Journal of Tropical Ecology (2001) 17:21–40. With 7 figures
Copyright © 2001 Cambridge University Press

Avian predation upon lizards and frogs in a neotropical forest understorey

BRIGITTE POULIN[1], GAËTAN LEFEBVRE, ROBERTO IBÁÑEZ, CÉSAR JARAMILLO, CARLOS HERNÁNDEZ *and* A. STANLEY RAND

Smithsonian Tropical Research Institute, Apartado 2072, Ancón, Republic of Panama
(Accepted 9th July 2000)

ABSTRACT. Although tropical forest birds are known to prey upon small lizards and frogs, no study has documented the attributes of vertebrate-eating birds or whether birds prey opportunistically on the different elements of the herpetofauna within tropical communities. This study is based on a 14-mo investigation on avian diet, supplemented with a 3-y census of frogs and a 1-y census of lizards in a humid forest of central Panama. From 91 bird species, 1086 regurgitates were collected, in which were found 75 lizards and 53 frogs. Over 50% of the common, primarily insectivorous bird species preyed upon lizards or frogs, with a mean frequency of 0.26 prey/sample. These birds (22 species, nine families) foraged on various substrates from different strata of the forest, fed on invertebrates averaging from 3.3 to 17.2 mm in length, weighed from 11 to 195 g, and had bill lengths that varied from 12.2 to 49.8 mm. Based on a logistic regression analysis, intensity of foraging at army-ant swarms was the variable that best explained the likelihood that a bird species preyed upon lizards, leading to a classification that was 91% correct. In contrast, bill length and body length classified correctly 88% of the frog-eating birds, which showed a fairly constant 1:7 bill length/body length ratio (as opposed to a mean but highly variable 1:10 ratio in other species). A multiple regression analysis showed that seasonal variation in intensity of lizard predation was positively related to arthropod abundance except during the breeding season when lizard intake decreased, presumably because nesting birds did not follow ant swarms. Intensity of frog predation correlated with frog abundance over time, the latter being inversely related to arthropod availability. Ninety-seven per cent of all lizards and frogs identified in the diet samples (n = 105) were from two genera, *Anolis* and *Eleutherodactylus*, respectively. Prey size distribution in the regurgitates suggested an optimal prey size of 33.5 mm snout-vent length (SVL) for lizards and 14.5 mm SVL for frogs. Birds preyed opportunistically on the different *Anolis* species, but almost exclusively upon juvenile individuals. Abundances of the different *Eleutherodactylus* species correlated with their predation rates, but these frogs represented only 10% of all the frogs observed during the censuses. The two most common local anurans, *Colostethus flotator* and *Bufo typhonius*, were not taken by any bird species.

[1] Correspondence: Brigitte Poulin, Station Biologique de la Tour du Valat, Le Sambuc, 13200 Arles, France.

RESUMEN. Aunque las aves del bosque tropical son conocidas por depredar pequeñas lagartijas y ranas, ningún estudio había intentado determinar los atributos de las aves que se alimentan de vertebrados dentro de las comunidades tropicales, y si éstas depredan oportunísticamente a diferentes elementos de la herpetofauna. Este estudio se basa en una investigación de 14 meses sobre la dieta de las aves, complementado con un programa de censos de tres años sobre la abundancia de ranas y lagartijas en el bosque húmedo tropical de Panamá central. Se recolectaron 1086 regúrgitos de 91 especies, en los cuales se encontraron 75 lagartijas y 53 ranas. Más del 50 por ciento de las especies de aves comunes, principalmente insectívoras, depredaron lagartijas o ranas con una frecuencia promedio de 0.26 presas/muestra. Estas aves (22 especies, 9 familias) forrajearon en varios substratos de estratos diferentes del bosque, se alimentaron de invertebrados que promediaban de 3.3 a 17.2 mm de longitud, pesaron de 11 a 195 g, y la longitud del pico varió de 12.2 a 49.8 mm. En base a un análisis de regresión logística, la intensidad del forrajeo en los enjambres de hormigas guerreras es la variable que explicó mejor la probabilidad que una especie de ave deprede lagartijas, llevando a una clasificación 91 por ciento correcta. En contraste, la longitud del pico y la longitud del cuerpo clasificaron correctamente al 88 por ciento de las aves que se alimentan de ranas, las cuales mostraron una estricta relación longitud del pico/longitud del cuerpo de 1 a 7 (opuestamente a un promedio, pero altamente variable, 1:10 en otras especies). Un análisis de regresión múltiple mostró que la estacionalidad en la depredación de lagartijas está inversamente relacionada con la crianza de las aves (las aves que anidan no siguen a los enjambres de hormigas), pero positivamente relacionada a la abundancia de artrópodos. La intensidad de la depredación de ranas varió similarmente a la abundancia de ranas a través del tiempo, esta última estando inversamente correlacionada con la disponibilidad de artrópodos. El 97 por ciento de todas las lagartijas y ranas identificadas en las muestras de dieta (n = 105) pertenecían a dos géneros, *Anolis* y *Eleutherodactylus*, respectivamente. La distribución del tamaño de la presa en los regúrgitos sugirió un tamaño óptimo de presa de 33.5 mm en longitud hocico-cloaca (LHC) para las lagartijas y 14.5 mm en LHC para las ranas. Las aves depredaron oportunísticamente diferentes especies de *Anolis*, pero casi exclusivamente a individuos juveniles. La distribución de la abundancia de las diferentes especies de *Eleutherodactylus* se ordenó similarmente a sus tasas de depredación, pero éstas representaron solamente el 10 por ciento de todas las ranas observadas durante los censos. Los dos anuros localmente más comunes, *Colostethus flotator* y *Bufo typhonius*, no fueron depredados por especie de ave alguna.

