

Feeding Ecology of Thirteen Syntopic Species of Anurans in a Seasonal Tropical Environment

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Summary. Thirteen species of anurans belonging to three families forage diurnally for arthropods in the leaf litter of the lowland rainforest at the Río Lullapichis in Amazonian Perú. This paper investigates the diets and patterns of coexistence in this group of ecologically similar species. All thirteen species use the forest floor habitat without apparent differentiation. Most species take prey in proportions significantly different from those occurring in the leaf litter and comprise two specialist guilds: dendrobatids and bufonids that eat hard-bodied, slow-moving arthropods such as ants and mites; and leptodactylids that eat soft-bodied, mobile arthropods, primarily orthopterans and large spiders. *Dendrobates femoralis* (Boulenger) is a generalist, taking prey in proportions not significantly different from those in the leaf litter. Within specialist guilds, body sizes of species vary and are correlated with the size of prey taken. Foraging behavior and predator defense also correlate with the type and sizes of prey taken. Ant specialists tend to be poisonous and active searchers, taking many small prey per day. Non-ant specialists are cryptic, sit-and-wait foragers that take few large prey per day. Similarity in diet within guilds tends to be lowest in the dry season when food is less abundant, suggesting that food is in short supply in the dry season.

Introduction

More than 50 species of anurans belonging to six families occur in the lowland rainforest in the Río Lullapichis region in Amazonian Perú (Toft and Duellman, 1979). Of these, 13 species in three families forage diurnally for arthropods in the leaf litter on the forest floor. Superficially, all 13 species, some of which are closely related, appear to be ecologically similar.

How do these species coexist? Is there a limit to how similarly they can use common resources that may often be in short supply (MacArthur and Levins, 1967)? According to the "theory of limiting similarity," species ought to show regular, not random, differences in their use of resources; empirical work shows that species differ most commonly in three ways: in the space they occupy, in what they eat; or when they are active (Schoener, 1974a). For example, if species differ only in the sizes of food they take and if food is continuously variable, the coexisting species should be regularly spaced along a spectrum of food sizes. May and MacArthur (1972) suggested that the differences (d) between mean sizes of food of adjacent species should be approximately equal to one standard deviation (w or the width of the utilization function), that is $d/w = 1$. Subsequent modifications of the theory of

limiting similarity (Abrams, 1975; Roughgarden, 1974, 1975, 1976; Turelli, 1978) have questioned whether the theoretical justification for $d/w = 1$ is valid. Nonetheless, empirical studies have found d/w to be approximately one along the relevant resource spectrum in several, very different communities: antbirds (Terborgh in MacArthur, 1972); sunfish (Werner, 1977); snails (Fenchel, 1975; Fenchel and Kofoed, 1976). Others have proposed new theories to deal with coexisting species (Lawlor and Maynard Smith, 1975; Roughgarden, 1976; Schoener, 1974b, 1976), but the qualitative prediction, that a limiting similarity should exist, remains open to question.

Moreover, variation in resource availability has been postulated to affect specific use of resources and therefore patterns of coexistence (MacArthur, 1969, 1970; MacArthur and Pianka, 1966). Where resource variation is seasonal, the common expectation is that species diverge in their use of a limiting resource during the season when resources are less abundant (Lack, 1947; Svardson, 1949). This expectation seems to be confirmed in several studies in which resources are assumed to vary: in populations of tropical stream fishes (Zaret and Rand, 1971), birds (Karr, 1976), and others (see review by Smith et al., 1978). Inger and Colwell (1977), Inger and Greenberg (1966), and Inger and Marx (1961) found seasonal differences in diet of amphibians in various tropical amphibians. Janzen (1973) and Robinson and Robinson (1979) showed that abundance of arthropods, the food source for many of the above species, varies seasonally in the tropics. However, only a few studies have included an independent sampling of the resources involved (Smith et al., 1978).

The question, in testing any of these notions in the field, is whether resources are truly limiting. Such a question may be difficult or impossible to answer; in fact, at any point in time an answer, if attainable, might be irrelevant. Undoubtedly, the time scale over which these communities have been shaped is closer to tens of thousands of years than the tens, at most, available for study. Rather than be stymied by the question "Is this resource now or has it ever been limiting?" one might begin to get approximate answers to the questions dealt with by the theory of limiting similarity and related hypotheses by examining the qualitative predictions in the above theory. Further, monitoring species' use of resources as those resources change can be an alternative to direct manipulation (Smith et al., 1978), and this approach can be made more effective in combination with the use of predictive theory.

The litter anurans of lowland Perú provide an opportunity to examine these ideas about coexisting species. They apparently coexist in time and space and share common resources, some of which potentially could be in short supply. Their environment

is seasonal (Toft and Duellman, 1979) and thus possibly their resources vary seasonally as well. The object of this study is to examine how these 13 species use common resources and to determine whether that use is affected by the abundance or variability of those resources.

Habitat and food are the two resources examined in this study. Because the litter anurans do not depend on highly localized bodies of water for reproduction as do other anurans, resources related to reproduction are not likely to be limiting in this group (Toft and Duellman, 1979). Both predation and parasitism could influence how similarly coexisting species use resources (Caswell, 1978, Connell, 1975, MacArthur, 1972, Roughgarden and Feldman, 1976). Predation and parasitism were not examined directly because predation cannot be observed frequently enough and because so little is known about anuran parasites at this location (Guerrero and Ayala, 1972).

Specifically I ask: First, do species differ in their use of food or habitat? Second, what is the availability of resources and does it vary, perhaps seasonally? Last, is the use of resources by the litter anurans consistent with ideas put forth by theory on the ecological similarity of coexisting species?

Methods

This study was conducted at the biological station, Panguana, on the lower Río Lullapichis, at approximately 9° 35' S, 74° 48' W, in lowland Amazonian Perú. Panguana, at about 210 M elevation, has a mean annual temperature of 24° C and a mean annual rainfall of 2,200 mm distributed in a distinctly seasonal pattern (Fig. 1). Toft and Duellman (1979) described the study area in detail.

I censused frogs and arthropods in 12 areas during two four week periods, once in mid-dry season (June and July) and one in mid-wet season (January and February). Censuses were conducted between 1,000 and 1,300 h.

In order to determine the spatial distribution of frogs on the forest floor, i.e., along a habitat gradient, I conducted censuses at varying distances from a stream and a pond (Table 1). However, I could discern no significant differences along this possible moisture gradient, nor any other obvious differences in the qualities of the forest floor; therefore, I combined these censuses with others that I chose randomly from a grid of the area for a total of 12 censuses each season. For the remainder of this paper I consider the forest floor to be homogenous, probably a valid assumption because of the even topography at this location.

Frogs were censused by a technique designed to estimate relative densities of frogs (Sexton et al., 1964; Lloyd et al., 1968). An assistant and I searched the leaf litter, removing it and all vegetation in a 6 × 6 m plot. We attempted to catch all frogs, and recorded the species and approximate size of frogs that we were unable to catch. Frogs both from the censuses and from general collection of the area were fixed as soon as possible in 10% formalin so as to preserve stomach contents with minimum digestion. Snout-vent length (SVL) and the width of the head at the angle of the jaws (mouth width or MW) were recorded for each frog.

Prey items were sorted to size class and broad taxonomic type: ants (Formicidae) and mites; orthopterans; coleopterans; lumped miscellaneous orders of insects and non-insect arthropods; and holometabolous larvae. I estimated the dry weight of all types and sizes of arthropods from length-weight regressions based on dried samples of arthropods of representative length classes from the litter censuses.

