January (\bar{x} = 441.0 mm) and February (\bar{x} = 381.1 mm), and the lowest is in June (\bar{x} = 64.7 mm) and July (\bar{x} = 60.4 mm). Two types of forest are recognized; terra firma forest is well drained, and inundated forest is flooded by the accumulation of runoff water during heavy rains. There are fewer ferns and less herbaceous ground cover but more *Heliconia* and *Calathea* in inundated forest than in terra firma forest (Duellman and Koechlin, 1991).

Specimens used in this study were collected during a 10-year biotic survey; the numbers of specimens by year are: 1981: 2; 1983: 17; 1984: 34; 1985: 12; 1986: 444; 1987: 1; 1988: 6; 1989: 129; 1990: 145; and 1991: 8. Fifty-five percent of the specimens were captured in 1986. The number of specimens captured per month is as follows: January: 222; February: 233; March: 7; June: 53; July: 45; October: 18; November: 158; December: 50. Most frogs were captured

in January and February (28% and 30%, respectively). Collecting was done both during day and at night; most specimens were collected from 2100 to 2400 hr. This yearly, monthly, and daily variation in the number of frogs collected reflects both variation in weather conditions (Duellman, 1995) and collecting effort. Frogs were collected by hand and preserved a few hours after capture—usually within 6 hr and rarely more than 12 hr later. Time of collection, frog activity (sleeping, calling, etc.), heights above ground, and other notes were recorded in the field. All but three specimens examined are preserved in the collection of the Natural History Museum, The University of Kansas (Appendix 1).

The rank order of the 20 most abundant frogs appears in Duellman (1995); hylids make up 12 of the 20 most abundant species. Body size and natural history data on the species of frogs from Cuzco Amazónico is presented in Table 1. The alimentary canals (esophagus to cloaca) and body cavities of all frogs were examined for parasites. Para-

Table 1. Sample sizes, average size of adults, foraging mode, reproductive mode (as in Duellman and Trueb, 1986), and general categorization of habitat use (from Duellman, 1990, and Rodríguez and Cadle, 1990) of the frog species studied at Cuzco Amazónico, Peru (A = arboreal, B = bush, T = terrestrial; N = nocturnal, D = diurnal; * = both sexes combined, from Duellman and Lizana, 1994).

Family and species	<i>n</i>	\bar{x} SVL (mm)	\bar{x} mass (g)	Foraging mode	Habitat	Diel	Reproductive mode	General habitat
BUFONIDAE	34							
<i>Bufo glaberrimus</i>	1	44.83	6.51	Active	T	N	1	Forest
<i>Bufo marinus</i>	5	104.17	128.06	Active	T	N	1,2	Clearings
<i>Bufo "typhonius"</i>	28	50.77	11.94	Active	T	D, N	1	Forest
DENDROBATIDAE	54							
<i>Colostethus marchesianus</i>	28	16.59	0.57	Active	T	D	14	Forest
<i>Epipedobates femoralis</i>	13	23.78	1.20	Active	T	D	14	Forest
<i>Epipedobates pictus</i>	13	20.43	0.88	Active	T	D	14	Forest
HYLIDAE	432							
<i>Hyla allenorum</i>	4	21.37	0.64	Sit and wait	A	N	1	Forest
<i>Hyla boans</i>	3	89.99	31.63	Sit and wait	A	N	3	Forest, river edge
<i>Hyla brevifrons</i>	4	18.85	0.64	Sit and wait	A	N	18	Forest
<i>Hyla calcarata</i>	2	42.61	3.82	Sit and wait	A	N	1	Forest
<i>Hyla fasciata</i>	25	39.35	3.17	Sit and wait	A	N	1	Forest
<i>Hyla granosa</i>	12	35.91	2.03	Sit and wait	A	N	1	Forest
<i>Hyla koechlini</i>	25	22.83	1.01	Sit and wait	A	N	1	Forest
<i>Hyla leali</i>	25	23.81	0.94	Sit and wait	A	N	1	Forest
<i>Hyla leucophyllata</i>	25	33.22	1.97	Sit and wait	A	N	18	Forest
<i>Hyla marmorata</i>	2	47.81	5.19	Sit and wait	A	N	1	Forest
<i>Hyla parviceps</i>	25	21.60	0.85	Sit and wait	A	N, D	1	Forest
<i>Hyla punctata</i>	5	33.11	2.21	Sit and wait	B	N	1	Forest
<i>Hyla rhodopepla</i>	23	23.73	1.02	Sit and wait	A	N	1	Forest
<i>Hyla schubarti</i>	20	21.68	0.83	Sit and wait	A	N	1	Forest
<i>Osteocephalus taurinus</i>	33	81.46	22.99	Sit and wait	A	N	1	Forest
<i>Osteocephalus</i> sp.	2	—	—	Sit and wait	A	N	1	Forest
<i>Phrynohyas coriacea</i>	25	56.21	12.92	Sit and wait	A	N	1	Forest
<i>Phrynohyas venulosa</i>	9	78.67	30.40	Sit and wait	A	N	1	Forest
<i>Phyllomedusa atelopoides</i>	9	39.81	4.29	Sit and wait	T	N	18	Forest
<i>Phyllomedusa palliata</i>	5	39.56	2.94	Sit and wait	A	N	18	Forest
<i>Phyllomedusa tomopterna</i>	22	48.78	4.60	Sit and wait	A	N	18	Forest
<i>Phyllomedusa vaillanti</i>	7	48.96	4.29	Sit and wait	A	N	18	Forest
<i>Scarthyla ostinodactyla</i>	25	19.34	0.63	Sit and wait	B	D, N	1	Forest
<i>Scinax garbei</i>	12	42.78	4.16	Sit and wait	B, A	N	1	Forest
<i>Scinax icterica</i>	25	30.26	1.60	Sit and wait	A	N	1	Forest
<i>Scinax pedromedinai</i>	25	27.26	1.24	Sit and wait	A	N, D	1	Forest
<i>Scinax rubra</i>	18	37.25	2.86	Sit and wait	A	N	1	Forest, clearings
<i>Sphaenorhynchus lacteus</i>	15	39.26	3.68	??	B	N	18	Forest
LEPTODACTYLIDAE	366							
<i>Adenomera</i> sp.	34	22.92	1.17	??	T	N, D	22	Forest
<i>Ceratophrys cornuta</i> *	72	79.55	74.48	Sit and wait	T	N	1	Forest
<i>Edalorhina perezii</i>	28	30.11	2.51	??	T	D	8	Forest
<i>Eleutherodactylus altamazonicus</i>	3	24.24	1.15	Sit and wait	B	N, D	17	Forest
<i>Eleutherodactylus cruralis</i>	5	25.61	1.52	Sit and wait	A	N	17	Forest
<i>Eleutherodactylus fenestratus</i>	29	35.70	3.93	Sit and wait	B, T	N	17	Forest
<i>Eleutherodactylus imitatrix</i>	11	16.08	0.53	Sit and wait	A	N, D	17	Forest
<i>Eleutherodactylus peruvianus</i>	21	24.79	1.32	Sit and wait	B	N, D	17	Forest
<i>Eleutherodactylus toftae</i>	30	21.79	0.88	Sit and wait	B	N, D	17	Forest
<i>Leptodactylus bolivianus</i>	14	86.92	43.65	Sit and wait	T	N, D	8	Forest
<i>Leptodactylus leptodactyloides</i>	33	41.65	5.90	Sit and wait	T	N, D	8	Forest
<i>Leptodactylus mystaceus</i>	25	51.28	11.76	Sit and wait	T	N	8	Forest
<i>Leptodactylus pentadactylus</i>	7	119.21	150.50	Sit and wait	T	N	21	Forest
<i>Leptodactylus petersii</i>	24	28.99	2.31	Sit and wait	T	N	8	Forest

Table 1 continued

Family and species	<i>n</i>	\bar{x} SVL (mm)	\bar{x} mass (g)	Foraging mode	Habitat	Diel	Reproductive mode	General habitat
burrows								
<i>Lithodytes lineatus</i>	2	46.33	7.13	Sit and wait	T	N	21	Forest
<i>Physalaemus petersi</i>	7	25.17	1.56	Active	T	N	8	Forest
MICROHYLIDAE								
	43							
<i>Altigius alios</i>	2	49.98	—	Sit and wait?	T	N	??	Forest
<i>Chiasmocleis ventrimaculata</i>	2	22.24	0.84	Sit and wait	T	N, D	1	Forest
<i>Ctenophryne geayi</i>	3	40.81	8.42	Sit and wait	T	N	3	Forest
<i>Elachistocleis ovalis</i>	11	36.31	3.95	Sit and Wait	T	N	1	Forest
<i>Hamptophryne boliviana</i>	25	33.19	3.73	Sit and Wait	T	N, D	1	Forest
PIPIDAE								
	6							
<i>Pipa pipa</i>	6	79.34	34.04	??	Aquatic	D, N	11	Ponds
PSEUDIDAE								
	2							
<i>Pseudis paradoxa</i>	2	53.72	22.74	Sit and Wait	Aquatic	N	1	Ponds

sites from 374 anurans (43% of individuals) were placed in 70% ethanol and identified by Charles Bursley and Stephen Goldberg (Parmelee et al., In prep.).

The taxonomy of two of the most common leaf-litter inhabitants at Cuzco Amazónico, *Bufo typhonius* and *Colostethus marchesianus*, may soon change. *Bufo typhonius* is a widespread and variable species that is being revised by Marinus Hoogmoed (Hoogmoed, 1990). According to Hoogmoed (pers. comm. to W. E. Duellman, 1997), there are at least two different species differing in size at Cuzco Amazónico. Because I could not distinguish them and they have not been formally described, I treat all of these toads as one taxon. Similarly, there may be several species of *Colostethus* at this site; revisionary studies of the widespread *C. marchesianus* are in progress by Víctor Morales, who (1994) suggested that *Colostethus trilineatus* is the available name for this taxon.

Two juveniles of an undescribed species of *Osteocephalus* were available, and I report on their diet in Appendix 2. *Scinax rubra*, as currently recognized, may be a composite of several species; this wide-ranging taxon occurs from coastal Brazil to St. Lucia in the Lesser Antilles (Frost, 1993). There may be two species of *Adenomera* at Cuzco Amazónico. According to Heyer (pers. comm. to W. E. Duellman), *Adenomera andreae* and *A. hylaedactyla* occur at this location. I examined the specimens and could not distinguish the species; therefore, they are treated as one taxon. The taxonomy of the medium-sized species of *Leptodactylus* is complex, but it is thought that the specimens previously reported as *L. podicipinus* (Duellman and Salas, 1991) are *Leptodactylus petersii* (Heyer, 1994).

RELIABILITY OF DIETARY DATA

Ideally, studies of anuran diet should be conducted on animals that are preserved as soon as possible after capture. The animals used in this study were not captured with the goal of performing a detailed dietary analysis. Surely many prey were digested. Because all frogs were handled similarly, I assume that there is no bias between species in length of time between capture and preservation. However, most certainly there is a bias toward hard-bodied prey such as beetles and ants. Beetle elytra, ant heads, and orthopteran appendages certainly are over-represented compared to annelid worms, collembolans, flies, and soft-bodied larvae. Many curculionid weevils were nearly intact in the lower intestine.

Caldwell (1996) discussed the necessity of reliable data and the importance of preservation immediately following capture. She preserved a sample of *Acris crepitans* every 6 hr after capture and found an average of seven prey items/stomach in frogs preserved immediately, 3.6 prey/stomach in those preserved after 6 hr, and an average of one prey item/stomach after 12 hr. Other studies (Johnson and Christiansen, 1976; Woolbright and Stewart, 1987) reported similar results.

In order to determine if time between capture and preservation had an effect in this study, I compared my data on *Colostethus marchesianus* with past studies on this species. Toft (1980a) reported 10.4 (wet season) and 24.6 (dry season) prey items/stomach, and Caldwell (1996) reported 22.0 prey items/stomach in this species. I found an average of 15.4 prey items/stomach (removal of one individual with 104 prey items resulted in an average of 12.0 prey

items/stomach). My findings fall between Toft's wet and dry season results, but may be low, indicating greater digestion of prey items in this study.

Several authors (e.g., Toft) have emphasized the importance of knowing the abundances of those prey taxa in nature that are available to anurans. The argument is that one cannot truly know if anurans are specialists if the relative abundances of available prey are unknown. I made no assumptions about the abundance of prey in the habitat; I consider the total diets of all species combined to represent the set of prey available to the anuran assemblage. The combined prey abundances of all anurans certainly cannot be taken as a direct measure of the relative prey abundances at this site. A similar dietary analysis of 212 lizards of 22 species at Cuzco Amazónico revealed a different pattern of prey abundances (Parmelee and Duellman, In prep.). Ants are still the most numerous prey items, but roaches and larvae are much more important volumetrically to the lizard fauna.

Insect activity is not uniform throughout the year, and insect activity varies from group to group (Bigger, 1976; Penny and Arias, 1982). Wolda (1978) found distinct differences in homopteran populations in Panama between wet and dry seasons. Other insect groups and species within a family varied in abundance at different times as well. Diet may vary between days, seasons, or years with availability of prey. A more complete profile of the diets of these species (and possibly intraspecific variation) will require larger samples from throughout the year and including juveniles and adults of both sexes. The absence of a particular prey item in a sample of a given species does not mean that the species never eats it. The more varied the diet of a species, the greater the sample size needed to obtain a complete picture of its diet (Hurtubia, 1973; Kovács and Török, 1997). Thus, for species with specialized diets, such as microhylids or other ant/termite specialists, the estimated niche breadths and diet percentages are probably most accurate. In species in which the diet is probably variable but sample sizes are small (e.g., *Pseudis paradoxa* or *Lithodytes lineatus*), the actual dietary percentages probably vary from the limited sample analyzed here.

Diet was analyzed by two general categories—size and taxon. These are the two variables that are most easily measured and seem to the human observer to be most important to the anuran predator. Unmeasured, but potentially important prey characteristics include caloric content, digestibility, prey hardness, prey behavior, and difficulty of capture. Prey items vary in the number of calories and protein content, even in prey of the same volume or mass (Anderson, 1997; Anderson and Smith, In press; Jaeger, 1990). Anurans may include a variety of prey types in order to balance essential minerals or other required sub-

stances (as in mammals: Clark, 1982; Westoby, 1978). For example, it is thought that dendrobatids eat a high percentage of ants because they gain a precursor to their toxic skin secretions from this prey item (Daly et al., 1987, 1994).

Hardness of prey items may also affect diet selection. Freeman (1981) ranked invertebrate prey of bats on a qualitative scale from 1 (softest) to 5 (hardest). Examples include (1) Isoptera, Diptera; (2) Araneida, Homoptera; (3) Orthoptera, Scorpionida; (4) Hymenoptera, Hemiptera; (5) Coleoptera. Insect exoskeletons are a composite with fibers running in different directions to resist crack propagation (Hepburn and Joffe, 1976; Vincent, 1980); frogs, as well as bats, may need specialized dentition or greater jaw musculature to handle prey with tougher exoskeletons. Bats specializing on beetles generally had fewer, but larger, teeth, whereas moth-eaters had more, smaller teeth (Freeman, 1979). A similar arrangement might be found to occur in anurans. Canine-like teeth have been linked to the need to pierce chitinous shells of arthropods in lizards (Mateo and López-Jurado, 1992).

Relative sizes of teeth (relative to SVL or jaw length) never have been compared among anurans. Bragg (1957, p. 190) observed feeding in toads for more than 20 years and described a juvenile *Bufo cognatus* capturing a large June beetle and "Soon the beetle's head appeared between the toad's lips and in spite of gulping on the part of the toad, [the beetle] crawled out and went on its way." I believe the edentate condition of bufonids and other groups hinders their ability to capture large, active prey.

Leaf-litter herpetofaunal communities in numerous tropical locations reveal a commonality of ant specialists ("advanced" dendrobatids and bufonids) being edentate, generalists being intermediate, and non-ant feeders having relatively large teeth (Duellman, 1978; Toft, 1980a,b, 1981). Hedges (1989) listed 19 species in the *Eleutherodactylus ricordii* group from the West Indies that can be confidently placed in this group (partially defined by having large vomerine odontophores), yet have short odontophores. He hypothesized that vomerine dentition may be correlated with feeding habits—short odontophores for soft-bodied prey such as Diptera and Lepidoptera, and long for hard-bodied prey such as Orthoptera and Coleoptera. He noted that this might explain why most arboreal species (i.e., those that would encounter soft-bodied prey more frequently) have short odontophores and most terrestrial species long odontophores. He mentioned that preliminary data on stomach contents lends initial support to this idea but that a much more extensive survey is warranted.

Prey activity could be quantified in a general manner. Categories could be delimited such as those defined by Emerson (1985): small, slow (e.g., ants, worms), small fast

(e.g., flies), large, slow (e.g., snails, vertebrates), large, fast (e.g., grasshoppers). These general descriptors of prey size and activity could affect diet selection or which prey elicit feeding responses in different species of frogs. There have been studies on the neurophysiology of the amphibian eye, which found that there are certain neurons that determine how an individual recognizes an appropriate size of prey to pursue (Ingle, 1973; Ingle and Cook, 1977; Schoener, 1979).

The number of resource categories to choose is a complex decision that must be made prior to analysis. The goal should be identification of the prey categories important to the species being studied. The obvious answer "as many as possible" proves to be overly facile and erroneous (Pianka, 1986:77). If resource categories are too broad, patterns of differential use will be obscured and ecological similarity will be overestimated. If resource categories are too narrow, problems of meaningless differences may be generated, but simply using ordinal differences in prey can misrepresent important food-niche and community parameters (Greene and Jaksic, 1983). I concur with Pianka (1986) that one must rely on prior knowledge of the organisms concerned, as well as on biological intuition, in choosing resource categories to recognize.

DIETARY ANALYSES

Dietary data were obtained from samples of 1–72 individuals of each species (Table 1). A dissecting microscope was used to identify stomach and intestinal contents of at least 25 individuals, or all available specimens (Table 1) of each species at least to order, and in most cases to family. Taxonomy of prey categories is consistent with Borror et al. (1992). If the family of a prey item could not be identified (e.g., only a beetle elytra or an orthopteran leg present), the prey was reported as an "Unid." subcategory of its respective order. Length and width of each intact prey item was measured to 0.01 mm (with digital calipers) and a volume calculated using the formula for a prolate spheroid:

$$V = 4/3\pi(\text{length}/2) * (\text{width}/2)^2.$$

Length measurements exclude antennae and ovipositors. Width was recorded at the midpoint of the prey item, excluding any protruding legs. In many cases, estimates of prey size were made if the general shape of the prey item could be determined from the available fragments. Unidentifiable prey fragments were not analyzed further. Many of the frogs contained leaves, twigs, and other plant debris in their digestive tracts. The only plant items reported were seeds, buds, or flowers (under the prey category: Plant material) that might have been ingested accidentally, but not incidentally, with other prey items. Some authors have suggested that anurans (e.g., *Bufo marinus*) may purposely ingest vegetation to provide roughage to assist grinding invertebrate exoskeletons, aid in elimina-

tion of intestinal parasites, or to provide moisture (Evans and Lampo, 1996; Zug et al., 1975). Possibly these plant pieces may have had an insect on them, and both were ingested together, but it is also possible that the movement of such prey-sized plant pieces appeared to the frog as animal prey.

Diets are described in detail (62 prey categories) for individual species in Appendix 2. More generalized prey categories (16 prey categories; e.g., all beetle families and types of larvae combined) also are graphed for several species to illustrate specific differences in major prey categories.

A prey resource matrix was constructed with numbers and volumes of each prey category. Proportional utilizations were calculated by dividing the number and volume of prey categories by the corresponding totals. Differential utilization of prey is revealed by comparisons of the species. Specialization is revealed by differences in each individual diet to the total "prey base" and with comparisons of niche breadths. Niche breadth was calculated for each species, using the reciprocal of Simpson's (1949) measure:

$$B = 1 / \sum_{i=1}^n p_i^2,$$

where i is the resource category, p is the proportion of resource category i used by that species, and n is the total number of prey categories (Pianka, 1986). Niche-breadth values vary from 1.0 (exclusive use of a single prey category) to n (all prey categories used equally). Diet analyses were performed with BugRun 5.1, a relational analysis database programmed in 4th Dimension®. All statistical analyses were performed with Statview Ver. 4.5® (Abacus Concepts, 1995) and Minitab Ver. 11.1® (Minitab Inc., 1991).

An ANOVA on mean (and maximum) individual prey volume per anuran for all species was performed to examine differences in sizes of prey taken by different species. Average number of prey per individual also was analyzed. The residuals of a common regression of SVL versus prey size for all species combined were used to account for body-size differences. I treated terrestrial and arboreal communities separately in many analyses.

MORPHOLOGICAL ANALYSES

Snout-vent-length (SVL, the linear distance from the tip of the snout to the end of the urostyle), jaw length (JL, [lateral head length of Trueb, 1977] the linear distance from the tip of the snout to the jaw articulation), and head width at level of jaw articulation (HW) were measured on all frogs. Jaw length did not include the fleshy snout of *Bufo typhonius* or several microhylids. Trueb (1977) defined these osteological measurements and all had low coefficients of variation. I also measured head height (HH) at a

level just anterior to the eyes. This was measured with the mouth open, and did not include the depth of the lower jaw. Sex was determined for all frogs by examination of the gonads. All immature individuals that could not be sexed were classified as juveniles.

Each anuran was processed in the same manner. The frog was removed from alcohol and quickly blotted dry with a paper towel. The five external measurements were taken, and the venter of the frog was cut open on the left side. If the frog contained an excess of internal liquid, this was removed. The stomach was excised and the excess liquid quickly removed; the stomach was weighed immediately. A frog mass was then obtained; the stomach mass was added to this measurement. Live and preserved masses of the anuran specimens utilized in this study were not significantly different (Parmelee and Ron, In prep.). The stomach was opened and the contents placed in a dish. Measurements of the gut then were taken.

To test for accuracy and repeatability of my measurements I measured three specimens of North American anurans (*Bufo woodhousii*, *Hyla versicolor*, and *Rana blairi*) on three separate dates. The measurements proved repeatable and fairly precise. Mass, SVL, and head width seem to be the most repeatable, whereas jaw length and head height were more variable, especially in *Bufo woodhousii* and *Rana blairi*.

To examine morphological variation, all morphological variables were log-transformed so that regressions with size (SVL) would be linearized. All p values for reported regressions < 0.05 . I then calculated means of all variables on a species-by-species basis, and removed the effect of size (SVL) by calculating residuals from the common regressions for all species combined. This avoids the problems associated with using ratios, and removes the effects of body size. A principal-component analysis was performed on the residuals along with SVL and body mass to determine which characters contributed most to variation in morphology among species (Miles, 1994; Vitt and Zani, 1996).

COMMUNITY ANALYSES

Resource matrices were constructed with prey categories as columns and anuran species as rows. Proportional utilization coefficients (p_i) were calculated by dividing actual resource utilizations (by volume) by the row-totals for each species. I then constructed a matrix of electivities (e_i), calculated by dividing the volume of a particular prey category by the column total (the total volume of a prey category for all frogs). These electivities, which vary from -1.0 (total avoidance) to $+1.0$ (total selection), were scaled so that values vary from 0.0 to 1.0 and columns sum to 1.0 (Winemiller and Pianka, 1990). Proportional utilizations

are positively correlated with resource availabilities and electivities are negatively correlated with resource availabilities (Winemiller & Pianka, 1990); therefore, the geometric mean (g_i) of p_i and e_i was used as a measure of resource utilization. This measure has been shown to introduce less bias into community analysis because correlations between g_i and resource availabilities balance the biases associated with p_i and e_i values (Winemiller and Pianka, 1990; Vitt and Zani, 1996). I tested this assumption for my anuran data as well.

Geometric means were used in place of proportional utilizations to calculate overlaps. Similarity in resource utilization was estimated with the symmetric niche overlap coefficient (Pianka, 1973):

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

where the symbols are the same as above and j and k represent the two species being compared. Overlaps vary from 0.0 (no overlap) to 1.0 (complete overlap). Overlaps and the following pseudocommunity analysis were performed separately for the 19 species of terrestrial and arboreal frogs with the greatest sample sizes.

Although the overlap matrix provides information on diet similarity between frog species, the possibility exists that resource utilization is random, with no structure among the species. To test for any structure, I performed two separate bootstrap (pseudocommunity) analyses (as in Winemiller and Pianka, 1990). In the first analysis, all values in the resource utilization matrix were randomized 100 times with respect to position for each species (scrambled zeros), and the new sets of overlaps calculated. Therefore, niche breadths and numbers of resources are retained and guild structure (if any) was destroyed. In the second analysis, all values in the resource-utilization matrix, except zero entries, were randomized 100 times with respect to position for each species (conserved zeros), and new sets of overlaps calculated, thus retaining niche breadths, number of resource states, and zero structure. These randomizations were performed on a Pascal computer program, MacScramble, based on analyses developed by Winemiller and Pianka (1990).

Randomization of resource utilization data provided pseudocommunities to compare to the actual anuran community to examine if members of this community are using resources in a random fashion, or if there is structure. Mean overlaps were ranked from greatest to lowest and compared at each nearest-neighbor rank following Inger

and Colwell (1977). Statistical comparisons reflect the fraction of randomized means below or above the real means at each rank. The real community was considered different (structured) from the pseudocommunities only if 95% of the ranked pseudocommunity overlaps fall below or above those of the real community.

Feeding guilds were revealed by plotting ranked dietary overlap of each species with all of its neighbors in niche space (Winemiller and Pianka, 1990; Vitt and Caldwell, 1994; Vitt and Zani, 1996). Rank 1 overlaps represent nearest neighbor comparisons, whereas lower overlaps represent comparisons between target species and more distant neighbors in niche space. As there were only five strictly diurnal species, I included seven other species

that seem to be active both day and night (Table 1) in the terrestrial, diurnal analysis.

To examine further the community structure of the anurans of Cuzco Amazónico, I performed a hierarchical cluster analysis of dietary overlaps (based on g_i data). The variables were standardized and Euclidean distances and single linkages were used (Minitab Inc., 1991). For the terrestrial matrix, I added an additional variable. Species were scored as: Diurnal (0), Diurnal and nocturnal (0.5), and nocturnal (1) to further separate species (as in Table 1). A similar hierarchical cluster analysis was performed on 49 species using mean prey volume and mean number of prey per individual to obtain an overall picture of differences in feeding strategy.

RESULTS

DIETS OF ANURANS

Prey in diets of all anurans.—Numerically, ants are the most abundant prey item. Only 15 of 58 species (25.9%) did not consume ants; most of these are hylids (Table 2). All other species consumed at least one ant, and many species are ant specialists (Appendix 2). Numerically, ants are more than four times as important as the next most abundant prey category, termites (Fig. 2). Beetles also were ubiquitous. Volumetrically, ants are only the fourth most important prey item; in decreasing order of importance are orthopterans, beetles, and hemipterans/homopterans (Fig. 2).

Hypothetically, softer prey are digested more quickly than hard-bodied prey, and therefore, intestinal contents are biased toward harder-bodied prey; Schoener (1989) suggested that the entire digestive tract should be exam-

Table 2. Species of anurans that did not contain ants in the gastrointestinal tract.

Species	<i>n</i>
HYLIDAE:	
<i>Hyla parviceps</i>	25
<i>Hyla rhodopepla</i>	23
<i>Scinax icterica</i>	25
<i>Scinax garbei</i>	12
<i>Phyllomedusa tomopterna</i>	22
<i>Phyllomedusa palliata</i>	5
<i>Hyla punctata</i>	5
<i>Hyla brevifrons</i>	4
<i>Hyla allenorum</i>	4
<i>Hyla boans</i>	3
<i>Hyla marmorata</i>	2
<i>Hyla calcarata</i>	2
LEPTODACTYLIDAE:	
<i>Physalaemus petersi</i>	7
PIPIDAE:	
<i>Pipa pipa</i>	6
PSEUDIDAE:	
<i>Pseudis paradoxa</i>	2

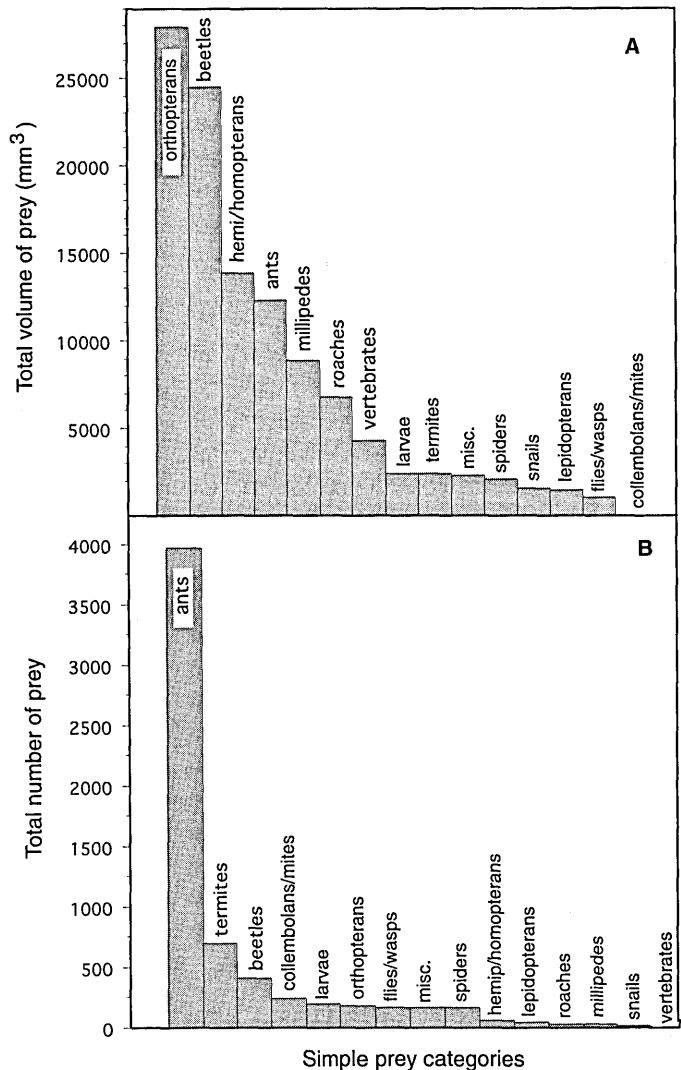


Fig. 2. Ranked (A.) Volumetric and (B.) Numeric importance of prey categories in the combined diets of 867 anurans of 58 species.

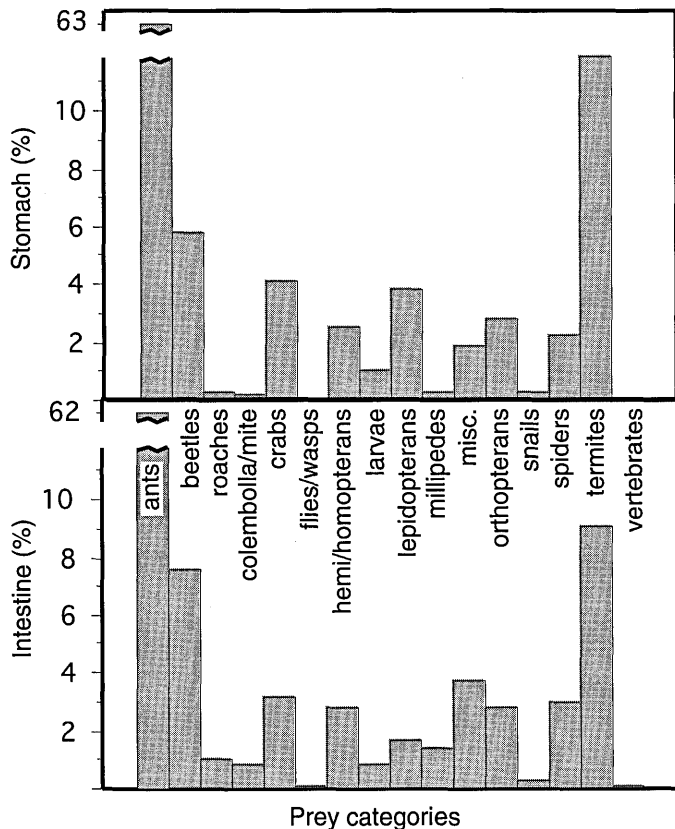


Fig. 3. Percentage of major prey categories obtained from stomachs and intestines of anurans.

ined in individuals with few prey items. A greater proportion of hard-bodied prey was found in the hind gut than in the stomach in a sample of 188 *Bufo bufo* (Wheater, 1986). In this study, there was no significant difference between prey obtained from the stomach compared to the intestines (Fig. 3; paired *t*-test, $t = 1.589$, $p = 0.1328$). However, when ants are excluded from the analysis, there was a significant difference between stomach and intestinal contents ($t = 2.383$, $p = 0.0319$). Differences in prey composition include more larvae, termites, and collembola in stomachs than in intestines and more miscellaneous arthropods, beetles, and lepidoptera in intestines. Beetle elytra and lepidopteran scales can be easily identified anywhere in the digestive tract. Seventy-seven percent of prey items (4316) were recovered from stomachs, compared to 2077 prey items from intestines. These results reveal how much in-

formation would have been lost had only the stomach contents been examined.