KEY WORDS: *Anolis* lizards, avian diet, *Eleutherodactylus* frogs, neotropical birds, Panama, predator–prey interactions, social foraging, tartar emetic

INTRODUCTION

Although food webs are a central concept in community ecology (Wilbur 1997), many trophic relationships are poorly documented, especially within tropical ecosystems. Predator–prey interactions are rarely observed in the field, and most attempts to identify and quantify their occurrence have focused on a narrow range of species. Because food webs within natural communities are complex, understanding their trophic links requires the study of a significant subset of a predator–prey assemblage.

Small lizards and frogs are preyed upon by a great variety of animals (Duellman & Trueb 1986, Greene 1988, Zug 1993). They are a food source to many passerines and other bird species in neotropical forests (Stiles *et al.* 1989; Wetmore 1965, 1968, 1972; Wetmore *et al.* 1984). Because of their low aerobic capacities relative to avian predators, frogs and lizards are expected to be cryptic and to rely on brief movements into inaccessible microhabitats for escape (Evans 1947, Greene 1988). In contrast to lizards, skin toxins are relatively common among anurans, especially within the Bufonidae and Dendrobatidae (Daly & Myers 1967, Daly *et al.* 1987).

Most of the potential lizard- and frog-eating birds in tropical forests are primarily insectivorous. Given the relationships between predator and prey size (Brandl *et al.* 1994, Lederer 1975), we would expect larger birds to prey more extensively upon vertebrates than smaller ones. Social behaviour while foraging is also potentially important since cryptic, immobile prey are often more vulnerable to predation when flushed out of cover by the activity of other animals (Bennetts & Dreitz 1997, Rand 1954). Environmental factors such as prey availability, abundance of alternate food types, and cover for prey hiding (Wunderle 1981) are also likely to affect avian predation on frogs and lizards, at least on a seasonal basis.

This study reports on frog and lizard intake by understorey birds from a humid forest in central Panama. A 14-mo investigation of avian diet is combined with information on local prey composition and abundance to infer prey selection by avian predators. Data on the birds' morphology and foraging behaviour are further used to assess attributes of lizard-eating and frog-eating species. Finally, bird abundance and breeding activity, as well as availability of invertebrates and vertebrates, are used as independent variables to explain seasonal variation in frog and lizard intake by birds.

We hypothesized that (1) vertebrate-eating species are of larger size and feed on larger invertebrates than species not preying upon lizards or frogs; (2) social foraging contributes to increase the intake of frogs and lizards by birds; (3) birds feed more extensively on vertebrates when arthropod availability is low; and (4) frog-eating species are more selective in their prey choice than lizard-eating species.

STUDY SITES

This study was conducted in Soberanía National Park, central Panama (9°10′ N, 79°7′W). Data on bird diet and arthropod abundance were collected within a 3.2-ha plot of second-growth humid forest along Pipeline Road including the margins of Frijoles and Frijolito streams. Data on frog and lizard abundance were collected at Rio Limbo in a mature forest 2.3 km northwest from the 3.2-ha plot. Mean height of canopy and emergent trees (n = 15) was measured with a range-height Finder model 'K' made by Topcon (75-1 Hasunuma-cho,

Tokyo, Japan) at each plot. The bird plot included 2.2 ha of young second-growth where mean height of canopy and emergent trees was 15.5 and 25.9 m, respectively. This plot, which is not representative of the park, was selected because its denser understorey was expected to improve bird capture rates in ground-level nets. Heights of canopy and emergent trees in the older second-growth at the bird plot averaged 16.5 and 28.7 m, respectively. The mature forest at Rio Limbo where herpetofauna censuses were conducted had a canopy of 18.1 m with emergent trees reaching 33.9 m on average. Although bird and herpetofauna censuses were not conducted at the same plot we are confident that we can infer prey selection by birds because (1) several visits at the bird plot revealed that the most common frog and lizard species at the Limbo plot were also present there, and (2) a 100-ha capture–recapture programme on birds conducted at Rio Limbo during our study showed that most bird species forage over large areas, several individuals being captured at both the second-growth and mature forest plots.