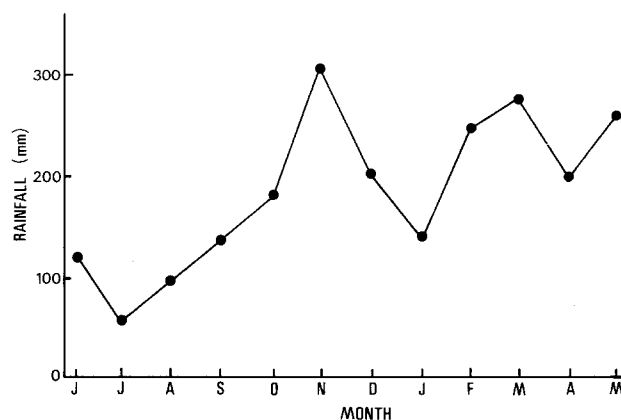


Fig. 1. Approximate monthly rainfall (mm) at the Río Lullapichis, Perú, during the year beginning with the onset of the dry season

Table 1. Numbers of frogs and frog species and estimated dry weight of arthropods in censuses (36 M² and 845 cm² respectively) taken at increasing distances from a pond and a stream respectively (1 = nearest; 3, 4 = farthest)

Census	Wet season			Dry season		
	Frogs	Species	Arthropods (mg)	Frogs	Species	Arthropods (mg)
<i>A. Pond</i>						
1	10	7	69.9	3	3	17.5
2	6	5	145.4	2	2	6.9
3	6	6	35.6	1	1	11.2
4	12	4	40.1	3	3	14.5
<i>B. Stream</i>						
1	2	2	7.2	0	0	16.6
2	4	3	98.2	1	1	7.8
3	4	3	25.3	1	1	20.8

Adjacent to each frog census plot, I collected an 845 cm² sample of leaf litter by putting it as quickly as possible into a plastic bag and weighing it. I used kerosene to extract arthropods from the litter (Strickland 1945), and sorted them into the same type and size categories as the arthropods from the stomach contents.

Statistical tests were performed on the natural logarithms of numbers and dry weight, as Janzen (1973), Schoener and Janzen (1968) and Toft and Levings (in press) found that numbers and dry weights of arthropods are log-normally distributed for large numbers of samples at other tropical sites.

Electivities [D] were calculated by the formula given by Jacobs (1974). Values of electivity run from +1 for complete preference, through 0, for no selection at all, to -1, for complete avoidance of a particular prey item. The niche breadth [B_s] and overlap [α_{ij}] measures used are those given by Schoener (1974c). In this paper, α_{ij} is not necessarily intended to be a true competition coefficient, i.e., to measure the intensity of competition, but is presented primarily as a measure of similarity in diets among species. Both B_s and α_{ij} of Schoener (1974) incorporate the availability of prey items in the environment as well as in the diet. One of their features is extreme sensitivity to rare prey in the

Table 2. Types of prey in the diet of 13 species of litter anurans and in the leaf litter: proportions and electivities of prey types; deviation of stomachs from the leaf litter (X^2); niche breadths (B_s) based on 5 and 4 categories of prey (see text). Prey categories: Ants, orthopterans (Ort.), coleopterans (Col.), misc. adult arthropods (Art.), and misc. larvae (Lar.). NA: sample size too small (Siegel, 1956); NS: not significant; *: $p=0.05$; **: $0.05 < p < 0.001$

Species	Sample Size		Proportions							Niche Breadth	
	Frogs	Prey	Electivity					X ²			
			Ants	Ort.	Col.	Art.	Lar.				
A. Wet Season											
Bufonidae											
<i>Dendrophryniscus minutus</i> (Melin)	15	681	0.90	0	0.02	0.01	0.07	**	0.06	0.06	
<i>Bufo typhonius</i> (L.)	13	528	0.84	0	0.14	0.01	0.01	**	0.07	0.07	
Dendrobatidae											
<i>Colostethus marchesianus</i> (Melin)	32	361	0.52	0.01	0.06	0.28	0.13	NA	0.05	0.05	
<i>Dendrobates quinquevittatus</i> Steindachner	2	65	0.95	0	0.05	0	0	**	0.07	0.07	
<i>Dendrobates pictus</i> (Bibron in Tschudi)	19	503	0.59	0	0.06	0.09	0.26	NS	0.20	0.28	
<i>Dendrobates femoralis</i> (Boulenger)	24	189	0.13	0.26	0.25	0.28	0.08	**	0.07	0.07	
<i>Dendrobates petersi</i> (Silverstone)	26	921	0.85	0.04	0.05	0.06	0.01	**	0.09	0.09	
<i>Dendrobates trivittatus</i> (Spix)	35	2,804	0.72	0.02	0.11	0.08	0.07	**	0.09	0.09	
Leptodactylidae											
<i>Eleutherodactylus ockendeni</i> (Boulenger)	9	45	0.01	0.73	0.06	0.20	0	NA	0.08	0.23	
<i>Eleutherodactylus toftae</i> Duellman	5	16	0.15	0.53	0.06	0.18	0.09	NA	0.13	0.27	
<i>Adenomera andreae</i> (Müller)	11	78	0.08	0.18	0.33	0.20	0.21	NS	0.10	0.14	
<i>Eleutherodactylus peruvianus</i> (Melin)	7	13	0.01	0.56	0.40	0.03	0.01	NA	0.10	0.21	
<i>Edalorhina perezi</i> Jiménez de la Espada	5	5	0	0.34	0.23	0.43	0	NA	0.14	0.25	
Leaf litter arthropods	12 ^a	1,183	0.22	0.22	0.23	0.23	0.10				
B. Dry Season											
Bufonidae											
<i>Dendrophryniscus minutus</i>	3	102	0.99	—	0.08	0.01	0.00	NA	—	0.09	
<i>Bufo typhonius</i>	4	161	0.81	—	0.18	0	0.01	**	—	0.12	
Dendrobatidae											
<i>Colostethus marchesianus</i>	8	197	0.34	—	0.02	0.33	0.31	NS	—	0.15	
<i>Dendrobates quinquevittatus</i>	—	—	—	—	—	—	—	—	—	—	
<i>Dendrobates pictus</i>	12	171	0.72	—	0.02	0.10	0.16	**	—	0.13	
<i>Dendrobates femoralis</i>	10	57	0.29	—	0.18	0.46	0.08	NS	—	0.25	
<i>Dendrobates petersi</i>	—	—	—	—	—	—	—	—	—	—	
<i>Dendrobates trivittatus</i>	9	507	0.82	—	0.03	0.08	0.07	**	—	0.12	

Table 2. Continued.

Species	Sample Size		Proportions								
	Frogs	Prey	Electivity						X ²	Niche Breadth	
			Ants	Ort.	Col.	Art.	Lar.	k=5		k=4	
Leptodactylidae											
<i>Eleutherodactylus ockendeni</i>	8	14	0.01	—	0	0.95	0.04	NA	—	0.11	
			−0.95	—	−1.00	0.94	−0.02				
<i>Eleutherodactylus toftae</i>	8	13	0	—	0.03	0.97	0	NA	—	0.10	
			−1.00	—	−0.82	0.97	−1.00				
<i>Adenomera andreae</i>	—	—	—	—	—	—	—	—	—	—	
			—	—	—	—	—				
<i>Eleutherodactylus peruvianus</i>	12	14	0	—	0.17	0.82	0.01	NA	—	0.13	
			−1.00	—	−0.21	0.83	0.13				
<i>Edalorhina perezi</i>	—	—	—	—	—	—	—	—	—	—	
			—	—	—	—	—				
Leaf litter arthropods	12 ^a	871	0.29	—	0.24	0.32	0.15				

^a Number of censuses

environment; therefore prey categories were combined so that no categories of prey in the leaf litter were less than 10% of the total. In the wet season, the five categories of prey described above were used in the calculations. In the dry season, I combined orthopterans with miscellaneous adult arthropods because the former were very rare in the leaf litter samples at that time. In order to compare niche breadth between and dry seasons, I present niche breadths computed with and without orthopterans as a separate category for the wet season. Therefore, categories for non-ant prey are somewhat arbitrary.