Anurans with and without prey.—There are familial differences in the percentage of frogs with empty gastrointestinal tracts (Table 3, $\chi^2 = 82.627$, $p < 0.0001$, excluding Pseudidae and Pipidae). Hylids clearly are more likely to have an empty gastrointestinal tract than members of other families. More than 40% of hylids contained no prey items. This might be expected for two reasons. First, they are thought to be sit-and-wait predators, and probably feed at irregular intervals, unlike active foragers that eat many prey items daily. Second, several species of hylids are only seen, and thus captured, while calling; it is likely that calling anurans suspend feeding activities. Calling males of *Eleutherodactylus coqui* ate fewer prey items and ended the night with less food volume in their stomachs than non-calling males (Woolbright and Stewart, 1987). This may explain the higher percentage of empty gastrointestinal tracts in the hylids (Table 3). Other than the study by Woolbright and Stewart (1987), evidence that calling males do not feed while vocalizing is largely circumstantial (reviewed by Woolbright, 1983). A small percentage of bufonids and dendrobatids had empty gastrointestinal tracts.

A comparison of the percentage of frogs with empty gastrointestinal tracts when calling or in amplexus or when captured when hiding, jumping, sitting, or sleeping revealed significant differences. Of those frogs calling or in amplexus, 60.7% (91 of 150) had prey in their gastrointestinal tract. Frogs engaged in other activities had prey in their gastrointestinal tract in 71.2% (401 of 563) of individuals ($\chi^2 = 6.174$, $p = 0.013$). Although this is a rough estimate, frogs engaged in mating activities apparently suspend feeding.

Among all frogs studied, there is no significant difference between the number of empty gastrointestinal tracts among the categories male, female, and juvenile (females, 73.1%, males, 66.5%, juveniles 75.0% with prey, $\chi^2 = 4.911$, $p = 0.086$). When juveniles are excluded, males have a significantly higher percentage of empty gastrointestinal tracts ($\chi^2 = 3.99$, $p = 0.046$). Of the females, those that were gravid had an empty gastrointestinal tract more often (71 of 111, 32.4%) than non-gravid females (40 of 193, 20.7%, $\chi^2 = 7.128$, $p = 0.008$).

Table 3. Comparison of numbers of individuals of five families of anurans with and without identifiable prey items in the gastrointestinal tract and the percentage either calling or in amplexus.

	Bufonidae	Dendrobatidae	Hylidae	Leptodactylidae	Microhylidae
With prey	33 (97%)	53 (96%)	248 (58%)	226 (78%)	40 (93%)
Without prey	1 (3%)	2 (4%)	183 (42%)	63 (22%)	3 (7%)
Percent mating	4%	15%	30%	7%	18%

Table 4. Familial means of number of prey per individual (of those frogs containing prey), relative prey size (\bar{x} prey volume [mm³]/ \bar{x} frog mass), total prey volume per individual, and relative total prey volume (\bar{x} total prey volume (mm³)/ \bar{x} frog mass). One SE of the mean included in parenthesis.

Family	\bar{x} Number of prey / individual	Relative prey size	Total prey volume	Total prey volume / frog mass
Bufo	60.04 (24.79)	1.08 (0.37)	891.03 (331.45)	37.38 (4.93)
Dendrobatidae	19.08 (7.62)	1.00 (0.18)	42.29 (3.19)	15.25 (3.21)
Hylidae	2.24 (0.28)	10.51 (1.49)	114.71 (19.62)	19.79 (1.65)
Leptodactylidae	6.20 (1.56)	5.14 (0.80)	208.54 (43.63)	21.11 (1.56)
Microhylidae	53.05 (20.32)	0.49 (0.16)	85.29 (8.91)	23.51 (2.74)
Pipidae	2.00 (0.58)	19.39 (14.71)	1072.85 (605.32)	35.90 (20.65)

Size of prey and number of prey per frog.—Different families of frogs reveal different strategies of energy acquisition (Table 4). Hylids and pipids eat a few, large prey. Microhylids consume a great number of small prey. Bufonids are one of the most prodigious consumers, with the greatest number of (relatively small) prey consumed. A comparison of the total prey volume consumed by members of different families reveals that not only do bufonids consume the greatest average amount of prey, but even when adjusted for size (total prey volume/frog mass), they still eat the greatest relative amount of prey (Table 4). Dendrobatids are smaller than bufonids, but still eat a large number of small prey (Table 4). Leptodactylids are intermediate in number and size of prey consumed. On the average, they eat three times the number of prey items than do hylids, but the average prey size is approximately half that of hylids.

An ANOVA on species means of relative prey size between families (excluding Pipidae, Pseudidae, and species with less than three individuals with prey), revealed a significant overall difference in comparative prey volume/frog mass ($F_{(4, 43)} = 5.463, p = 0.0012$), and residuals of the common regression of the log-transformed values of mean prey volume and SVL ($F_{(56, 553)} = 5.23, p < 0.0001$). Hylids eat significantly relative larger prey than do members of other families (all $p < 0.05$). Also, significant differences exist among anuran families in the average number of prey per individual ($F_{(4, 43)} = 22.657, p < 0.0001$). All pairs are significantly different ($p < 0.05$), except leptodactylids and dendrobatids, leptodactylids and bufonids, and microhylids and bufonids.

There are distinct differences in the number of prey consumed by different species of frogs (Table 5). As expected, the large *Bufo marinus* eats the most prey per individual of the three species of *Bufo*. This species also eats the relatively smallest prey. Of the dendrobatids, *Epipedobates femoralis* eats fewer, larger prey than its congener, *E. pictus*, and *Colostethus marchesianus*. *Colostethus marchesianus* and *E. pictus* eat about the same average size of prey (the smallest relative size of prey except for the microhylids), but the latter eats almost twice the number

of prey items. Dietarily, *Sphaenorhynchus lacteus* is clearly distinct among the hylids; it is an ant specialist, and eats more than twice the number of prey than any other hylid and eats the smallest prey relative to its own size. Hylids that ingest relatively large prey include *Hyla parviceps*, *H. koechlini*, *Phyllomedusa vaillanti*, *P. tomopterna*, *Scinax garbei*, and *S. icterica*; except for *Sphaenorhynchus lacteus*, *Phrynohyas coriacea*, and *Scinax rubra* eat the greatest number of prey per individual.

Among leptodactylids, *Physalaemus petersi* is the most distinctive in that it is a small-prey specialist that eats the greatest number of small prey (termites). *Lithodytes lineatus*, which has a body shape similar to dendrobatids, eats the second largest average number of prey, and the smallest-sized prey. Species of *Eleutherodactylus* (especially *E. fenestratus* and *E. peruvianus*) eat relatively large prey. Of the leptodactylids, *Leptodactylus mystaceus* eats the relatively largest prey.

Microhylids are alike in eating large numbers of the relatively smallest prey (mostly ants). *Elachistocleis ovalis* consumes large numbers of extremely small prey for its body size. Apparently *Pipa pipa* eats a few relatively large prey items.

Neither numeric ($F_{(1, 49)} = 2.874, p = 0.0963$) or volumetric ($F_{(1, 49)} = 3.534, p = 0.0661$) niche breadths are correlated with number of prey items per frog (3 species with fewer than 3 prey items removed from analysis). There is a sample size bias when niche breadths are compared to number of anurans examined. Both numeric ($r^2 = 0.208, F_{(1, 52)} = 13.644, p = 0.0005$) and volumetric ($r^2 = 0.362, F_{(1, 52)} = 29.513, p < 0.0001$) niche breadths increase with the number of frogs examined (Fig. 4). Hence, diets of species with small sample sizes should be interpreted with caution. General prey categories of several species of anurans are illustrated in Figure 5.

Diets of species.—Detailed dietary results for each species are given in Appendix 2. Ants and beetles are most important in the diet of bufonids. *Bufo marinus* at Cuzco Amazónico were collected in the camp clearing; the difference in diet from its congeners may be a consequence of this difference in habitat.

Table 5. Number of prey categories (total 62), total number of prey, mean number of prey per frog, size, and relative size of prey items consumed by anurans. In columns 5-7, 1 SE in parenthesis after mean, with range below.

Species	Number of prey categories	Number of prey	\bar{x} Number of prey / frog	Prey length (mm)	Prey width (mm)	Prey volume (mm ³)	\bar{x} Prey volume / \bar{x} frog mass
BUFONIDAE:							
<i>Bufo glaberrimus</i>	7	34	34.0	6.47 (0.54) 1.97-11.92	1.24 (0.14) 0.37-3.42	10.01 (2.74) 0.14-73.00	1.5
<i>Bufo marinus</i>	12	548	109.6	5.82 (0.14) 1.61-27.95	1.42 (0.06) 0.41-13.47	28.52 (8.24) 0.14-2655.31	0.4
<i>Bufo "typhonius"</i>	23	986	36.5	5.64 (0.11) 1.34-22.38	1.42 (0.03) 0.35-10.16	13.63 (1.48) 0.14-1172.32	1.4
DENDROBATIDAE:							
<i>Colostethus marchesianus</i>	22	478	17.1	1.44 (0.04) 0.33-5.89	0.52 (0.01) 0.18-2.08	0.45 (0.05) 0.01-10.92	0.8
<i>Epipedobates femoralis</i>	13	91	7.0	1.83 (0.18) 0.29-10.67	0.62 (0.06) 0.17-2.62	1.50 (0.50) 0.00-38.35	1.4
<i>Epipedobates pictus</i>	19	431	33.2	1.93 (0.04) 0.38-7.83	0.51 (0.02) 0.17-2.83	0.73 (0.14) 0.01-21.47	0.8
HYLIDAE:							
<i>Hyla allenorum</i>	6	8	2.0	2.75 (0.30) 1.54-3.88	1.29 (0.17) 0.64-2.00	2.87 (0.72) 0.33-5.42	5.4
<i>Hyla boans</i>	4	5	2.5	13.19 (5.06) 3.22-28.74	3.70 (0.91) 1.48-5.26	168.70 (79.09) 3.69-396.02	5.3
<i>Hyla fasciata</i>	9	31	2.2	5.93 (0.69) 1.44-15.58	1.91 (0.18) 0.53-3.81	20.00 (4.61) 0.21-94.3	6.3
<i>Hyla granosa</i>	5	10	1.4	5.12 (1.37) 0.54-13.3	1.33 (0.30) 0.31-3.33	13.13 (7.59) 0.03-77.22	6.5
<i>Hyla koechlini</i>	7	15	1.4	8.28 (1.57) 0.54-22.41	1.96 (0.27) 0.39-4.91	31.80 (14.59) 0.04-189.22	31.5
<i>Hyla leali</i>	12	44	2.9	3.97 (0.36) 1.30-9.8	1.18 (0.09) 0.53-2.81	4.94 (0.95) 0.24-23.81	5.2
<i>Hyla leucophyllata</i>	11	25	1.7	7.43 (0.79) 2.79-17.71	2.38 (0.20) 0.79-5.41	33.77 (9.87) 0.99-251.02	17.4
<i>Hyla marmorata</i>	3	4	2.0	6.33 (3.41) 1.61-16.07	1.90 (0.53) 1.05-3.24	26.58 (20.89) 0.93-88.33	5.1
<i>Hyla parviceps</i>	13	26	1.6	5.79 (0.70) 2.16-17.16	1.76 (0.14) 0.87-3.91	14.42 (3.97) 0.94-79.26	17.0
<i>Hyla punctata</i>	3	6	2.0	6.53 (1.00) 3.65-9.32	1.75 (0.29) 1.32-3.20	11.77 (4.75) 4.31-34.96	5.3
<i>Hyla rhodopepla</i>	6	11	1.6	4.77 (0.90) 1.45-12.38	1.50 (0.19) 0.86-2.57	8.95 (3.63) 0.84-37.34	8.8
<i>Hyla schubarti</i>	9	20	1.7	3.49 (0.53) 0.60-10.00	1.39 (0.19) 0.47-3.44	7.41 (2.67) 10.11-45.66	9.2
<i>Osteocephalus taurinus</i>	18	53	2.0	14.11 (1.26) 1.77-41.71	3.78 (0.30) 0.48-9.21	201.41 (39.40) 0.28-1522.69	10.0
<i>Phrynohyas coriacea</i>	14	70	4.7	9.42 (0.74) 0.83-35.49	2.36 (0.16) 0.58-8.60	5.63 (23.08) 0.15-1374.366	5.9
<i>Phrynohyas venulosa</i>	12	16	2.3	11.30 (2.99) 0.8-36.46	3.48 (0.89) 0.52-10.85	331.88 (154.34) 0.11-2247.37	14.4
<i>Phyllomedusa atelopoides</i>	9	22	2.4	6.20 (0.82) 0.42-13.67	1.82 (0.18) 0.23-3.38	17.98 (4.25) 0.01-63.35	4.2
<i>Phyllomedusa palliata</i>	4	6	1.5	5.40 (1.29) 0.68-8.98	1.40 (0.30) 0.43-2.12	9.28 (3.63) 0.07-19.25	3.2
<i>Phyllomedusa tomopterna</i>	5	8	1.3	11.34 (0.60) 9.07-14.13	3.50 (0.32) 1.91-4.77	6.82 (13.67) 23.23-139.61	18.2
<i>Phyllomedusa vaillanti</i>	5	5	1.0	7.46 (2.73) 1.99-14.37	2.27 (0.95) 0.59-4.92	62.58 (38.25) 0.48-174.78	18.5
<i>Scarthyla ostinodactyla</i>	12	25	2.5	4.03 (0.61) 0.53-11.64	1.35 (0.16) 0.41-4.27	7.72 (2.93) 0.05-69.6	12.7
<i>Scinax garbei</i>	6	11	1.1	10.48 (1.34) 2.92-16.26	3.62 (0.28) 2.46-5.19	82.59 (16.66) 10.90-161.10	19.8
<i>Scinax icterica</i>	7	13	1.4	7.33 (0.91) 2.32-12.28	2.25 (0.21) 0.99-3.31	25.7 (6.09) 1.50-70.45	16.1

Table 5 continued

Species	Number of prey categories	Number of prey	\bar{x} Number of prey / frog	Prey length (mm)	Prey width (mm)	Prey volume (mm ³)	\bar{x} Prey volume / \bar{x} frog mass
<i>Scinax pedromedinai</i>	10	25	1.8	4.83 (0.46) 1.59–11.46	1.71 (0.13) 0.5–3.01	9.73 (1.73) 0.21–32.47	8.0
<i>Scinax rubra</i>	7	31	3.1	4.64 (0.60) 0.57–10.64	1.34 (0.12) 0.46–2.51	7.54 (1.46) 0.07–35.1	2.6
<i>Sphaenorhynchus lacteus</i>	4	172	13.5	4.70 (0.21) 1.69–10.86	0.96 (0.03) 0.42–1.62	2.94 (0.29) 0.23–11.47	0.8
LEPTODACTYLIDAE:							
<i>Adenomera</i> sp.	24	192	6.2	3.14 (0.16) 0.56–11.59	0.92 (0.05) 0.29–3.96	3.32 (0.59) 0.03–78.17	3.0
<i>Edalorhina perezi</i>	17	53	2.7	5.63 (0.32) 1.94–12.91	1.75 (0.12) 0.35–4.28	13.21 (2.14) 0.12–67.72	5.5
<i>Eleutherodactylus fenestratus</i>	22	67	3.1	6.56 (0.57) 1.20–20.85	2.01 (0.15) 0.59–5.50	31.83 (6.92) 0.26–330.24	9.4
<i>Eleutherodactylus imitatrix</i>	8	10	2.0	2.89 (0.46) 1.14–5.94	1.04 (0.21) 0.45–2.43	2.68 (1.15) 0.12–11.35	5.2
<i>Eleutherodactylus peruvianus</i>	16	36	2.3	4.77 (0.53) 0.95–13.71	1.56 (0.14) 0.38–3.42	11.37 (3.00) 0.11–83.96	8.6
<i>Eleutherodactylus toftae</i>	21	62	2.8	3.72 (0.23) 0.61–8.19	1.32 (0.09) 0.36–3.44	5.58 (1.05) 0.04–44.74	6.5
<i>Leptodactylus bolivianus</i>	21	102	7.3	11.88 (0.93) 1.48–42.24	3.01 (0.21) 0.76–9.83	122.92 (22.1) 1.04–1212.97	2.8
<i>Leptodactylus leptodactyloides</i>	28	98	3.8	5.30 (0.30) 1.14–14.26	1.55 (0.11) 0.37–5.73	13.6 (2.71) 0.19–155.94	3.6
<i>Leptodactylus mystaceus</i>	20	50	2.4	11.12 (0.89) 2.02–28.10	3.51 (0.24) 0.58–6.79	109.88 (18.01) 0.39–607.12	11.5
<i>Leptodactylus pentadactylus</i>	12	30	4.3	19.07 (4.06) 2.72–101.21	4.19 (0.55) 0.77–13.13	523.18 (214.91) 0.84–5525.23	7.9
<i>Leptodactylus petersii</i>	19	68	4.0	5.18 (0.29) 1.64–12.49	1.58 (0.11) 0.41–3.96	11.17 (1.96) 0.19–60.54	5.0
<i>Leptodactylus rhodonotus</i>	26	83	4.4	9.83 (1.11) 0.75–53.11	2.35 (0.24) 0.29–11.62	83.67 (19.97) 0.11–839.19	3.2
<i>Lithodytes lineatus</i>	8	35	17.5	5.55 (0.9) 3.06–32.86	1.35 (0.12) 0.89–4.38	11.29 (4.46) 1.27–134	1.6
<i>Physalaemus petersi</i>	2	92	23.0	3.9 (0.07) 2.85–4.69	1.21 (0.04) 0.57–1.68	3.59 (0.26) 0.48–6.93	2.7
MICROHYLIDAE:							
<i>Chiasmocleis ventrimaculata</i>	3	71	35.5	2.48 (0.16) 1.58–11.68	0.57 (0.03) 0.32–1.36	0.75 (0.18) 0.1–11.31	0.9
<i>Ctenophryne geayi</i>	7	56	18.7	3.83 (0.37) 1.59–14.64	1.05 (0.12) 0.43–4.59	6.56 (1.85) 0.15–65.86	0.8
<i>Elachistocleis ovalis</i>	4	712	89.0	2.68 (0.03) 0.94–9.59	0.71 (0.01) 0.26–1.78	0.95 (0.05) 0.03–7.56	0.2
<i>Hamptophryne boliviana</i>	11	1287	51.5	3.27 (0.06) 0.99–16.6	0.75 (0.01) 0.32–3.02	1.69 (0.09) 0.07–29.52	0.5
PIPIDAE:							
<i>Pipa pipa</i>	5	8	2.0	12.27 (6.14) 0.99–40.02	3.62 (1.43) 0.80–10.06	536.43 (345.73) 0.36–2120.66	19.4

Dendrobatids eat a large number of small prey (including Collembola and Acari). *Colostethus marchesianus* eats a tremendously diverse diet (22 different prey categories). Ants and collembolans are the most numerous prey items, whereas termites and ants are volumetrically the most important. One female (16.9 mm SVL) had eaten 100 Collembola, and 19 of 28 individuals contained at least one collembolan. Small drosophilid and muscoid flies are common in the diet of this species and uncommon in other

anurans. *Epipedobates femoralis* consumes larger prey items than the other two species of dendrobatids (Table 5); this species also consumes considerably fewer prey items per individual than *E. pictus* (7.0 prey/individual versus 33.2 prey/individual). Eruciform larvae seem to be important numerically in *E. pictus*, because one male (17.7 mm SVL) had eaten 49 similar small larvae (1.71 mm × 0.30 mm) and one large larva (7.83 mm × 1.37 mm). Also, there were 28 mites in six different individuals. Volumetrically, seven

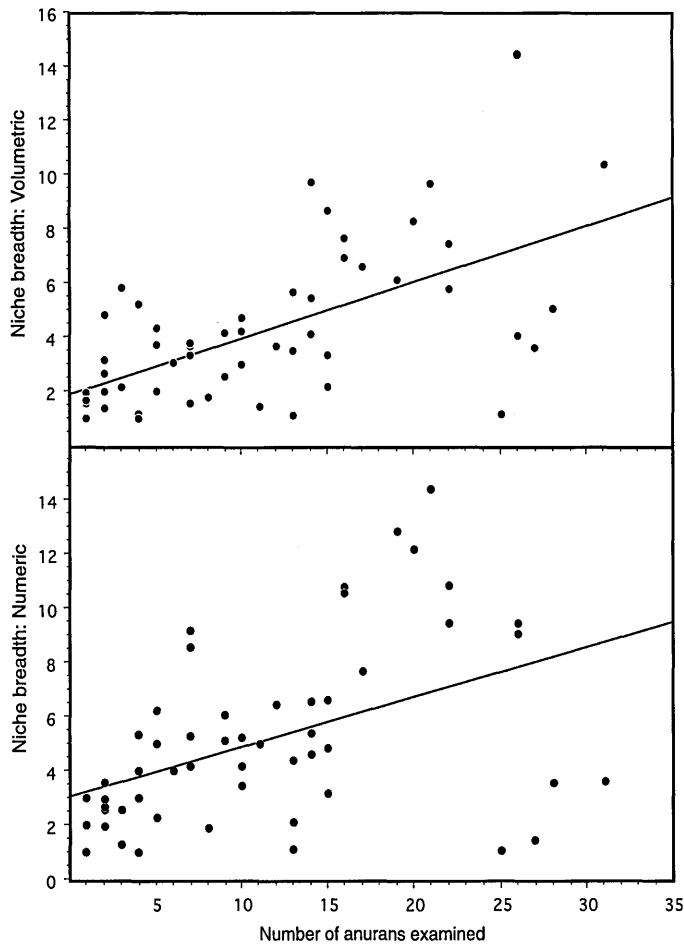


Fig. 4. Volumetric and numeric niche breadths versus number of specimens examined.

similar chrysomelid beetles (5.12 mm \times 2.83 mm) in one large male (23.3 mm SVL) contributed most to this category. *Epipedobates pictus* eats more prey, and consumes more prey categories than its congener, and is much more of an ant specialist (67.8% by number), whereas *E. femoralis* is more even in its consumption of several different prey categories

Some hylids are rather catholic in their diets, whereas others seem to specialize on large prey, mostly orthopterans and lepidopterans. *Hyla koehlini* eats the relatively largest prey of all frogs (Table 5). A male (22.1 mm SVL) had eaten a larva that was 22.41 \times 3.53 mm, and four individuals had each eaten one larva (average length: 16.77 mm). A gravid female *Hyla parviceps* (25.7 mm SVL) had eaten a tettigoniid orthopteran 67% of its body length. The anterior end of this orthopteran was intact in her stomach, whereas the posterior portion had been fairly well digested in the intestine. Tettigoniid orthopterans are the most important prey of several large hylids, such as *Osteocephalus*

taurinus and *Phrynohyas coriacea*. Katydidids are among the largest orthopterans in tropical rainforests, and only anurans such as large hylids and leptodactylids can handle these formidable, spiny prey items. Orthopterans eaten by *Osteocephalus taurinus* are usually 15–30 mm in length, but one tettigoniid was 41.71 \times 8.35 mm in size.

Surprisingly, collembolans and mites were found in a number of hylids; for example, a female *Hyla fasciata* (36.7 mm SVL) had eaten a collembolan (1.44 mm \times 0.53 mm). This small prey item may have been incidentally ingested with other prey or plant material. Collembolans and a mite were found in three *Hyla schubarti*, suggesting that these extremely small prey items may have been ingested purposely.

Spiders are important in the diets of *Scinax pedromedinai*, *Scarthyta ostinodactyla*, *Hyla fasciata*, and *Hyla rhodopepla*. Eight *Hyla fasciata* had eaten 10 spiders. The diet of *H. fasciata* is quite even over the prey categories, giving it a notably high niche breadth for a hylid. The small *Hyla leali* also has one of the largest niche breadths in its family. This species has a remarkable evenness to its diet and utilizes many prey categories nearly equally. *Hyla leali* has a high number of prey items per individual (2.9) for a small hylid (Table 5); about 70% of its diet is composed of flying insects, such as dipterans, winged ants, and lepidopterans. One gravid female (24.4 mm SVL) had eaten 12 winged ants; another gravid female (26.1 mm SVL) had consumed seven flies. *Hyla parviceps* also has a remarkably diverse diet of a few relatively large prey (Table 5). *Hyla leucophyllata* is a moth specialist; 10 of 16 individuals with prey had remains of lepidopterans in their gastrointestinal tracts. I assume these lepidopterans are moths, not butterflies, because hylids (like moths) are active at night.

Phyllomedusa atelopoides is the only terrestrial hylid at Cuzco Amazónico, and its diet reflects this difference in microhabitat. Unlike its three congeners, spiders are the most numerous and frequent prey item. Roaches, spiders, and crickets are most important volumetrically, and the presence of the primarily terrestrial crickets, isopods, and mites indicates feeding at the ground level. This species has a greater number of prey per individual than the other species of *Phyllomedusa* (2.4 versus 1.0, 1.3, and 1.5 for the other three species; Table 5). *Scinax icterica* also may forage at ground level; a male (27.0 mm SVL) had eaten a staphylinid and a scarabid beetle.

Scinax rubra often enters buildings (Rodríguez and Duellman, 1994), and at Cuzco Amazónico, it often was found around the buildings at the lodge. This species contains an average of 3.1 prey per individual, which is more than the other species of *Scinax*, and most other hylids (Table 5). Much like the other species of *Scinax*, spiders are

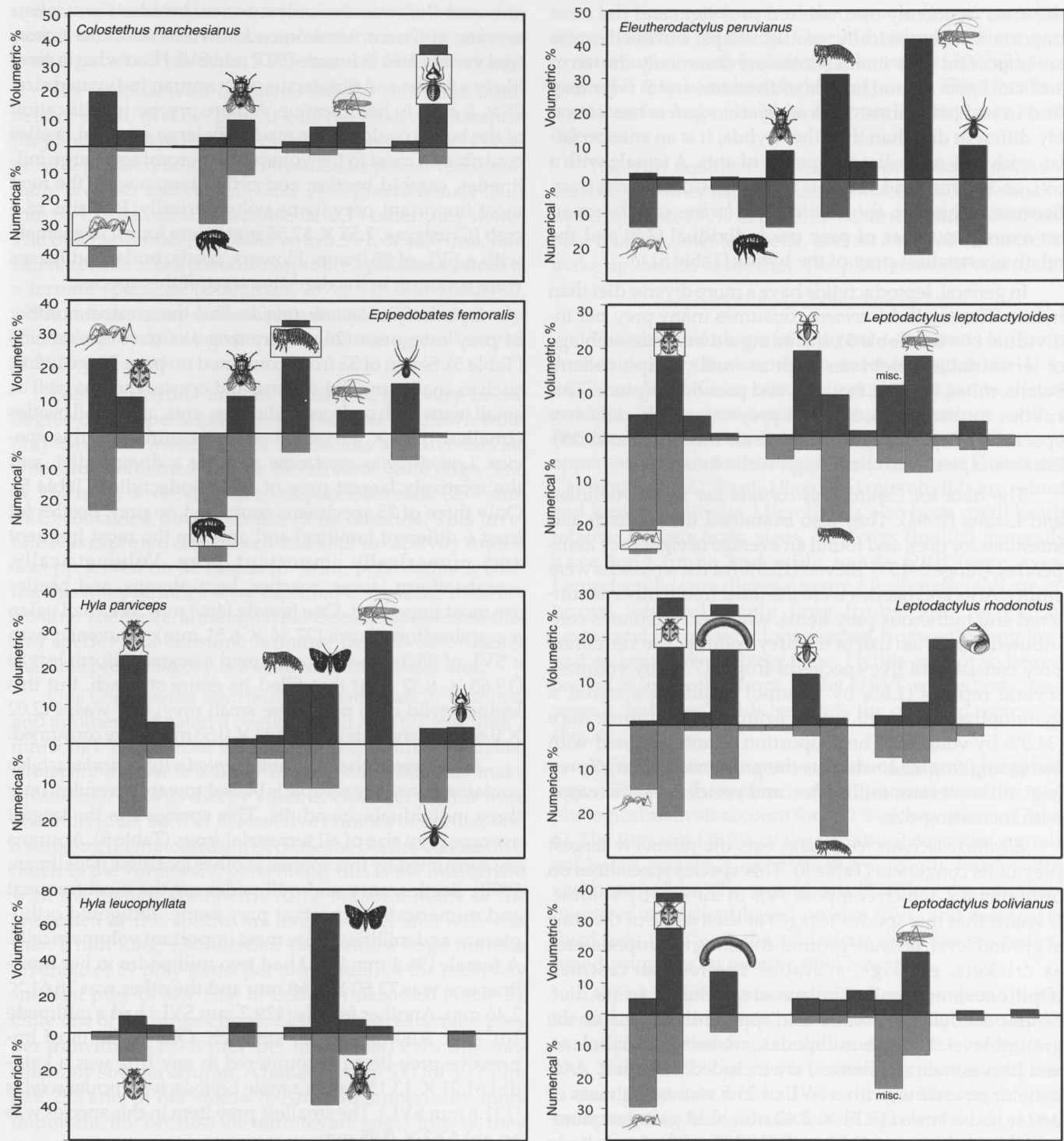


Fig. 5. Volumetric (above x-axis) and numeric (below x-axis) percentages of general categories of prey in the diets of *Colostethus marchesianus*, *Epipedobates femoralis*, *Hyla parviceps*, *Hyla leucophyllata*, *Eleutherodactylus peruvianus*, *Leptodactylus leptodactyloides*, *L. rhodonotus*, and *L. bolivianus*. Major prey categories illustrated by icons (e.g., major prey categories for *Colostethus marchesianus* are ants, collembolans, flies/wasps, orthopterans, and termites).

the most frequently encountered prey item and the most important volumetrically; moths, wasps, and beetles also are important prey items. Moths are commonly drawn to artificial lights around human settlements, and *S. rubra* may feed in such situations. *Sphaenorhynchus lacteus* has a notably different diet than the other hylids; it is an ant specialist, with 98% of its diet composed of ants. A female with a SVL of 36.6 mm had 112 ants in her gastrointestinal tract. Because of this diet, *Sphaenorhynchus lacteus* eats the greatest average number of prey per individual (7.5) and the relatively smallest prey of the hylids (Table 5).

In general, leptodactylids have a more diverse diet than hylids. The small *Adenomera* consumes many prey per individual ($\bar{x}=6.2$, Table 5), including a diverse assemblage of terrestrial invertebrates such as snails, thrips, collembolans, mites, spiders, isopods, and pseudoscorpions. This species consumed 24 different prey categories; only two species of *Leptodactylus* had eaten more (26 and 28). *Edalorhina perezii* also has a high niche breadth.

The data for *Ceratophrys cornuta* are from Duellman and Lizana (1994). They also examined the stomach and intestines for prey, and found an average of eight prey items per frog (range 0–159). Eleven (15.3%) of the stomachs were empty. Ants and beetles were the most frequently encountered and numerous prey items, whereas vertebrates contributed more than half of the prey volume. The vertebrate prey consisted of five species of frogs (17.2% by volume), several reptiles (1.6% by volume) including a snake, a gymnophthalmid lizard, and a lizard egg, and three mice (34.3% by volume). The proportion of ants declined with increasing frog size, whereas the proportion of large prey (e.g., orthopterans, millipedes, and vertebrates) increased with increasing size.

Eleutherodactylus fenestratus eats the relatively largest prey of its congeners (Table 5). This species specializes on orthopterans, which compose 74% of the diet by volume. It seems that this species forages at least some of the time at ground level, because ground-dwelling arthropods such as crickets, earwigs, scarabid beetles, harvestmen (Opiliones), and collembolans are included in its diet. *Eleutherodactylus peruvianus* also apparently forages on the ground level, because millipedes, crickets, collembolans, and harvestmen (Opiliones) are included in its diet. A female *E. peruvianus* with a SVL of 21.5 mm and a mass of 0.82 g had a larva (13.71 × 3.42 mm, 0.13 g) in her stomach; this larva accounted for nearly 16% of the frog's body weight. An *E. toftae* had a complete snail (3.09 × 1.91 mm in size) in its intestine.

