Society for the Study of Amphibians and Reptiles

Feeding Ecology of Panamanian Litter Anurans: Patterns in Diet and Foraging Mode
Author(s): Catherine A. Toft
Source: *Journal of Herpetology*, Vol. 15, No. 2 (Apr. 30, 1981), pp. 139-144
Published by: Society for the Study of Amphibians and Reptiles
Stable URL: http://www.jstor.org/stable/1563372
Accessed: 11/12/2009 12:09

Your use of the JSTOR archive indicates your acceptance of JSTOR's Terms and Conditions of Use, available at http://www.jstor.org/page/info/about/policies/terms.jsp. JSTOR's Terms and Conditions of Use provides, in part, that unless you have obtained prior permission, you may not download an entire issue of a journal or multiple copies of articles, and you may use content in the JSTOR archive only for your personal, non-commercial use.

Please contact the publisher regarding any further use of this work. Publisher contact information may be obtained at http://www.jstor.org/action/showPublisher?publisherCode=ssar.

Each copy of any part of a JSTOR transmission must contain the same copyright notice that appears on the screen or printed page of such transmission.

JSTOR is a not-for-profit service that helps scholars, researchers, and students discover, use, and build upon a wide range of content in a trusted digital archive. We use information technology and tools to increase productivity and facilitate new forms of scholarship. For more information about JSTOR, please contact support@jstor.org.

Society for the Study of Amphibians and Reptiles is collaborating with JSTOR to digitize, preserve and extend access to *Journal of Herpetology.*

http://www.jstor.org

1981 JOURNAL OF HERPETOLOGY 15(2):139–144

Feeding Ecology of Panamanian Litter Anurans: Patterns in Diet and Foraging Mode

Catherine A. Toft

Department of Zoology, University of California, Davis, California 95616

ABSTRACT—Litter frogs at two rainforest locations in Panamá elect prey in a pattern similar to that found for litter frogs in lowland Perú (Toft, 1980) despite differences in the frog fauna between Panamá and Perú. Species of litter frogs form a continuum from species that specialize on ants and mites, through generalists, to species that avoid ants and mites. Modes of foraging and predator defense and taxa of litter frogs are correlated with position along the continuum. *Atelopus* and *Bufo* (Bufonidae) and *Dendrobates* (Dendrobatidae) are poisonous, searching foragers which eat many small prey, primarily ants and mites, per day. *Colostethus* (Dendrobatidae) eat ants, but to a lesser degree, and have a more sedentary foraging behavior than *Dendrobates. Eleutherodactylus* (Leptodactylidae) are cryptic, sit-and-wait foragers which eat few large prey per day, with the exception of *E. vocator,* which eat ants in proportion similar to *Colostethus.* Evidence within the Dendrobatidae suggests that specialization on ants is derived from a generalized mode of foraging. Ecological correlates of foraging mode in litter anurans are summarized and are generally similar to those in desert lizards.

* * *

INTRODUCTION

Studies on diets of tropical anurans (Inger and Marx, 1961; Jones, in prep; Toft, 1980a) have found differences in diet among species at a given location but only one of these (Toft, 1980a) has related, for an entire group of syntopic species, composition of the diet with estimated availability of prey in the environment. In the latter study, the diurnal species of the forest litter in Amazonian Perú comprised a continuum of diet specialization along which most species selected ants in either far higher or far lower proportions than occur in the environment.

Along this continuum, the degree of specialization, or lack thereof, on ants by frogs was related to their morphology, prey size selection, foraging behavior, and mode of defense against predators (Toft, 1980a). The ant specialists are narrow-mouthed, poisonous, searching foragers and the "non-ant" specialists are wide-mouthed, cryptic, sit-and-wait foragers; generalists are intermediate in morphology and foraging mode. Huey and Pianka (1981) found, in a comparison of lizard communities, that syntopic species of lizards exhibit a similar dichotomy of foraging modes, with relatively sit-and-wait foragers on the one hand and more widely foraging species on the other. Their analysis established a series of ecological correlates of these two foraging modes. The question arises: how general are these patterns associated with foraging mode, for example in different groups of predators? My study at one site (Toft, 1980a) suggests that litter anurans may exhibit many of the same patterns as lizards. However, do the results I obtained at one site actually constitute a pattern, that is, do they obtain in other regions, in different communities of litter anurans?