Results and Discussion

Feeding Ecology

Certain patterns of feeding in the litter anurans at the Río Llullapichis are not affected by seasonal changes.

Prey type. The majority of anuran species in the leaf litter eat types of prey in proportions different from those found in the leaf litter (Table 2). Species of frogs can be arranged along a continuum, based on the proportions of two "types" of prey in the diet: slow-moving, hard-bodied arthropods, principally ants and mites (hereafter referred to only as ants because mites make up a small proportion of this category) and all other prey, characteristically soft-bodied mobile arthropods such as roaches, crickets, and large spiders. Values of electivities [*D*] of ants were used as a basis for the continuum: Electivities range from +1.0 representing "ant specialists," through 0 representing generalists, which eat prey in proportions similar to those found in the leaf litter, to −1.0, representing "non-ant specialists", which select soft-bodied mobile prey and disproportionately low proportions of ants in the diet. Species cluster at extremes of the continuum, i.e., in separate guilds (Root 1967) comprising and versus non-ant specialists. Only one species, *Dendrobates femoralis* (Boulenger), consistently eats prey in proportions that occur in the leaf litter and thereby is a generalist. Other species may specialize less in one season or other and perhaps the assignment of these species to a specialist guild to arbitrary.

Among the frogs that eat ants, niche breadths [*B_s*] reflect these designations of specialists and generalists. Specialists should have narrower food niches, or small values of *B_s*, and generalists wider niches, or larger values of *B_s*. As expected, frogs that strongly elect ants have small niche breadths, i.e., are ant specialists, and as electivity of ants decreases niche breadth increases, with the generalist *Dendrobates femoralis* having the largest niche breadth (Table 2; *R_s* = 0.93; *p* < 0.001 in the wet season; *R_s* = −0.89; 0.05 < *p* < 0.01 in the dry season).

As I have defined them above, frogs that do not eat ants in the same proportions as occur in the leaf litter are "specialists." This terminology might be in conflict with others who refer to these species as "generalists" or "opportunistic" because they do not differentiate among non-ant prey. Though the composition of diet of *Adenomera andreae* (Müller) is not significantly different from the proportions of prey in the leaf litter, I consider *A. andreae* a non-ant specialist because it has a large negative electivity of ants and because the sample size of its prey is small. *Eleutherodactylus toftae* Duellman exhibits a relatively small negative electivity of ants in the dry season, but samples, again, are small; most probably *E. toftae* belongs to the non-ant guild.

Composition of these guilds at the Río Llullapichis reflects taxonomic categories. Here, all frogs that eat ants, whether an ant specialist or the generalist, are bufonids or dendrobatids, as corroborated by others (Inger and Marx, 1961; Silverstone, 1975, 1976), although some *Eleutherodactylus* elsewhere are known to eat ants (Duellman, 1978; Jones MS, M. Stewart pers. comm.). The non-ant specialists are all leptodactylids; for the time being, *A. andreae* and especially *E. toftae* are included in this guild.

Prey sizes. Species of anurans at the Río Llullapichis differ in body size (Table 3). As in other insectivores (Hespenheide, 1975) the size of prey of an individual frog is correlated with the dimension associated with prey capture. There is a significant correlation between mouth width and the mean size of prey of an individual frog (Fig. 2). Moreover, this relationship is stronger within guilds than when all frogs are considered at once; and the slopes are significantly different for the three guilds (*F* = 51.5; 0.05 < *p* < 0.01). In other words, ant specialists take smaller prey for a given mouth

Table 3. Body size (mm), prey size (mm), and number of prey items per stomach in 13 species of litter anurans

Species	Body size		Prey size	No. items/stomach
	SVL \pm SE	MW \pm SE	$\bar{X} \pm SE \pm SD$	$\bar{X} \pm SE$
A. Wet Season				
Bufonidae				
<i>Dendrophryniscus minutus</i>	16.9 \pm 1.4	4.8 \pm 0.3	0.51 \pm 0.01 \pm 0.27	45.5 \pm 14.8
<i>Bufo typhonius</i>	41.9 \pm 3.2	15.9 \pm 1.2	1.60 \pm 0.03 \pm 0.63	40.6 \pm 9.6
Dendrobatidae				
<i>Colostethus marchesianus</i>	14.7 \pm 0.7	5.1 \pm 0.2	0.50 \pm 0.02 \pm 0.28	10.4 \pm 1.1
<i>Dendrobates quinquevittatus</i>	15.0	5.0	0.44 \pm 0.03 \pm 0.19	32.5 \pm 6.5
<i>Dendrobates pictus</i>	19.9 \pm 0.3	6.2 \pm 0.1	0.56 \pm 0.02 \pm 0.34	26.5 \pm 4.0
<i>Dendrobates femoralis</i>	23.8 \pm 1.4	8.1 \pm 0.5	1.16 \pm 0.09 \pm 0.63	7.9 \pm 1.0
<i>Dendrobates petersi</i>	28.9 \pm 0.7	8.4 \pm 0.7	0.94 \pm 0.01 \pm 0.56	32.2 \pm 5.0
<i>Dendrobates trivittatus</i>	39.7 \pm 4.7	11.1 \pm 1.2	0.79 \pm 0.02 \pm 0.45	75.8 \pm 9.0
Leptodactylidae				
<i>Eleutherodactylus ockendeni</i>	13.3 \pm 1.6	5.4 \pm 0.8	0.47 \pm 0.06 \pm 0.41	4.5 \pm 2.2
<i>Eleutherodactylus toftae</i>	14.3 \pm 2.1	5.7 \pm 0.8	0.65 \pm 0.12 \pm 0.46	3.2 \pm 0.9
<i>Adenomera andreae</i>	14.6 \pm 1.7	5.6 \pm 1.9	0.90 \pm 0.06 \pm 0.59	7.1 \pm 2.8
<i>Eleutherodactylus peruvianus</i>	21.2 \pm 2.0	7.7 \pm 1.6	1.30 \pm 0.21 \pm 0.29	1.9 \pm 0.4
<i>Edalorhina perezii</i>	31.5 \pm 0.7	11.0 \pm 0.5	2.20 \pm 0.15 \pm 0.33	1.0 \pm 0.0
Leaf litter arthropods			0.82 \pm 0.02 \pm 0.51	
B. Dry Season				
Bufonidae				
<i>Dendrophryniscus minutus</i>	13.0 \pm 1.0	3.7 \pm 0.3	0.33 \pm 0.01 \pm 0.12	34.0 \pm 3.6
<i>Bufo typhonius</i>	51.9 \pm 3.6	18.8 \pm 3.2	1.85 \pm 0.04 \pm 0.43	40.3 \pm 14.2
Dendrobatidae				
<i>Colostethus marchesianus</i>	14.1 \pm 0.7	4.2 \pm 0.2	0.44 \pm 0.02 \pm 0.23	24.6 \pm 6.2
<i>Dendrobates quinquevittatus</i>	—	—	—	—
<i>Dendrobates pictus</i>	17.3 \pm 1.1	4.5 \pm 1.0	0.44 \pm 0.05 \pm 0.34	14.5 \pm 2.8
<i>Dendrobates femoralis</i>	21.9 \pm 1.7	6.9 \pm 1.3	0.72 \pm 0.13 \pm 0.50	5.7 \pm 1.4
<i>Dendrobates petersi</i>	—	—	—	—
<i>Dendrobates trivittatus</i>	34.4 \pm 4.1	8.6 \pm 2.3	0.83 \pm 0.05 \pm 0.53	56.3 \pm 21.7
Leptodactylidae				
<i>Eleutherodactylus ockendeni</i>	15.9 \pm 0.6	5.8 \pm 0.6	0.99 \pm 0.28 \pm 0.33	1.8 \pm 0.5
<i>Eleutherodactylus toftae</i>	21.4 \pm 0.4	7.3 \pm 0.5	1.32 \pm 0.21 \pm 0.39	1.6 \pm 0.3
<i>Adenomera andreae</i>	—	—	—	—
<i>Eleutherodactylus peruvianus</i>	23.0 \pm 1.5	8.4 \pm 2.3	1.59 \pm 0.39 \pm 0.72	1.3 \pm 0.2
<i>Edalorhina perezii</i>	—	—	—	—
Leaf litter arthropods			0.66 \pm 0.02 \pm 0.46	