Species of *Leptodactylus* eat a great number of diverse, terrestrial prey. *Leptodactylus bolivianus* has the highest number of prey per individual ($\bar{x}=7.3$, Table 5), and all 14 specimens contained prey. Nearly all had eaten at least one

ant, and this was the only species, besides *Ceratophrys cornuta*, at Cuzco Amazónico known to consume terrestrial vertebrates. A female (90.7 mm SVL) had what is most likely a femur and tibiotarsus of an anuran (estimated size: 28 × 8 mm) in her intestine. A more precise identification of the bones could not be made. Six large scarabid beetles contributed most to the volumetric percentage. Large millipedes, carabid beetles, and orthopterans were the next most important prey items volumetrically. Remains of a crab (Crustacea, 7.57 × 12.55 mm) were found in a female with a SVL of 88.0 mm. Flowers, seeds, buds, and leaves were common in the digestive tract of this species.

Leptodactylus leptodactyloides had the greatest number of prey categories (28) of any frog at Cuzco Amazónico (Table 5). Seven of 33 frogs contained no prey. Large items, such as snails, annelid worms, and crustaceans, as well as small items such as drosophilid flies, ants, and small beetles (smallest: 1.95 × 1.04 mm) were consumed by this species. *Leptodactylus mystaceus* also has a diverse diet, and the relatively largest prey of all leptodactylids (Table 5). Only three of 25 specimens contained no prey. Beetles (at least 6 different families) and ants are the most frequent and numerically important prey. Volumetrically, scarabaeiform larvae, roaches, hemipterans, and beetles are most important. One female (46.3 mm SVL) had eaten a scarabaeiform larva (27.36 × 6.51 mm). A juvenile with a SVL of 25.5 mm had consumed a scarabaeiform larvae (19.65 × 6.32 mm) that filled its entire stomach. But this leptodactylid does not ignore small prey; tiny wasps (2.02 × 0.61 mm) and ants (some 2.24 × 0.58 mm) were consumed.

All seven of the available *Leptodactylus pentadactylus* contained prey. My sample is biased toward juveniles; only three individuals are adults. This species has the largest average prey size of all terrestrial frogs (Table 5). Anurans are consumed by this species at other locations (Duellman, 1990). Beetles, ants, and millipedes are the most frequent and numerically important prey items. Tettigoniid orthopterans and millipedes are most important volumetrically. A female (96.4 mm SVL) had two millipedes in her intestine; one was 73.50 × 6.68 mm and the other was 18.61 × 2.46 mm. Another female (129.7 mm SVL) had a millipede 101.21 × 8.00 mm in her stomach. One of the most impressive prey items encountered in any frog was a katydid 61.21 × 13.13 mm in a male *Leptodactylus pentadactylus* (131.6 mm SVL). The smallest prey item in this species was an ant 4.82 × 0.95 mm.

Leptodactylus rhodonotus has one of the highest numerical niche breadths; it eats members of 26 different prey categories. Millipedes and snails make up almost half of the diet volumetrically. These two uncommon prey categories are important prey items and make *L. rhodonotus* unique in its diet compared to its congeners. Other un-

usual prey items in this species include a crab, three centipedes, two annelids, nine campodeiform larvae, and two walking sticks (Phasmida, 33.58 mm and 31.43 mm long).

The leptodactylid *Lithodytes lineatus* eats large numbers of small, diverse prey. It eats the relatively smallest prey and the second highest number of prey per individual of all leptodactylids. Only *Physalaemus petersi* consumes more prey per individual (Table 5). A gravid female (50.1 mm SVL) had eaten 19 termites and 14 other prey items. The other specimen, a female with a SVL of 42.6 mm, had eaten a beetle and a pseudoscorpion. *Physalaemus petersi* is a termite specialist (Duellman, 1978; Vitt and Caldwell, 1994) and eats many of these prey items almost exclusively. The only prey item besides a termite was a small weevil (4.26×0.92 mm).

The microhylids are ant specialists, but vary in the degree of ant specialization. *Altigius alios* is known from only two post-metamorphic specimens and five larvae. One adult contained 12 ants (seven were quite large, 9.60×1.57 mm), a weevil, and a wasp; one juvenile (23.7 mm SVL) contained three termites in its intestine. This juvenile was captured on 3 March and kept in captivity until it was preserved on 31 March (E. Wild, pers. comm.). During this time, termites were captured and placed in its enclosure. Therefore, although it has been demonstrated that this species will consume termites, there is no evidence that this prey category is included in its natural diet.

One *Chiasmocleis ventrimaculata* had eaten 27 termites, and another had eaten a beetle and 43 ants (37 less than 2 mm long). This species is clearly an ant/termite specialist. *Ctenophryne geayi* is a fairly large microhylid; ants make up almost 99% of its diet by volume. Other prey items were one individual each of at least five families of beetles, and a stinkbug (Pentatomidae). Because the beetles contributed much to the volumetric percentage, this is the microhylid with the highest volumetric niche breadth. Many of the ants eaten by this species are large; only 21 ants were less than 2 mm long. *Elachistocleis ovalis* eats a large number (average of 89 prey items per individual) of the relatively smallest prey of any frog at Cuzco Amazónico (Table 5). Only one of the largest frogs, *Bufo marinus*, eats more prey per individual (109.6 prey per individual) than this considerably smaller anuran. A female with a SVL of 35.7 mm had 295 ants in her stomach. Ants are numerically more important, but because the termites are larger insects, they are more important volumetrically. *Hamptophryne boliviana*, the most common microhylid at Cuzco Amazónico, is an ant specialist (more than 92% in numbers and volume); the few other small prey were beetles. Beetles in the families Pselaphidae, Scolytidae, and Histeridae are small, and similar in size and shape to the ants that this species utilizes as its primary prey.

Only two specimens of the aquatic *Pseudis paradoxa* were available for study. One individual with no gastrointestinal contents had a scraped nose (KU 209762), suggesting it may have been held in captivity. The other had remains of a large (16.26×4.01 mm) orthopteran in its intestine.

The truly aquatic *Pipa pipa* has a predictably different diet than all other frogs at Cuzco Amazónico. Fish remains make up almost 99% of the prey volume. Unidentified tadpole remains, a water beetle, and an ostracod (Crustacea) make up the rest of the diet. The plant material was seeds.

MORPHOLOGICAL CORRELATES OF DIET

The size and shape of anurans.—Anurans at Cuzco Amazónico vary in size over an order of magnitude (11.4–142.7 mm SVL). Gross morphological types can be distinguished. The bizarre aquatic *Pipa pipa* is unique, with a flattened body, a wide flat head, and other modifications apparently correlated with its aquatic existence (Trueb and Cannatella, 1986). Toads (*Bufo*) and microhylids are robust and have short limbs. Microhylids also have small heads relative to their body sizes. Treefrogs (hylids) generally have long limbs and wide heads with large eyes. Leptodactylids are diverse; many *Eleutherodactylus* are arboreal with relatively long limbs, and terrestrial *Leptodactylus* are large, long-limbed frogs with long jaws and an impressively large gape. Hylids are not so heavy-bodied as most other frogs. A plot of SVL versus body mass reveals that most hylids lie below the common regression (Fig. 6).

Principal components analysis of external morphology.—The first three principal components from the morphological analysis account for 86.1% of the variation (Table 6). The first axis (38.5% of the variation) describes a gradient based primarily on relative jaw length, head width, and head height. The second axis (32.8% of the variation) describes a gradient based on size (SVL and mass). The third axis (14.8% of the variation) describes a gradient based primarily on relative tibia length.

A plot of the first two principal components (means for each species) reveals both differences and similarities in morphology among families and genera of frogs (Fig. 7A). The aquatic *Pipa pipa* is bizarre morphologically and is clearly separate from all other frogs. The microhylids group together, being characterized by relatively short jaws and narrow heads. Hylids are distributed throughout morphological space, with species such as *Hyla boans* and *H. calcarata* having relatively long jaws and wide heads, and *H. marmorata*, *H. leali*, and *H. allenorum* having relatively short jaws and narrow heads. The obvious outlier among hylids is *Sphaenorhynchus lacteus*; this species falls within the microhylid morphospace.

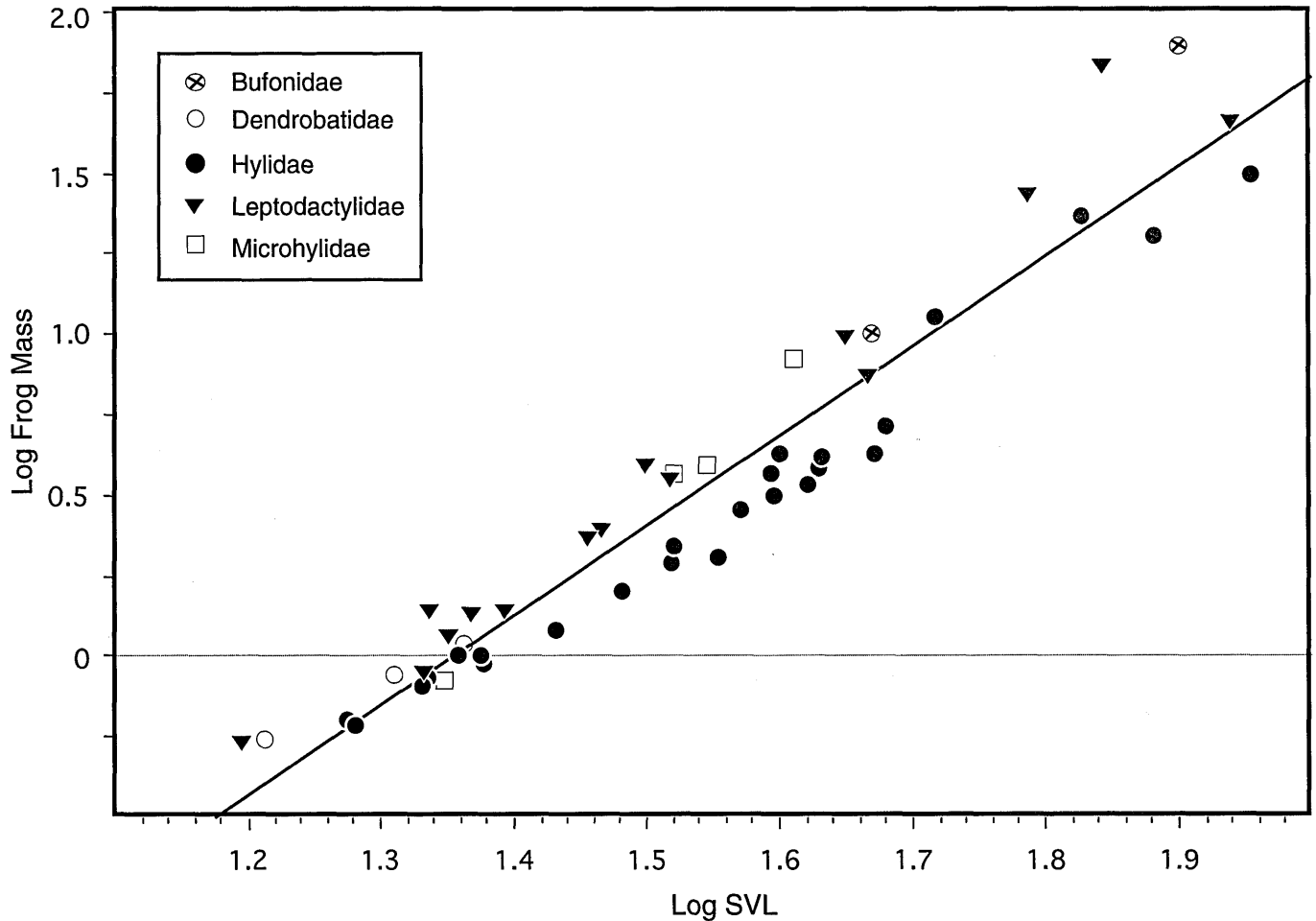


Fig. 6. Plot of SVL versus mass for 49 species of anurans.

The leptodactylids occur together toward the long-jaw, wide-head side of the PC 1 axis. *Eleutherodactylus* cluster together, with *E. fenestratus* having the longest jaw and widest head of all frogs. All species of *Leptodactylus* have the same general head shape (similar to *Eleutherodactylus*), but vary widely in overall size. Dendrobatids cluster in morphospace, as do the large and similarly shaped hylid genera *Osteocephalus* and

Phrynohyas. Three of the four species of *Phyllomedusa* are close together, but the terrestrial *Phyllomedusa atelopoides*, while similar in size, has a different head shape and falls within the morphospace occupied by *Leptodactylus*, with a longer jaw/wider head than its congeners.

A plot of the first and third principal components (means for each species) again reveals both differences and similarities in morphology among the families and gen-

Table 6. Loadings from a principal component analysis on size-free morphological variables for 58 species of adult frogs.

Variable	PC1	PC2	PC3
Head width	-0.523	0.050	0.301
Head height	-0.456	0.044	0.389
Jaw length	-0.612	0.088	-0.038
Tibia length	-0.353	0.102	-0.864
SVL	-0.083	-0.700	-0.098
Mass	-0.112	-0.698	0.013
Eigenvalue	2.311	1.968	0.887
Percentage of variance explained	38.5	32.8	14.8
Cumulative % of variance explained	38.5	71.3	86.1

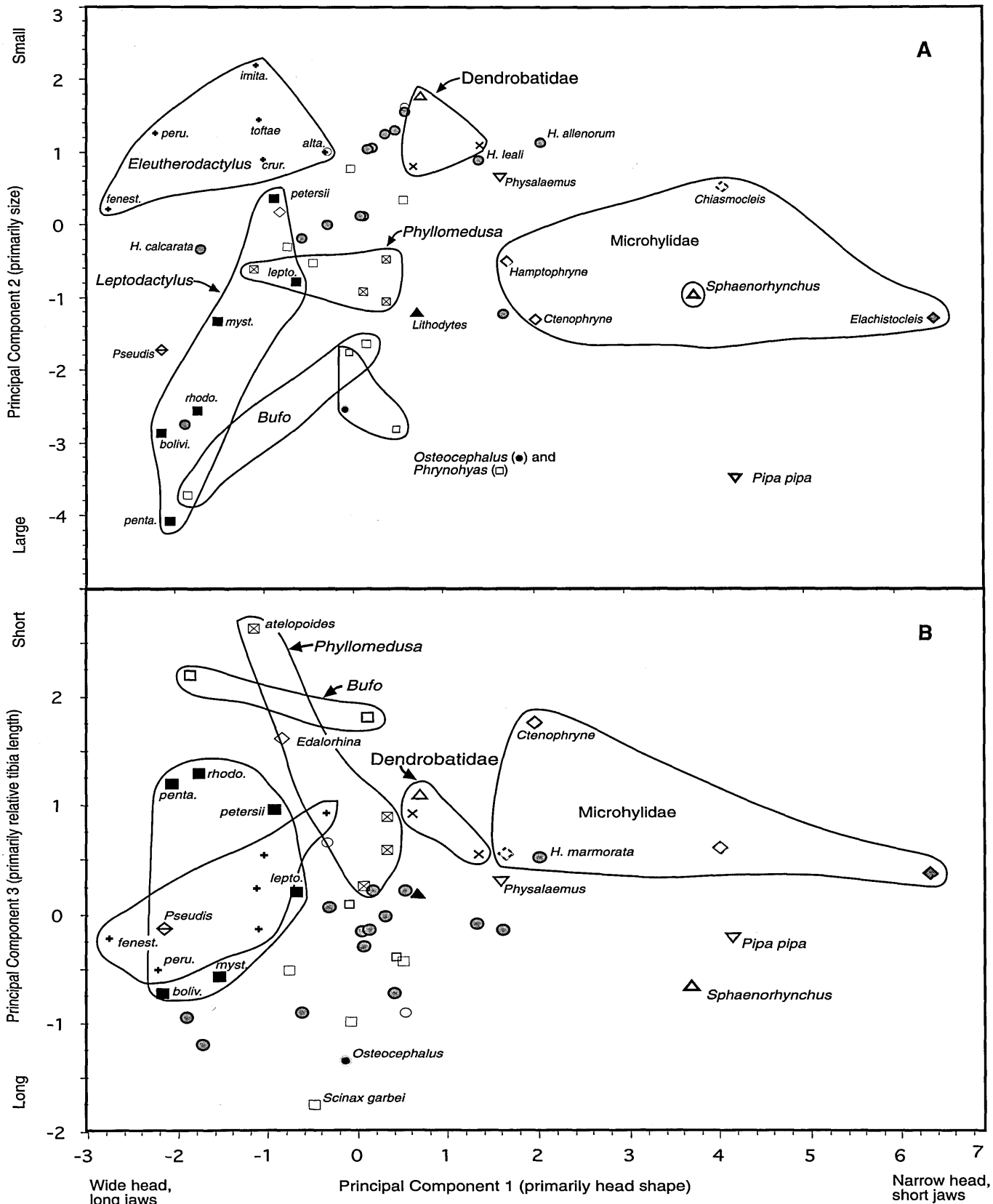


Fig. 7. (A) A plot of the first two principal components; (B) A plot of the first and third principal components of a PCA analysis on body size and several size-free morphological variables of 54 species of anurans. Symbols represent different genera.

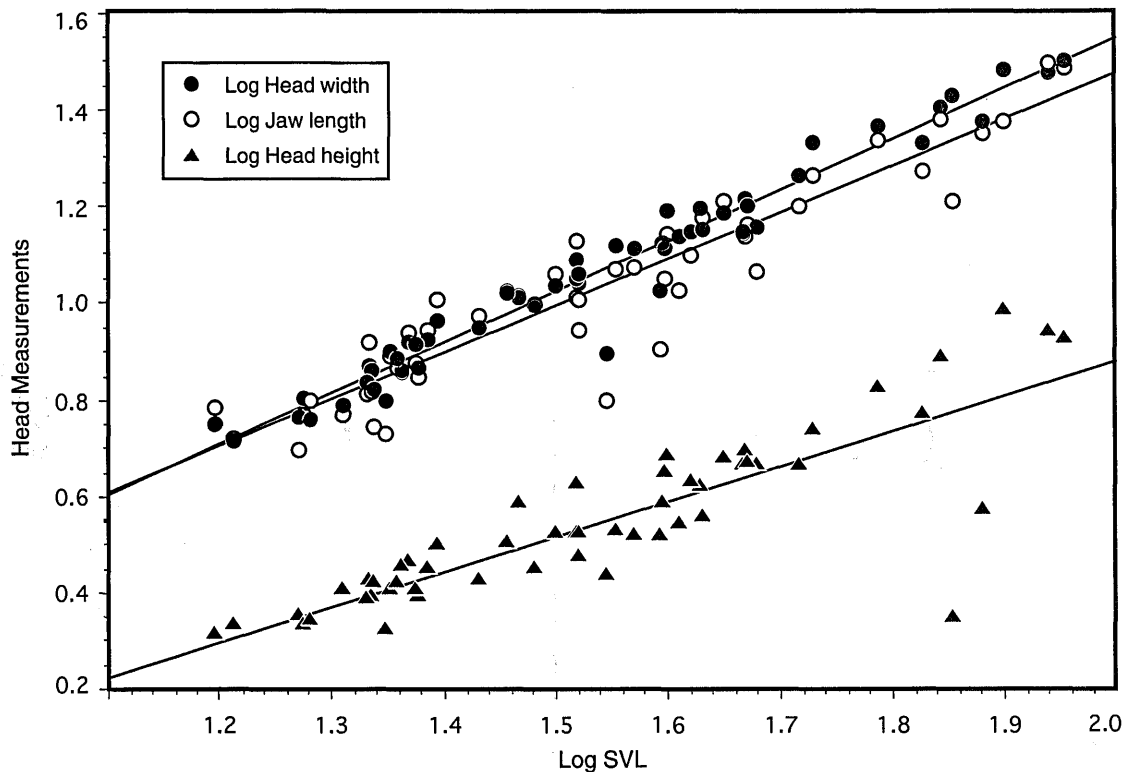


Fig. 8. Correlation of mean head measurements with mean SVL in 54 species of anurans.

era (Fig. 7B). The hylids clearly have the longest legs for their body size; *Sphaenorhynchus lacteus*, while having an atypical hylid head, has relatively long legs like other hylids. *Phyllomedusa atelopoides* differs from its congeners; it has the shortest relative tibia length of all species examined. Bufonids have the next shortest legs. Whereas *Eleutherodactylus* and *Leptodactylus* are distinguished by size (Fig. 7A), they cluster together by head shape and relative limb length. The species of *Leptodactylus* range from long-legged (*L. bolivianus* and *L. mystaceus*), intermediate (*L. leptodactyloides*), and relatively short-legged species (*L. rhodonotus*, *L. pentadactylus*, and *L. petersii*).

Comparative morphology of head and body.—Head measurements are closely correlated to SVL (Fig. 8). Head width is most closely correlated to SVL ($r^2 = 0.958$, $F_{(50, 10)} = 33.035$, $p < 0.0001$). Head height is the next-most correlated variable to SVL when the extremely shallow-headed *Pipa pipa* is removed (excluding *Pipa pipa*: $r^2 = 0.901$, $F_{(55, 804)} = 47.801$, $p < 0.0001$; including *Pipa pipa*: $r^2 = 0.849$, $F_{(56, 809)} = 76.637$, $p < 0.0001$). Jaw length is the most variable head measurement, but is still highly correlated to SVL ($r^2 = 0.888$, $F_{(56, 810)} = 92.904$, $p < 0.0001$). The slopes of head width (1.009) and jaw length (0.932) versus SVL are close to 1.0, whereas head height (0.781) has a lower slope (Fig. 8).

There are overall significant familial differences in all size-adjusted external morphological variables (Fig. 9):

head width ($F_{(6, 860)} = 51.856$, $p < 0.0001$), jaw length ($F_{(6, 860)} = 144.976$, $p < 0.0001$), head height ($F_{(6, 859)} = 240.549$, $p < 0.0001$), and tibia length ($F_{(6, 860)} = 85.614$, $p < 0.0001$). *Pipa pipa* has the relatively flattest head and shortest relative tibia length. Microhylids and dendrobatids have the narrowest heads, whereas *Pseudis paradoxa*, leptodactylids, and bufonids have the widest heads. Microhylids have shallow heads, and bufonids and leptodactylids have deep heads. Bufonids and microhylids have relatively short tibiae, and hylids and *Pseudis paradoxa* have the relatively longest tibiae.

Predator-prey size relationships.—There is a significant relationship between prey size and frog body size (Fig. 10; slope = 1.06, $r^2 = 0.430$, $F_{(1, 582)} = 439.025$, $p < 0.0001$). Generally, larger frogs eat larger prey. A comparison of prey length and width with frog size reveals that there is a tighter relationship and steeper slope between frog size and prey length (slope = 1.075, $r^2 = 0.448$) than between prey width and body size (slope = 0.868, $r^2 = 0.377$).

Prey size is not determined by predator size alone, because relative head and tibia dimensions also affect prey size. There are significant positive correlations between mean prey volume and the size-adjusted morphological variables head width ($r^2 = 0.04$, $F_{(1, 608)} = 25.437$, $p < 0.0001$), jaw length ($r^2 = 0.06$, $F_{(1, 608)} = 39.012$, $p < 0.0001$), head height

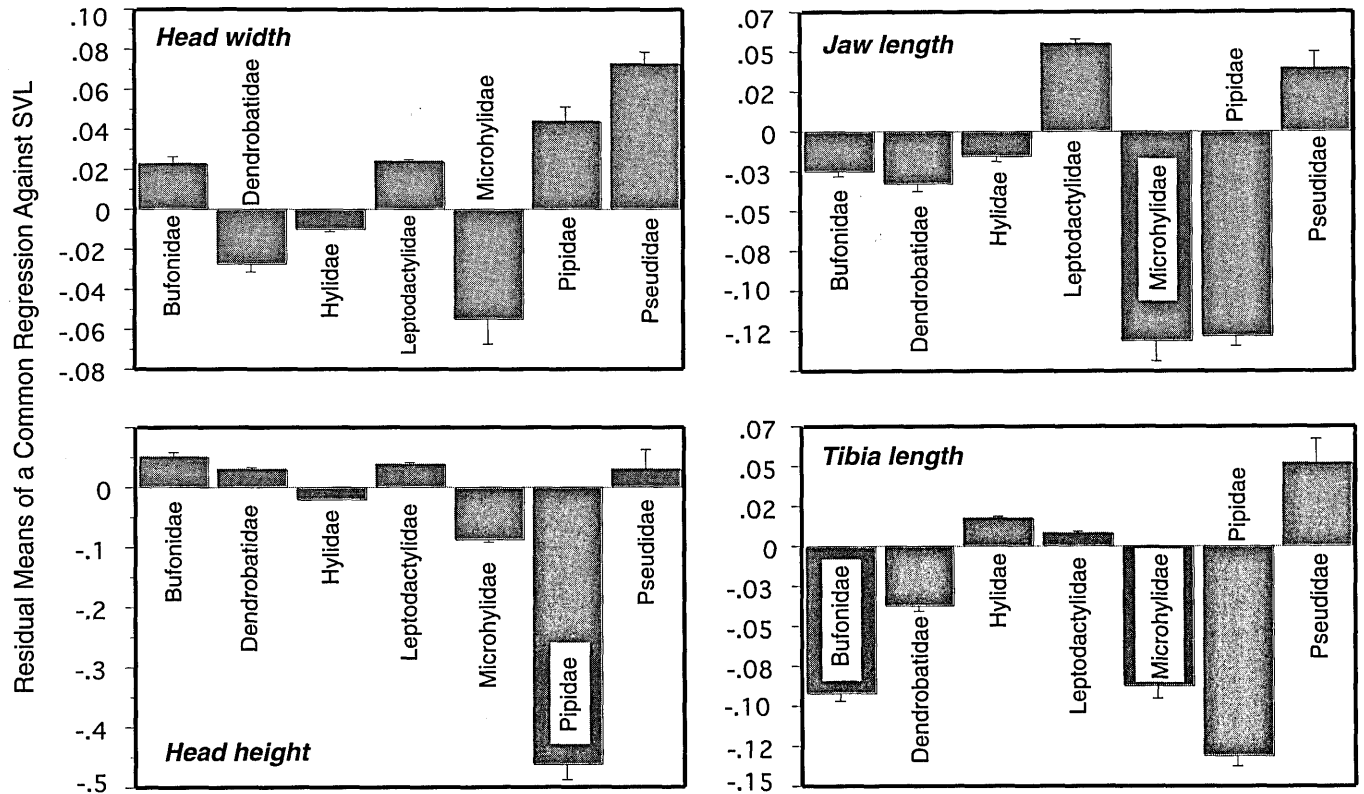


Fig. 9. Residual means for morphological measurements versus SVL split by family. Bars indicate one SE of the mean.

($r^2 = 0.007$, $F_{(1, 607)} = 4.043$, $p = 0.0448$), and tibia length ($r^2 = 0.056$, $F_{(1, 608)} = 36.340$, $p < 0.0001$). Head widths and jaw lengths are most closely correlated, and head heights are barely significant. Three of four of these morphological variables have a significant, negative correlation with mean number of prey per individual: head width ($r^2 = 0.039$, $F_{(1, 608)} = 24.401$, $p < 0.0001$), jaw length (Fig. 17B; $r^2 = 0.103$, $F_{(1, 608)} = 69.886$, $p < 0.0001$), and tibia length ($r^2 = 0.202$, $F_{(1, 608)} = 153.432$, $p < 0.0001$). Mean number of prey per individual is not correlated to head height ($p > 0.05$). Relative tibia lengths and jaw lengths are most closely correlated to prey size. Although legs are clearly not directly involved in prey capture, relatively short legs seem to be a correlate of active foraging behavior.

Obviously, frog size alone does not determine prey size; relative prey sizes vary considerably (Table 5). A plot of mean SVL against mean prey volume reveals that dendrobatids, microhylids, and bufonids consume smaller prey in relation to their body size (Fig. 11). Most hylids (*Sphaenorhynchus* being an exception) and leptodactylids (except *Physalaemus petersi* and *Lithodytes lineatus*) eat relatively larger prey compared to all frogs. This relationship seems to be linear and nonasymptotic.

Different groups of frogs have different predator-prey size relationships. Hylids and leptodactylids have steeper

head width-prey width slopes, and bufonids, dendrobatids, and microhylids have shallower slopes and tighter correlations (Fig. 12). The three species of *Bufo* eat nearly the same size of prey, even though one (*Bufo marinus*) has a much wider head (slope = 0.007, $r^2 = 0.317$). When comparing the two most speciose genera, *Hyla* and *Leptodactylus*, different predator-prey slopes are apparent (Fig. 13). *Leptodactylus* has a much tighter correlation and steeper slope between SVL and mean prey volume (Fig. 13A; $r^2 = 0.606$, slope = 2.614). *Hyla* has a significant, but less tightly correlated relationship (Fig. 13B; $r^2 = 0.103$, slope = 1.615). Many more species of *Hyla* share prey in the same prey-size range, whereas there is more separation in size ranges of prey among species of *Leptodactylus*. Still, *L. bolivianus*, *L. rhodonotus*, and *L. mystaceus* consume a similar range of prey sizes; thus, there may be competition if similar-sized prey are limited in availability.

Whereas average prey size is correlated to mean body size in frogs, frogs are limited by maximum prey size. The relationship between minimum prey size per species and frog size is only slightly significant ($r^2 = 0.131$, $F_{(1, 39)} = 5.867$, $p = 0.0202$), whereas maximum prey size and frog size is highly correlated ($r^2 = 0.592$, $F_{(1, 40)} = 57.926$, $p < 0.0001$). Within families, only leptodactylids have a significant, positive relationship between minimum prey size and SVL

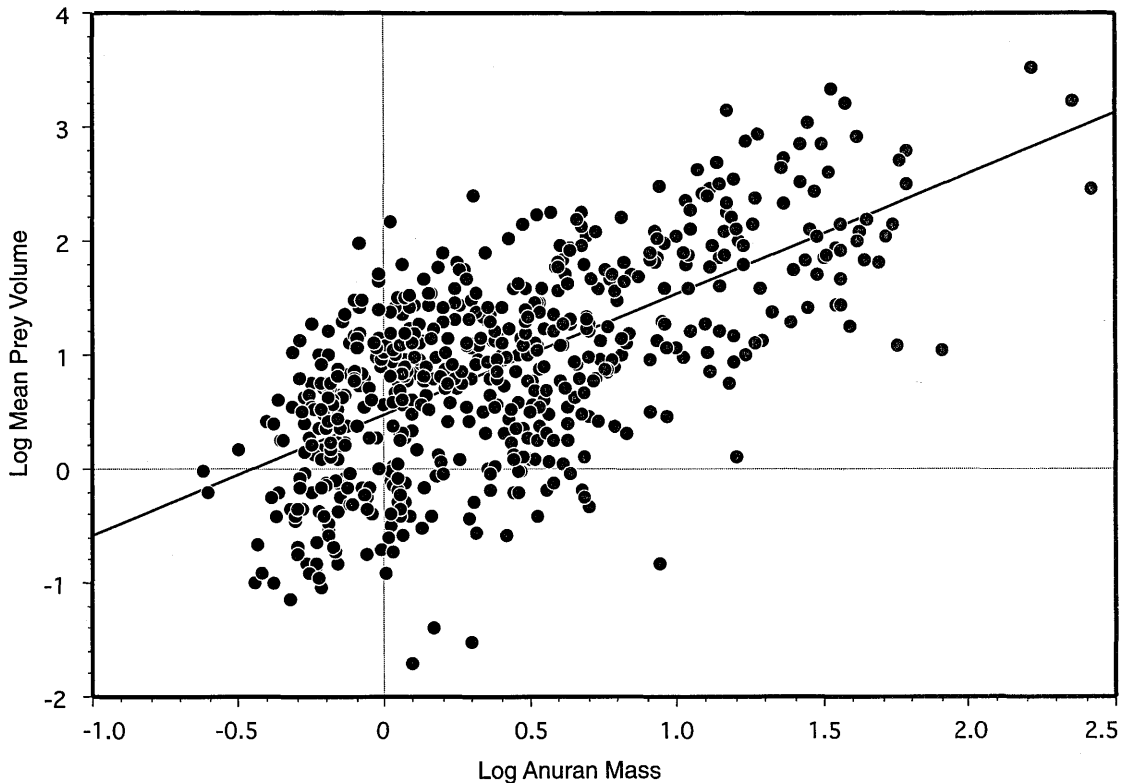


Fig. 10. Mean prey volume plotted against frog mass for 609 anurans.

($F_{(1,13)} = 9.647$, $p = 0.0084$). Both hylids ($F_{(1,16)} = 7.698$, $p = 0.0135$) and leptodactylids ($F_{(1,13)} = 39.784$, $p < 0.0001$) have a significant relationship between SVL and maximum prey size. Possibly, larger anurans are rarely limited by prey size. Maximum prey widths fall below head widths for all sizes of frogs, but the gap is especially evident in larger frogs (Fig. 14).