In this study I examine the feeding ecologies of diurnal litter anurans in two locations in the lowland tropics of Panamá to determine whether the modes of diet specialization are repeated in the same ecological association—diurnal litter anurans—composed from a different fauna. In attempting to document patterns of foraging modes in litter anurans, I have two goals: The first is to discern possible causes for specialization on food, which in turn may shed light on if, or how, diurnal litter anuran communities are structured (Toft, 1980a; 1980b). A second goal is to compare diurnal litter anurans with similar predators, lizards, to establish the generality of patterns in foraging modes and their ecological correlates in different predators.

METHODS

Frogs and arthropods were collected by standardized censuses (Sexton *et al.,* 1964; Toft, 1980a) and additional frogs were taken at random in the general study sites at two sites in Panamá. The first site was in secondary rainforest along the Pipeline Road, which runs north of Gamboa, Canal Zone, at approximately 9°5′N, 79°50′W and 30 m of elevation. The second was in primary rainforest along the El Llano-Cartí Road (or "Cartí Road") in the Department of Panamá at 9°20′N, 78°55′W and 300 m of elevation.

As soon as possible after collection, frogs were fixed in 10% formalin to preserve stomach contents. Snout-vent length (SVL) and width of the mouth (MW) were recorded for each frog. Arthropods were extracted from leaf litter samples by Berlese funnel (Toft and Levings, 1979). Arthropods and prey items were sorted to size and type categories: (1) ants and mites; (2) orthopterans; (3) miscellaneous orders of adult arthropods; and (4) holometabolous insect larvae. Lengths of arthropods and prey were transformed to natural logarithms because lengths of litter arthropods are log-normally distributed (Toft and Levings, 1979).

Electivities were calculated from Jacobs (1974):

$$D = \frac{d_k - f_k}{d_k f_k - 2\, d_k f_k} \qquad (1)$$

where d_k is the proportion of prey k in the stomach contents and f_k is the proportion of prey k in the environment. D varies from +1, for complete selection or preference of prey k, through 0, when prey k is taken in the same proportion as found in the environment, to −1 when prey k is absent in the diet but present in the environment. All prey categories were represented in the diet of at least one species of frog; that is, prey not eaten by any species of frog were excluded from the analyses.

RESULTS AND DISCUSSION

Foraging mode and its correlates in litter anurans.

In Panamá, species are distributed along a continuum based on electivity (Jacobs, 1974) of ants and mites, from strong ant and mite specialists (D = 1), through generalists (D = 0), to species that avoid ants and mites (D = −1) and instead eat a wide variety of non-ant prey, that is, "non-ant specialists." More specialists of either type are present than generalists (Tables 1 and 2). For practical purposes, these three groups, ant specialists, "non-ant" specialists, and generalists, may be considered as three separate guilds (*sensu* Root, 1967), although for some species on the continuum, inclusion in a particular guild may be arbitrary. Thus the litter anurans in Panamá exhibit the same patterns in diet as found in Amazonian litter anurans despite differences in the litter anuran fauna between Panamá and Perú—*Bufo typhonius* is the only species common to both areas—and despite differences in environmental conditions at the various locations (Toft, 1980a; 1980b). The spectrum of prey types available in the leaf litter is similar at the two Panamá sites (Tables 1 and 2) and the Perú site (Toft, 1980a), suggesting that the general composition of the anuran litter fauna at a given site may be partly an ecological response to the range of prey available.

TABLE 1. Types of prey (proportions and electivity) in the diets of litter frogs and proportions of prey in the litter at Carti Road; wet and dry seasons combined. Prey categories: ants and mites (Ants); orthopterans (Ort.); coleopterans (Col.); misc. adult arthropods and larvae (Art.).