width than do non-ant specialists, and generalists are intermediate. Finally, although ranges of body sizes overlap between adjacent species (Table 3), mean sizes of prey are significantly different among species for the most part, and are correlated with the average mouth width among species ($R_s = 0.80$; $0.5 < p < 0.01$ ant; $R_s = 1.00$ non-ant). Other aspects of morphology reflect this tendency: ant specialists have narrower mouths for a given body size than do non-ant specialists (Fig. 3) but this relationship is not greatly different at small body sizes.

Comparing the ratios of snout-vent length and mouth width, respectively, of adjacent species in the ant specialist guild (Table 4), one sees the classic ratios of linear dimensions observed by Hutchinson (1959) in closely related species sharing common resources. These size ratios are 1.2 to 1.4 consistently for mouth width but not body length. *Dendrobates femoralis*, which is closely related

but does not eat the same types of prey, does not fit into this series. The three species of *Eleutherodactylus* also exhibit size ratios between 1.2 to 1.4.

Foraging behavior. Because ant specialists take relatively smaller prey for a given body size than do non-ant specialists, they should take more prey per unit time than non-ant specialists, all other things being equal. Indeed, and specialists have more prey per stomach by an order of magnitude than do non-ant specialists (Table 3). The generalist *Dendrobates femoralis* tends to have an intermediate but not significantly different number of prey per stomach than the non-ant specialists (Table 3).

The foraging behavior of these frogs under natural conditions confirms the above relationships. I have observed that *Dendrobates pictus*, *D. trivittatus* and dendrobatids elsewhere forage constantly, searching actively for prey and eating many prey per unit time.

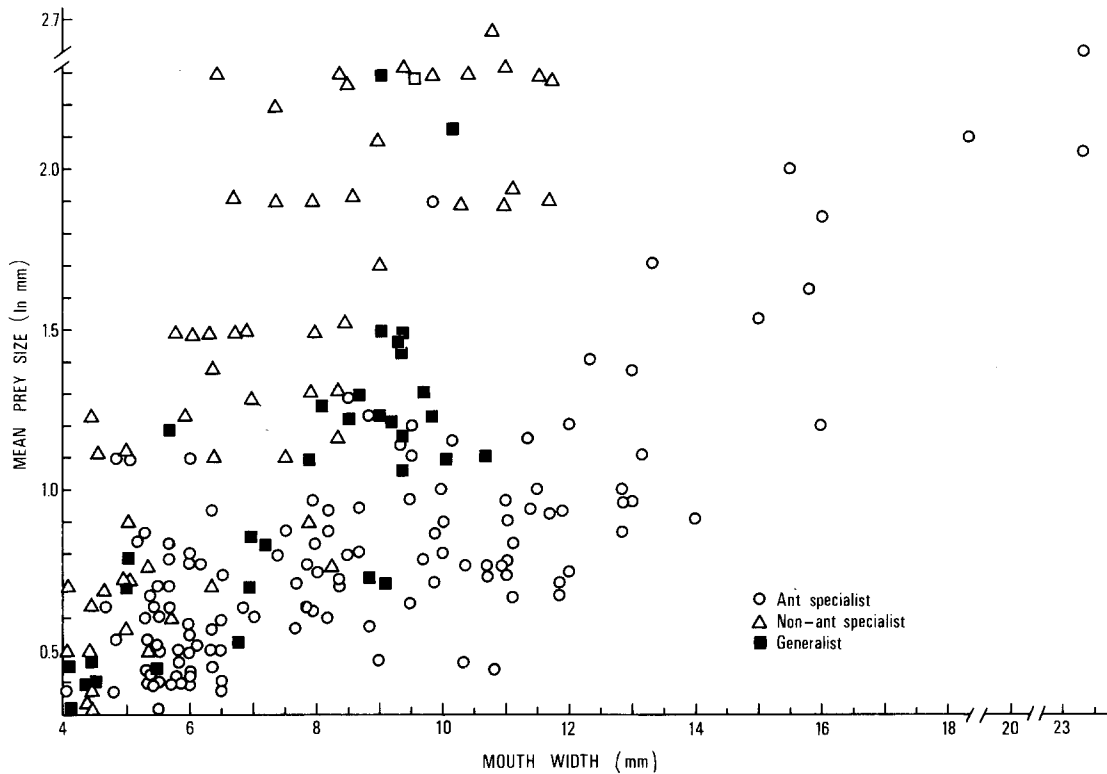


Fig. 2. Mean prey size (in mm) versus mouth width (mm) in three guilds of litter anurans: ant specialists ($r=0.4$, $p<0.001$); non-ant specialists ($r=0.9$, $p<0.001$); and generalists ($r=0.8$, $p<0.001$)

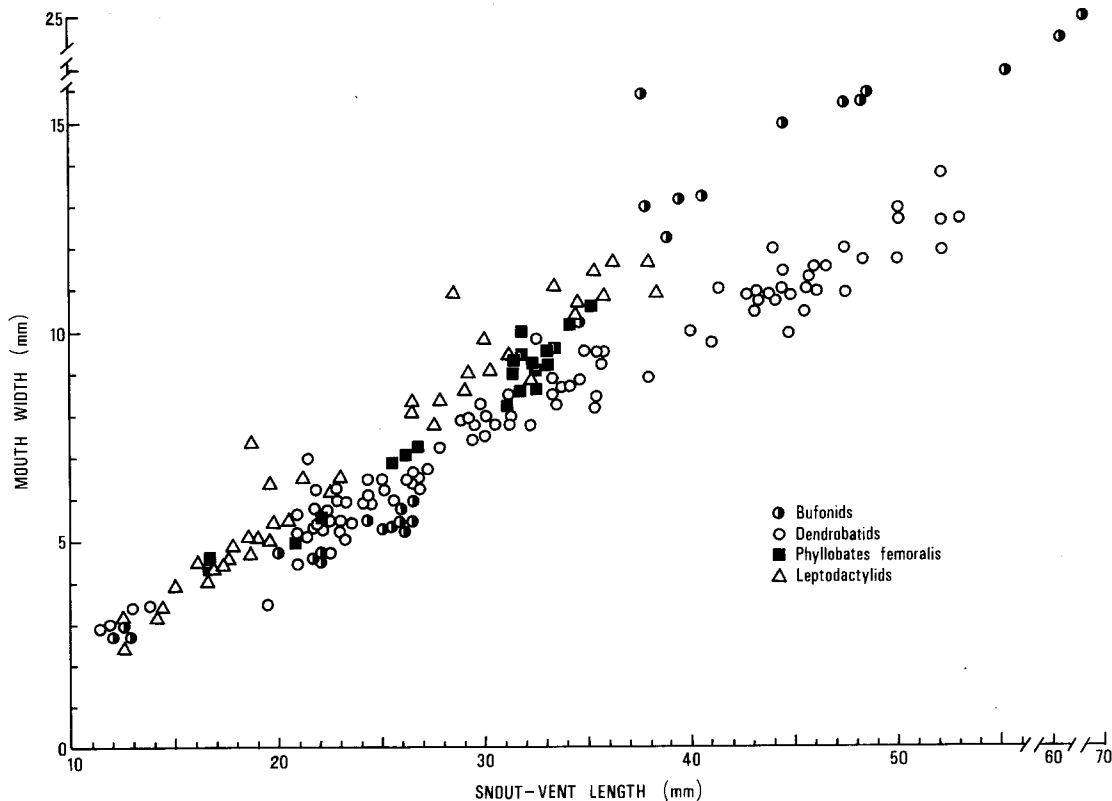


Fig. 3. Mouth width (mm) versus snout-vent length (mm) for: bufonids ($r=0.9$, $p<0.001$); dendrobatids ($r=0.8$, $p<0.001$); leptodactylids ($r=0.9$, $p<0.001$), and *Dendrobates femoralis* ($r=0.9$, $p<0.001$)