Because most species consume ants, I examined whether the distribution of ant size was related to frog size. Overall, there is a significant, positive correlation between frog size (SVL) and mean ant volume ($r^2 = 0.695$, $F_{(1,28)} = 63.747$, $p < 0.0001$). In general, larger frogs eat larger ants. When separated by family, only the leptodactylids demonstrated a significant relationship ($F_{(1,11)} = 56.794$, $p < 0.0001$). Examination of mean ant size of ant-consuming frogs ranked by SVL reveals a progression of larger ants with increasing size of frogs (Fig. 15). Microhylids eat very small ants, even though some (e.g., *Ctenophryne geayi*) are quite large. Although it was the second largest frog studied, *Bufo marinus* eats relatively small ants.

A comparison of ant sizes within three species of microhylids reveals that *Elachistocleis ovalis* eats significantly smaller ants than *Ctenophryne geayi* or *Hamptophryne boliviana*, and there is no significant difference in ant size between the latter two species ($F_{(2,1758)} = 26.082$, $p < 0.0001$). This relationship is independent of body size, because

Hamptophryne boliviana is the smallest frog (\bar{x} SVL = 33.2 mm), *Elachistocleis ovalis* (\bar{x} SVL = 36.3 mm) intermediate in size, and *Ctenophryne geayi* the largest frog (\bar{x} SVL = 40.8 mm).

Head shape influences relative prey size and mean number of prey per individual consumed. Examination of the species means for these variables plotted against the first principal components axis of the size-adjusted morphology (see foregoing section on Principal Components Analysis) reveals that anurans with narrower heads/shorter jaws eat more prey and smaller prey than other frogs (Fig. 16). The exceptions to this trend are *Pipa pipa* for both variables, and *Bufo marinus* for number of prey. Species with a greater percentage of ants and termites in their diet have relatively narrower heads (Fig. 17).

Number of prey per frog and mean individual prey volume per frog are negatively correlated; as the number of prey per frog increases, the volume of individual prey items decreases (Fig. 18; $r^2 = 0.103$, $F_{(1,603)} = 67.666$, $p < 0.0001$). Overall, the number of prey per frog is not related to frog size ($r^2 = 0.001$, $F_{(1,608)} = 0.579$, $p = 0.447$).

COMMUNITY ANALYSES

Diet overlaps.—Most diet overlaps between species are low (Tables 7, 8; Fig. 19). They range from 0 (several pairs of species) to 0.919 (between *Ctenophryne geayi* and both *Bufo "typhonius"* and *Epipedobates pictus*) for terres-

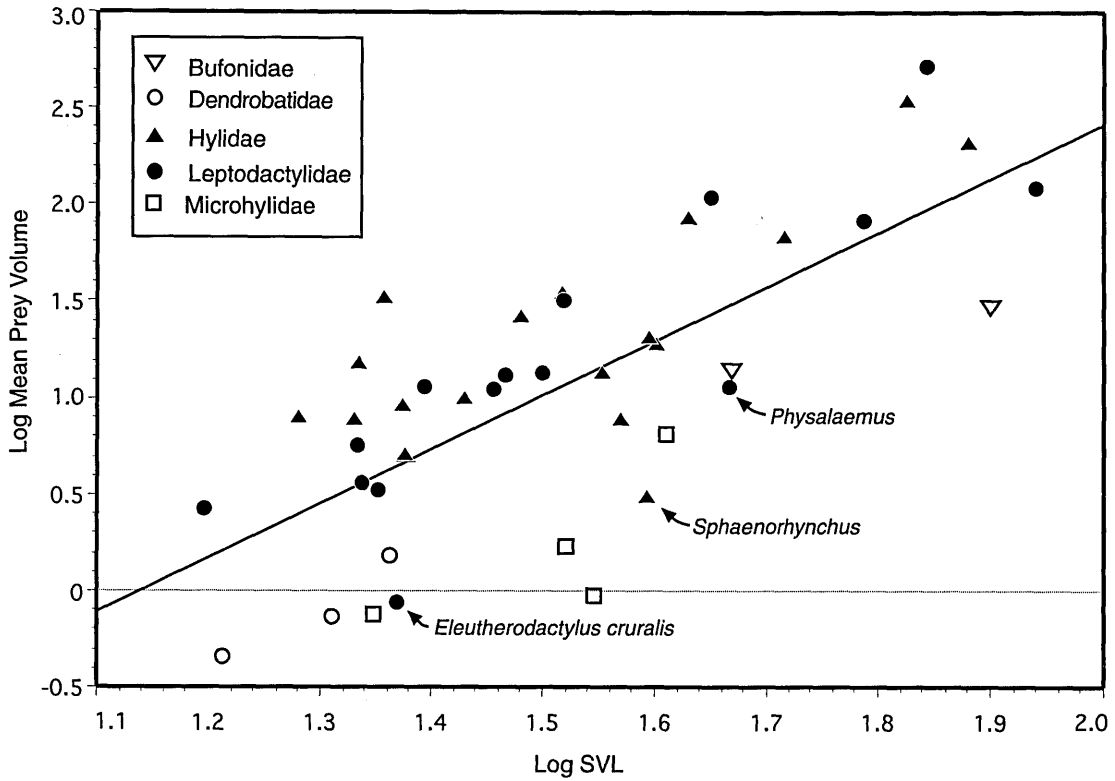


Fig. 11. Mean prey volume versus mean SVL for 40 species of anurans. Species with fewer than 10 prey items excluded.

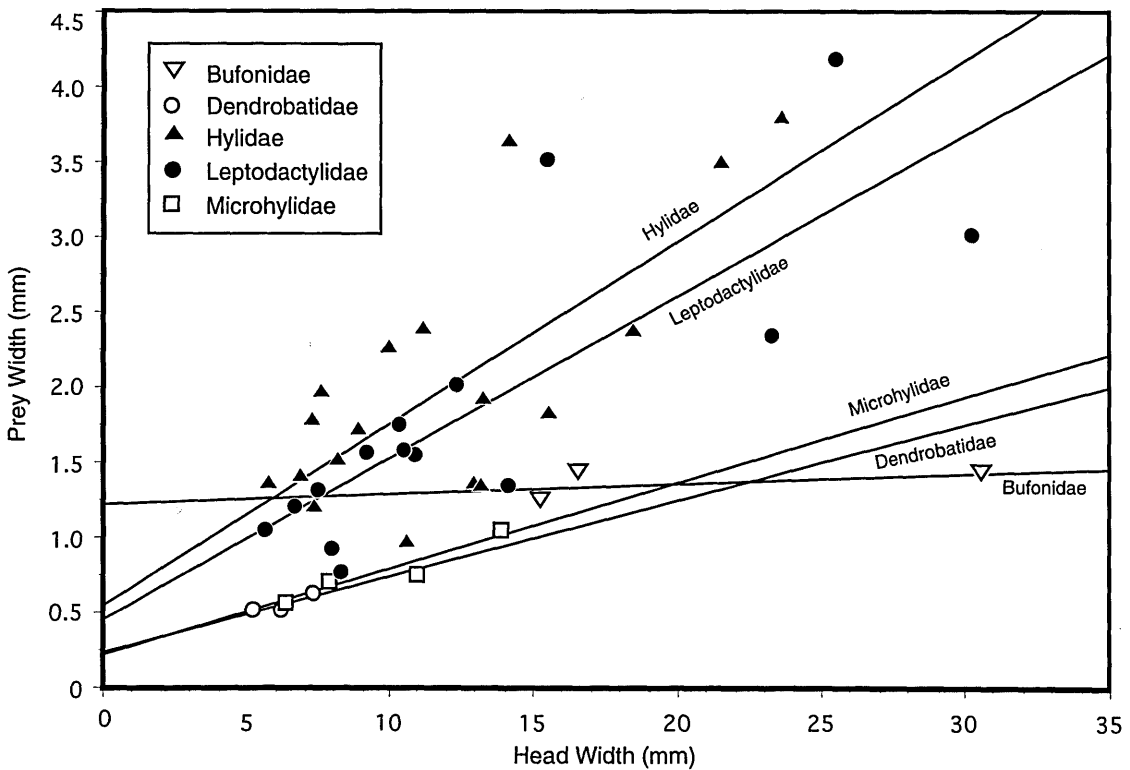


Fig. 12. Species means of prey width versus head width for five families of anurans.

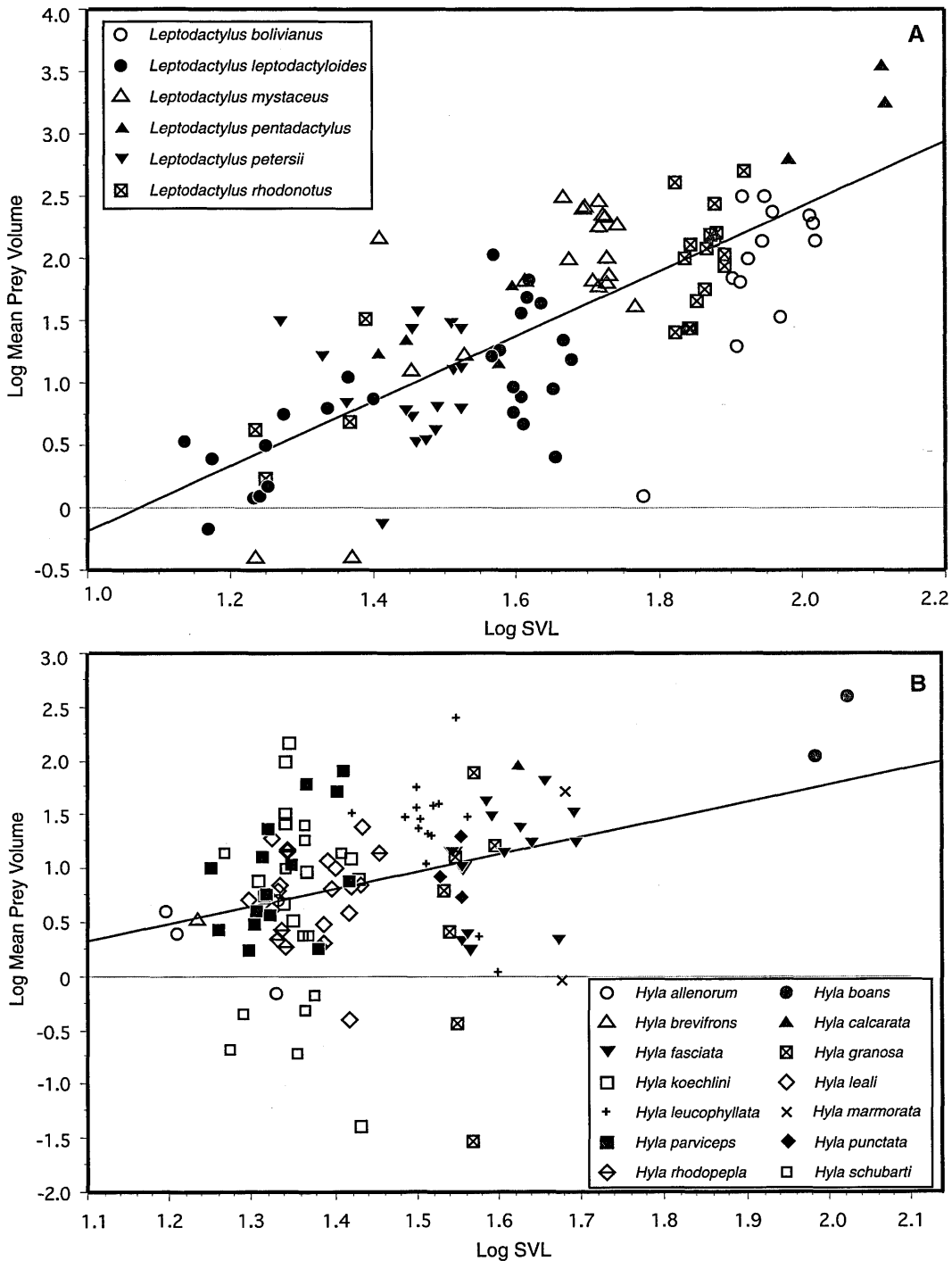


Fig. 13. (A) Mean prey volume versus mean SVL for six species of *Leptodactylus* and (B) 14 species of *Hyla*.

trial anurans (Table 7). Overlaps range between 0 (between the ant specialist *Sphaenorhynchus lacteus* and several other species) and 0.976 (between the large orthopteran specialists *Osteocephalus taurinus* and *Eleutherodactylus fenestratus*) for the arboreal species (Table 8).

Examination of the distribution of overlap values (Fig. 19) reveals that arboreal species have more pairs with higher overlaps than do terrestrial species. There is a pronounced lack of species pairs with overlaps between 0.300 and 0.399 and then a greater number with overlaps be-

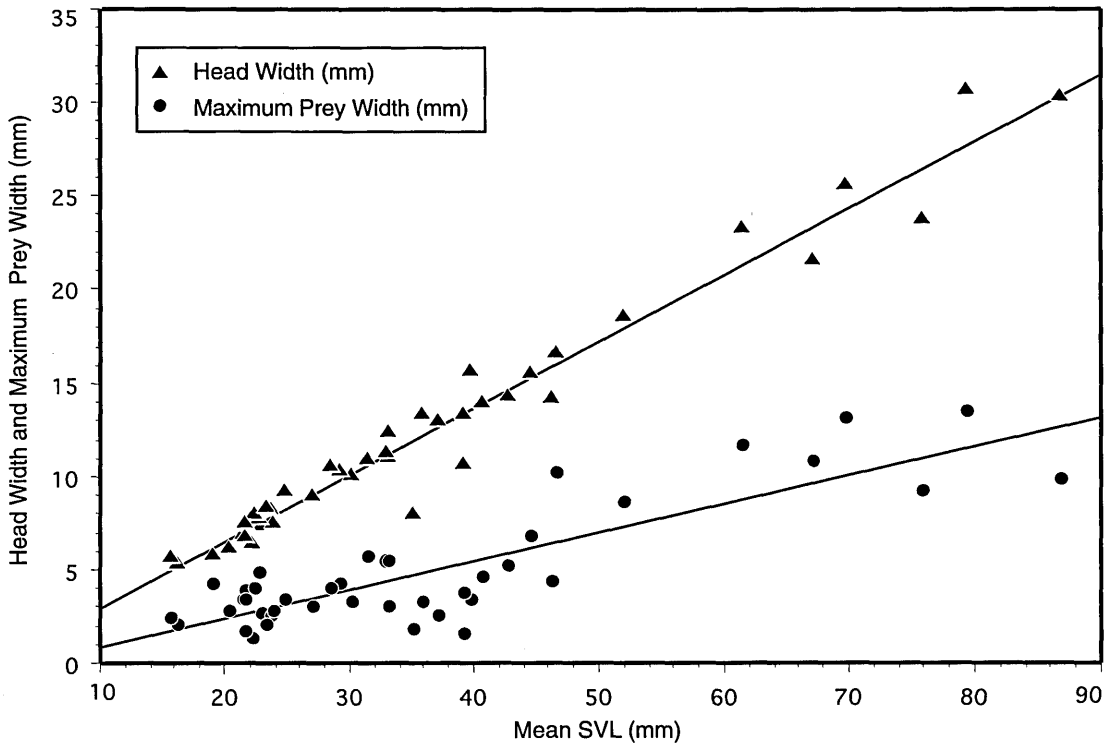


Fig. 14. Mean head width and maximum prey width versus mean SVL in the diets of 46 species of anurans.

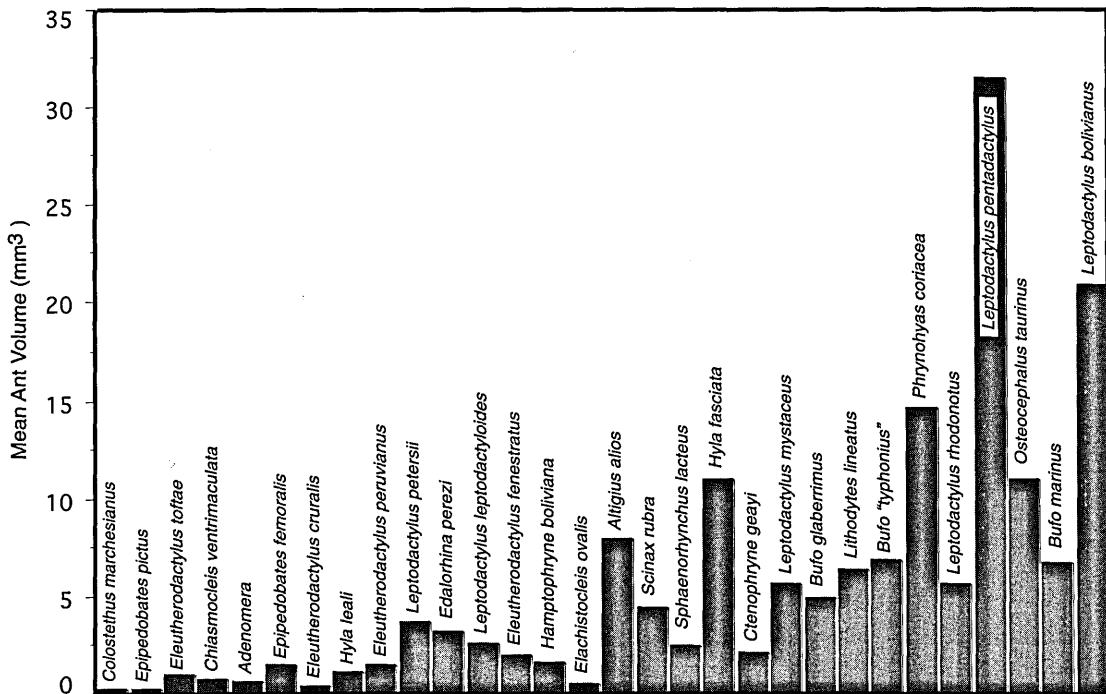


Fig. 15. Species means of mean ant volume consumed, ranked by mean SVL.

Table 7. Diet overlaps for terrestrial anurans. Overlaps are based on g_i data. The order of species in rows and columns is the same.

	B. m.	B. t.	C. m.	E. f.	E. p.	P. a.	A. sp.	E. p.	L. b.	L. l.	L. m.	L. pen.	L. pet.	L. r.	L. l.	P. p.	C. g.	E. o.	H. b.
<i>Bufo marinus</i>	1																		
<i>Bufo "typhonius"</i>	0.294	1																	
<i>Colostethus marchesianus</i>	0.126	0.313	1																
<i>Epipedobates femoralis</i>	0.087	0.395	0.366	1															
<i>Epipedobates pictus</i>	0.346	0.888	0.429	0.344	1														
<i>Phyllomedusa atelopoides</i>	0.008	0.026	0.098	0.375	0.036	1													
<i>Adenomera sp.</i>	0.181	0.515	0.355	0.662	0.575	0.322	1												
<i>Edalorhina perezii</i>	0.070	0.156	0.377	0.636	0.126	0.484	0.489	1											
<i>Leptodactylus bolivianus</i>	0.240	0.411	0.142	0.195	0.470	0.124	0.445	0.249	1										
<i>Leptodactylus leptodactylus</i>	0.694	0.414	0.247	0.365	0.504	0.374	0.674	0.405	0.528	1									
<i>Leptodactylus mystaceus</i>	0.435	0.387	0.128	0.464	0.505	0.701	0.595	0.347	0.411	0.724	1								
<i>Leptodactylus pentadactylus</i>	0.092	0.084	0.120	0.105	0.091	0.197	0.291	0.392	0.526	0.343	0.310	1							
<i>Leptodactylus petersii</i>	0.213	0.288	0.280	0.803	0.342	0.653	0.709	0.471	0.269	0.580	0.832	0.222	1						
<i>Leptodactylus rhodonotus</i>	0.267	0.225	0.053	0.070	0.276	0.077	0.476	0.079	0.409	0.323	0.374	0.541	0.215	1					
<i>Lithodytes lineatus</i>	0.091	0.101	0.356	0.223	0.126	0.199	0.638	0.305	0.266	0.585	0.228	0.292	0.353	0.076	1				
<i>Physalaemus petersi</i>	0.059	0.004	0.683	0.003	0.254	0	0.045	0	0.002	0.010	0.002	0	0.069	0.001	0.083	1			
<i>Ctenophryne geayi</i>	0.556	0.919	0.201	0.261	0.919	0.008	0.479	0.100	0.469	0.578	0.504	0.102	0.255	0.309	0.049	0.004	1		
<i>Elachistocleis ovalis</i>	0.117	0.278	0.751	0.142	0.364	0.009	0.120	0.020	0.030	0.047	0.005	0.006	0.129	0.005	0.115	0.907	0.178	1	
<i>Hamptophryne boliviana</i>	0.162	0.682	0.343	0.350	0.363	0.025	0.216	0.052	0.087	0.112	0.035	0.017	0.183	0.020	0.103	0.036	0.448	0.452	1

Table 8. Diet overlaps for arboreal anurans. Overlaps are based on g_i data. The order of species in rows and columns is the same.

	H. f.	H. k.	H. l.	H. l.	H. p.	H. r.	H. s.	O. t.	P. c.	P. t.	S. o.	S. g.	S. i.	S. p.	S. r.	S. l.	E. f.	E. p.	E. t.
<i>Hyla fasciata</i>	1																		
<i>Hyla koechlini</i>	0.037	1																	
<i>Hyla leali</i>	0.539	0.280	1																
<i>Hyla leucophyllata</i>	0.242	0.050	0.440	1															
<i>Hyla parviceps</i>	0.711	0.376	0.616	0.518	1														
<i>Hyla rhodopepla</i>	0.584	0.766	0.507	0.314	0.712	1													
<i>Hyla schubarti</i>	0.482	0.299	0.216	0.046	0.360	0.507	1												
<i>Osteocephalus taurinus</i>	0.501	0.082	0.285	0.154	0.598	0.162	0.280	1											
<i>Phrynohyas coriacea</i>	0.255	0.120	0.232	0.146	0.642	0.114	0.109	0.697	1										
<i>Phyllomedusa tomopterna</i>	0.188	0.013	0.262	0.172	0.358	0.078	0.037	0.560	0.536	1									
<i>Scarthyla ostinodactyla</i>	0.514	0.288	0.131	0.018	0.308	0.475	0.457	0.348	0.225	0.237	1								
<i>Scinax garbei</i>	0.508	0.050	0.180	0.068	0.431	0.204	0.493	0.815	0.562	0.644	0.729	1							
<i>Scinax icterica</i>	0.195	0.012	0.268	0.135	0.341	0.085	0.046	0.524	0.506	0.996	0.209	0.611	1						
<i>Scinax pedromedinae</i>	0.536	0.096	0.228	0.086	0.410	0.302	0.545	0.542	0.477	0.280	0.891	0.844	0.243	1					
<i>Scinax rubra</i>	0.672	0.088	0.708	0.611	0.557	0.548	0.274	0.102	0.079	0.154	0.53	0.283	0.140	0.507	1				
<i>Sphaenorhynchus lacteus</i>	0.194	0.026	0.184	0.005	0.007	0.006	0.031	0.018	0.050	0	0.095	0	0	0.028	0.243	1			
<i>Eleuth. fenestratus</i>	0.438	0.050	0.263	0.122	0.547	0.081	0.118	0.976	0.716	0.499	0.346	0.764	0.455	0.539	0.089	0.024	1		
<i>Eleuth. peruvianus</i>	0.312	0.700	0.459	0.194	0.611	0.597	0.235	0.584	0.481	0.247	0.493	0.478	0.208	0.479	0.306	0.052	0.610	1	
<i>Eleuth. toftae</i>	0.659	0.202	0.770	0.161	0.550	0.457	0.418	0.424	0.301	0.165	0.468	0.457	0.162	0.588	0.644	0.120	0.416	0.502	1

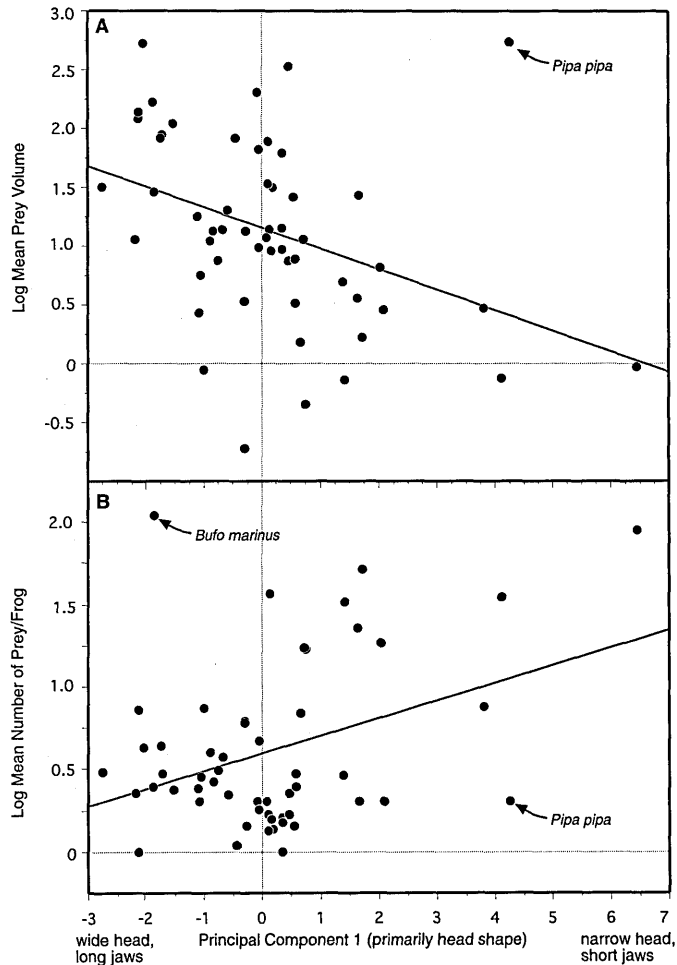


Fig. 16. (A) Mean prey size and (B) mean number of prey per frog versus the first Principal component of a Principal components analysis of frog size and several size-free morphological variables.

tween 0.400 and 0.599 in the arboreal species, and an opposite distribution in the terrestrial species.

As has been shown in other studies (Winemiller and Pianka, 1990; Vitt and Caldwell, 1994; Vitt and Zani, 1996), correlations between column (prey resource) totals in the g matrix (geometric means) and g_{ij} values are intermediate between correlations of p matrix (proportional utilization coefficients) column totals and p_{ij} and correlations of e matrix (electivities) column totals and e_{ij} (Table 9). Therefore, the g -matrix data balances biases of p matrix and e matrix data, and therefore, are most appropriate for use in calculating overlaps.

Pseudocommunity analyses.—Pseudocommunity analyses of dietary data reveals that at nearly all ranks, scrambled zero pseudocommunity results are significantly different from the real community. The only ranks in which

Table 9. Correlations between matrix column totals (prey categories) and calculated values for pseudocommunity analyses of diet; standard errors of estimated r values are given.

	Correlations
TERRESTRIAL ANURANS:	
p matrix column totals versus p_{ij}	0.443 ± 1.056
e matrix column totals versus e_{ij}	0.168 ± 0.462
g matrix column totals versus g_{ij}	0.314 ± 0.748
ARBOREAL ANURANS:	
p matrix column totals versus p_{ij}	0.472 ± 1.158
e matrix column totals versus e_{ij}	0.153 ± 0.400
g matrix column totals versus g_{ij}	0.344 ± 0.774

more than 5% of the number of overlaps in randomly generated pseudocommunities are greater than real overlaps are at ranks 3, 4, and 18 for terrestrial species (Fig. 20C), and at the first three ranks for the arboreal species (Fig. 21C). This means that the zero structure of the resource matrix (i.e., what the animals are not eating) is important, and the species are sharing several important prey categories.

There is evidence for guild structure in both the terrestrial and arboreal portions of the anuran assemblage. The observed mean overlap is greater than the scrambled zero communities at all ranks in both communities (Figs. 20A, 21A). This means that consumers are concentrated in utilization of certain resource states. If there is no difference between the observed overlaps and that of the completely randomized community, anurans are utilizing resources in a random manner relative to each other.

There is a distinct difference between the terrestrial and arboreal communities in the way in which they differ from the "conserved zero" pseudocommunities. The conserved zero communities have greater mean overlaps than the real community at all but the second rank for the terrestrial species, and the conserved zero community overlaps are all less than the real prey overlaps in the arboreal species. Comparisons with the conserved zero pseudocommunities distinguish between random and hyperdispersed patterns of resource utilization. Resource partitioning is evident when the conserved zero overlap values float above the observed overlap values (Winemiller and Pianka, 1990). Therefore, just as the distribution of overlap values indicated (Fig. 19), the terrestrial community seems to demonstrate more resource partitioning than the arboreal one. Additional evidence comes from the steeper slope of the mean overlap plots for the terrestrial anurans (Figs. 20A, 21A). There are seven species of arboreal frogs with greater than 40% mean dietary overlaps, and only five terrestrial ones.

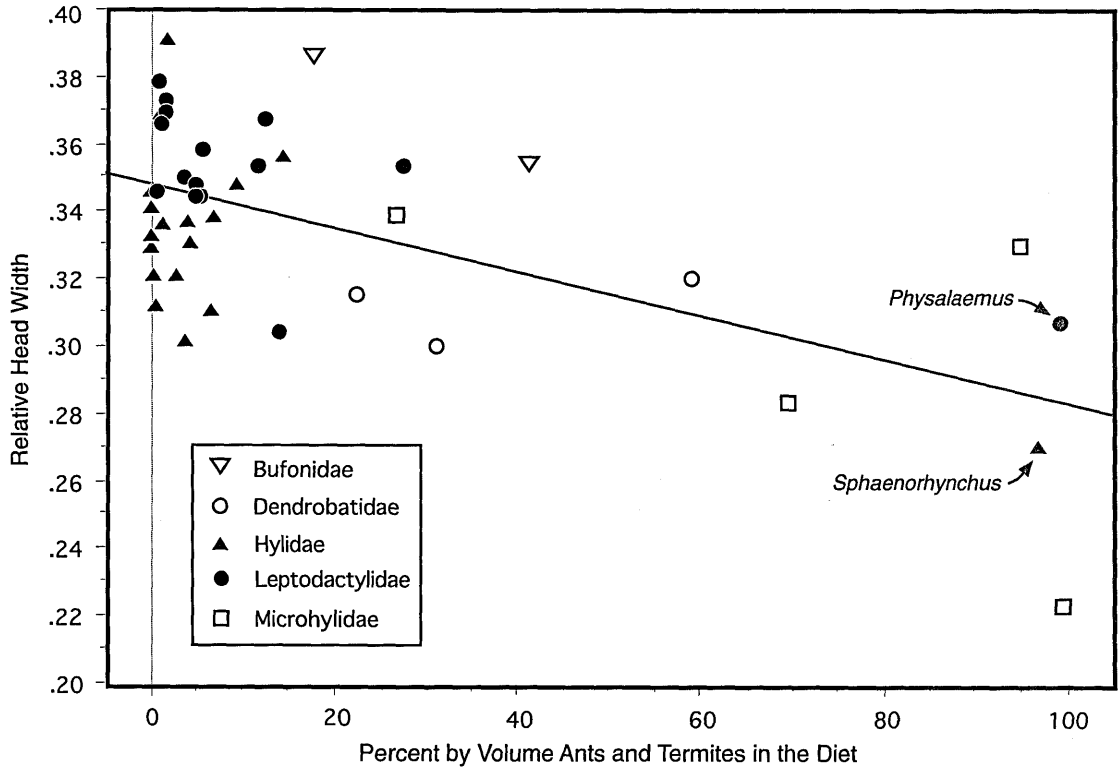


Fig. 17. Relative head width (head width/SVL) versus volumetric percent of diet composed of ants and termites.