	Sample Size		Proportions				Electivity				No. items/ stomach	
Species	Frogs	Prey	Ants	Ort.	Col.	Art.	Ants	Ort.	Col.	Art.	$\bar{X}$	(± SE)
Atelopus varius	23	697	.59	.06	.10	.24	0.51	0.85	−0.10	0.22	34.8	(6.0)
Bufo coniferus	6	233	.91	.01	.06	.02	0.91	−0.96	−0.22	−0.79	56.3	(23.5)
*B. haemititicus**	8	60	.64	0	.24	.12	0.61	−1.00	0.57	−0.03	8.6	(3.2)
B. typhonius	48	1296	.94	0	.02	.04	0.94	−1.00	−0.61	−0.65	39.1	(7.9)
Colostethus ingunialis	12	80	.37	.23	.12	.28	0.11	−0.42	0.19	0.30	7.3	(2.1)
C. nubicola	30	336	.40	.08	.09	.43	0.18	−0.79	0.04	0.57	11.6	(2.0)
*C. pratti**	8	26	.06	.78	.09	.07	−0.74	0.57	0.10	−0.35	5.1	(1.2)
C. talamancae	27	200	.53	0	.07	.36	0.50	−1.00	−0.13	0.46	10.5	(1.5)
Dendrobates auratus	7	224	.70	0	.15	.15	0.67	−1.00	0.30	−0.70	44.8	(6.7)
D. fulguritus	4	122	.97	0	0	.03	0.97	−1.00	−1.00	−0.70	25.8	(4.8)
D. minutus	26	458	.81	0	0	.19	0.80	−1.00	−1.00	0.07	24.1	(5.7)
*Eleutherodactylus altae**	1	4	0	.68	0	.32	−1.00	0.89	−1.00	−0.70	4.0	(—)
E. biporcatus	3	8	.15	.54	0	.31	−0.44	0.22	−1.00	0.37	4.0	(0.0)
*E. bransfordi**	1	2	0	0	0	1.00	−1.00	−1.00	−1.00	1.00	2.0	(—)
*Eleutherodactylus cruentus**	4	3	0	.71	0	.29	−1.00	0.43	−1.00	0.46	1.5	(0.4)
E. frater	12	12	0	.70	0	.30	−1.00	0.52	−1.00	0.35	1.5	(0.2)
*E. golmeri**	6	2	0	1.00	0	0	−1.00	1.00	−1.00	−1.00	1.0	(0.0)
E. longirostris	18	28	.03	.31	.44	.19	−0.86	−0.24	0.79	0.08	2.8	(0.7)
E. talamancae	27	54	.03	.50	.33	.15	−0.90	0.14	0.68	−0.08	2.6	(0.4)
E. vocator	35	113	.37	.07	.03	.53	0.11	−0.82	−0.50	0.69	4.4	(0.5)
Leaf litter		3702	.32	.43	.09	.17						

*One season only

TABLE 2. Types of prey (proportions and electivities) in the diets of litter frogs and proportions of prey in the litter at Pipeline Road) wet and dry seasons combined. Prey categories and abbreviations as in Table 1.

	Sample Size		Proportions				Electivity				No. items/ stomach	
Species	Frogs	Prey	Ants	Ort.	Col.	Art.	Ants	Ort.	Col.	Art.	$\bar{X}$	(± SE)
B. typhonius	24	536	.87	.03	.03	.07	0.87	−0.90	−0.63	−0.56	25.5	(3.6)
C. nubicola	111	763	.27	.06	.13	.45	−0.13	−0.79	0.04	0.51	10.9	(2.0)
E. bransfordi	2	3	0	0	0	1.00	−1.00	−1.00	−1.00	1.00	2.0	(0.0)
E. bufoniformis	1	2	0	.61	.39	0	−1.00	0.06	0.71	−1.00	2.0	(—)
*E. cruentus**	4	14	.34	.66	0	0	−0.12	0.56	−1.00	−1.00	4.1	(3.7)
E. fitzingeri	2	2	0	.99	0	.01	−1.00	0.99	−1.00	−0.97	1.0	(0.0)
E. frater	3	3	0	.98	0	.02	−1.00	0.98	−1.00	−0.88	1.0	(0.0)
E. longirostris	7	13	.14	.08	.24	.54	−0.48	−0.74	0.41	0.64	2.2	(0.6)
E. vocator	12	46	.77	0	.02	.21	0.75	−1.00	−0.72	0.00	4.6	(1.9)
Leaf litter		4020	.32	.35	.12	.21						