Table 4. Ratio of snout-vent lengths and mouth widths and d/w for common, closely-related species in the litter

Species	SVL ratio	MW ratio	d/w
<i>Colostethus marchesianus</i>			
<i>Dendrobates pictus</i>	1.4	1.2	0.2
<i>Dendrobates petersi</i>	1.5	1.4	0.8
<i>Dendrobates trivittatus</i>	1.4	1.3	0.3
<i>Eleutherodactylus ockendeni</i>			
<i>Eleutherodactylus toftae</i>	1.2	1.2	0.4–0.9
<i>Eleutherodactylus peruvianus</i>	1.2	1.3	1.6–0.6

Bragg (1957) and Lescure (1965) made similar observations for *Bufo americanus* Holbrook and *B. bufo* L., both known to eat ants. In contrast, non-ant specialists sit and wait for prey, presumably recognizing prey at a distance, springing at prey suddenly and feeding only a few times a day at most. I have never observed *Dendrobates femoralis* foraging, but observations on captive *Dendrobates* and *Phylllobates* indicate that some dendrobatids are searchers and others relatively more sit-and-wait foragers (Polder, 1975); unfortunately we lack adequate information on the natural diets of these captive frog species. Differentiation between ants and other prey and correlation with searching versus sit-and-wait foraging are not unique to litter frogs but also are seen in spiders (Enders, 1975) and other frogs (Lescure, 1971). Lizards, on the other hand, show the reverse trend, with ant specialization being associated with sit-and-wait foraging (Pianka and Pianka, 1970).

Correlates with foraging behavior. The anti-predator tactics of frogs in ant and non-ant guilds differ, and these differences correspond to differences in feeding behavior. Nearly all the active foragers are poisonous frogs; *Dendrobates* and *Phylllobates* are well known for their skin toxins (Daly and Myers, 1967; Myers et al., 1978) and the bufonids possess poisons in the parotid glands. Active, constant foraging surely exposes the frogs to higher risks of predation. Their poisons are known to work against natural predation by snakes (Lüling, 1971) and to be toxic to birds and mammals (Tokuyama et al., 1969). However, not all predators are susceptible to these poisons; some snakes (Myers et al., 1978) and spiders (personal observation) eat dendrobatids without apparent harm. The dendrobatids showing the least tendency to take ants, *Colostethus marchesianus* (Melin) and *Dendrobates femoralis*, and the leptodactylids of the leaf litter are not known to be poisonous (C. Myers, personal communication) and are cryptic; both cryptic coloration and sit-and-wait behavior hide them equally well from predator and prey. Thus within guilds, particularly of specialists, the foraging behavior and anti-predator tactics are complementary and perhaps coevolved.

Physiology of these frogs also may vary according to feeding and anti-predator behaviors. Bennett and Licht (1976) reported that in slow-moving poisonous anurans, exemplified by *Bufo boreas*, lactate production is very small; that is, these animals are capable of long periods of sustained activity and they do not tire. Conversely, palatable frogs such as ranids, which rely on rapid movement for escape and possibly prey capture, produce large amounts of lactate and, although they exhibit extreme bursts of activity, they are unable to sustain this maximal activity. Perhaps these physiological correlates apply here to species in the ant and non-ant guilds with their divergent feeding and anti-predator behaviors.

Table 5. Abundance of anurans and arthropods and species diversity of anurans per census plot

	Anurans		Arthropods	
	Wet season	Dry season	Wet season	Dry season
Numbers				
Mean	5.6	1.6	98.6	72.6
Standard error	1.0	0.3	24.1	10.2
Total	67	19	1,173	871
Biomass				
Mean	3.9	0.5 (g)	55.1	16.7 (mg)
Standard error	1.2	0.2	12.5	3.3
Total	47.0	6.5	451.1	164.7
No. species				
Mean	3.8	1.5		
Standard error	0.5	0.3		
Species diversity	5.4	3.7		
No. censuses	12	12	12	12

Seasonal Changes

Abundance, in both numbers and biomass, of frogs per unit area is lower in the dry season than in the wet (Table 5). Species diversity of frogs is also lower, due to decreases in both the number of species and the equitability of their relative abundances (Table 6). Estimated dry weight of arthropods per census is lower in the dry season; numbers of arthropods per census are lower, but not significantly so, in the dry season, indicating that small arthropods decrease less in numbers than large. Indeed, mean size of arthropods decreases slightly in the dry season (Table 3).

Are changes in frog populations caused by changes in their food supply or are frogs and arthropods responding to the same seasonal changes in physical factors? It seems unlikely that frogs are affected to such an extent by physical factors. Some species are equally or more abundant in the dry season, and these often breed preferentially at this time (Toft and Duellman, 1979). At least some deep forest dendrobatids are able to tolerate a wider range of microclimates than occur on the forest floor; *Dendrobates auratus* (Girard) on the island of Taboga in Panamá exhibit classic niche expansion where they forage in sunny and dry open fields (personal observation). Seasonal changes in the diets, if any, might suggest, alternatively, whether changes in frog populations are due to changes in the food supply.

The major feeding patterns of the litter anurans do not change seasonally. Species shift slightly in prey sizes but with no apparent pattern from wet to dry season. *Colostethus marchesianus* changes from a moderate ant specialist ($D=0.58$) to a generalist in the dry season taking prey in proportions not significantly different from those in the leaf litter. This change is partly due to the relative increase in the abundance of ants over other prey in the leaf litter (Table 3), which results in an apparent decrease in electivity of ants in the niche breadth formula used; indeed, several of the ant specialists have greater niche breadths in the dry season.