Both sites have a tropical monsoon climate under the Köppen system of climatic classification (Croat 1978). Mean monthly temperatures are 27 °C in April and 26 °C in all other months. Annual rainfall averages 2133 mm. A dry season, which receives *c.* 13% of annual rainfall, begins in December, or rarely November, and ends in April, or rarely May (data from the meteorological station of the Panama Canal Commission in Gamboa, 4.5 km SE from the bird study plot).

METHODS

Bird sampling

Diet and breeding condition of birds were monitored though mist-netting sessions conducted from October 1993 through November 1994. Mist nets were operated during 7 h starting at sunrise for three consecutive days twice a month. A total of 36 nets (3-m × 10-m, 32-mm mesh) were used, with a single net placed every 25 m along eight transects 35 m apart. Each bird captured was banded, weighed, checked for the presence of brood patch and primary molt, forced to regurgitate, and released. Because the trapping effort was held constant during the whole sampling period, we used the number of frogs and lizards taken by birds as an indicator of predation rate, as well as the number of frog- and lizard-eating birds captured as an indicator of predator abundance.

Data on bill length (culmen from the base), body length, intensity of attendance at army-ant swarms, frequency of foraging in monospecific (including pairs and family groups) or multispecific flocks, and main foraging substrate used for all bird species are from Wetmore (1965, 1968, 1972) and Wetmore *et al.* (1984). Vertical distribution of bird foraging was divided into six categories: ground, low understorey, upper understorey, midstorey, subcanopy and canopy (D. Robinson, unpubl. data).

Hummingbirds (Trochilidae) and manakins (Pipridae) were excluded from

this study because their physiological adaptations to efficiently assimilate nectar and fruit are incompatible with vertebrate digestion. Their particular morphology (e.g. small size of hummingbirds, short bill of manakins) would have strongly influenced the results and decreased the relevance of our analyses. With the exception of the ruddy quail-dove (*Geotrygon montana*) and the lesser seed-finch (*Oryzoborus angolensis*), all the bird species dealt with in this paper had arthropods as a significant fraction (> 40% of items taken) of their diet (B. Poulin, unpubl. data).

Diet estimation

Regurgitates were obtained by orally administering tartar emetic to the birds following the method of Poulin & Lefebvre (1995). Food items were preserved in 70% ethanol and taxonomically identified in the laboratory using a dissecting scope. Because most arthropods were highly fragmented and digested, they were generally identified to order, and their body length measured (or estimated) to the nearest 5 mm. Among the Hymenoptera, we distinguished between ants, flying ants and wasps. Early stages of insects were clumped as eggs or larvae, without taxonomic distinction except for Lepidoptera larvae. Frog and lizard prey were identified to species or genus and measured to the nearest mm using a reference collection of skeletons from animals which had previously been identified, measured, sexed and aged. Length of specific bones, mainly the maxilla and mandibula (lizard), and the ilium (frog), were used for both taxonomic identification and estimation of the snout-vent length (SVL). The minimum adult size for each species was estimated using the reference collection. Nomenclature follows Rand & Myers (1990).

Availability of frogs and lizards

Seasonal abundance of each frog and lizard species was estimated along an 800-m trail route that included the margins, slopes and a ridge adjacent to the Limbo stream. Diurnal censuses were carried out twice a month from October 1993 to November 1994 (lizards), and from March 1992 to May 1995 (frogs). An observer walked slowly, poking the leaf litter with a stick, and counting the number of individuals of each species found within 1 m width and 2 m height along the trail.

Frog size (SVL) was measured or estimated to the nearest mm whenever possible during the censuses. Several *Eleutherodactylus* were not identified to species, but instead combined based on their similarity in appearance as follows: Group 1: *E. cerasinus*, *E. ridens*, *E. cruentus*, *E. taeniatus*; Group 2: *E. vocator*, *E. diastema*; Group 3: *E. fitzingeri*, *E. crassidigitus*; and Group 4: *E. bransfordii*, *E. bufoniformis*. This same grouping was used for the *Eleutherodactylus* found in the birds' regurgitates.

A monthly index of prey availability (Poulin & Lefebvre 1997) was calculated using the relative abundance of each frog or lizard species censused (mean monthly values divided by mean annual numbers) multiplied by its overall

predation rate (i.e. the proportion of items it represents in the bird regurgitates) and summed across species. Only lizards and frogs identified to species or group of species (i.e. *Eleutherodactylus*) were used. We therefore assumed that unidentified species within a genus were distributed similarly to identified ones. This assumption relies on the fact that the unidentified species in a regurgitate lacked sufficient bone fragments rather than failing to conform to the reference collection.