*One season only

In Panamá, as in Perú, body size and prey size of litter anurans is highly correlated within guilds (Fig. 1). Ant specialists take the smallest prey for a given mouth width, and non-ant specialists the largest (analysis of covariance: $F = 31.1$, $p << 0.001$). Generalists tend to take intermediate sized prey, but the relationship is not significantly different from that of either specialist guild. Reflecting these tendencies, ant specialists have the greatest number (but not necessarily volume) of prey per stomach, often by an order of magnitude; generalists have an intermediate number and close to that of non-ant specialists, which have few prey per stomach (Tables 1 and 2).

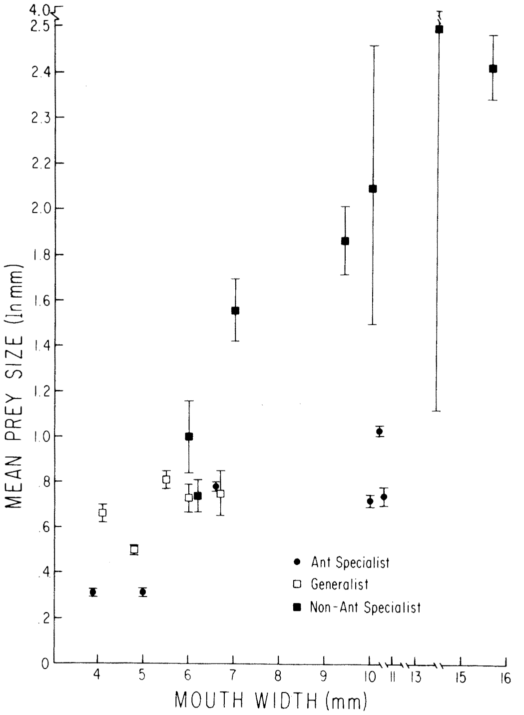

FIGURE 1. Mean size of prey (ln mm, ± standard error) versus mouth width (mm) for species of litter anurans in three guilds from Carti Road. Symbols and standard error bars represent species of frogs of respective guilds (in order of average mouth size): ant-specialists, *D. minutus, D. fulguritus, A. varius, D. auratus, B. typhonius, B. coniferus;* generalists, *E. vocator, C. nubicola, C. talamancae, C. inguinalis, C. pratti;* non-ant specialists, *E. talamancae, E. biporcatus, E. longirostris, E. frater, E. bransfordi, E. golmeri, E. cruentus. B. haemititicus, E. altae,* and *E. fitzgingeri* are not illustrated.

The above patterns within and among guilds are corroborated by observations of representatives from all three guilds foraging in their natural habitat. *Dendrobates auratus* and *Atelopus varius,* pronounced ant specialists, search actively for prey and often range over wide areas. *Dendrobates auratus* feeds frequently while moving over the surface of leaves and tree trunks or logs and captures prey by leaning forward slightly and then snapping up the prey with its tongue. The *Colostethus* ssp., which tend to be more generalized in diet, also forage on the surface of the leaf litter, but are more sedentary than *Dendrobates. Colostethus* ssp. often move only within a radius of a few centimeters up to a meter or so while foraging; and capture prey in the same manner as *Dendrobates,* by hopping toward it, leaning forward slightly and snapping it up with the tongue. *Eleutherodactylus* sit and wait for prey while hiding beneath the leaf litter; they typically wait for prey to walk by on the surface of adjacent leaves, and lunge, with open mouth, at the prey.

Thus differences among diurnal litter anurans in foraging behavior and in the number of prey in the stomach correlate with the degree of specialization on ants: The more active the searcher, the higher proportion of ants in the diet, and the less time spent in pursuit of prey; conversely, the sit-and-wait foragers rarely take ants, and instead eat one or two large prey, for which they expend more effort to capture, per day.