If, as food abundance goes down, competition for food becomes increasingly likely, then species might exhibit some mechanisms for reducing potential competition when food is in shortest supply. One way might be to reduce, over evolutionary time,

Table 6. Relative abundances, based on numbers and biomass, of anuran species in leaf litter censuses in the wet and dry seasons. Proportions are in parentheses. “p” indicates that a species was observed but not found in a census plot

Species	Wet season		Dry season	
	Number	Biomass (g)	Number	Biomass (g)
<i>Dendrophryniscus minutus</i>	3 (0.06)	0.1 (>0.01)	2 (0.17)	0.2 (0.07)
<i>Bufo typhonius</i>	1 (0.02)	5.5 (0.15)	p —	— —
<i>Colostethus marchesianus</i>	12 (0.23)	4.2 (0.12)	5 (0.42)	1.3 (0.45)
<i>Dendrobates quinquevittatus</i>	p —	— —	1 (0.08)	0.8 (0.28)
<i>Dendrobates pictus</i>	5 (0.09)	3.2 (0.09)	2 (0.17)	0.3 (0.10)
<i>Dendrobates femoralis</i>	1 (0.02)	0.2 (0.01)	2 (0.17)	0.3 (0.10)
<i>Dendrobates petersi</i>	1 (0.02)	1.1 (0.03)	0 (0.00)	0 (0.00)
<i>Dendrobates trivittatus</i>	3 (0.06)	14.0 (0.38)	p —	— —
<i>Eleutherodactylus ockendeni</i>	12 (0.23)	1.7 (0.05)	p —	— —
<i>Eleutherodactylus toftae</i>	p —	— —	1 (0.08)	0.8 (0.28)
<i>Adenomera andreae</i>	13 (0.25)	4.1 (0.11)	0 (0.00)	0 (0.00)
<i>Eleutherodactylus peruvianus</i>	2 (0.04)	2.3 (0.06)	p —	— —
<i>Edalorhina perezi</i>	p —	— —	0 (0.00)	0 (0.00)
Total	53 (1.00)	36.4 (1.00)	12 (1.00)	2.9 (1.00)
Number of Species	13		9	

the amount of similarity among species during the lean season (Smith et al., 1978, Zaret and Rand, 1971), for, if there were no similarity in diet or habitat among species, competition could not occur among them. Thus, if similarity in diet represents the potential for competition – of course such similarity does not demonstrate that species compete – the litter anurans, as a group, might be expected to exhibit reduced similarity in diet in the dry season.

The average similarity in diet, as measured by α_{ij} , for all species present in the community is significantly lower in the dry season than in the wet, as is the mean α_{ij} for species in the ant guild (Tables 7 and 8). However, mean α_{ij} within the non-ant guild increases significantly in the dry season. This increase could mean: that competition is more intense in the dry season than in the wet; that competition is reduced in the dry season so that species can tolerate more overlap; or that the arbitrary categories or small sample sizes of non-ant prey in the diets do not give biologically meaningful values of α_{ij} .

Another way of considering similarity in diet within guilds is to examine which species in each guild are absent in the dry season. In Table 7 and 8 species are arranged within guilds according to increasing body size. Perhaps significantly, in both guilds, species that are absent in the dry season are of alternate sizes, i.e., the “middle” species between two potential competitors. An example is the pair, *Adenomera andreae* and *Eleutherodactylus toftae*, which are similar in size; in the wet season, *A. andreae* is very common while *E. toftae* is present but rare – in the dry season, *E. toftae* becomes common enough to be encountered in the censuses, while *A. andreae* is totally absent from the leaf litter. By this criterion of similarity, albeit less sensitive to composition of the diet than are α_{ij} 's, both guilds show reduced similarity in the dry season.

Where individuals of these species go in the dry season is not at all clear. I doubt that all adults in the population die during the dry season. I cannot find them in the leaf litter or

in other habitats in the dry season, and I observed the same patterns in two different dry seasons, so these disappearances are not spurious. I can only presume that these individuals aestivate somewhere, but no one has reported such behavior for tropical amphibians.

If degree of similarity in diet is associated with the absence of some species in the dry season, can changes in relative abundances of species present in both seasons be related to similarity in diet with other species? If α_{ij} is proportional somehow to the intensity of competition and all else being equal, larger α_{ij} 's would be associated with small abundances, N_i , of species (Schoener 1974b). When a mean α_{ij} values of all species j on a given species i are compared to the abundance of that species i , both within and between seasons in case time lags occur, no significant relationships emerge; thus the overlap or the degree of similarity in diet cannot explain changes in relative abundance in species present in both seasons.

Perhaps the abundances of species, even if competitors, cannot be expected to vary in any systematic way with α_{ij} because carrying capacities may be greatly different (Schoener 1974b). The two species that increase most in relative abundance in the dry season, *Colostethus marchesianus* and *Dendrobates femoralis*, are generalists during that time. This observation suggests that generalists may have greater carrying capacities as others have pointed out (e.g., MacNaughton and Wolf, 1970).

Conclusions: Mechanisms of Coexistence

Several kinds of evidence indicate that food is, or has been, an important factor both in the evolution of these anuran species and in the organization of the community at this location.

First, body morphology, feeding behavior, and anti-predator tactics all co-vary with the diets of these species, from narrow-mouthed, poisonous, searching foragers that eat hard-bodied, slow-moving prey, such as ants and mites to wide-mouthed, palat-

Table 7. Similarity in diet as measured by α_{ij} (see text) based on prey types and sizes of 13 species of anurans. Species are arranged by size within guilds

Species i	Species j												
	D.m.	C.m.	D.q.	D.p.	D.pr.	D.t.	B.t.	E.o.	E.t.	A.a.	E.p.	Ed.p.	D.f.
A. Wet Season													
Ant Specialists													
<i>Dendrophryniscus minutus</i>	—	0.62	0.93	0.80	0.62	0.86	0.37	0.02	0.21	0.37	0.16	0.00	0.35
<i>Colostethus marchesianus</i>	1.19	—	1.23	1.07	0.62	0.80	0.51	0.57	0.56	0.66	0.49	0.05	0.39
<i>Dendrobates quinquevittatus</i>	0.86	0.59	—	0.70	0.33	0.49	0.03	0.01	0.23	0.37	0.17	0.00	0.13
<i>Dendrobates pictus</i>	1.13	0.77	1.07	—	0.76	0.94	0.62	0.15	0.28	0.52	0.46	0.03	0.54
<i>Dendrobates petersi</i>	0.40	0.20	0.23	0.34	—	0.84	2.54	0.07	0.08	0.22	0.26	0.03	0.54
<i>Dendrobates trivittatus</i>	0.63	0.30	0.39	0.49	0.97	—	1.78	0.03	0.11	0.25	0.17	0.10	0.56
<i>Bufo typhonius</i>	0.02	0.02	0.00	0.03	0.26	0.16	—	0.01	0.00	0.04	0.03	0.01	0.10
Non-Ant Specialists													
<i>Eleutherodactylus ockendeni</i>	0.02	0.27	0.01	0.10	0.10	0.04	0.12	—	0.43	0.12	0.43	0.28	0.13
<i>Eleutherodactylus toftae</i>	0.52	0.73	0.62	0.51	0.33	0.37	0.16	1.15	—	0.51	0.71	0.71	0.43
<i>Adenomera andreae</i>	0.45	0.41	0.49	0.45	0.42	0.41	0.69	0.16	0.24	—	0.39	0.21	0.45
<i>Eleutherodactylus peruvianus</i>	0.17	0.27	0.20	0.35	0.44	0.25	0.56	0.50	0.30	0.34	—	0.96	0.55
<i>Edalorhina perezi</i>	0.00	0.01	0.00	0.00	0.08	0.03	0.04	0.07	0.06	0.04	0.20	—	0.10
Generalist													
<i>Dendrobates femoralis</i>	0.34	0.20	0.14	0.37	0.84	0.76	1.52	0.14	0.17	0.37	0.51	0.43	—
α_{ij}													
				Ant specialists			Non-Ant specialists			Overall			
Mean				0.67			0.40			0.53			
Standard error				0.08			0.07			0.12			
B. Dry Season													
Ant Specialists													
<i>Dendrophryniscus minutus</i>	—	0.23	*	0.75	*	0.14	0.02	0.08	0.00	*	0.01	*	0.42
<i>Colostethus marchesianus</i>	0.09	—	*	0.19	*	0.04	0.01	0.06	0.03	*	0.03	*	0.08
<i>Dendrobates quinquevittatus</i>	*	*	—	*	*	*	*	*	*	*	*	*	*
<i>Dendrobates pictus</i>	1.23	0.72	*	—	*	0.48	0.06	0.22	0.07	*	0.08	*	0.62
<i>Dendrobates petersi</i>	*	*	*	*	—	*	*	*	*	*	*	*	*
<i>Dendrobates trivittatus</i>	0.03	0.02	*	0.05	*	—	0.08	0.10	0.01	*	0.10	*	0.06
<i>Bufo typhonius</i>	0.00	0.00	*	0.00	*	0.02	—	0.03	0.08	*	0.09	*	0.54
Non-Ant Specialists													
<i>Eleutherodactylus ockendeni</i>	0.02	0.03	*	0.03	*	0.11	0.16	—	1.30	*	1.08	*	0.42
<i>Eleutherodactylus toftae</i>	0.00	0.01	*	0.00	*	0.00	0.15	0.54	—	*	1.03	*	0.19
<i>Adenomera andreae</i>	*	*	*	*	*	*	*	*	*	—	*	*	*
<i>Eleutherodactylus peruvianus</i>	0.00	0.00	*	0.00	*	0.04	0.15	0.38	0.87	*	*	—	0.10
<i>Edalorhina perezi</i>	*	*	*	*	*	*	*	*	*	*	*	—	*
Generalist													
<i>Dendrobates femoralis</i>	0.35	0.16	*	0.31	*	0.29	1.00	1.68	1.79	*	1.21	*	—
α_{ij}													
				Ant specialists			Non-Ant specialists			Overall			
Mean				0.21			0.87			0.28			
Standard error				0.07			0.14			0.05			