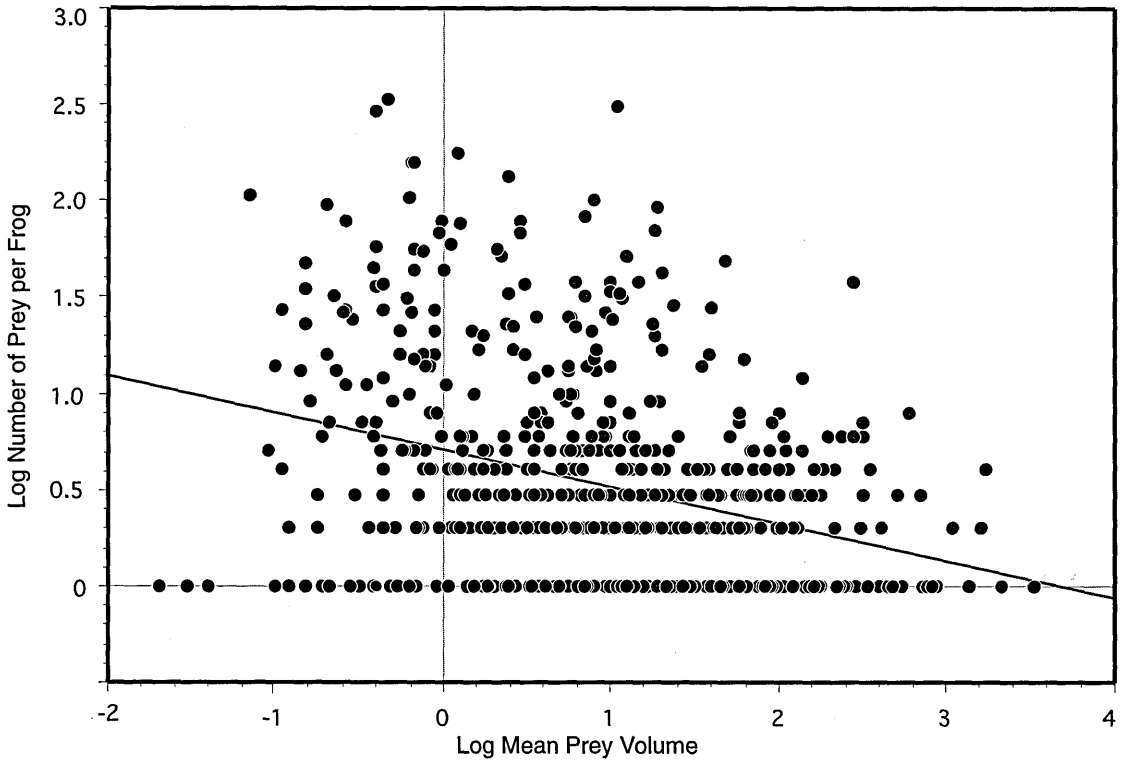


Fig. 18. Mean number of prey per frog versus mean prey volume for 603 anurans.

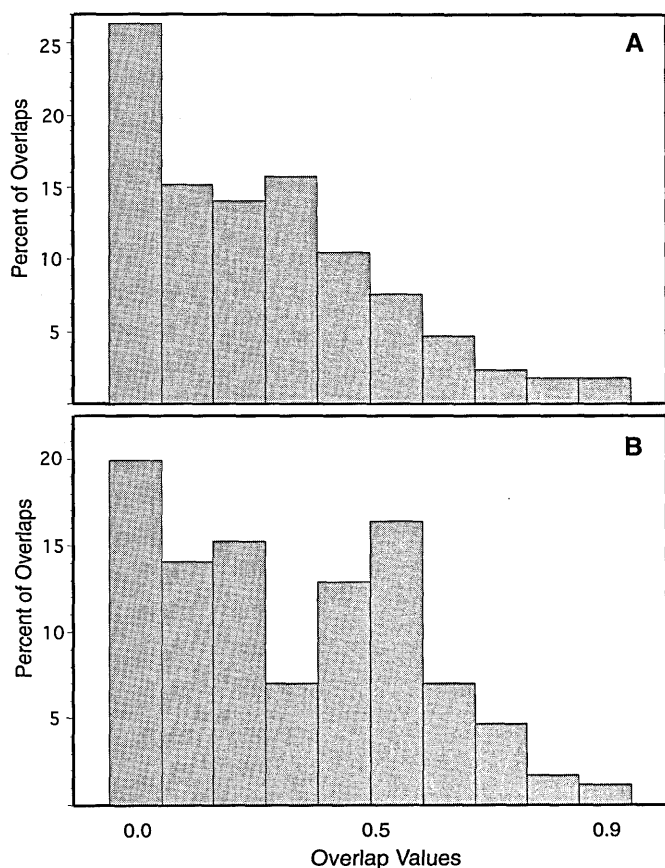


Fig. 19. Distribution of prey overlaps (based on g_i data) for (A) 19 species of terrestrial anurans, and (B) 19 species of arboreal anurans. Bars are in 10% increments.

The "humps" in standard deviations (Figs. 20B, 21B) are characteristic of guild structure. If small sets of species closely resemble each other, their niches will form a closely overlapping cluster in resource space. A different cluster in some other region of the resource space also will have high overlaps among its own members, but overlaps between each member of the first cluster and each member of the second will be small. If clusters differ in number of members, variance (or standard deviation) in niche overlap between pairs of species are small for low nearness orders, because most pairs share membership in the same cluster. As the order of nearness begins to exceed average cluster size, variance in pairwise niche overlap increases rapidly, because some overlaps are between members of different clusters, whereas other overlaps are still between members of larger clusters. When the size of the larger clusters begins to be exceeded at more distant neighbors, variance in niche overlap falls, because nearly all overlaps are between members of different clusters (Inger and Colwell, 1977).

Several guilds are apparent in both terrestrial and arboreal frogs when ranked on a species-by-species basis (Fig.

22). Species lines with steep negative slopes reflect comparatively unique diets.

The plot of terrestrial, nocturnal species (Fig. 22A) features four main guilds, the distinctive *Physalaemus petersi* is in a guild by itself as a termite specialist. The two microhylids, *Hamptophryne boliviana* and *Elachistocleis ovalis* (and most likely the other microhylids), form another ant/small prey guild. *Elachistocleis ovalis* and *Physalaemus petersi* overlap greatly as nearest neighbors, whereas *Hamptophryne boliviana* has the lowest mean overlap with the other species at the first nearness order. A distinctive guild of four members—*Adenomera* and *Leptodactylus petersii*, *L. mystaceus*, and *L. leptodactyloides* cluster through the first five nearness ranks. *Leptodactylus pentadactylus*, *L. bolivianus*, *L. rhodonotus*, and *Eleutherodactylus peruvianus* also cluster loosely.

The terrestrial, diurnal members are depicted in Figures 22B and 22C. Two species have rather distinct diets—viz., *Hamptophryne boliviana* and *Colostethus marchesianus*. *Bufo "typhonius"* and *Epipedobates pictus* have similar diets and cluster at most ranks. *Adenomera* and *Leptodactylus* have shallow slopes, indicating a diverse diet with high dietary overlaps with many other species.

Because there is a large number of hylids, the mean overlap plots are split into three figures for ease of visualization. Figure 22D depicts species that have sharp initial slopes, indicating a relatively specialized diet compared to other members of this assemblage. As expected, the ant-specialist, *Sphaenorhynchus lacteus*, overlaps little with any other treefrog. *Hyla leucophyllata* and *H. koechlini* have distinctive diets. *Hyla leucophyllata* is a lepidopteran specialist and *H. koechlini* consumes over 80% by volume of eruciform larvae. Figure 22E depicts species that generally have higher overlaps at all ranks than the previous group of species. *Hyla parviceps* has a remarkably diverse diet and a high overlap up until the last rank with the other treefrogs. *Scinax garbei* and *Hyla fasciata* also overlap greatly with other arboreal species in niche space. *Eleutherodactylus fenestratus* and *Osteocephalus taurinus* have similar diets and dietary overlaps throughout the ranks. The final graph of overlaps for this arboreal assemblage (Fig. 22F) depicts species with intermediate slopes. *Eleutherodactylus toftae*, *Hyla leali*, *Phrynohyas coriacea*, and *Scinax rubra* form a group for the first six rankings, with *Scinax pedromedinai* joining the group at the third ranking.

Mean overlaps for all species within three general ecological guilds—terrestrial diurnal, terrestrial nocturnal, and arboreal nocturnal—are plotted in Figure 23A. The terrestrial groups have much steeper slopes than the arboreal group, but the curves generated by this procedure are close to what would be expected because of differences in species density (Inger and Colwell, 1977; Fig. 7). A combina-

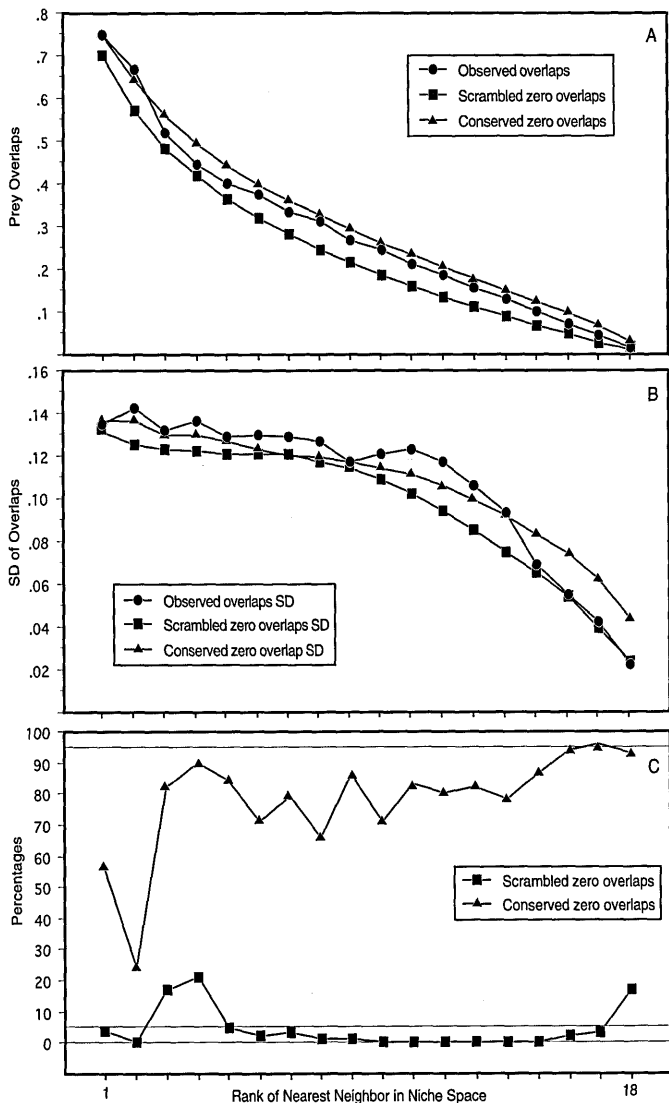


Fig. 20. Results of pseudocommunity analysis of dietary data for 19 species of terrestrial anurans. (A) Compares ranked observed overlaps (based on geometric means) with ranked overlaps based on scrambled zero and conserved zero simulations. (B) Compares the standard deviations in (A). (C) Shows the percentage of pseudocommunity overlaps above or below observed overlaps on a rank by rank basis. Five percent of less of the pseudocommunity overlaps falling above or below observed overlaps indicates significant differences.

tion of the terrestrial groups results in a comparison of two communities of nearly equal size (Fig. 23B). That comparison clearly indicates much higher average overlaps in arboreal species after the second rank. Examining the mean standard deviations for the arboreal and terrestrial communities (Fig. 23C) reveals a striking difference over what would be expected in the absence of any community structure. The theoretical distribution of standard deviations is essentially constant (slightly monotonically increasing) for all orders of nearness and for any niche density (Thomp-

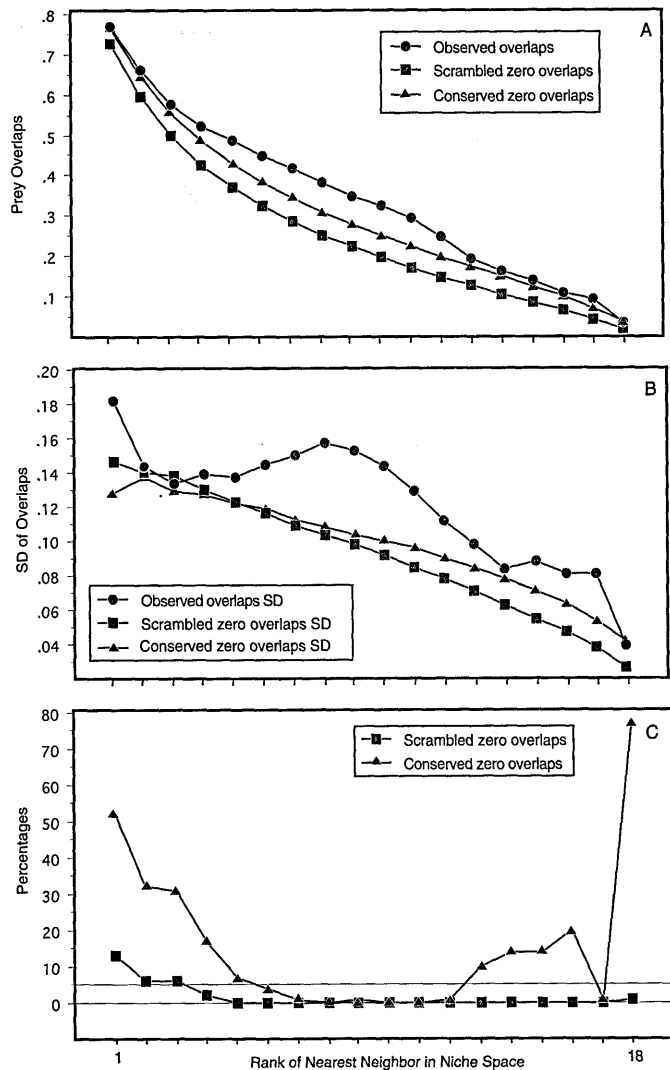
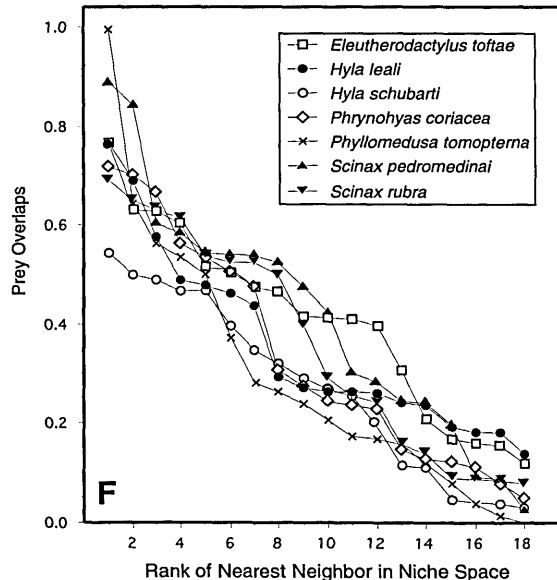
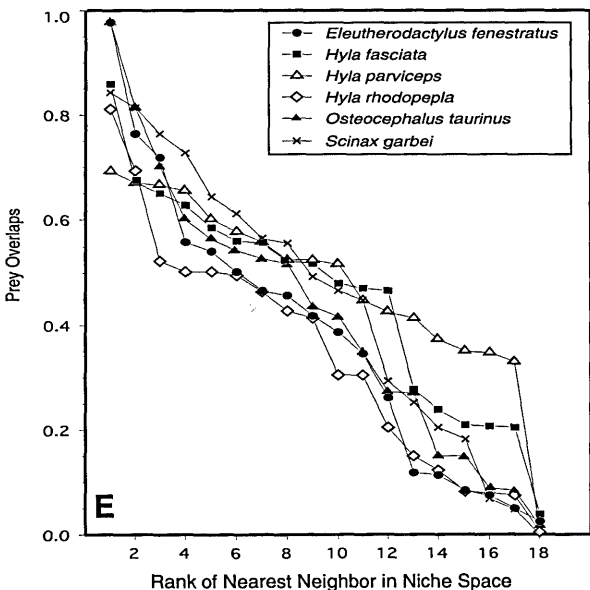
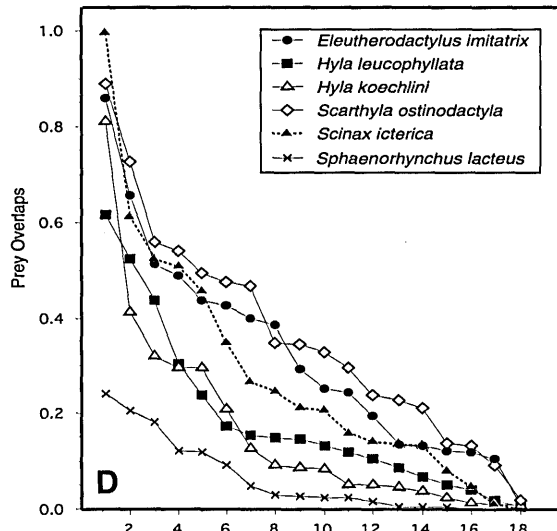
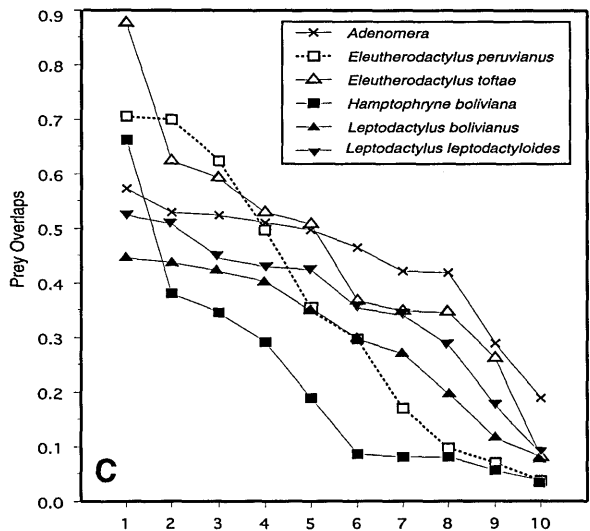
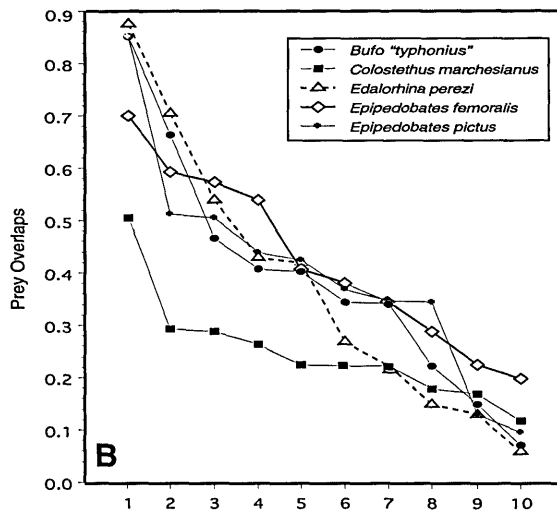
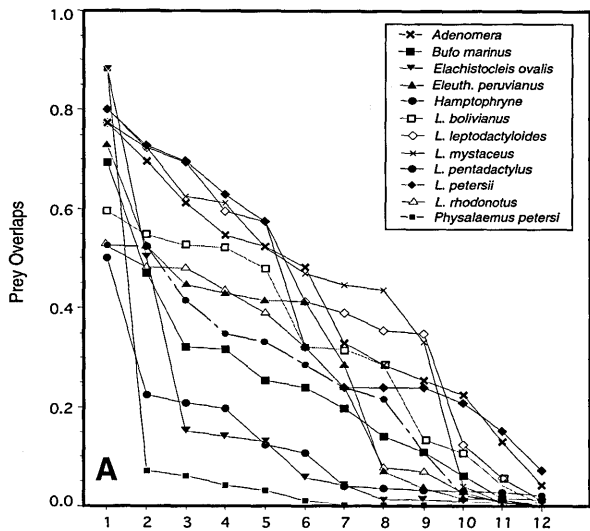


Fig. 21. Results of pseudocommunity analysis of dietary data for 19 species of arboreal anurans. (A) Compares ranked observed overlaps (based on geometric means) with ranked overlaps based on scrambled zero and conserved zero simulations. (B) Compares the standard deviations in (A). (C) Shows the percentage of pseudocommunity overlaps above or below observed overlaps on a rank by rank basis. Five percent of less of the pseudocommunity overlaps falling above or below observed overlaps indicates significant differences.

son, 1956). The definite peaks in standard deviations of prey overlaps indicate guild structure in both communities of the anuran assemblage. Moreover, the pattern of the peaks suggests that guilds tend to be tighter and smaller

Fig. 22. Plot of dietary overlaps (based on volumetric data, g_i) of (A) 12 species of terrestrial, nocturnal anurans, (B) five species of terrestrial, diurnal anurans, (C) six species of terrestrial, diurnal anurans, (D) six species of arboreal anurans, (E) six species of arboreal anurans, (F) seven species of arboreal anurans, and ranked neighbors in niche space. Lines for species with relatively unique diets have steep negative slopes.



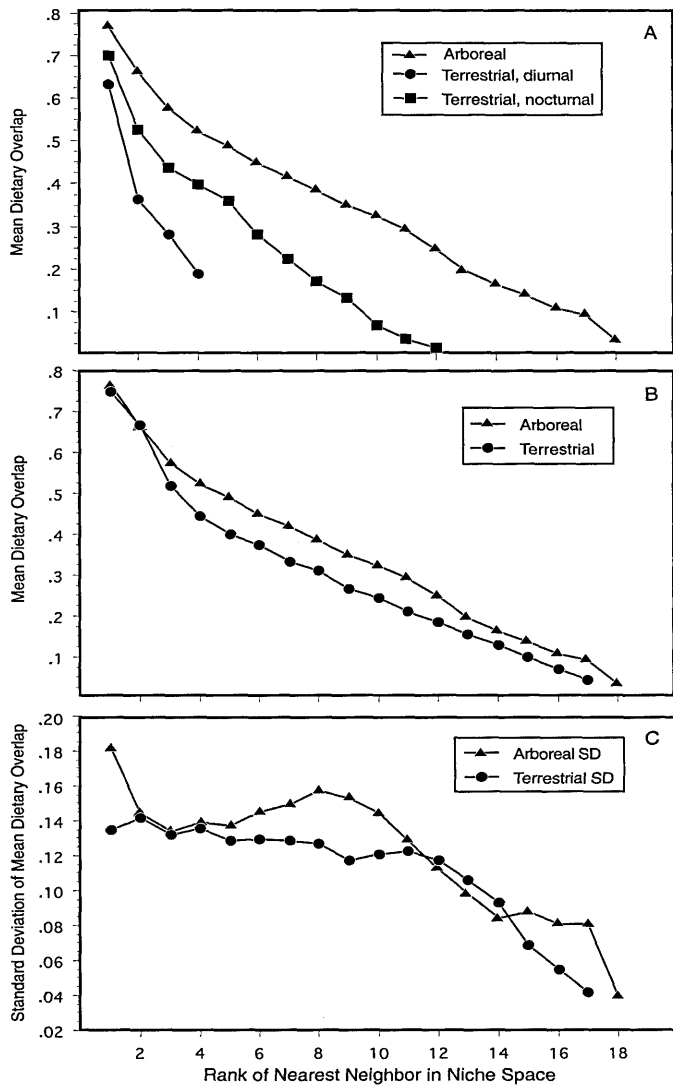


Fig. 23. A. Ranked mean prey overlaps for three communities (terrestrial, diurnal; terrestrial, nocturnal; arboreal, nocturnal) of anurans. B. Ranked mean prey overlaps for two communities (terrestrial and arboreal) of anurans. C. Standard deviation of niche overlaps between first through last nearest neighbors for two anuran communities (terrestrial and arboreal). Overlaps are based on g_i values of volumetric data.

in the terrestrial community and larger in the arboreal community. There is one large peak at rank seven for the arboreal species, and three small peaks at ranks two, four, and eleven for the terrestrial species. Pianka (1980) found that systems with larger guilds peak at more distant ranks in niche space.

Cluster analyses.—The cluster analysis using mean number of prey per individual and mean volume of prey of all frogs (with adequate sample sizes) reveals a distinct cluster of 27 of the 49 species (Fig. 24). These are mainly the small to medium-sized hylids and leptodactylids. *Bufo marinus* and *Elachistocleis ovalis* are distinct from all other

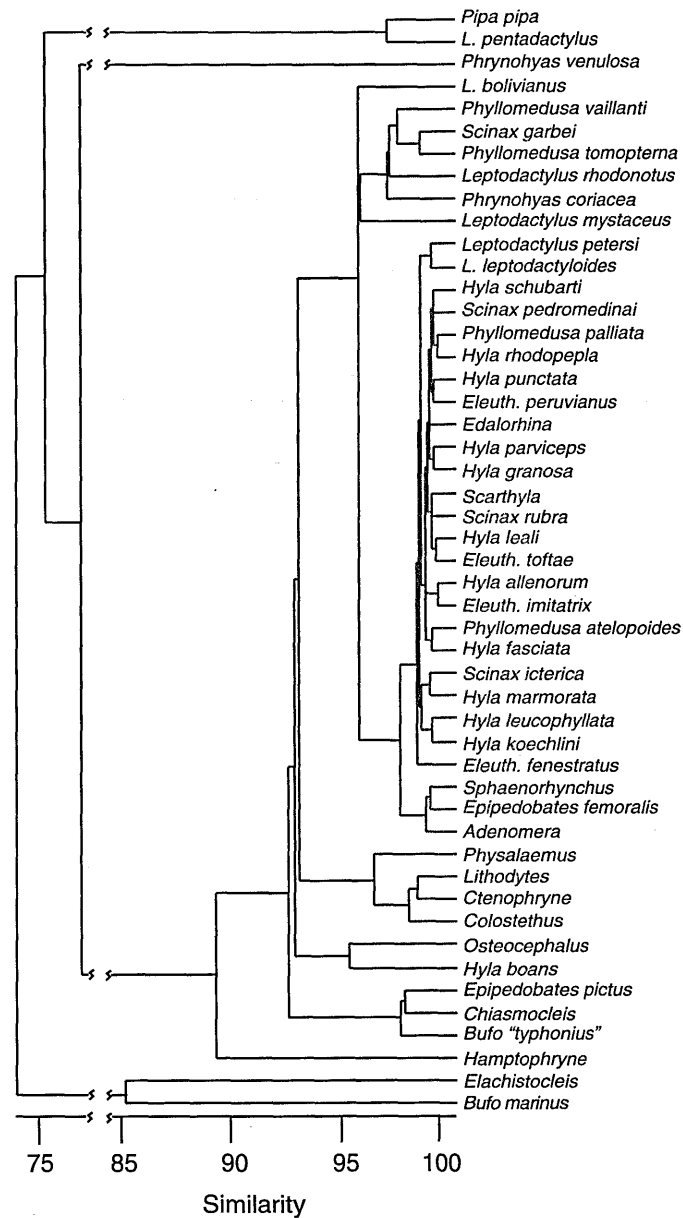


Fig. 24. Cluster diagram of 49 species of anurans. Similarity values based on means of number of prey per individual, and prey volume.

frogs in eating the greatest number of prey, and *Leptodactylus pentadactylus* and *Pipa pipa* constitute a group that eats the largest prey. The large *Leptodactylus* and large hylids are grouped in mixed clusters outside the largest cluster. Other groups are composed of species that eat many, smaller prey (e.g., *Physalaemus petersi*, all microhylids except *Elachistocleis ovalis*).

Cluster analysis of the arboreal and terrestrial communities reveals several feeding guilds in both communities (Figs. 25, 26). It is important to note that the cluster analysis is based on g_i data, which means that both volu-

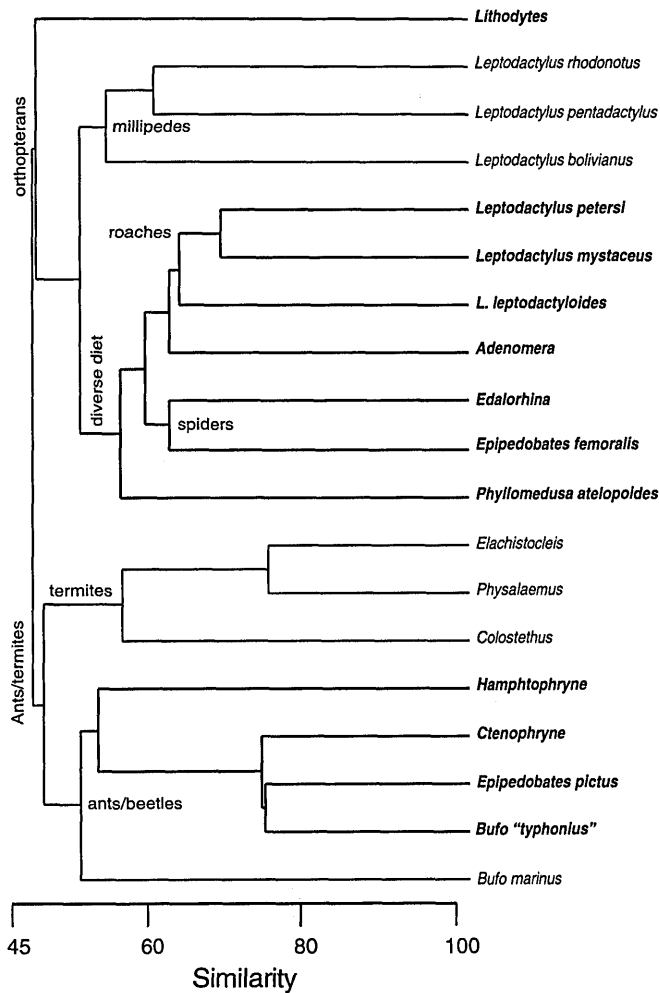


Fig. 25. Cluster diagram of 19 species of terrestrial anurans. Similarity values based on diet (g_i values of volumetric data) and diel activity. Groups that seem to have similar diets denoted by alternating normal and bold type.

metric percentage of diet and electivity (high importance for relatively rare prey items) contribute to the overlap values. The terrestrial species include two members with unique diets, and four groups with more than three members each. There are four groups of arboreal species, each with more than two members and three species with unique diets.

The terrestrial species are in two groups, an ant/termite consumer group with eight members, and a larger-prey group with 11 members (Fig. 25). The ant/termite specialist group is divided into *Bufo marinus* (with a substantial amount of hemipterans and beetles in its diet), a group with a diet of 50–60% beetles and most of the rest ants (*Bufo "typhonius," Epipedobates pictus, Ctenophryne geayi*) with *Hamptophryne boliviana* (which eats 92% by volume of ants), and a group of three species that specialize on relatively small prey including termites (38%, 99%, and

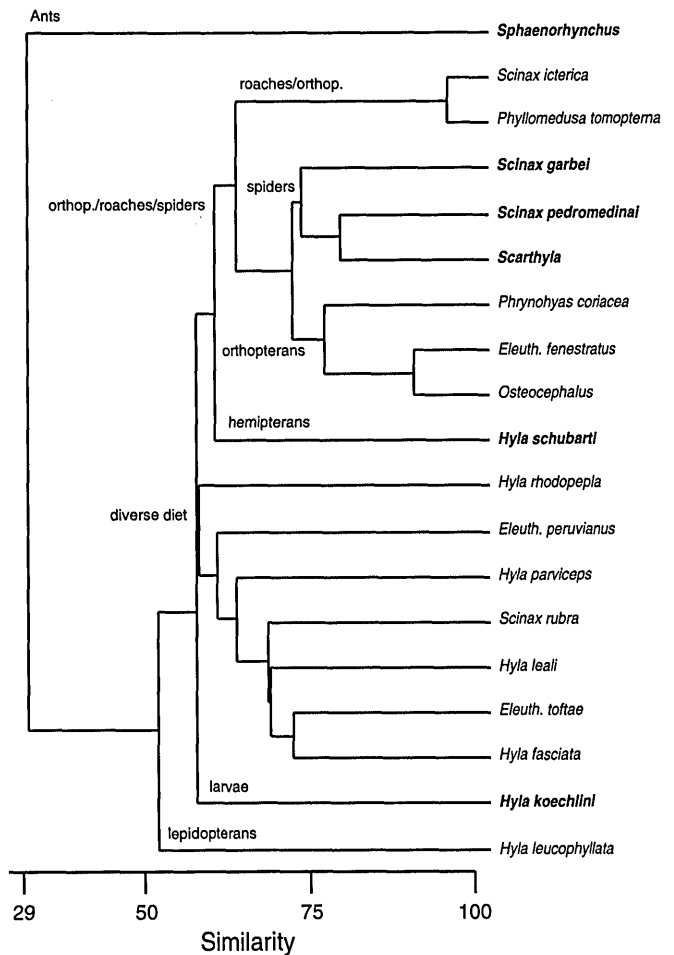


Fig. 26. Cluster diagram of 19 species of arboreal anurans. Similarity values based on g_i values of volumetric dietary data. Groups that seem to have similar diets denoted by alternating normal and bold type.

65% by volume, respectively; *Colostethus marchesianus, Physalaemus petersi,* and *Elachistocleis ovalis*).

In the larger-prey group, *Lithodytes lineatus* is distinct in having a diverse diet with a high percentage of relatively unique prey items such as annelid worms and isopods. The rest of this group falls into one of two guilds—the large species of *Leptodactylus* (*L. bolivianus, L. pentadactylus, L. rhodonotus*) that include millipedes as a major component of their diets, and the other medium-sized leptodactylids that have a more diverse diet that includes beetles, roaches, spiders, and orthopterans.

The cluster analysis reveals two main dietary groups in the arboreal community, *Sphaenorhynchus lacteus* (an ant specialist), and all others (Fig. 26). *Hyla leucophyllata* (a lepidopteran specialist) and *Hyla koechlini* (an eruciform larvae specialist) have relatively unique diets. The largest group (with 7 members) eats a diverse diet with beetles, flies/wasps, and moderate amounts of orthopterans. Spi-

ders are included in the diets of all of the remaining arboreal species. *Osteocephalus taurinus*, *Eleutherodactylus fenestratus*, and *Phrynohyas coriacea* have similar diets with the greatest percentage of orthopterans of any frogs, and with roaches as the next most important prey item. Another group eats a high percentage of spiders—*Scarthyla ostinodactyla*, *Scinax pedromedinai*, and *Scinax garbei*. Finally,

Phyllomedusa tomopterna and *Scinax icterica* have similar diets of roaches and orthopterans.