I have restricted this study to diurnal litter anurans. Other species of litter anurans forage at night (Toft and Duellman, 1979). Do nocturnal foragers, which are subject to different constraints due to predation, exhibit the same patterns of diet and foraging mode? Studies of nocturnal litter anurans (Duellman, 1978; K. L. Jones, in prep.) indicate that they exhibit similar patterns of diet specialization; many of the nocturnal leptodactylids, including some of the *Eleutherodactylus* that also forage diurnally, seem to be non-ant specialists with few prey per stomach, and the microhylids are ant specialists with many prey per stomach (Toft, unpublished data; C. Nelson, in prep.). There exists insufficient data on the foraging behavior of nocturnal litter anurans to determine whether they exhibit similar patterns of foraging mode.

Evolution of foraging mode.

In Panamá and Perú, the three guilds are represented by the same families of anurans, even though genera differ from site to site. Bufonids and dendrobatids all eat ants to some degree, with *Bufo* and *Dendrobates* ssp. all ant-specialists, and with the *Colostethus* ssp. tending to be generalists or slight ant specialists (Tables 1 and 2). The same is true of litter anurans in Perú, with

Dendrobates femoralis being the only true generalist (Toft, 1980a). The leptodactylids tend to be exclusively non-ant specialists; *E. vocator* is a definite exception and eats ants in proportions similar to some *Colostethus* (Tables 1 and 2 Figure 1; Toft, 1980a). These correspondences at the family level suggest that specializations on food type is a fairly conservative trait which arose concomitantly with the divergence of families and which may have coevolved with other characteristics such as mode of defense against predators (Toft, 1980a). Further, patterns within families of litter anurans present evidence that specialization on ants is derived from either a generalist or non-ant specialist mode of foraging. For instance, consider the Dendrobatidae, which originated in South America (Savage, 1973) and which may have diverged from leptodactyloid stock (Lynch, 1971). The dendrobatids in which specialization on ants is least developed are the *Colostethus,* which are considered primitive (Myers *et al.,* 1978) and *Dendrobates femoralis,* which is an anomolous species perhaps not closely related to other *Dendrobates* (Myers et al., 1978). In fact, Myers *et al.* (1978) state that the evolution of powerful skin toxins in the *Dendrobates-Phyllobates* group "was a major evolutionary development that opened new avenues of adaptation within the Dendrobatidae." One such avenue may have been the opportunity to adopt an actively searching mode of diurnal foraging, allowing them to exploit more efficiently an abundant resource such as ants.

Patterns in foraging mode: generality in unrelated predators.

At least one end, if not both, of the continuum of foraging modes appear to be derived in litter frogs. The ecological correlates associated with the evolution of these modes in litter anurans (Table 3) are similar to those in reptilian predators (Andrews, 1979; Huey and Pianka, 1981; Moermond, 1979). As in desert lizards (Huey and Pianka, 1981), the two specialist foraging modes probably represent an evolutionary commitment as reflected by wide and correlated divergences in many traits, including morphological, physiological, and behavioral (Table 3). Within each mode, certain trade-offs and constraints are apparent. Sit-and-wait foragers surely have lower search costs, because their prey come to them, and almost certainly the physiological costs of digesting their prey is less; at the same time, their larger prey are harder to subdue and handle. Searching foragers, in contrast, incur a much smaller cost of capture per prey item, but they have to capture many more prey, which are probably more costly to digest. Mode of defense against predators may put constraints on foraging mode, with searching foragers being susceptible to more kinds of

TABLE 3. General correlates of foraging mode in litter anurans.