able but cryptic, sit-and-wait foragers that eat soft-bodied, mobile prey such as orthopterans. Such morphological and ecological differences may be the result of food limitation, caused by competition for food among predators (Lack, 1947; MacArthur, 1972) or coevolution between predator and prey (Roughgarden, 1976). Closely related species in both guilds exhibit Hutchinsonian size

ratios, which is a form of circumstantial evidence for resource competition. However, the interpretation of these size ratios in an ecological context is still being debated (Horn and May, 1977). Also, the expected consequence of these size differences, a constant d/w respect to food size, does not occur in either guild, and values of d/w are often below one.

Second, the composition of this community changes from wet to dry season, as food abundance changes. MacArthur (1969) predicted that, if food is limiting, similarity among species should be sensitive to changes in resource abundance with similarity among species being set by the season of lower food abundance; Turelli (personal communication) suggests that species will adjust their similarity to the yearly "average" over seasons. At the Río Llullapichis, species within guilds show reduced similarity in diets when food is less abundant; mean α_{ij} overall and within the ant guild are significantly lower in the dry season, and in both guilds, species of intermediate sizes drop out. This result of lower similarity in the season of lower food abundance is consistent with other empirical studies reviewed by Smith et al. (1978).

The results for ant and non-ant specialists differ somewhat, and one reason may be the differing nature of their respective resources. Most of the ants eaten by frogs are workers and not reproductive units, unlike the prey taken by members of the non-ant guild; ant specialists are more like grazers or browsers that eat the leaves of a tree rather than like predators that take whole individuals. Also, non-ant specialists probably share their food resource with more kinds of predators than do ant-eating frogs. Perhaps for these reasons, ants are apparently a less variable resource than, for example, orthopterans, the principal prey of non-ant specialists. Such a resource would allow a greater degree of specialization of species sharing it (MacArthur, 1970, 1972).

Evidence presented in this study suggests that food is, or has been limiting periodically and that at this location morphological and behavioral differences among species and changing relative abundances of litter anurans are in response to this limitation by food. However, not all the evidence presented here, is consistent with this hypothesis. Further tests could involve the gathering of more detailed information relevant to the various models of limiting similarity and their assumptions. Better yet, one could manipulate parameters in this system, but the latter may be difficult or impossible for vertebrates in such a complex tropical system.

Many of the arguments that I have pursued make the basic assumption that the community is self-contained and therefore in local equilibrium. What of the possibility that coexistence of these species, whether or not they are competing for food, is mediated by migration and local extinction (Levin, 1974; Levins and Culver, 1971; Slatkin, 1974; Wiens, 1977)? Most probably, migration and local extinction do not play a role in the coexistence of litter anurans at the Río Llullapichis, where the habitat is uniform over wide areas and species appear to be evenly distributed.

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References

Abrams, P.: Limiting similarity and the form of the competition coefficient. *Theoretical Population Biology* **8**, 356–375 (1975)

- Andrews, R.M., Rand, A.S., Guerrero, S.: Regulation of population size in a tropical lizard, *Anolis limifrons* (abstract). *Herpetological Review* **8**(3) supplement, 1 (1977)
- Bennett, A.F., Licht, P.: Anaerobic metabolism during activity in amphibians. *Comparative Biochemistry and Physiology* **48A**, 319–327 (1974)
- Bragg, A.N.: Some factors in the feeding of toads. *Herpetologica* **13**, 189–191 (1957)
- Caswell, H.: Predator-mediated coexistence: a nonequilibrium model. *American Naturalist* **112**, 127–154 (1978)
- Connell, J.H.: Some mechanisms producing structure in natural communities. In: *Ecology and evolution of communities* (M.L. Cody and J.M. Diamond, editors). Cambridge, Massachusetts: Belknap Press of Harvard University Press, USA 1975
- Daly, J.W., Myers, C.W.: Toxicity of Panamanian poison frogs (*Dendrobates*): some biological and chemical aspects. *Science* **156**, 970–973 (1976)
- Duellman, W.E.: The biology of an equatorial herpetofauna in Amazonian Ecuador. The University of Kansas, Museum of Natural History Miscellaneous Publications **65**, 1–352 (1978)
- Enders, F.: The influence of hunting manner on prey size, particularly in spiders with long attack distances (Araneidae, Linyphiidae, and Salticidae). *American Naturalist* **109**, 737–763 (1975)
- Feldman, M.W., Roughgarden, J.: A population's stationary distribution and chance of extinction in a stochastic environment with remarks on the theory of species packing. *Theoretical Population Biology* **7**, 197–207 (1975)
- Fenchel, T.: Character displacement and coexistence of mud snails (Hydrobiidae). *Oecologia (Berl.)* **20**, 19–32 (1975)
- Fenchel, T., Kofoed, L.H.: Evidence for interspecific competition in mud snails (Hydrobiidae). *Oikos* **27**, 367–376 (1976)
- Guerrero, S., Ayala, S.C.: Hemoparasitos de algunos reptiles y anfibios de la selva amazónica del Perú. *Rev. Inst. Med. trop. Sao Paulo* **19**, 283–288 (1977)
- Hespenheide, H.A.: Prey characteristics and predator niche width. In: *Ecology and evolution of communities* (M.L. Cody and J.M. Diamond, editors). Cambridge, Massachusetts: Belknap Press of Harvard University Press, USA 1975
- Horn, H.S., May, R.M.: Limits to similarity among coexisting competitors. *Nature* **270**, 660–661 (1977)
- Hutchinson, G.E.: Homage to Santa Rosalia or why are there so many kinds of animals. *American Naturalist* **93**, 145–159 (1959)
- Inger, R.F., Colwell, R.K.: Organization of contiguous communities of amphibians and reptiles in Thailand. *Ecological Monographs* **47**, 229–253 (1977)
- Inger, R.F., Marx, H.: The food of amphibians. *Exploration du Parc national de l'Upemba* 64. Mission G.F. de Witte et al., Imprimerie Hayes, Brussels, Belgium (1961)
- Jacobs, J.: Quantitative measurement of food selection: a modification of the forage ratio and Ivlev's electivity index. *Oecologia* **14**, 413–417 (1974)
- Janzen, D.H.: Sweep samples of tropical foliage insects: description of study sites, with data on species abundances and size distributions. *Ecology* **54**, 659–686 (1973)
- Jones, K.L.: Prey size, trophic niche overlap, movement and feeding in four species of *Eleutherodactylus*, manuscript
- Karr, J.R.: Seasonality, resource availability, and community diversity in tropical bird communities. *American Naturalist* **110**, 973–994 (1976)
- Lack, D.: Darwin's finches. Cambridge University Press, Cambridge (1974)