The cluster diagrams are further evidence of the greater similarity in diet of the arboreal species. The closest similarity value for a pair of terrestrial species is 85%; two pairs of arboreal species have similarity values of over 90%, and most of the major separations in the arboreal community are at higher similarity values than the terrestrial species.

DISCUSSION

It is clear that anurans at Cuzco Amazónico feed on many different types of prey. Ants, beetles, and orthopterans are the most common prey items in many species. Ants probably are taken opportunistically by almost all of the frog species, and ant specialization has occurred independently in most families. There are no true ant specialists among leptodactylids at Cuzco Amazónico, but *Physalaemus petersi* specializes on termites, and *Lithodytes lineatus* eats a high percentage of termites and ants. At other Amazonian localities, some leptodactylids, including *Phyllonastes myrmecoides* and *Eleutherodactylus acuminatus* (Duellman, 1978; Rodríguez and Duellman, 1994), specialize on ants. At Cuzco Amazónico, all bufonids and especially microhylids specialize on ants. Most dendrobatids eat a large percentage of ants, and the hylid *Sphaenorhynchus lacteus* eats ants almost exclusively. Tropical lizard communities reveal a pattern similar to anurans in having ant specialists (Tropiduridae) (Vitt and Zani, 1996; Parmelee, pers. obser.).

Ant consumers must spend considerable time feeding, because their prey is small and low in nutritional value. It is thought that ant specialists commonly occur because ants represent an abundant and concentrated food source (Pianka and Parker, 1975). Ants are known to be diverse and extremely abundant in lowland tropical forests (Hölldobler and Wilson, 1990; Lieberman and Dock, 1982). A preliminary analysis of the ants of Cuzco Amazónico revealed at least 256 species belonging to 64 genera (Cover et al., 1990). Ants should be available as prey to all frogs because ants occur at all levels of the forest, from leaf litter to canopy. Therefore, it seems that many arboreal hylids avoid eating ants. Whether hylids are susceptible to toxins in ants, don't react to their small size, or find them simply unprofitable as prey is unknown.

Diet is a complex phenomenon and can be described in many ways. Three important indices of diet are presented. Frequency is a measure of the number of times a particular prey category occurs in the predator species. Relative numerical and volumetric contributions contribute different information about a predator's diet. For example, one large orthopteran can contribute the same number of calories to the predator as 100 small ants. Some au-

thors combine these three measures in an importance index by multiplying frequency of occurrence by the sum of relative numerical and volumetric contributions (Pinkas, 1971). In order to convey the most information possible, I choose to present and discuss the three individual variables separately. In addition to volume, several authors have used biomass (Toft, 1980a; Zug and Zug, 1979), or calculated volume by a liquid displacement technique (Whitaker et al., 1977).

CORRELATIONS OF DIET WITH PHYLOGENY, MORPHOLOGY, MICROHABITAT, AND FORAGING MODE

Phylogeny.—Unfortunately, phylogenetic hypotheses of the relationships among the taxa of anurans at this site do not exist, but it is probably a safe assumption that members of the same family and probably genera are each other's closest relatives. Thus, with a few exceptions, members of the same clade tend to have more similar diets.

All bufonids have similar diets. Ants and beetles are the most numerous prey items, but a variety of other small prey are eaten. The larger *Bufo marinus* differs from its congeners because of the volumetric contribution of several large hemipterans, and the numerical contribution of termites. It also differs from its congeners in habitat; it frequents clearings around human habitations where the prey base certainly must be different than in primary forest.

Diet has been most closely examined in a phylogenetic framework in dendrobatids. The genera thought to be more basal (e.g., *Colostethus* and *Epipedobates*) have wider and more generalized diets, than the more derived taxa, which have narrower and more specialized diets (Toft, 1995). These specialized diets consist of ants and mites. Although *Colostethus* is considered to be more basal than *Epipedobates*, at Cuzco Amazónico, *C. marchesianus* did not have the greatest niche breadth. Its niche breadth is similar to that of *E. femoralis*; *E. pictus* has a considerably narrower diet, possibly a consequence of its smaller size, which restricts the size of prey that can be ingested. Another explanation for the unexpectedly broad diet of *E. femoralis* is that it may belong in a separate genus (K. Summers, pers. comm.).

Hylids generally eat a few, large prey. Anuran body size has an effect on the major prey categories consumed

Table 10. Species of Hylidae, arranged by increasing average SVL. Primary, secondary, and tertiary general prey categories were selected by the greatest volumetric contribution to the diet (categories contributing less than 10% excluded).

Species	\bar{x} SVL (mm)	1° prey	2° prey	3° prey
<i>Hyla brevifrons</i>	18.85	Beetles	Flies/wasps	Spiders
<i>Scarthyla ostinodactyla</i>	19.34	Spiders	Orthopterans	Larvae
<i>Hyla allenorum</i>	21.37	Beetles	Flies/wasps	Spiders
<i>Hyla parviceps</i>	21.60	Orthopterans	Beetles	Larvae
<i>Hyla schubarti</i>	21.68	Hemipterans	Spiders	Larvae
<i>Hyla koechlini</i>	22.83	Larvae	—	—
<i>Hyla rhodopepla</i>	23.73	Larvae	Beetles	Spiders
<i>Hyla leali</i>	23.81	Beetles	Flies/wasps	Lepidopterans
<i>Scinax pedromedinai</i>	27.26	Spiders	Orthopterans	Hemipterans
<i>Scinax icterica</i>	30.26	Roaches	Orthopterans	Spiders
<i>Hyla punctata</i>	33.11	Spiders	Lepidopterans	—
<i>Hyla leucophyllata</i>	33.22	Lepidopterans	—	—
<i>Hyla granosa</i>	35.91	Orthopterans	Lepidopterans	—
<i>Scinax rubra</i>	37.25	Spiders	Lepidopterans	Beetles
<i>Sphaenorhynchus lacteus</i>	39.26	Ants	—	—
<i>Hyla fasciata</i>	39.35	Beetles	Orthopterans	Spiders
<i>Phyllomedusa palliata</i>	39.56	Orthopterans	—	—
<i>Phyllomedusa atelopoides</i>	39.81	Roaches	Orthopterans	Spiders
<i>Hyla calcarata</i>	42.61	Orthopterans	Spiders	—
<i>Scinax garbei</i>	42.78	Orthopterans	Spiders	Roaches
<i>Hyla marmorata</i>	47.81	Orthopterans	Hemipterans	—
<i>Phyllomedusa tomopterna</i>	48.78	Roaches	Orthopterans	Spiders
<i>Phyllomedusa vaillanti</i>	48.96	Hemipterans	Orthopterans	—
<i>Phrynohyas coriacea</i>	56.21	Orthopterans	Roaches	Winged termites
<i>Phrynohyas venulosa</i>	78.67	Roaches	Orthopterans	Hemipterans
<i>Osteocephalus taurinus</i>	81.46	Orthopterans	Roaches	—
<i>Hyla boans</i>	89.99	Orthopterans	Spiders	—

(Table 10). In general, the largest hylids (e.g., *Osteocephalus taurinus* and *Phrynohyas venulosa*) consume orthopterans and roaches as their primary prey. Medium-sized hylids (e.g., *Hyla calcarata* and *Scinax pedromedinai*) usually eat mostly orthopterans and spiders, whereas small hylids (e.g., *H. allenorum* and *H. rhodopepla*) generally eat beetles, larvae, and spiders. No small hylid consumes more than 10% by volume of roaches, and with the exception of *Hyla parviceps*, orthopterans rarely are a major prey category. Orthopterans, and especially roaches, are some of the largest prey items eaten by anurans at Cuzco Amazónico; presumably there is a gape limitation on smaller frogs eating these large insects. The smaller hylids eat more beetles, larvae, spiders, flies, and wasps—a more varied diet of smaller prey items.

The major prey categories consumed by leptodactylids differ from those of hylids (Tables 10, 11), even though the size distribution of hylids and leptodactylids is similar (but hylids are more numerous). Spiders, roaches, and lepidopterans are absent from the primary prey categories, and

flies/wasps, lepidopterans, and roaches are rare or absent in any of the major prey categories of leptodactylids, but important to hylids. Leptodactylids eat primarily beetles and orthopterans, and unlike hylids, eat millipedes and snails, which are primarily terrestrial organisms. Within leptodactylids, the most obvious size-related difference in primary prey items is the importance of millipedes to the largest frogs. Most millipedes recovered from the frogs were quite large (some more than 100 mm long), and only the largest frogs can consume such impressive prey.

Vertebrates were only found in two of the largest frog species, *Ceratophrys cornuta* and *Leptodactylus bolivianus*; *L. pentadactylus* (Duellman, 1990) and *Bufo marinus* (Evans and Lampo, 1996) have been reported to eat small vertebrates by other authors. Only four frogs in this assemblage commonly reach lengths of over 100 mm SVL—*Bufo marinus*, *Ceratophrys cornuta*, *Leptodactylus bolivianus*, and *L. pentadactylus*. *Bufo marinus* eats many small prey items; ants and termites make up over 90% of its prey. The two species of *Leptodactylus* are most similar to each other, with

Table 11. Species of Leptodactylidae, arranged by increasing average SVL. Primary, secondary, and tertiary general prey categories were selected by the greatest volumetric contribution to the diet (categories contributing less than 10% excluded).

Species	\bar{x} SVL (mm)	1° prey	2° prey	3° prey
<i>Eleutherodactylus imitatrix</i>	16.08	Beetles	Orthopterans	—
<i>Eleutherodactylus toftae</i>	21.79	Orthopterans	Beetles	Flies/wasps
<i>Adenomera</i> sp.	22.92	Beetles	Larvae	Orthopterans
<i>Eleutherodactylus altamazonicus</i>	24.24	Thrips	Beetles	—
<i>Eleutherodactylus peruvianus</i>	24.79	Orthopterans	Larvae	—
<i>Physalaemus petersi</i>	25.17	Termites	—	—
<i>Eleutherodactylus cruralis</i>	25.61	Snails	Ants	Beetles
<i>Leptodactylus petersii</i>	28.99	Larvae	Orthopterans	Beetles
<i>Edalorhina perezi</i>	30.11	Orthopterans	Spiders	—
<i>Eleutherodactylus fenestratus</i>	35.70	Orthopterans	—	—
<i>Leptodactylus leptodactyloides</i>	41.65	Beetles	Hemipterans	Orthopterans
<i>Lithodytes lineatus</i>	46.33	Annelids	Orthopterans	Larvae
<i>Leptodactylus mystaceus</i>	51.28	Beetles	Roaches	Orthopterans
<i>Leptodactylus rhodonotus</i>	72.27	Beetles	Millipedes	Snails
<i>Ceratophrys cornuta</i>	79.55	Vertebrates	Orthopterans	—
<i>Leptodactylus bolivianus</i>	86.92	Beetles	Orthopterans	Millipedes
<i>Leptodactylus pentadactylus</i>	119.21	Orthopterans	Millipedes	—

ants and beetles comprising the highest percentage of prey numerically (about 50% for both species). For *L. pentadactylus*, orthopterans and millipedes are most important volumetrically (52% and 33%, respectively) and for *L. bolivianus*, beetles, orthopterans, and millipedes (38%, 20% 13%, respectively) are most important. For *Ceratophrys cornuta*, ants make up 70% of its prey numerically, and volumetrically, vertebrates represent 53% and orthopterans 22%. Leptodactylids can handle large prey, which make up the bulk of their diet volumetrically. *Ceratophrys* eats a much higher percentage of vertebrates than the species of *Leptodactylus*. In both genera, however, a high percentage of the number of prey items is ants. It seems that these prodigious eaters probably consume any prey item that comes before them, but gain a majority of their energy from consumption of relatively large prey.

Like hylids, small leptodactylids have a greater variety of different prey items as their primary prey categories. Division of leptodactylids into the eight smallest and nine largest species reveals that the smaller leptodactylids have six different primary prey categories, and the nine largest leptodactylids have only four different primary prey categories (Table 11).

To varying degrees, microhylids are ant specialists. In all species, ants are the primary prey in terms of numbers, and in all but *Elachistocleis ovalis* (termites being most important), ants are the primary prey volumetrically. Given its body size, *Elachistocleis ovalis* eats an unexpectedly large number of extremely small prey. Although microhylids are ant specialists, ants and termites are not the only prey they

consume. All five species of microhylids eat small beetles; *Hamptophryne boliviana* consumes members of at least five families of beetles. Moreover, small beetles, wasps, and larvae are not rejected as prey items by microhylids.

Pipa pipa consumes relatively large fish and tadpoles and a few smaller aquatic arthropods. No terrestrial prey was found in the limited sample size from Cuzco Amazónico. The diet of *Pseudis paradoxa* cannot be characterized from a sample size of two frogs and one prey item. All that can be said is that they do consume orthopterans.

Morphology.—Smaller frogs (and the juvenile stages of all frogs) are limited to small prey. From this and other studies (e.g., Duellman and Lizana, 1994; Emerson et al., 1994; Lima and Moreira, 1993), it is clear that most large frogs also include smaller prey in their diet. This causes the maximum and mean prey sizes ingested to increase with frog size, with a lesser effect on minimum prey size. Prey taxa and prey size are not independent. Small dendrobatids eat a large proportion of Acari and Colembolla because they are the few prey available in the size ranges capable of being ingested (Simon and Toft, 1991). Vertebrates are found only in anurans large enough to consume such a large prey item.

The relationship between frog size and prey size seems to be linear, with no asymptote. This same relationship in an assemblage of 22 tropical lizards was not linear; larger lizards ate disproportionately smaller prey (Vitt and Zani, 1996). Possibly, lizards reach a point at which prey size does not increase, because there are few invertebrate prey any larger (although only one lizard had a greater mean

prey volume than the anurans studied herein). Lizards may spend more time handling prey than frogs, and this may limit the upper limit of prey size for lizards more than for frogs. The energetic cost of handling various types of prey seems to be trivial (Grimmond et al., 1994), but this time may be ecologically important as lizards are probably more vulnerable to predation while handling prey. The lizard *Lacerta vivipara* spent 15 min or more consuming large mealworms (Avery and Mynott, 1990), and *Scincella lateralis* spent up to 54 min subduing and swallowing crickets (Preest, 1991).

Other studies (Inger and Marx, 1961; Toft, 1982) have found a significant body size-prey size correlation between, but not within, species. This lack of correlation is probably the result of the small range of body sizes within species relative to among species. For many taxa, I had a wide spectrum of body sizes available.

I did not anticipate the observed close relationship between ant size and frog size. If the larger frogs are eating ants opportunistically, and there is no gape-limitation on such a small prey item, I would not expect such a strong correlation. Possibly, very small ants are either not worth the energy to pursue, or are not detected by larger anurans. *Bufo marinus* and the larger microhylids differ from this pattern and eat relatively small ants.

The importance of head shape to morphological variation among anurans is demonstrated by head shape measurements contributing more to overall variation than does body size. The variation from relatively large to small head widths and jaw lengths correlates with the percentage of ants and termites in the diet. A wide head and longer jaw contributes to a larger gape (Emerson, 1985), which is necessary to consume relatively large prey. A shorter jaw may facilitate a faster feeding cycle and may be advantageous for an animal that needs to consume large quantities of relatively low quality prey such as ants. Head height demonstrates negative allometry; smaller frogs have relatively deeper heads. Although differences exist among families in head height, there is little correlation with prey size.

The most striking deviations of morphology within families are with two hylids with unique diets. *Phyllomedusa atelopoides* has a leptodactylid-like head and the relative leg length of a bufonid. *Sphaenorhynchus lacteus* has a typical leg length for a hylid, but a head morphology strikingly different than other hylids, indeed more like the head shape of the small-prey specialist microhylids.

As head dimensions are correlated with body size and body size is correlated with prey size, it is not unexpected that head dimensions are significantly related to prey size. Use of residuals of the common regression of head dimensions with body size allowed an examination of relative head shape. There is a significant correlation between head

width and jaw length and prey size. The relationship is even stronger within the guilds of ant-specialists and non-ant specialists than with all frogs considered at once. As in other studies (e.g., Toft, 1980a), ant specialists take smaller prey for a given head width than non-ant specialists. If the smallest dimension of a prey item (its width) limits anurans, it seems that most of the prey consumed are much smaller than what could possibly be ingested. Gape dimensions may be important during times of higher competition for limited prey, when the ability to feed on a greater spectrum of prey sizes may aid survival. Also, it is important to note that the dietary data reported herein are a cross-sectional sample of what the predators ate during a specific time period. The reported maximum prey sizes are actually maximum prey sizes consumed during some unit of time; the true maximum ingestible prey size is probably larger than this.

Ecological foraging theory may provide another explanation. Optimal foraging theory predicts that in maximization of net energy intake, prey types can be ranked in desirability by their ratio of handling time to energy content (or prey body size) (Charnov, 1976; Stephens and Krebs, 1986). As prey body size increases, at some point handling time escalates steeply (Andrews et al., 1987; Werner, 1974). Therefore, trophic morphology may not directly limit prey size, except in rare cases when a large prey item is consumed.

Microhabitat.—It is difficult to separate the effects of phylogeny and microhabitat on diet, because phylogeny seems strongly correlated with microhabitat choice. Hylids are arboreal, with only one exception at this site (*Phyllomedusa atelopoides*). Microhylids, bufonids, and dendrobatids at Cuzco Amazónico are terrestrial, leaf-litter inhabitants. Leptodactylids include the terrestrial leptodactylines and the mostly arboreal eleutherodactylines.

Evidence for microhabitat determining diet exists in the terrestrial hylid, *Phyllomedusa atelopoides*. In arboreal members of this genus, roaches and orthopterans are important prey items, but *P. atelopoides* clearly has the most diverse diet among its congeners by including many primarily terrestrial prey such as crickets, isopods, and mites; it also has twice the number of prey items per individual as found in other species of *Phyllomedusa*.

The largest *Eleutherodactylus*, *E. fenestratus*, has the relatively longest jaws and widest head and eats mostly large orthopterans. Its diet is most similar to that of a large hylid. The smaller species of *Eleutherodactylus* have a more diverse diet, but volumetrically, orthopterans are the primary prey. Many arboreal *Eleutherodactylus* also are active on the ground and have a diet similar only to the terrestrial *Edalorhina perezii* among the leptodactylids in percent-

age of orthopterans consumed. Most other terrestrial leptodactylids (e.g., *Adenomera*, small *Leptodactylus*) eat a greater percentage of beetles and larvae.

Tettigonid orthopterans and lepidopterans probably are more common in the arboreal strata of the forest, whereas beetles, larvae, and ants may be more common at ground level. Spiders are important to both terrestrial and arboreal anurans; a more detailed identification of the spiders might reveal differences in types of spiders in the diets of anurans foraging in these two microhabitats. Dipterans were the most abundant arboreal insects at an Amazonian rainforest site (84–91%, Penny and Arias, 1982), and at El Verde, Puerto Rico (89%; Garrison and Willig, 1996), followed by Hymenoptera (5%), Homoptera (2%), and Coleoptera (1%). Mites, followed by ants, were the most numerous arthropod taxa in the leaf-litter layer at El Verde, Puerto Rico (Pfeiffer, 1996). Some arthropods exploit both terrestrial and arboreal habitats. For example, roaches and crickets migrate from the litter to arboreal habitats each night, and flies and moths emerge as winged adults from the litter during the wet season (Pfeiffer, 1996). The importance of the leaf litter for the larval stages of many arthropods, which as adults live at higher levels of the forest, creates the possibility for competition for resources among anurans differing in habitats.

Foraging mode.—Foraging modes in anurans range from species that are active foragers to sit-and-wait strategists. Dendrobatids and bufonids, and the leptodactylid *Physalaemus petersi* are active foragers. Most hylids and leptodactylids are sit-and-wait predators, often relying on crypsis to ambush prey. These are end points of a continuum, and several species such as the small leptodactylids *Adenomera*, *Edalorhina perezii*, and *Eleutherodactylus* may be intermediate in foraging strategy, or switch strategies according to prey abundances. It would be interesting to determine the foraging behavior of the ant specialist *Sphaenorhynchus lacteus*.

Some small-prey specialists are active foragers (e.g., dendrobatids and bufonids), whereas others (e.g., microhylids) apparently are sit-and-wait predators. It is unknown whether the ant species consumed by these two groups are divergent in behavior. Active foragers may capture more solitary species, whereas sit-and-wait species may feed on colonial ants at their trails or colonies.

Foraging behavior has a great influence on diet. Active foragers often eat 10–40 times the number of smaller prey than sit-and-wait foragers (Table 5). Either strategy has benefits and costs; active foragers are more vulnerable to predation and must expend more energy to search for prey (Huey and Pianka, 1981; Pough and Taigen, 1990). Sit-and-wait foragers can be cryptic and use less energy to search for prey, but may encounter fewer prey per unit time.

COMMUNITY ANALYSES AND FEEDING GUILDS

There is structure in the feeding ecology of the anurans of Cuzco Amazónico, Peru. The majority of dietary overlaps are fairly low even within the same general microhabitat, with different frog species eating different prey in different proportions. This discounts the common hypothesis that the pattern of anuran prey utilization follows the relative abundances of prey in the environment, except for a few specialized species.

There are clearly two separate dietary guilds among the terrestrial anurans examined. About half of the species specialize on ants or termites, and the other half (including the smaller species of *Leptodactylus*) has a diverse diet dominated by orthopterans, beetles, and millipedes. Not surprisingly, the three largest *Leptodactylus* are a separate guild from other terrestrial anurans, because these large, morphologically similar predators consume large millipedes. The single hylid in the terrestrial group, *Phyllomedusa atelopoides*, eats a diverse diet with orthopterans, spiders, and larvae dominating volumetrically.

The arboreal species are more similar to each other in diet. There is only one small-prey specialist among arboreal frogs—*Sphaenorhynchus lacteus*. Possibly the larger gut and more bulbous bodies associated with ant-eating are not compatible with arboreality. *Sphaenorhynchus lacteus* has the body shape of a typical hylid (but with a narrower head and shorter jaws), and ants certainly are abundant on higher vegetation, so it seems the arboreal ant-eating niche contains only one species of frog.

Hylids as a whole eat fewer prey items, and possibly as a consequence have smaller niche breadths than terrestrial (non-ant-specialist) anurans. Several hylids (e.g., *Hyla schubarti* and *Hyla koechlini*) seem to have unique diets, but this may be a consequence of sampling error. Possibly examination of more specimens would reveal these taxa to be aligned with other groups. *Hyla leucophyllata* seems to be unique in the high percentage of Lepidoptera consumed (similar diet reported by Duellman, 1978). The hylids are divided into two large groups—a diverse-diet group (similar to the terrestrial, diverse-diet group in being medium-sized), and a second characterized by the presence of orthopterans, roaches, and spiders. Frogs of the genus *Hyla* either had unique diets or were in the diverse-diet group. *Eleutherodactylus toftae* and *E. peruvianus* are in the diverse-diet group, whereas *E. fenestratus* is with two of the largest arboreal anurans, *Osteocephalus taurinus* and *Phrynohyas coriacea*. *Eleutherodactylus fenestratus* is 10 mm longer and three times the mass of the smaller pair (*E. toftae* and *E. peruvianus*), that are similar in size (Table 1). The species of *Scinax* fall out among three groups; *Scinax rubra* is the most divergent in diet from its congeners.

No one has determined whether adult anurans in similar feeding guilds also have larvae that separate out into similar feeding guilds. Resource utilization was documented for the larval stages of the anurans of Cuzco Amazónico. Wild (1996) separated 16 species into five ecomorphological guilds based primarily on oral morphology. One guild (Suspension feeding) was composed of five microhylids. A Suspension-rasper Guild was composed of *Phyllomedusa tomopterna* and *P. vaillanti*. *Colostethus marchesianus* and *Leptodactylus mystaceus* have benthic tadpoles, and eight hylids were grouped into a Macrophagous Guild (*Hyla brevifrons*, *H. koechlini*, *H. leali*, *H. leucophyllata*, and *H. parviceps*) and a Nektonic Guild (*H. fasciata* and *Scinax icterica*).

The microhylids seem to form distinctive guilds in both larval and adult stages. The phyllomedusids differed in which large-prey group dominated. Both the terrestrial *Colostethus marchesianus* and *Leptodactylus mystaceus* have benthic tadpoles, but differ greatly in size as adults, thereby affecting their adult diets. *Hyla fasciata* and *Scinax icterica* are both members of a large cluster of species eating similar numbers of similar-sized prey (Fig. 24), but had a low dietary overlap (0.195). The largest tadpole guild consisted of five small to medium-sized hylids. As adults, one specialized on lepidopterans, another on larvae, and the other three had a typical small-hylid diet.

The natural feeding ecology of no tadpole is well known (Altig and Johnston, 1989). Putative larval feeding guilds are not based on diet directly, but are extrapolated from features of oral morphology. There is insufficient information available on the tadpole guilds at Cuzco Amazónico to accurately divide the larval stages into feeding guilds. It seems as though phylogeny has a great impact on tadpole morphology, and in many cases on adult diet. The only known larvae of *Phyllomedusa atelopoides* are early stages and have not developed characters for meaningful comparisons with other, arboreal members of the genus (Duellman et al., 1988). Adult *Sphaenorhynchus lacteus* has a head morphology and diet similar to microhylids, but the tadpoles are not morphologically convergent. *Scarthyla ostinodactyla* does not have a unique diet as an adult, but has a bizarre oral morphology as a tadpole (Duellman and de Sá, 1988).

COMPARISONS WITH OTHER ASSEMBLAGES

The dietary data from Cuzco Amazónico were compared to dietary studies conducted at other locations in tropical areas. Differences in diet in the same species at different locations could be related to a number of factors, including for example, habitat differences, historical factors causing differences in prey resources, and different competitors at the two sites. Several studies have docu-

mented intraspecific dietary differences among habitats (Korschgen and Baskett, 1963; McKamie and Heidt, 1974; Kovács and Török, 1992). Santa Cecilia, Ecuador, is one of the most diverse (and most comprehensively analyzed) tropical anuran communities in the world (Duellman, 1978), and is compared here to Cuzco Amazónico. Duellman (1978) reported on the stomach contents of up to 25 individuals of each of approximately 86 species of anurans. Thirty-six species occur both at Santa Cecilia and Cuzco Amazónico. The three most important prey categories are compared in Table 12.

Bufo throughout the world commonly eat high proportions of ants (Berry, 1970; Berry and Bullock, 1962; Clarke, 1974; Inger and Marx, 1961; Lajmanovich, 1995; Toft, 1981, 1982). The diet of all species of *Bufo* is remarkably similar between Santa Cecilia and Cuzco Amazónico (Table 12). *Bufo glaberrimus* and *B. "typhonius"* had nearly identical diets, whereas *B. marinus* differed in the greater frequency of orthopterans at Santa Cecilia, and possibly the greater frequency of plant material at Cuzco Amazónico. Duellman (1978) did not report plant materials. The diet of *B. marinus* has been examined in several natural populations (Brazil: Strüssmann et al., 1984; Ecuador: Duellman, 1978; Panama: Zug and Zug, 1979; Venezuela: Evans and Lampo, 1996, Lampo and Medialdea, 1996), and in areas where this species has been introduced to control insect populations (Hawaii: Illingworth, 1941; Fiji: Hinckley, 1963; Puerto Rico: Wolcott, 1937; Papua New Guinea: Zug et al., 1975). In Panama, ants and beetles were the most numerous prey items. Of four localities studied in Panama, ants were the most important by weight at two, snails at another site, and beetles at another (Zug and Zug, 1979). *Bufo marinus* has successfully colonized a wide range of habitats—e.g., forests, savannas and grasslands, arid, riparian, and urban environments. Open areas seem to be preferred, and they are often found in areas of human disturbance. This species has adapted so well to human habitation that it has been observed eating dog food set out for pets (Alexander, 1965). Because *B. marinus* was found only in open areas, it may not be appropriate to compare the diet of this species to other anurans, which were found in the forest.

In Rondônia, Brazil, *Bufo typhonius* ate 70.24% ants and 24.67% beetles by volume (Vitt and Caldwell, 1994). The most common beetles (after Unid.) were the families Curculionidae (2.70%), Buprestidae (1.68%), and Chrysomelidae (1.32%); two of those families are common prey of *Bufo "typhonius"* at Cuzco Amazónico.

The primary prey categories are similar in the diet of dendrobatids from Santa Cecilia and Cuzco Amazónico (Table 12). Ants have a similar importance in all three species, with the same numerical percentage at both localities

Table 12. Comparison of dietary data for 35 species of anurans at Cuzco Amazónico, Peru, and Santa Cecilia, Ecuador (Duellman, 1978). Sample sizes are for only individuals containing prey, and are for Cuzco Amazónico, Santa Cecilia ? = exact number with prey not reported. The type of data reported by Duellman (1978) varied between frequency (number of frogs containing the category of prey) and numerical (numbers of different prey items in all frogs). Duellman's study reported stomach contents only; data from Cuzco Amazónico also include intestinal contents.

Species	<i>n</i>	Type of data	Cuzco Amazónico	Santa Cecilia
BUFONIDAE:				
<i>Bufo glaberrimus</i>	1, 3?	Numerical	Ants 71 Beetles 21 Spiders, wasps, plants 8	Ants 76 Beetles 15 Termites, millip, whip scorpions 9
<i>Bufo marinus</i>	5, 25?	Frequency	Ants 100 Beetles 100 Plants 50	Ants 68 Beetles 64 Orthopterans 40
<i>Bufo "typhonius"</i>	27, 25	Numerical	Ants 82 Beetles 14 Larvae 1	Ants 89 Beetles 10 Isopods, millip., hemip., orthop. 1
DENDROBATIDAE:				
<i>Colostethus marchesianus</i>	28, 25	Numerical	Ants 44 Collembolans/mites 29 Flies/wasps 10	Ants 45 Beetles 30 Termites 14
<i>Epipedobates femoralis</i>	13, 21?	Numerical (ranked)	Collembolans/mites Ants Flies/wasps	Ants Beetles Wasps, spiders
<i>Epipedobates pictus</i>	13, 26?	Frequency	Ants 68 Larvae 13 Beetles 5	Ants 92 Beetles 62 Termites 23
HYLIDAE:				
<i>Hyla boans</i>	3, 13?	Frequency	Orthopterans 100 Spiders 50 Plants 50	Orthopterans 85 Eruciform larvae 15 Lepidopterans 8
<i>Hyla brevifrons</i>	1, 25?	Frequency	Beetles 33 Flies/wasps 33 Spiders 33	Beetles 44 Eruciform larvae 20 Homopterans, spiders 16
<i>Hyla calcarata</i>	1, 25?	Frequency	Orthopterans 100 Spiders 100	Orthopterans 40 Spiders 24 Beetles, homop., eruc. larvae 8
<i>Hyla fasciata</i>	14, 23	Frequency	Spiders 57 Beetles, ants 21 Orthopterans, lepidopterans 14	Flies 27 Roaches 22 Spiders 17
<i>Hyla granosa</i>	7, 8?	Numerical	Lepidopterans, ants 30 Orthopterans 20 Flies/wasps/coll./mites 10	Beetles 36 Orthopterans 27 Lepidopterans, spiders 18
<i>Hyla leucophyllata</i>	15, 3	Numerical	Lepidopterans 40 Beetles 16 Plants 12	Lepidopterans 50 Beetles 25 Roaches 25
<i>Hyla marmorata</i>	2, 13?	Frequency	Orthopterans 50 Hemipterans 50 Plants 50	Beetles, orthopterans 38 Spiders, mites, larvae 8 Dermopterans 8
<i>Hyla parviceps</i>	16, 25?	Frequency	Beetles 31 Orthopterans, spiders 25 Lepidopterans, larvae, flies 19	Beetles 36 Eruciform larvae 32 Orthop., homop., flies, ants 12
<i>Hyla punctata</i>	3, 9?	Numerical	Lepidopterans 50 Spiders 33 Flies/wasps 17	Homopterans 44 Orthopterans 33 Flies, wasps 11
<i>Hyla rhodopepla</i>	7, 10?	Numerical	Spiders 27 Lepidopterans, hemip, larvae 18 Beetles, flies/wasps 9	Beetles 23 Flies, orthopterans, spiders 15 Hemi, homop., lepid., roach 8
<i>Osteocephalus taurinus</i>	26, 10?	Frequency	Orthopterans 58 Beetles 27 Ants 15	Orthopterans 80 Roaches 20 Ants, spiders, pedipalps 10

Species	n	Type of data	Cuzco Amazónico	Santa Cecilia
<i>Phrynohyas coriacea</i>	15, 2?	Numerical	Termites 54 Orthopterans 13 Flies/wasps 6	Roaches, orthopterans, ants 20 Beetles, spiders 20
<i>Phyllomedusa palliata</i>	4, 20?	Frequency	Orthopterans 75 Flies/wasps, coll./mite, larvae 25 Spiders 25	Orthopterans 40 Homopterans 35
<i>Phyllomedusa tomopterna</i>	6, 6	Numerical	Orthopterans, roaches 38 Spiders, lepidopterans 13 Homopterans 14	Orthopterans 43 Roaches 43
<i>Phyllomedusa vaillanti</i>	5, 18	Frequency	Orthopterans, larvae 20 Homop., isopods, ants 20	Orthopterans 89 Spiders 11
<i>Scinax garbei</i>	10, 23?	Frequency	Orthopterans, spiders 40 Hemip., roaches, plants 10 Flies, larvae 4	Orthopterans 70 Spiders 30
<i>Scinax rubra</i>	10, 25?	Frequency	Spiders, ants 40 Beetles, coll./mites 30 Lepidopterans 20	Orthopterans 40 Eruciform larvae 24 Lepidopterans, beetles 20
LEPTODACTYLIDAE:				
<i>Adenomera</i>	31, 11	Frequency	Ants 65 Beetles 36 Larvae 29	Ants 45 Beetles, roaches 18 Dermapterans, termites, hemip., homop., chilop., spiders, annelids 9
<i>Edalorhina perezi</i>	4, 20	Frequency	Orthopterans 50 Flies/wasps 40 Ants 30	Flies 50 Wasps 25 Orthopterans 25
<i>Eleutherodactylus altamazonicus</i>	1, 26?	Numerical	Thrips 67 Ants 17 Beetles 17	Orthopterans 35 Ants 27 Beetles, spiders 15
<i>Leptodactylus mystaceus</i>	21, 26?	Volumetric	Beetles 30 Roaches 17 Orthopterans 15	Orthopterans 81 Beetles 8
<i>Leptodactylus pentadactylus</i>	7, 27?	Volumetric	Orthopterans 52 Millipedes 33 Beetles 9	Orthopterans 42 Beetles 22 Millipedes 11
<i>Leptodactylus leptodactyloides</i>	26, 25?	Volumetric	Beetles 26 Hemi./homopterans 19 Orthopterans 18	Orthopterans 27 Beetles 14 Ants 12
<i>Lithodytes lineatus</i>	2, 9?	Frequency	Termites, ants, larvae 50 Isopods, annelids, orthop., beetles 50	Ants 78 Larvae 33 Beetles, hemip., orthop. 22
<i>Physalaemus petersi</i>	4, 6	Volumetric	Termites 99 Beetles 1	Termites 100
MICROHYLIDAE:				
<i>Chiasmocleis ventrimaculata</i>	2, 3?	Volumetric	Ants 55 Termites 45 Beetles 0.4	Ants 100
<i>Ctenophryne geayi</i>	3, 1	Volumetric	Beetles 61 Ants 27 Hemipterans 12	Beetles 100
<i>Hamptophryne boliviana</i>	25, 25	Frequency	Ants 100 Beetles 32 Termites, larvae 12	Ants 96 Termites 8 Beetles, larvae, dermapterans 4
PIPIDAE:				
<i>Pipa pipa</i>	4, 1	Volumetric	Fish 98.8 Tadpoles 0.8 Beetles 0.3	Fish 100

for *Colostethus marchesianus*. Collembolans and mites seem to be more important at Cuzco Amazónico, but this may also be a sampling error, because these extremely small prey items may have been overlooked, or may have been digested in the Santa Cecilia sample.