	Sit and Wait	Widely Foraging
Prey type	large, mobile prey, depend on escape as I° predator defense	small, slow-moving prey that sting, or are distasteful or chitinous
Number of prey	lower	higher
Volume of prey	might be the same for both modes	
Search Cost	lower* (*costs may be ameliorated by physiology, see below)	higher*
Handling Cost:		
Capture (cost/capture)	higher	lower
Digestion (net)	lower	higher
Predator defense	crypticity, escape detection	skin toxins; may be aposomatic
Morphology	stocky, wide-mouthed	slim, narrow-mouthed
Physiology (Bennett and Licht, 1974)	anaerobic; capable of large bursts of energy, tire easily	aerobic; maintain constant but low levels of activity

predators as Huey and Pianka (1981) postulate for lizards; at any rate, in litter anurans searching foragers apparently cannot rely solely on concealment, and without exception these species possess powerful skin toxins (Myers *et al.,* 1978, Toft, 1980a). Although not all the correlates of foraging mode in litter anurans are the same as those found in desert lizards (Huey and Pianka, 1981), enough traits are shared by the two groups to establish the generality of many foraging patterns in unrelated predators in very different habitats.

ACKNOWLEDGMENTS

I am grateful to the staff and associates of the Smithsonian Tropical Research Institute for providing logistical support and advice and to the many who accompanied and assisted me in the field. R. Andrews, R. Huey, and R. Ruibal made helpful comments and suggestions on the manuscript. This study was funded by the Smithsonian Tropical Research Institute.

LITERATURE CITED

Andrews, R. M. 1979. Evolution of life histories: a comparison of *Anolis* lizards from matched island and mainland habitats. Breviora 454:1–51.

Bennett, A. F. and P. Licht. 1974. Anaerobic metabolism during activity in amphibians. Comparative biochemistry and Physiology 48A:319–327.

Duellman, W. E. 1978. The biology of an equatorial herpetofauna in Amazonian Ecuador. Univ. Kansas, Mus. Nat. Hist. Misc. Publ. 65:1–352.

Huey, R. B. and E. R. Pianka. 1981. Ecological correlates of foraging mode. Ecology, in press.

Inger, R. F. and H. Marx. 1961. The food of amphibians. Exploration du Parc national de l'Upemba. Mission C. F. de Witte *et al.* Imprimerie Hayes, Brussels, Belgium. pp. 3–85.

Jacobs, J. 1974. Quantitative measurement of food selection: a modification of the forage ratio and Ivlev's electivity index. Oecologia 14:413–417.

Lynch, J. D. 1971. Evolutionary relationships, osteology, and zoogeography of leptodactylid frogs. Univ. Kansas Mus. Natur. Hist. Misc. Pub. 53:1–238.

Moermond, T. C. 1979. The influence of habitat structure on *Anolis* foraging behavior. Behaviour 70:147–167.

Myers, C. W., J. W. Daly and B. Malkin. 1978. A dangerously toxic new frog (*Phyllobates*) used by Embera Indians of Western Colombia, with discussion of blowgun fabrication and dart poisoning. Bull. Am. Mus. Nat. Hist. 161:309–365.

Root, R. 1967. The niche exploitation pattern of the blue-gray gnatcatcher. Ecol. Monogr. 37:317–350.

Savage, J. M. 1973. The geographic distribution of frogs: patterns and predictions. *In* J. L. Vial (ed.), Evolutionary Biology of the Anurans, pp. 351–455. Univ. of Missouri Press, Columbia, MO.

Sexton, O. J., H. Heatwole, and D. Knight. 1964. Correlation of micro-distribution of some Panamanian reptiles and amphibians with structural organization of the habitat. Carib. J. Sci. 4:261–295.

Toft, C. A. and W. E. Duellman. 1979. Anurans of the lower Río Llullapichis, Amazonian Perú: a preliminary analysis of community structure. Herpetologica 35:71–77.

Toft, C. A. and S. C. Levings. 1979. Seasonal trends in litter arthropod populations. *In* H. Wolda (ed.), Actas del IV Symposium Internacional de Ecologia tropical, marzo 7–11, 1977 2:559–576.

Toft, C. A. 1980a. Feeding ecology of thirteen syntopic species of anurans in a seasonal tropical environment. Oecologia 45:131–141.

———. 1980b. Seasonal variation in populations of Panamanian litter frogs and their prey: a comparison of wetter and drier sites. Oecologia, 47:34–38.

Accepted 20 Oct 1980

●