- Lawlor, L.R., Maynard-Smith, J.: The coevolution and stability of competing species. *American Naturalist* **110**, 79–99 (1976)
- Lescure, J.: L'alimentation et le comportement de prédation chez *Bufo bufo* (Linnaeus, 1758). Doctoral thesis. University of Paris, Paris, France (1965)
- Lescure, J.: L'alimentation du Crapaud *Bufo regularis* Reuss et de la Grenouille *Dicroglossus occipitalis* (Günther) au Sénégal. *Bulletin de l'I.F.A.N.* **33(s)**, 446–466 (1971)
- Levin, S.A.: Dispersion and population interactions. *American Naturalist* **108**, 207–228 (1974)
- Levins, R., Culver, D.: Regional coexistence of species and competition between rare species. *Proceedings of the National Academy of Sciences, USA* **68**, 1246–1248 (1971)
- Lloyd, M.R., Inger, R.F., King, R.W.: On the relative diversity of reptile and amphibian species in a Bornean rain forest. *American Naturalist* **102**, 497–515 (1968)
- Lüling, K.H.: Der Färberfrosch *Phyllobates bicolor* Bibron der Cordillera Azul (Peru). *Bonner. Zool. Beitr.* **22**, 161–174 (1971)
- MacArthur, R.H.: Species packing or what competition minimizes. *Proceedings of the National Academy of Sciences of the USA* **64**, 1369–1371 (1969)
- MacArthur, R.H.: Species packing and competitive equilibrium for many species. *Theoretical Population Biology* **1**, 1–11 (1970)
- MacArthur, R.H.: *Geographical Ecology*. Harper and Row, New York, New York USA (1972)
- MacArthur, R.H., Levins, R.: The limiting similarity, convergence and divergence of coexisting species. *American Naturalist* **101**, 377–385 (1967)
- May, R.M., MacArthur, R.H.: Niche overlap as a function of environmental variability. *Proceedings of the National Academy of Sciences of the USA* **69**, 1109–1113 (1972)
- McNaughton, S.I., Wolf, L.L.: Dominance and the niche in ecological systems. *Science* **167**, 131–139 (1970)
- Myers, C.W., Daly, J.W., Malkin, B.: A dangerously toxic new frog (*Phyllobates*) used by Emberá Indians of Western Colombia, with discussion of blowgun fabrication and dart poisoning. *Bulletin of the American Museum of Natural History* **161**, 309–365 (1978)
- Oficina nacional de evaluación de recursos naturales: Inventario, evaluación e integración de los recursos naturales de la zona del Río Pachitea. Lima, Perú (1966)
- Pianka, E.R., Pianka, H.D.: The ecology of *Moloch horridus* (Lacertilia: Agamidae) in Western Australia. *Copeia* (1970), 90–103 (1970)
- Polder, W.N.: *Dendrobates, Phyllobates en Colostethus*. *Het Aquarium* **46**, 260–266 (1967)
- Robinson, M.H., Robinson, B.: Prey caught by a sample population of the spider *Argiope argentata* (Araneae: Araneidae) in Panama: a year's census data. *Zoological Journal of the Linnean Society* **49**, 345–357 (1970)
- Root, R.: The niche exploitation pattern of the blue-gray gnatcatcher. *Ecological Monographs* **37**, 317–350 (1967)
- Roughgarden, J.D.: Species packing and the competitive function with illustrations from coral reef fish. *Theoretical Population Biology* **5**, 163–186 (1974)
- Roughgarden, J.D.: Population dynamics in a stochastic environment: spectral theory for the linearized N-species Lotka-Volterra competition equations. *Theoretical Population Biology* **7**, 1–12 (1975)
- Roughgarden, J.D.: Resource partitioning among species – a coevolutionary approach. *Theoretical Population Biology* **9**, 388–424 (1976)
- Roughgarden, J.D., Feldman, M.: Species packing and predation pressure. *Ecology* **56**, 489–492 (1975)
- Schoener, T.W.: Resource partitioning in ecological communities. *Science* **189**, 27–39 (1974a)
- Schoener, T.W.: Competition and the form of habitat shift. *Theoretical Population Biology* **6**, 265–301 (1974b)
- Schoener, T.W.: Some methods for calculating competition coefficients from resource-utilization spectra. *American Naturalist* **108**, 332–340 (1974c)
- Schoener, T.W.: Alternatives to Lotka-Volterra competition: models of intermediate complexity. *Theoretical Population Biology* **10**, 309–333 (1976)
- Schoener, T.W., Janzen, D.H.: Notes on environmental determinants of tropical versus temperate insect size patterns. *American Naturalist* **102**, 207–224 (1968)
- Sexton, O.J., Heatwole, H., Knight, D.: Correlation of micro-distribution of some Panamanian reptiles and amphibians with structural organization of the habitat. *Caribbean Journal of Science* **4**, 261–295 (1964)
- Siegel, S.: *Nonparametric statistics for the behavioral sciences*. pp. 1–312. McGraw-Hill Book Co. New York, New York, USA (1956)
- Silverstone, P.A.: A revision of the poison-arrow frogs of the genus *Dendrobates* Wagler. *Natural History Museum of Los Angeles County Science Bulletin* **21**, 1–55 (1975)
- Silverstone, P.A.: A revision of the poison-arrow frogs of the genus *Phyllobates* Bibron in Sagra (Family Dendrobatidae). *Natural History Museum of Los Angeles County Science Bulletin* **27**, 1–53 (1976)
- Slatkin, M.: Competition and regional coexistence. *Ecology* **55**, 128–34 (1974)
- Smith, J.N.M., Grant, P.R., Grant, B.R., Abbott, I.J., Abbott, L.K.: Seasonal variation in feeding habits of Darwin's ground finches. *Ecology* **59**, 1137–1150 (1978)
- Strickland, A.H.: A survey of arthropod soil and litter fauna of some forest reserves and cacao estates in Trinidad. *J. Animal Ecology* **14**, 1–11 (1945)
- Svardson, G.: Competition and habitat selection in birds. *Oikos* **1**, 157–174 (1974)
- Toft, C.A., Duellman, W.E.: Anurans of the lower Río Lullapichis, Amazonian Perú: a preliminary analysis of community structure. *Herpetologica* **35**, 71–77 (1979)
- Toft, C.A., Levings, S.: Seasonal trends in litter arthropod populations. In: *Proceedings of the IV International Symposium of Tropical Ecology* (H. Wolda, editor). (In press.)
- Tokuyama, T., Daly, J., Witkop, B.: The structure of batrachotoxin, a steroidal alkaloid from the Colombian arrow poison frog, *Phyllobates aurotaenia* and partial synthesis of batrachotoxin and its analogs and homologs. *Journal of the American Chemical Society* **91**, 3931 (1969)
- Turelli, M.: A reexamination of stability in randomly varying versus deterministic environments with comments on the stochastic theory of limiting similarity. *Theoretical Population Biology* **13**, 222–246 (1978)
- Werner, E.E.: Species packing and niche complementarity in three sunfishes. *American Naturalist* **111**, 553–578 (1977)
- Wiens, J.A.: On competition and variable environments. *Scientific American* **65**, 590–597 (1977)
- Zaret, T., Rand, A.S.: Competition in tropical stream fishes: support for the competitive exclusion principle. *Ecology* **52**, 336–342 (1971)

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