Several studies have demonstrated that *Colostethus* eat a more generalized diet than the more derived members of the family Dendrobatidae (Toft, 1995). Caldwell (1996) examined the evolution of myrmecophagy in the family Dendrobatidae and found *Colostethus* to have diets with relatively low percentages of ants (12–16% volumetrically), lower numbers of prey per individual, and greater niche breadths. The *C. marchesianus* she studied from Amazonian Ecuador had a similar diet composition to that which I found, except for more eruciform larvae in Ecuador (most important volumetrically: termites, ants, eruciform larvae, Coleoptera; numerically: ants, Collembola, eruciform larvae, Acari). Toft (1980a) studied this species in lowland rainforest at the Río Lullapichis in Amazonian Peru and reported relative proportion (by dry weight) of only five prey categories. She found *C. marchesianus* ate low numbers of orthopterans and beetles. The primary prey categories were: ants/mites: 52% (wet season), 34% (dry season); misc. adult arthropods: 28% (wet season), 33% (dry season).

Epipedobates femoralis had the highest diet niche breadth of six species of dendrobatids studied by Toft (1980a) at another Peruvian rainforest site ($B_s = 0.28$ versus all others less than 0.09). *Epipedobates femoralis* ate similar proportions ($\pm 26\%$ by weight) of orthopterans, coleopterans, and miscellaneous adult arthropods, 13% of ants/mites and 8% of larvae. Because of this evenness (both numerically and volumetrically), niche breadth values were high. My data confirm Toft's (1980a) findings that this species eats a more diverse diet than its congener, *E. pictus*. In Rondônia, Brazil, this species consumed flies, 27.4%, crickets 15.1%, wasps 14.3% by volume (Vitt and Caldwell, 1994). These proportions are considerably different than the prey proportions presented here, although many flies and wasps were consumed by *E. femoralis* at Cuzco Amazónico. Larvae also were important at Rondônia (8.27% by volume, but ants made up only 4.37% of the diet). *Epipedobates femoralis* also had the highest dietary niche breadth (numerically) of nine species of dendrobatids (second highest by volume) studied by Caldwell (1996). She found beetles to be most important in the diet of a population in Ecuador. At the Río Lullapichis, Toft (1980a) found *E. pictus* to consume 59% (by weight) ants/mites, 26% larvae, no orthopterans, and small numbers of beetles and other arthropods. These results are similar to mine except for the greater contribution of beetles in my sample.

There are 17 species of hylids common to Santa Cecilia and Cuzco Amazónico; 11 (65%) species have the same

primary prey category (Table 12). Commonly, when the primary prey category differs, that prey category is still one of the three major prey categories.

Major prey differences occur between sites for *Hyla punctata*. Besides the similar contribution of the fly/wasp category (17% versus 11%), the primary and secondary prey categories are completely different. *Hyla punctata* at Santa Cecilia eats primarily homopterans and orthopterans, whereas those at Cuzco Amazónico eat mostly moths and spiders. Sample sizes of this species were low at both localities. *Scinax rubra* also differs in diet between the sites and the sample sizes seem adequate. At Cuzco Amazónico, this species most frequently eats spiders and ants, followed by beetles and collembolans/mites; at Santa Cecilia, orthopterans, then eruciform larvae are most frequently encountered in their diet. Moths are found at equal frequency (20%) in the diets of *S. rubra* at these two localities. Only two specimens of *Phrynohyas coriacea* were examined at Santa Cecilia; therefore differences between sites may be a consequence of the low sample size. Another potential source of differences is that winged termites are numerically most important in the sample from Cuzco Amazónico because one individual had eaten 38 of them. If this individual were removed, the next most important prey category would be orthopterans, which was one of the prey items reported in the diet of this species at Santa Cecilia. The limited sample from Santa Cecilia ($n = 2$) contained one each of a roach, ant, orthopteran, beetle, and spider. Specimens from Cuzco Amazónico had eaten individuals from all of these prey categories.

Santa Cecilia and Cuzco Amazónico share eight species of leptodactylids, and their diets at the two localities are similar (Table 12). Only three of eight (38%) have the same primary prey category, but many have the same three major prey categories, but in a different order. *Physalaemus petersi* is confirmed to be a termite specialist. The greatest differences in diets are those of *Eleutherodactylus altamazonicus*, but this is certainly the result of the sample size of one individual (with prey) at Cuzco Amazónico. The primary prey categories are thrips at Cuzco Amazónico and orthopterans at Santa Cecilia; after this, the next two prey categories are quite similar. The three species of *Leptodactylus* could be compared by using the volumetric contribution to the diet. All revealed similar diets between the sites, with orthopterans, beetles, and millipedes being most important.

Vitt and Caldwell (1994) provided dietary data on *Adenomera andreae*, *A. hylaedactyla*, and a hybrid between these two species from Rondônia, Brazil. There were differences between these taxa, but termites were always most important volumetrically (32.51, 37.85, and 47.16%). Crickets (29.00%) and ants (18.65%) were the next most important prey items for *A. andreae*, eruciform larvae (32.17%),

and ants (8.45%) for *A. hylaedactyla*, and roaches (30.75%) and ants (11.04%) for the hybrids. Termites were far less important at Cuzco Amazónico, but other categories such as ants and crickets were important at both localities.

Toft (1980a) studied the diet of five *Edalorhina perezi* (which contained only 5 prey items total) at the Río Lullapichis in Amazonian Peru and reported the percentages by weight to be: miscellaneous arthropods 43%, orthopterans 34%, and beetles 23%. She found no ants or larvae, prey items that I found in the diet of my larger sample of frogs.

At a rainforest site in Rondônia, Brazil, *Eleutherodactylus fenestratus* had eaten the same two principal prey categories as at Cuzco Amazónico—49.39% by volume of orthopterans, 18.43% roaches, and 11.73% beetles (Vitt and Caldwell, 1994). Toft (1980a) studied the diet of seven *E. peruvianus* at the Río Lullapichis in Amazonian Peru and found the percentages by weight to be: orthopterans 56%, beetles 40%, miscellaneous arthropods 3%, larvae 1%, and ants 1%. Orthopterans are clearly an important prey category for this species. *Eleutherodactylus toftae* had the following percentages (by weight) at the Río Lullapichis, Peru: Orthoptera 53%, miscellaneous arthropods 18%, ants 15%, larvae 9%, beetles 6% (Toft, 1980a). This species had the highest niche breadth of four species of *Eleutherodactylus* she studied; these results are similar to the diets reported herein.

Pipa pipa consumes relatively large fish and tadpoles, and a few smaller aquatic arthropods. *Pipa pipa* fed mainly on fish at both Cuzco Amazónico and Santa Cecilia, and a few more prey items were documented at Cuzco Amazónico (Table 12). The three microhylids common to both Cuzco Amazónico and Santa Cecilia all had the same primary prey category. The greatest similarity in diet is between the samples of *Hamptophryne boliviana*; ants were found in 100% (Cuzco Amazónico) and 96% (Santa Cecilia) of the frogs, with similar small numbers of termites and larvae, and relatively more beetles at Cuzco Amazónico. Only beetles were found in the one specimen of *Ctenophryne geayi* examined at Santa Cecilia; at Cuzco Amazónico, beetles make up the greatest volumetric percentage (61%), followed by ants (27%), and Hemiptera (12%).

Only ants were found in *Chiasmocleis ventrimaculata* at Santa Cecilia, but at Cuzco Amazónico, ants and termites each make up about equal volumetric contributions to the diet. At Tambopata, Peru, *C. ventrimaculata* can live in a commensal relationship with a burrowing theraphosid spider, *Xenesthis immanis* (Cocroft and Hambler, 1989); frogs emerged from spiders' burrows about 1.5 hr after sundown and adopted a modified sit-and-wait foraging mode, remaining at one location for 1–56 min (\bar{x} = 14.0) before moving to another location 2–40 cm (\bar{x} = 12.3) away. A conservative estimate of feeding attempts was 2.6 per hour. No dietary analysis was reported, but this behavior is further evidence that microhylids eat many small prey in a sit-and-wait fashion.

CONCLUSIONS

Clearly diet is a complex phenomenon that is affected by body size and head shape, phylogeny, microhabitat, and foraging behavior. There may be present-day interactions (e.g., competition or predation) that influence diet selection or availability of prey. Each of the foregoing factors is interrelated, and teasing apart their relative contributions is difficult. Most likely, frog diets evolve; when phylogenetic hypotheses of relationships are available a more detailed picture of dietary evolution should emerge. Generalizations can be formulated about anuran communities by combining and comparing my data with those of other dietary studies. There seems to be a strong phylogenetic component to anuran diets. Specialization on certain types of prey has occurred in several families and genera; rather than focusing on competition at a local scale, we should look at species interactions from a historical perspective—specialization may have allowed certain taxa to be successful in colonizing and persisting in different communities.

Unexamined, but potentially important variables include ontogenetic changes in diet and individual variation in diet. *Colostethus stephensi* consumes different prey taxa, not only larger prey sizes, with increasing body size

(Lima and Moreira, 1993). Several other studies have demonstrated ontogenetic changes in diet (Christian, 1982; Donnelly, 1991; Flowers and Graves, 1995; Labanick, 1976; Lima, 1998). Therefore, the ecological relationships among anurans may depend more on interactions among individuals of different sizes (adults of a smaller species interacting with juveniles of a larger species) than on the relationships among the adults (Polis, 1984; Resetarits, 1995). The stomach contents reported in this study represent a population niche breadth. However, a population with a narrow, specialized niche must be composed of individuals with narrow, specialized niches. On the other hand, a population with a broad niche breadth consists of individuals with either narrow or wide niches, or a combination of both. Individual diet preferences could be influenced by intra- and inter-individual components of niche width (Amundsen, 1995; Amundsen et al., 1996; Pierotti and Annett, 1987).

The data reported herein describe a pattern at one locality; experiments are necessary to understand the causes of the observed pattern. The problem with natural studies (such as the comparison of anuran diets in differ-

ent localities) is not the discovery of pattern, but the inference of mechanism (McGuinness, 1988). Predation may generate patterns in the structure of communities similar to those produced by competition (Holt, 1984). Both predator and prey abundances may depend on the level of a third, unmeasured variable. We do not know if predators control prey community structure, or if prey assemblages dictate predator community structure. One must also note that simple community patterns may also arise from complex interactions among many factors. The trajectory of falling rain is determined by a complex interaction of wind speed, air temperature, and other factors, yet the spatial pattern of raindrops is "random" (Simberloff, 1980) and can be described by a Poisson distribution. Description of the pattern of dietary differences and similarities in this complex assemblage of species should give insight into anuran community dynamics, and provide the impetus for much needed future research.

This study is descriptive in the sense that diets and morphological variation among species are presented for an assemblage of tropical anurans. Hypotheses such as whether predator-prey relationships differ among taxa, or if the community is structured in a non-random manner,

are also tested. My data could not address the hypothesis that competition is responsible for structuring anuran diets, and if there is competition for food resources among most tropical anurans at the present time. There may be diffuse competition for food at certain times of the year or in certain habitats, or competition may have occurred in the past. Toft (1980b) found evidence supporting a pattern that may be expected in the presence of competition—lower dietary similarity among guilds in the dry season, a time of low food availability. The only way to examine whether competition for food occurs in nature is to design experiments to manipulate species or prey densities and observe the results. The different species of frogs at Cuzco Amazónico undoubtedly evolved under different conditions, with different potential competitors, than they have today. The dietary and ecological data in this study is only a "snapshot" in ecological time (Duellman and Pianka, 1990). Many interactions and selective pressures may have occurred in evolutionary time. Each species has evolved differences in their trophic apparatus—head shape, extent of dentition, tongue morphology, and overall size, all of which contribute to their ability to capture different kinds and sizes of prey.

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APPENDIX 1

SPECIMENS EXAMINED

Unless noted otherwise, all specimens are in the herpetological collection in the Natural History Museum, The University of Kansas. Three anurans—two *Osteocephalus* sp. and one *Lithodytes lineatus*—are in the Museum of Vertebrate Zoology, University of California, Berkeley (MVZ). All specimens are from the Reserva Cuzco Amazónico, 15 km ENE of Puerto Maldonado, Departamento Madre de Dios, Amazonian Peru (12°35' S, 69°05' W) at an elevation of 200 m above sea level.

- Adenomera* sp.: 205049, 205052–205056, 205060, 207691–207692, 207694–207695, 209164–209172, 215126–215127, 215434, 215436–215446
- Altigius alios*: 215544, 216021
- Bufo "typhonius"*: 194915, 205237–205246, 207541–207546, 209156, 215115, 215117, 215145, 215149, 215159, 220162–220166
- Bufo glaberrimus*: 194913
- Bufo marinus*: 194914, 205234–205236, 220161
- Chiasmocleis ventrimaculata*: 215540, 215542
- Colostethus marchesianus*: 205270–205282, 207547–207550, 209157, 215160–215165, 215172–215175
- Ctenophryne geayi*: 205775, 215543, 215545
- Edalorhina perezii*: 205082–205094, 207705–207707, 209173, 215128–215129, 215447–215454, 215458
- Eleutherodactylus altamazonicus*: 209956, 215459, 215460
- Eleutherodactylus cruralis*: 207749, 215461–215462, 215479–215480
- Eleutherodactylus fenestratus*: 205109–205116, 205119–205121, 205124–205130, 207708, 209174–209175, 215463–215467, 215471–215473
- Eleutherodactylus imitatrix*: 207709–207714, 215474–215476, 215478
- Eleutherodactylus peruvianus*: 194909, 205107, 205132–205135, 205137–205138, 205142, 205304, 207715–207717, 215481–215488
- Eleutherodactylus toftae*: 205099–205106, 205117–207718, 209177–209181, 209957, 215489–215497, 215499–215503
- Epipedobates femoralis*: 205285, 205287, 205289–205291, 205293, 205295, 207551–207552, 215176–215181
- Epipedobates pictus*: 194917, 205299–205303, 207553–207554, 215182–215186
- Hamptophryne boliviana*: 194931–194932, 205781–205782, 205785–205786, 205788–205790, 205794, 207752–207754, 207757–207758, 207761–207763, 209193, 215555, 215557–215558, 215570, 215573–215574
- Hyla allenorum*: 215187–215190
- Hyla boans*: 215191–215193
- Hyla brevifrons*: 215202, 220167–220168
- Hyla calcarata*: 207555, 215205
- Hyla fasciata*: 205461–205463, 205467, 205475, 205478, 207557–207558, 207564–207566, 209158–209159, 215120, 215206–215207, 215210–215216, 216082–216083
- Hyla granosa*: 205479–205486, 215217–215219, 216081
- Hyla koechlini*: 205697, 205701, 205703, 205708, 205712, 205715, 205723, 205725–205727, 205729, 205732, 205751, 215220–215222, 215235–215238, 215244–215246, 215249, 221877
- Hyla leali*: 205490, 205492, 205504, 205507, 205517–205518, 205520–205521, 205536, 205544, 205548, 205550, 205552, 205566, 205573, 215254–215263
- Hyla leucophyllata*: 194920, 205591, 205596–205597, 205601, 205604, 205606–205607, 205609–205613, 205616, 207583–207585, 209950, 215264, 215266–215267, 215269–215270, 215274, 215278
- Hyla marmorata*: 215280, 216084
- Hyla parviceps*: 205621–205622, 205633–205634, 205659–205660, 205663, 205665, 205667, 205669, 207586–207588, 207593, 209951, 215281–215284, 215289–215294
- Hyla punctata*: 205672, 215123, 216085, 220172–220173
- Hyla rhodopepla*: 205673–205676, 205678–205690, 207595, 215295–215299
- Hyla schubarti*: 194922–194923, 207596–207605, 209952, 215300, 215302–215307
- Leptodactylus bolivianus*: 194911, 205144, 205152, 205154–205155, 205158–205159, 205161–205162, 205165, 207732–207734, 209182
- Leptodactylus leptodactyloides*: 194912, 205043–205048, 205050–205051, 205057–205059, 205222–205232, 207747–207748, 209187, 215526–215529, 215531–215533
- Leptodactylus mystaceus*: 194910, 205169–205171, 205180, 205182, 205187, 207735–207740, 209183–209186, 215132, 215504–215505, 215509–215512
- Leptodactylus pentadactylus*: 205188–205194
- Leptodactylus petersii*: 205195–205204, 207741–207743, 209188, 215513–215522
- Leptodactylus rhodonotus*: 205205–205208, 205211–205221, 207744–207746, 209959, 215523–215525
- Lithodytes lineatus*: 207750, MVZ 197104
- Osteocephalus* sp.: MVZ 199505–199506
- Osteocephalus taurinus*: 194925, 194927–194928, 205403–205408, 205411–205413, 207641–207649, 209161, 215358–215369
- Phrynohyas coriacea*: 194930, 205414–205416, 207651, 207653–207656, 207659–207661, 207663–207669, 215370, 215372–215376

Phrynosoma venulosus: 194929, 205417–205419, 207670, 215377–215380
Phyllomedusa atelopoides: 204765, 204767–204770, 206623, 215383–215384, 220178
Phyllomedusa palliata: 205420, 215385–215386, 215387–215388
Phyllomedusa tomopterna: 205421–205422, 205424–205433, 207671–207672, 215389–215396
Phyllomedusa vaillanti: 205435–205439, 205442, 215407
Physalaemus petersi: 209189–209192, 215133, 215534–215535
Pipa pipa: 205801, 215134, 215575–215576, 216086–216087
Pseudis paradoxa: 209762, 215536

Scarthyla ostonodactyla: 205757, 205759, 205762, 205765–205767, 205769, 205771–205772, 206625–206626, 206629–206631, 209163, 215125, 215414, 215418–215422, 215425, 215428–215429
Scinax garbei: 205339–205342, 207617–207618, 215323–215328
Scinax icterica: 205347–205348, 205350–205351, 205374–205378, 205401–205402, 207624–207626, 207638, 215337–215343, 215355–215357
Scinax pedromedinai: 194924, 205321, 205324–205327, 205329–205330, 205332, 205336, 207612–207614, 207616, 215309–215314, 215316–215318, 215321–215322
Scinax rubra: 205343–205346, 207619–207623, 209160, 215329–215336
Sphaenorhynchus lacteus: 205446–205456, 215432–215433, 220177

APPENDIX 2

DIETARY DATA

The following dietary data are presented in descending order of volumetric importance. Genera and species are arranged alphabetically within families.

Prey category	No.	% No.	Volume	% Vol.	Frequency	Prey category	No.	% No.	Volume	% Vol.	Frequency
BUFONIDAE:						<i>Bufo "typhonius" continued</i>					
<i>Bufo glaberrimus</i> (n = 1)						Isopoda	1	0.10	8.68	0.06	1
Coleoptera unid.	2	5.88	132.16	38.85	—	Annelid	1	0.10	6.32	0.05	1
Formicidae	26	76.47	126.41	37.16	—	Isoptera	4	0.41	4.57	0.03	1
Curculionidae	2	5.88	32.70	9.61	—	Histeridae	1	0.10	4.58	0.03	1
Araneae	1	2.94	25.28	7.43	—	Camptodeiform larvae	1	0.10	2.58	0.02	1
Carabidae	1	2.94	20.96	6.16	—	Pseudoscorpiones	1	0.10	0.77	0.01	1
Plant material	1	2.94	1.39	0.41	—	Sums	986	100	13434.74	100	—
Wasp	1	2.94	1.32	0.39	—	Niche breadths	—	1.47	—	3.61	—
Sums	34	100	340.22	100	—	DENDROBATIDAE:					
Niche breadths	—	1.68	—	3.25	—	<i>Colostethus marchesianus</i> (n = 28)					
<i>Bufo marinus</i> (n = 5)						Isoptera	28	5.86	82.18	38.55	6
Pentatomidae	3	0.55	5623.85	35.98	1	Formicidae	212	44.35	35.29	16.55	25
Coleoptera unid.	11	2.01	3403.61	21.78	5	Diptera	37	7.74	17.22	8.08	11
Hemiptera unid.	2	0.36	2771.65	17.73	2	Coleoptera unid.	6	1.26	11.84	5.55	4
Formicidae	318	58.03	2111.48	13.51	5	Isopoda	3	0.63	11.3	5.30	3
Isoptera	174	31.75	686.69	4.39	1	Gryllidae	1	0.21	10.92	5.12	1
Plant material	31	5.66	470.23	3.01	4	Tetrigidae	3	0.63	8.89	4.17	1
Scarabaeidae	3	0.55	331.28	2.12	1	Winged Formicidae	4	0.84	8.67	4.07	1
Orthoptera unid.	1	0.18	107.79	0.69	1	Collembola	128	26.78	6.71	3.15	19
Isopoda	1	0.18	66.82	0.43	1	Araneae	7	1.46	4.96	2.33	7
Carabidae	2	0.36	22.59	0.14	2	Wasp	12	2.51	3.89	1.82	8
Scarabaeiform larvae	1	0.18	21.35	0.14	1	Vermiform larvae	8	1.67	3.82	1.79	6
Tettigoniidae	1	0.18	12.25	0.08	1	Diplura	8	1.67	1.73	0.81	2
Sums	548	100	15629.59	100	—	Pseudoscorpiones	1	0.21	1.54	0.72	1
Niche breadths	—	2.27	—	4.35	—	Plant material	2	0.42	1.48	0.69	1
<i>Bufo "typhonius" (n = 26)</i>						Acari	10	2.09	0.80	0.38	7
Formicidae	810	82.15	5555.18	41.35	26	Larvae	2	0.42	0.66	0.31	2
Coleoptera unid.	75	7.61	4039.01	30.06	17	Chilopoda	1	0.21	0.55	0.26	1
Carabidae	11	1.12	1395.77	10.39	8	Pselaphidae	2	0.42	0.39	0.18	2
Curculionidae	26	2.64	637.79	4.75	12	Staphylinidae	1	0.21	0.16	0.08	1
Staphylinidae	11	1.12	448.38	3.34	1	Cicadellidae	1	0.21	0.12	0.06	1
Wasp	7	0.71	315.40	2.35	6	Miridae	1	0.21	0.05	0.02	1
Chrysomelidae	11	1.12	277.03	2.06	1	Sums	478	100	213.17	100	—
Vermiform larvae	6	0.61	191.20	1.42	3	Niche breadths	—	3.57	—	5.08	—
Scarabaeidae	3	0.30	174.58	1.30	3	<i>Epipedobates femoralis</i> (n = 13)					
Erucoform larvae	3	0.30	77.00	0.57	2	Larvae	3	3.30	39.82	29.22	2
Plant material	3	0.30	71.55	0.53	2	Formicidae	21	23.08	30.34	22.26	8
Coccinellidae	1	0.10	70.18	0.52	1	Araneae	7	7.69	20.36	14.94	6
Tetrigidae	1	0.10	60.75	0.45	1	Tettigoniidae	1	1.10	9.39	6.89	1
Hemiptera unid.	5	0.51	49.73	0.37	2	Carabidae	1	1.10	8.70	6.38	1
Orthoptera unid.	1	0.10	15.52	0.12	1	Wasp	8	8.79	8.51	6.24	3
Homoptera unid.	1	0.10	15.95	0.12	1	Diptera	9	9.89	6.49	4.76	5
Diptera	2	0.20	12.22	0.09	2	Vermiform larvae	2	2.20	6.29	4.62	1

Appendix 2 continued

Prey category	No.	% No.	Volume	% Vol.	Frequency	Prey category	No.	% No.	Volume	% Vol.	Frequency
<i>Epidobates femoralis</i> continued						<i>Hyla fasciata</i> continued					
Curculionidae	1	1.10	5.09	3.73	1	Coleoptera unid.	4	12.90	143.8	23.20	3
Scolytidae	1	1.10	0.74	0.54	1	Araneae	10	32.26	134.63	21.72	8
Isoptera	1	1.10	0.19	0.14	1	Carabidae	1	3.23	76.97	12.42	1
Staphylinidae	1	1.10	0.19	0.14	1	Formicidae	4	12.90	43.67	7.04	3
Acari	35	38.46	0.18	0.13	3	Hemiptera unid.	1	3.23	37.15	5.99	1
Sums	91	100	136.29	100	—	Lepidoptera	2	6.45	25.84	4.17	2
Niche breadths	—	4.41	—	5.69	—	Plant material	6	19.35	11.13	1.80	3
<i>Epidobates pictus</i> (n = 13)						Collembola	1	3.23	0.21	0.03	1
Chrysomelidae	7	1.62	150.29	47.84	1	Sums	31	100	619.88	100	—
Formicidae	292	67.75	58.73	18.69	13	Niche breadths	—	5.37	—	5.47	—
Isoptera	14	3.25	39.27	12.50	5	<i>Hyla granosa</i> (n = 12)					
Coleoptera unid.	8	1.86	20.35	6.48	7	Orthoptera unid.	2	20	102.00	77.70	2
Eruciform larvae	50	11.60	11.64	3.71	1	Lepidoptera	3	30	27.22	20.73	3
Hemiptera unid.	2	0.46	7.65	2.43	2	Formicidae	3	30	1.49	1.13	2
Scarabaeidae	1	0.23	6.94	2.21	1	Diptera	1	10	0.54	0.41	1
Pseudoscorpiones	3	0.70	3.70	1.18	2	Acari	1	10	0.03	0.02	1
Scolytidae	3	0.70	3.30	1.05	3	Sums	10	100	131.28	100	—
Vermiform larvae	3	0.70	2.75	0.88	2	Niche breadths	—	4.17	—	1.55	—
Acari	28	6.50	2.44	0.78	6	<i>Hyla koechlini</i> (n = 25)					
Wasp	4	0.93	2.01	0.64	4	Eruciform larvae	4	26.67	393.86	82.58	4
Larvae	2	0.46	1.76	0.56	2	Diptera	3	20.00	34.93	7.32	2
Diptera	3	0.70	1.29	0.41	3	Araneae	4	26.67	25.33	5.31	4
Elateriform larvae	1	0.23	0.76	0.24	1	Hemiptera unid.	1	6.67	8.09	1.70	1
Curculionidae	2	0.46	0.58	0.18	2	Orthoptera unid.	1	6.67	7.58	1.59	1
Annelid	1	0.23	0.37	0.12	1	Formicidae	1	6.67	7.12	1.49	1
Thysanoptera	2	0.46	0.19	0.06	1	Acari	1	6.67	0.04	0.01	1
Collembola	5	1.16	0.15	0.05	2	Sums	15	100	476.95	100	—
Sums	431	100	314.17	100	—	Niche breadths	—	5	—	1.45	—
Niche breadths	—	2.09	—	3.49	—	<i>Hyla leali</i> (n = 25)					
HYLIDAE:						Wasp	4	9.09	39.49	18.18	2
<i>Hyla allenorum</i> (n = 4)						Coleoptera unid.	4	9.09	31.34	14.43	3
Coccinellidae	1	12.50	5.42	23.59	1	Lepidoptera	4	9.09	27.33	12.58	3
Curculionidae	1	12.50	4.95	21.54	1	Chrysomelidae	1	2.27	23.81	10.96	1
Wasp	1	12.50	4.69	20.41	1	Orthoptera unid.	1	2.27	22.89	10.54	1
Araneae	2	25.00	3.61	15.71	2	Eruciform larvae	2	4.55	19.81	9.12	2
Hemiptera unid.	1	12.50	3.35	14.58	1	Blattaria	1	2.27	19.32	8.89	1
Diptera	2	25.00	0.96	4.18	1	Diptera	9	20.45	13.15	6.05	3
Sums	8	100	22.98	100	—	Winged Formicidae	12	27.27	7.39	3.40	1
Niche breadths	—	5.33	—	5.22	—	Formicidae	1	2.27	7.22	3.32	1
<i>Hyla boans</i> (n = 3)						Araneae	3	6.82	3.92	1.80	2
Acrididae	1	20	396.02	46.95	1	Plant material	2	4.55	1.59	0.73	2
Orthoptera unid.	1	20	302.77	35.89	1	Sums	44	100	217.26	100	—
Araneae	1	20	137.32	16.28	1	Niche breadths	—	6.59	—	8.67	—
Plant material	2	40.00	7.39	0.88	1	<i>Hyla leucophyllata</i> (n = 25)					
Sums	5	100	843.5	100	—	Lepidoptera	10	40.00	561.89	66.55	10
Niche breadths	—	3.57	—	2.66	—	Plant material	3	12.00	60.01	7.11	1
<i>Hyla brevifrons</i> (n = 4)						Diptera	1	4.00	45.7	5.41	1
Elateridae	1	33.33	6.74	68.64	1	Coleoptera unid.	3	12.00	41.46	4.91	2
Diptera	1	33.33	1.64	16.70	1	Chrysomelidae	1	4.00	37.14	4.40	1
Araneae	1	33.33	1.44	14.66	1	Blattaria	1	4.00	33.10	3.92	1
Sums	3	100	9.82	100	—	Orthoptera unid.	1	4.00	31.73	3.76	1
Niche breadths	—	3	—	1.92	—	Campodeiform larvae	1	4.00	25.31	3.00	1
<i>Hyla calcarata</i> (n = 2)						Isoptera	2	8.00	5.87	0.70	1
Tetrigoniidae	1	33.33	208.89	78.71	1	Wasp	1	4.00	1.06	0.13	1
Araneae	1	33.33	35.00	13.19	1	Formicidae	1	4.00	0.99	0.12	1
Orthoptera unid.	1	33.33	21.5	8.10	1	Sums	25	100	844.26	100	—
Sums	3	100	265.39	100	—	Niche breadths	—	4.84	—	2.18	—
Niche breadths	—	3	—	1.55	—	<i>Hyla marmorata</i> (n = 2)					
<i>Hyla fasciata</i> (n = 25)						Orthoptera unid.	1	25.00	88.33	83.08	1
Orthoptera unid.	2	6.45	146.48	23.63	2	Hemiptera unid.	1	25.00	16.13	15.17	1

Appendix 2 continued

Prey category	No.	% No.	Volume	% Vol.	Frequency	Prey category	No.	% No.	Volume	% Vol.	Frequency
<i>Hyla marmorata</i> continued						<i>Osteocephalus taurinus</i> continued					
Plant material	2	50.00	1.86	1.75	1	Curculionidae	1	1.89	27.99	0.26	1
Sums	4	100	106.32	100	—	Wasp	1	1.89	19.14	0.18	1
Niche breadths	—	2.67	—	1.4	—	Larvae	1	1.89	12.18	0.11	1
<i>Hyla parviceps</i> (n = 25)						Isoptera	2	3.77	10.45	0.10	2
Tettigoniidae	1	3.85	79.26	21.14	1	Mordellidae	1	1.89	6.39	0.06	1
Coleoptera unid.	3	11.54	73.94	19.72	3	Sums	53	100	10674.64	100	—
Lepidoptera	3	11.54	57.42	15.32	3	Niche breadths	—	9.46	—	4.05	—
Eruciform larvae	2	7.69	55.05	14.68	2	<i>Osteocephalus</i> sp. (n = 2)					
Orthoptera unid.	3	11.54	31.15	8.31	3	Blattaria	1	100	173.48	100	1
Blattaria	1	3.85	20.24	5.40	1	<i>Phrynohyas coriacea</i> (n = 25)					
Isoptera	2	7.69	15.44	4.12	2	Tettigoniidae	5	7.14	2280.15	49.63	4
Araneae	4	15.38	15.17	4.05	4	Blattaria	1	1.43	765.63	16.67	1
Chrysomelidae	2	7.69	12.07	3.22	2	Winged Isoptera	38	54.29	565.86	12.32	1
Cicadellidae	1	3.85	7.96	2.12	1	Eruciform larvae	2	2.86	280.67	6.11	2
Wasp	2	7.69	2.65	0.71	2	Orthoptera unid.	4	5.71	250.06	5.44	3
Larvae	1	3.85	2.65	0.71	1	Lepidoptera	3	4.29	196.99	4.29	2
Diptera	1	3.85	1.89	0.50	1	Homoptera unid.	1	1.43	64.10	1.40	1
Sums	26	100	374.89	100	—	Formicidae	6	8.57	51.40	1.12	3
Niche breadths	—	10.56	—	6.97	—	Winged Formicidae	1	1.43	50.49	1.10	1
<i>Hyla punctata</i> (n = 5)						Coleoptera unid.	2	2.86	33.19	0.72	2
Araneae	2	33.33	40.35	57.12	2	Wasp	3	4.29	30.15	0.66	2
Lepidoptera	3	50.00	25.98	36.78	1	Diptera	1	1.43	16.11	0.35	1
Wasp	1	16.67	4.31	6.10	1	Araneae	2	2.86	9.04	0.2	1
Sums	6	100	70.64	100	—	Acari	1	1.43	0.15	0.0	1
Niche breadths	—	2.57	—	2.15	—	Sums	70	100	4593.99	100	—
<i>Hyla rhodopepla</i> (n = 23)						Niche breadths	—	3.15	—	3.35	—
Eruciform larvae	2	18.18	39.35	39.99	2	<i>Phrynohyas venulosa</i> (n = 9)					
Elateridae	1	9.09	25.31	25.72	1	Blattaria	1	6.25	2247.37	42.32	1
Araneae	3	27.27	18.28	18.58	3	Orthoptera unid.	1	6.25	950.27	17.90	1
Lepidoptera	2	18.18	10.43	10.6	2	Cicadidae	1	6.25	870.01	16.38	1
Hemiptera unid.	2	18.18	3.76	3.82	2	Coleoptera unid.	1	6.25	825.85	15.55	1
Diptera	1	9.09	1.27	1.29	1	Tettigoniidae	1	6.25	276.35	5.20	1
Sums	11	100	98.4	100	—	Histeridae	1	6.25	101.14	1.90	1
Niche breadths	—	5.26	—	3.66	—	Formicidae	1	6.25	12.12	0.23	1
<i>Hyla schubarti</i> (n = 20)						Membracidae	1	6.25	11.69	0.22	1
Hemiptera unid.	4	20.00	62.61	42.22	2	Plant material	1	6.25	6.28	0.12	1
Araneae	5	25.00	27.01	18.21	4	Araneae	1	6.25	5.08	0.10	1
Eruciform larvae	1	5.00	26.3	17.74	1	Thysanoptera	2	12.50	3.53	0.07	1
Coleoptera unid.	3	15.00	26.1	17.6	3	Acari	4	25.00	0.45	0.01	1
Formicidae	2	10.00	2.23	1.50	2	Sums	16	100	5310.14	100	—
Isoptera	1	5.00	2.17	1.46	1	Niche breadths	—	8.53	—	3.77	—
Wasp	1	5.00	1.26	0.85	1	<i>Phyllomedusa atelopoides</i> (n = 9)					
Collembola	2	10.00	0.42	0.28	2	Blattaria	3	13.64	152.7	38.60	3
Acari	1	5.00	0.19	0.13	1	Araneae	7	31.82	72.83	18.41	5
Sums	20	100	148.29	100	—	Gryllidae	2	9.09	69.66	17.61	2
Niche breadths	—	6.45	—	3.64	—	Eruciform larvae	1	4.55	54.92	13.88	1
<i>Osteocephalus taurinus</i> (n = 33)						Orthoptera unid.	2	9.09	29.48	7.45	2
Tettigoniidae	10	18.87	4459.72	41.78	7	Formicidae	2	9.09	7.35	1.86	1
Orthoptera unid.	9	16.98	2348.15	22.00	8	Isopoda	1	4.55	5.03	1.27	1
Blattaria	3	5.66	1250.21	11.71	3	Larvae	2	9.09	3.56	0.90	2
Hemiptera unid.	1	1.89	883.39	8.28	1	Acari	2	9.09	0.02	0.01	2
Scarabaeidae	1	1.89	339.24	3.18	1	Sums	22	100	395.55	100	—
Eruciform larvae	2	3.77	306.57	2.87	2	Niche breadths	—	6.05	—	4.18	—
Coleoptera unid.	3	5.66	281.38	2.64	3	<i>Phyllomedusa palliata</i> (n = 5)					
Dermoptera	1	1.89	251.24	2.35	1	Orthoptera unid.	3	50.00	51.92	93.26	3
Araneae	3	5.66	195.06	1.83	3	Larvae	1	16.67	2.46	4.42	1
Lepidoptera	1	1.89	122.18	1.14	1	Wasp	1	16.67	1.22	2.19	1
Formicidae	6	11.32	65.96	0.62	4	Acari	1	16.67	0.07	0.13	1
Plant material	6	11.32	64.70	0.61	2	Sums	6	100	55.67	100	—
Carabidae	1	1.89	30.69	0.29	1	Niche breadths	—	3	—	1.15	—

Appendix 2 continued

Prey category	No.	% No.	Volume	% Vol.	Frequency	Prey category	No.	% No.	Volume	% Vol.	Frequency
<i>Phyllomedusa tomopterna</i> (n = 22)						<i>Scinax pedromedinai</i> continued					
Blattaria	3	37.50	315.44	51.33	3	Sums	25	100	243.33	100	—
Orthoptera unid.	2	25.00	113.61	18.49	2	Niche breadths	—	4.63	—	4.1	—
Tettigoniidae	1	12.50	79.60	12.95	1	<i>Scinax rubra</i> (n = 18)					
Araneae	1	12.50	66.43	10.81	1	Araneae	8	25.81	75.52	32.3	4
Lepidoptera	1	12.50	39.51	6.43	1	Lepidoptera	3	9.68	57.38	24.54	2
Sums	8	100	614.59	100	—	Wasp	2	6.45	28.44	12.16	1
Niche breadths	—	4	—	3.03	—	Coleoptera unid.	4	12.90	28.04	11.99	3
<i>Phyllomedusa vaillanti</i> (n = 7)						Formicidae	5	16.13	22.16	9.48	4
Cicadidae	1	20	174.78	55.86	1	Cerambycidae	1	3.23	21.61	9.24	1
Orthoptera unid.	1	20	135.27	43.23	1	Acari	8	25.81	0.65	0.28	3
Isopoda	1	20	1.82	0.58	1	Sums	31	100	233.8	100	—
Formicidae	1	20	0.55	0.18	1	Niche breadths	—	5.25	—	4.73	—
Larvae	1	20	0.48	0.15	1	<i>Sphaenorhynchus lacteus</i> (n = 15)					
Sums	5	100	312.9	100	—	Formicidae	173	97.74	276.03	95.71	13
Niche breadths	—	5	—	2	—	Chrysomelidae	1	0.56	5.06	1.75	1
<i>Scarthyla ostinodactyla</i> (n = 25)						Diptera	2	1.13	5.06	1.75	1
Araneae	13	52.00	103.57	53.67	8	Wasp	1	0.56	2.26	0.78	1
Orthoptera unid.	1	4.00	28.04	14.53	1	Sums	177	100	288.41	100	—
Larvae	1	4.00	19.09	9.89	1	Niche breadths	—	1.09	—	1.09	—
Gryllidae	1	4.00	15.02	7.78	1	LEPTODACTYLIDAE:					
Hemiptera unid.	1	4.00	12.45	6.45	1	<i>Adenomera</i> sp. (n = 34)					
Formicidae	2	8.00	7.68	3.98	2	Coleoptera unid.	9	4.69	122.25	19.21	8
Eruciform larvae	1	4.00	4.19	2.17	1	Vermiform larvae	10	5.21	75.72	11.90	6
Cicadellidae	1	4.00	1.65	0.86	1	Gryllidae	3	1.56	62.78	9.86	2
Wasp	1	4.00	0.61	0.32	1	Formicidae	98	51.04	62.68	9.85	20
Homoptera unid.	1	4.00	0.35	0.18	1	Isopoda	8	4.17	62.17	9.77	5
Diptera	1	4.00	0.28	0.15	1	Araneae	10	5.21	42.66	6.70	7
Collembola	1	4.00	0.05	0.03	1	Gastropoda	8	4.17	38.13	5.99	7
Sums	25	100	192.98	100	—	Nitulidae	5	2.60	29.56	4.64	2
Niche breadths	—	3.42	—	3.02	—	Eruciform larvae	2	1.04	27.36	4.30	2
<i>Scinax garbei</i> (n = 12)						Orthoptera unid.	1	0.52	24.81	3.90	1
Orthoptera unid.	3	27.27	308.20	33.93	3	Staphylinidae	5	2.60	17.98	2.83	4
Araneae	4	36.36	237.86	26.18	4	Campodeiform larvae	1	0.52	13.65	2.14	1
Blattaria	1	9.09	139.99	15.41	1	Isoptera	10	5.21	12.32	1.94	1
Hemiptera unid.	1	9.09	122.24	13.46	1	Wasp	2	1.04	12.04	1.89	2
Tettigoniidae	1	9.09	89.26	9.83	1	Thysanura	1	0.52	8.07	1.27	1
Plant material	1	9.09	10.90	1.20	1	Tettigoniidae	1	0.52	7.84	1.23	1
Sums	11	100	908.45	100	—	Diplopoda	1	0.52	6.42	1.01	1
Niche breadths	—	4.17	—	4.25	—	Carabidae	2	1.04	4.08	0.64	1
<i>Scinax icterica</i> (n = 25)						Plant material	4	2.08	2.81	0.44	3
Blattaria	4	30.77	183.96	55.07	3	Pseudoscorpiones	2	1.04	1.18	0.19	2
Orthoptera unid.	2	15.38	92.76	27.77	2	Diptera	1	0.52	0.83	0.13	1
Araneae	3	23.08	34.33	10.28	3	Diplura	2	1.04	0.64	0.10	2
Lepidoptera	1	7.69	14.13	4.23	1	Acari	4	2.08	0.41	0.06	3
Scarabaeidae	1	7.69	4.60	1.38	1	Collembola	2	1.04	0.05	0.01	1
Staphylinidae	1	7.69	2.76	0.83	1	Sums	192	100	636.44	100	—
Coleoptera unid.	1	7.69	1.50	0.45	1	Niche breadths	—	3.6	—	10.41	—
Sums	13	100	334.04	100	—	<i>Ceratophrys cornuta</i> (n = 72)*					
Niche breadths	—	5.12	—	2.54	—	Vertebrata	—	3.35	—	53.05	—
<i>Scinax pedromedinai</i> (n = 25)						Orthoptera	—	4.54	—	22.42	—
Araneae	10	40.00	98.71	40.57	8	Crustacea	—	0.39	—	8.79	—
Orthoptera unid.	4	16.00	43.93	18.05	4	Diplopoda	—	1.38	—	3.95	—
Tettigoniidae	2	8.00	38.26	15.72	2	Araneae	—	1.97	—	3.27	—
Hemiptera unid.	1	4.00	32.47	13.34	1	Coleoptera unid.	—	8.28	—	1.95	—
Diptera	1	4.00	12.47	5.12	1	Formicidae	—	70.22	—	0.52	—
Isoptera	1	4.00	8.39	3.45	1	Annelida	—	0.59	—	0.27	—
Lepidoptera	1	4.00	5.08	2.09	1	Niche breadth	—1.14–6.71	—	—	—	—
Formicidae	3	12.00	2.33	0.96	2	<i>Edalorhina perezii</i> (n = 28)					
Larvae	1	4.00	1.48	0.61	1	Araneae	6	11.32	152.39	21.77	5
Thysanoptera	1	4.00	0.21	0.09	1	Gryllidae	2	3.77	115.79	16.54	2

Appendix 2 continued

Prey category	No.	% No.	Volume	% Vol.	Frequency	Prey category	No.	% No.	Volume	% Vol.	Frequency
<i>Edalorhina perezi</i> continued						<i>Eleutherodactylus imitatrix</i> continued					
Tetrigidae	3	5.66	95.96	13.71	3	Coleoptera unid.	1	10.00	4.74	17.7	1
Wasp	8	15.09	70.8	10.11	6	Tettigoniidae	1	10.00	2.64	9.86	1
Orthoptera unid.	5	9.43	48.31	6.90	4	Formicidae	3	30.00	1.50	5.60	2
Diptera	5	9.43	45.41	6.49	4	Hemiptera unid.	1	10.00	0.64	2.39	1
Coleoptera unid.	2	3.77	31.13	4.45	2	Araneae	1	10.00	0.29	1.08	1
Tettigoniidae	2	3.77	27.47	3.92	1	Collembola	1	10.00	0.12	0.45	1
Formicidae	5	9.43	24.6	3.51	5	Sums	10	100	26.78	100	—
Vermiform larvae	3	5.66	23.35	3.33	3	Niche breadths	—	6.25	—	3.75	—
Blattaria	3	5.66	18.43	2.63	3	<i>Eleutherodactylus peruvianus</i> (n = 21)					
Staphylinidae	1	1.89	17.61	2.52	1	Vermiform larvae	2	5.56	92.04	22.48	2
Miridae	1	1.89	12.6	1.80	1	Tettigoniidae	1	2.78	66.32	16.20	1
Isopoda	1	1.89	8.18	1.17	1	Orthoptera unid.	4	11.11	58.14	14.20	4
Campodeiform larvae	1	1.89	6.66	0.95	1	Tetrigidae	2	5.56	41.55	10.15	1
Winged Formicidae	3	5.66	1.01	0.14	1	Araneae	6	16.67	40.14	9.80	6
Pselaphidae	2	3.77	0.46	0.07	1	Eruciform larvae	2	5.56	35.03	8.55	2
Sums	53	100	700.16	100	—	Lepidoptera	1	2.78	21.31	5.20	1
Niche breadths	—	12.17	—	8.3	—	Wasp	1	2.78	18.16	4.44	1
<i>Eleutherodactylus altamazonicus</i> (n = 3)						Diptera	4	11.11	16.52	4.03	3
Thysanoptera	4	66.67	0.83	74.77	1	Winged Formicidae	1	2.78	5.66	1.38	1
Coleoptera unid.	1	16.67	0.17	15.32	1	Gryllidae	1	2.78	4.46	1.09	1
Formicidae	1	16.67	0.11	9.91	1	Histeridae	1	2.78	3.48	0.85	1
Sums	6	100	1.11	100	—	Diplopoda	1	2.78	3.16	0.77	1
Niche breadths	—	2	—	1.69	—	Collembola	4	11.11	1.90	0.46	2
<i>Eleutherodactylus cruralis</i> (n = 5)						Formicidae	4	11.11	1.34	0.33	2
Gastropoda	2	13.33	5.98	45.96	1	Opiliones	1	2.78	0.26	0.06	1
Formicidae	9	60.00	3.60	27.67	1	Sums	36	100	409.47	100	—
Scolytidae	1	6.67	1.54	11.84	1	Niche breadths	—	10.8	—	7.64	—
Plant material	1	6.67	1.36	10.45	1	<i>Eleutherodactylus toftae</i> (n = 30)					
Araneae	1	6.67	0.33	2.54	1	Orthoptera unid.	3	4.84	68.15	19.70	2
Acari	1	6.67	0.20	1.54	1	Araneae	7	11.29	62.47	18.06	7
Sums	15	100	13.01	100	—	Coleoptera unid.	10	16.13	59.01	17.06	7
Niche breadths	—	2.53	—	3.19	—	Wasp	6	9.68	55.25	15.97	6
<i>Eleutherodactylus fenestratus</i> (n = 29)						Eruciform larvae	2	3.23	14.45	4.18	2
Orthoptera unid.	11	16.42	677.87	31.78	7	Hemiptera unid.	2	3.23	14.09	4.07	1
Tettigoniidae	2	2.99	349.01	16.36	2	Tettigoniidae	1	1.61	12.93	3.74	1
Acrididae	2	2.99	333.3	15.63	2	Formicidae	13	20.97	12.64	3.65	8
Gryllidae	4	5.97	213.53	10.01	3	Buprestidae	1	1.61	9.69	2.80	1
Blattaria	4	5.97	181.54	8.51	4	Diptera	4	6.45	9.57	2.77	4
Araneae	10	14.93	69.28	3.25	7	Gastropoda	1	1.61	5.90	1.71	1
Hemiptera unid.	2	2.99	67.48	3.16	2	Lygaeidae	1	1.61	4.75	1.37	1
Dermaptera	1	1.49	61.46	2.88	1	Lepidoptera	1	1.61	4.23	1.22	1
Coleoptera unid.	4	5.97	51.78	2.43	3	Cicadellidae	1	1.61	3.61	1.04	1
Wasp	1	1.49	42.51	1.99	1	Isoptera	1	1.61	3.44	0.99	1
Formicidae	10	14.93	19.68	0.92	6	Curculionidae	1	1.61	3.05	0.88	1
Vermiform larvae	1	1.49	16.15	0.76	1	Winged Formicidae	2	3.23	1.12	0.32	1
Isoptera	4	5.97	13.35	0.63	2	Vermiform larvae	1	1.61	0.76	0.22	1
Scarabaeidae	1	1.49	12.36	0.58	1	Dermaptera	1	1.61	0.35	0.10	1
Larvae	2	2.99	10.77	0.50	2	Acari	2	3.23	0.21	0.06	2
Pseudoscorpiones	2	2.99	4.10	0.19	2	Collembola	1	1.61	0.20	0.06	1
Lepidoptera	1	1.49	3.93	0.18	1	Sums	62	100	345.87	100	—
Scolytidae	1	1.49	1.60	0.08	1	Niche breadths	—	9.47	—	7.43	—
Coccinellidae	1	1.49	1.66	0.08	1	<i>Leptodactylus bolivianus</i> (n = 14)					
Curculionidae	1	1.49	0.69	0.03	1	Scarabaeidae	6	5.88	2418.39	19.29	4
Opiliones	1	1.49	0.36	0.02	1	Carabidae	4	3.92	1764.99	14.08	4
Collembola	1	1.49	0.31	0.01	1	Diplopoda	6	5.88	1646.56	13.13	4
Sums	67	100	2132.72	100	—	Orthoptera unid.	6	5.88	1197.4	9.55	5
Niche breadths	—	10.81	—	5.76	—	Vertebrata	1	0.98	938.29	7.48	1
<i>Eleutherodactylus imitatrix</i> (n = 11)						Tettigoniidae	1	0.98	816.02	6.51	1
Histeridae	1	10.00	11.35	42.38	1	Formicidae	30	29.41	626.75	5.00	11
Orthoptera unid.	1	10.00	5.50	20.54	1	Hemiptera unid.	3	2.94	613.76	4.90	3

Appendix 2 continued

Prey category	No.	% No.	Volume	% Vol.	Frequency	Prey category	No.	% No.	Volume	% Vol.	Frequency
<i>Leptodactylus bolivianus</i> continued						<i>Leptodactylus mystaceus</i> continued					
Coleoptera unid.	6	5.88	450.34	3.59	6	Hemiptera unid.	1	2.00	81.95	1.49	1
Eruciform larvae	1	0.98	435.24	3.47	1	Araneae	3	6.00	66.02	1.20	3
Crustacea	1	0.98	376.56	3.00	1	Coccinellidae	1	2.00	65.73	1.20	1
Gryllidae	2	1.96	262.30	2.09	1	Wasp	2	4.00	56.28	1.02	2
Lepidoptera	1	0.98	202.33	1.61	1	Eruciform larvae	2	4.00	47.90	0.87	2
Plant material	22	21.57	180.17	1.44	4	Formicidae	5	10.00	28.00	0.51	5
Tetrigidae	3	2.94	173.81	1.39	2	Gryllidae	1	2.00	20.86	0.38	1
Araneae	2	1.96	119.16	0.95	2	Sums	50	100	5493.86	100	—
Histeridae	1	0.98	113.10	0.90	1	Niche breadths	—	14.37	—	9.65	—
Vermiform larvae	2	1.96	112.03	0.89	2	<i>Leptodactylus pentadactylus</i> (<i>n</i> = 7)					
Curculionidae	2	1.96	62.72	0.50	1	Tettigoniidae	3	10.00	6657.08	42.41	1
Phasmida	1	0.98	19.44	0.16	1	Diplopoda	4	13.33	5183.48	33.03	3
Dermaptera	1	0.98	7.99	0.06	1	Orthoptera unid.	2	6.67	1474.65	9.40	2
Sums	102	100	12537.35	100	—	Carabidae	1	3.33	621.02	3.96	1
Niche breadths	—	6.56	—	9.72	—	Hemiptera unid.	2	6.67	578.75	3.69	2
<i>Leptodactylus leptodactyloides</i> (<i>n</i> = 33)						Scarabaeidae	2	6.67	527.60	3.36	1
Gryllidae	2	2.04	170.15	12.77	2	eruciform larvae	2	6.67	212.45	1.35	2
Coleoptera unid.	13	13.27	147.64	11.08	12	Formicidae	5	16.67	186.38	1.19	3
Cicadidae	1	1.02	140.78	10.56	1	Coleoptera unid.	5	16.67	143.35	0.91	4
Aradidae	1	1.02	107.94	8.10	1	Curculionidae	2	6.67	96.21	0.61	1
Crustacea	1	1.02	106.59	8.00	1	Gastropoda	1	3.33	11.70	0.07	1
Curculionidae	2	2.04	76.82	5.76	2	Winged Formicidae	1	3.33	2.75	0.02	1
Formicidae	26	26.53	66.10	4.96	16	Sums	30	100	15695.42	100	—
Blattaria	1	1.02	61.54	4.62	1	Niche breadths	—	9.18	—	3.31	—
Orthoptera unid.	5	5.10	50.05	3.76	4	<i>Leptodactylus petersii</i> (<i>n</i> = 24)					
Scarabaeidae	2	2.04	45.81	3.44	1	Vermiform larvae	7	10.29	251.12	33.06	4
Araneae	3	3.06	43.79	3.29	3	Blattaria	3	4.41	84.62	11.14	3
Vermiform larvae	6	6.12	41.95	3.15	5	Formicidae	18	26.47	62.18	8.19	6
Campodeiform larvae	8	8.16	41.45	3.11	4	Tettigoniidae	3	4.41	60.28	7.94	3
Carabidae	2	2.04	37.56	2.82	1	Coleoptera unid.	3	4.41	58.83	7.75	3
Cicindelidae	1	1.02	37.08	2.78	1	Araneae	5	7.35	36.86	4.85	5
Eruciform larvae	1	1.02	27.68	2.08	1	Wasp	1	1.47	29.89	3.94	1
Tetrigidae	1	1.02	22.02	1.65	1	Lygaeidae	1	1.47	28.38	3.74	1
Isopoda	2	2.04	19.06	1.43	2	Isoptera	12	17.65	26.15	3.44	1
Annelid	1	1.02	18.25	1.37	1	Carabidae	1	1.47	24.97	3.29	1
Lepidoptera	2	2.04	18.08	1.36	2	Tetrigidae	1	1.47	23.45	3.09	1
Larvae	4	4.08	12.45	0.93	3	Orthoptera unid.	4	5.88	18.74	2.47	2
Plant material	1	1.02	9.10	0.68	1	Gastropoda	1	1.47	13.91	1.83	1
Hemiptera unid.	1	1.02	8.81	0.66	1	Isopoda	1	1.47	11.92	1.57	1
Diplopoda	1	1.02	8.45	0.63	1	Membracidae	2	2.94	11.51	1.52	2
Isoptera	2	2.04	5.07	0.38	2	Gryllidae	1	1.47	7.46	0.98	1
Diptera	5	5.10	4.87	0.37	2	Winged Formicidae	1	1.47	6.79	0.89	1
Gastropoda	2	2.04	3.25	0.24	2	Plant material	2	2.94	1.42	0.19	1
Pseudoscorpiones	1	1.02	0.38	0.03	1	Chrysomelidae	1	1.47	1.06	0.14	1
Sums	98	100	1332.72	100	—	Sums	68	100	759.54	100	—
Niche breadths	—	9.03	—	14.42	—	Niche breadths	—	7.68	—	6.63	—
<i>Leptodactylus mystaceus</i> (<i>n</i> = 25)						<i>Leptodactylus rhodonotus</i> (<i>n</i> = 21)					
Scarabaeiform larvae	2	4.00	1018.08	18.53	2	Diplopoda	7	8.43	1889.36	27.21	6
Blattaria	3	6.00	923.93	16.82	3	Gastropoda	3	3.61	1352.83	19.48	3
Lygaeidae	2	4.00	585.10	10.65	1	Carabidae	5	6.02	1085.17	15.63	3
Coleoptera unid.	7	14.00	517.44	9.42	5	Cicadidae	1	1.20	792.93	11.42	1
Carabidae	5	10.00	507.43	9.24	5	Coleoptera unid.	5	6.02	755.83	10.88	3
Tettigoniidae	1	2.00	283.25	5.16	1	Orthoptera unid.	4	4.82	183.77	2.65	3
Orthoptera unid.	3	6.00	275.51	5.01	3	Blattaria	1	1.20	183.25	2.64	1
Tetrigidae	3	6.00	247.94	4.51	3	Chrysomelidae	2	2.41	124.39	1.79	1
Curculionidae	2	4.00	211.59	3.85	2	Phasmida	2	2.41	96.15	1.38	2
Staphylinidae	2	4.00	197.25	3.59	1	Vermiform larvae	12	14.46	80.47	1.16	5
Scarabaeidae	3	6.00	162.60	2.96	2	Tetrigidae	1	1.20	80.89	1.16	1
Diplopoda	1	2.00	101.00	1.84	1	Dermaptera	1	1.20	69.96	1.01	1
Gastropoda	1	2.00	96.00	1.75	1	Formicidae	12	14.46	66.90	0.96	9

Appendix 2 continued

Prey category	No.	% No.	Volume	% Vol.	Frequency	Prey category	No.	% No.	Volume	% Vol.	Frequency
<i>Leptodactylus rhodonotus</i> continued						<i>Chiasmocleis ventrimaculata</i> continued					
Curculionidae	2	2.41	36.62	0.53	2	Sums	71	100	52.84	100	—
Crustacea	1	1.20	30.97	0.45	1	Niche breadths	—	1.95	—	2.01	—
Campodeiform larvae	9	10.84	27.21	0.39	1	<i>Ctenophryne geayi</i> (n = 3)					
Annelid	2	2.41	22.58	0.33	1	Formicidae	49	87.5	98.55	26.83	3
Araneae	2	2.41	13.77	0.20	2	Histeridae	1	1.79	65.86	17.93	1
Isopoda	1	1.20	14.11	0.20	1	Coleoptera unid.	2	3.57	64.36	17.52	2
Lygaeidae	1	1.20	13.21	0.19	1	Pentatomidae	1	1.79	44.41	12.09	1
Thysanura	1	1.20	11.87	0.17	1	Carabidae	1	1.79	35.41	9.64	1
Chilopoda	3	3.61	6.07	0.09	2	Curculionidae	1	1.79	30.51	8.31	1
Diptera	1	1.20	3.10	0.04	1	Scarabaeidae	1	1.79	28.21	7.68	1
Scolytidae	2	2.41	2.48	0.04	1	Sums	56	100	367.31	100	—
Acari	1	1.20	0.15	0.00	1	Niche breadths	—	1.3	—	5.83	—
Pselaphidae	1	1.20	0.24	0.00	1	<i>Elachistocleis ovalis</i> (n = 11)					
Sums	83	100	6944.28	100	—	Isoptera	254	35.67	438.89	64.91	4
Niche breadths	—	12.83	—	6.11	—	Formicidae	455	63.9	235.6	34.84	7
<i>Lithodytes lineatus</i> (n = 2)						Coleoptera unid.	2	0.28	1.17	0.17	2
Gryllidae	1	2.86	134.00	33.90	1	Larvae	1	0.14	0.53	0.08	1
Annelid	1	2.86	87.10	22.04	1	Sums	712	100	676.19	100	—
Isopoda	2	5.71	49.93	12.63	1	Niche breadths	—	1.87	—	1.8	—
Vermiform larvae	5	14.29	49.13	12.43	1	<i>Hamptophryne boliviana</i> (n = 25)					
Formicidae	5	14.29	31.87	8.06	1	Formicidae	1257	97.67	2000.79	92.18	25
Isoptera	19	54.29	24.11	6.10	1	Isoptera	13	1.01	61.60	2.84	3
Pseudoscorpiones	1	2.86	15.02	3.80	1	Coleoptera unid.	5	0.39	28.56	1.32	4
Coleoptera unid.	1	2.86	4.12	1.04	1	Histeridae	1	0.08	21.49	0.99	1
Sums	35	100	395.28	100	—	Carabidae	2	0.16	20.98	0.97	2
Niche breadths	—	2.92	—	4.84	—	Eruciform larvae	1	0.08	18.78	0.87	1
<i>Physalaemus petersi</i> (n = 7)						Vermiform larvae	3	0.23	11.23	0.52	2
Isoptera	91	98.91	328.94	99.43	4	Larvae	1	0.08	5.17	0.24	1
Curculionidae	1	1.09	1.89	0.57	1	Scolytidae	2	0.16	1.30	0.06	1
Sums	92	100	330.83	100	—	Acari	1	0.08	0.21	0.01	1
Niche breadths	—	1.02	—	1.01	—	Pselaphidae	1	0.08	0.31	0.01	1
MICROHYLIDAE:						Sums	1287	100	2170.42	100	—
<i>Altigius alios</i> (n = 2)						Niche breadths	—	1.05	—	1.18	—
Formicidae	12	70.59	95.00	65.22	1	PIPIDAE:					
Curculionidae	1	5.88	29.84	20.48	1	<i>Pipa pipa</i> (n = 6)					
Wasp	1	5.88	14.29	9.81	1	Fish	2	25.00	4241.32	98.83	2
Isoptera	3	17.65	6.54	4.49	1	Tadpole	1	12.50	35.48	0.83	1
Sums	17	100	145.67	100	—	Water beetle	1	12.50	12.54	0.29	1
Niche breadths	—	1.86	—	2.09	—	Plant material	3	37.50	1.72	0.04	2
<i>Chiasmocleis ventrimaculata</i> (n = 2)						Ostracod	1	12.50	0.36	0.01	1
Formicidae	43	60.56	28.93	54.75	1	Sums	8	100	4291.42	100	—
Isoptera	27	38.03	23.55	44.57	1	Niche breadths	—	4	—	1.02	—
Coleoptera unid.	1	1.41	0.36	0.68	1						

*72 *Ceratophrys cornuta* from Cuzco Amazónico, Peru (from Duellman and Lizana, 1994). The niche breadth values are based on numerical percentages and varied seasonally.

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