Availability of alternate food types

Arthropod abundance was estimated through sweep-net samples during the bird-netting sessions. Arthropods were captured twice monthly along the mist-net transects by sweeping the first 2 m of vegetation for a 20-min period as soon as the vegetation was dry (late morning) to maximize capture efficiency. We used a constant sampling effort under similar meteorological conditions to allow comparison of samples.

Data from sweep-net and regurgitation samples were combined to produce a monthly index of arthropod availability to frog- and lizard-eating birds. This index corresponds to the summed proportion of each arthropod taxon in the regurgitates of bird species eating frogs or lizards, multiplied by its relative abundance (mean monthly values divided by mean annual numbers) in sweep-net samples (Poulin & Lefebvre 1997). We calculated this index for all arthropods and for large ones only (> 5 mm).

Statistical analyses

We used a multiple logistic regression analysis with a forward stepwise-computed procedure to discriminate the frog- and lizard-eating bird species based on their morphology, feeding behaviour and taxonomy. Morphological variables included bill length, body length and body mass. Characteristics of feeding behaviour included mean size of invertebrate prey, proportion of invertebrate prey in different size classes (< 5, < 10, < 15, < 20, < 25 mm), main foraging substrate, main foraging strata, intensity of use of each foraging stratum, frequency of attendance at army-ant swarms, and frequency of foraging in mono- or multispecific flocks. The proportion of diet samples containing frogs was used in the analysis of lizard-eating birds and *vice versa*. Taxonomy refers to the family membership of each species (Ridgely & Gwynne 1989). For each computed model, the analysis was rerun excluding any selected variable to determine which model best discriminated the frog- and lizard-eating species.

We used a forward stepwise-computed multiple linear regression analysis to evaluate which factors accounted for the variation in frog and lizard intake over time. Only frogs and lizards identified at least to genus were considered in this analysis. Independent variables were avian breeding and molt (occurrence of birds with brood patch or primary molt), number of frog- and

lizard-eating birds caught, indices of availability of frogs, lizards and arthropods. All these variables were expressed as mean values for each calendar month (n = 12), and were normally distributed (Kolmogorov–Smirnov goodness-of-fit test, $P > 0.05$). For each computed model, the regression analysis was rerun excluding any selected variable to determine which model best explained the temporal variation in avian predation on vertebrates.

RESULTS

We collected 1086 regurgitation samples from 91 bird species. To reduce bias associated with small sample size in diet estimation, bird species represented by five samples or fewer were excluded, except when vertebrates occurred in their regurgitations (two species). The remaining 43 species were distributed in 12 families (Table 1). Predation on frogs and lizards occurred respectively in 16 and 15 bird species belonging to six and eight families, with nine species (41%) feeding on both lizards and frogs (Table 1). Frequency of lizard intake averaged 0.21 item/sample, being highest for *Attila spadiceus* with 1.22 (n = 9). Frequency of frog intake was lower (0.12 item/sample), reaching a maximal value of 0.47 (n = 15) for *Formicarius analis* (Table 1).

From the 75 lizards found in diet samples, 69 (92%) were identified at least to genus, of which 67 were *Anolis* and two were *Ameiva*. From the 53 frogs found in the regurgitates, 36 (68%) could be identified, and all were *Eleutherodactylus*. One bird species (*Leptotila cassinii*) fed on vertebrate eggs. Two regurgitates from the same individual bird in early and mid July totalled five lizard (*Anolis*) and four frog (*Eleutherodactylus*) eggs.

Prey selection

Eight species of lizards were recorded during the censuses (Figure 1). Four of these species were taken by birds in proportion to their relative abundance with *Anolis limifrons* being the most common prey. *Anolis auratus*, which is common in grassy open areas (Sexton *et al.* 1971), was observed in one regurgitate but not recorded during the (forest) censuses.

Fourteen species of frogs were recorded during the censuses (Figure 2). The two most abundant species, *Colostethus flotator* and *Bufo typhonius*, accounted respectively for 72% and 17% of all observations, but were not observed in our diet samples. They were followed by the four groups of *Eleutherodactylus* species whose abundance distributions ranked similarly to their predation rates. The remaining eight frog species were locally rare and did not appear in the regurgitates.

Anolis in diet samples averaged 33.5 mm SVL, ranging from 19 to 44 mm (n = 31). Size distribution of *Anolis* in diet samples (Figure 3) did not differ from a normal distribution (goodness-of-fit test, $G = 2.01$, $df = 5$, ns). Based on a minimum adult SVL of 40 mm for *Anolis limifrons* (Sexton *et al.* 1971), and 48

Table 1. Family membership, vertebrate intake, feeding behaviour and morphology of 43 neotropical understorey bird species.

Family Bird species	N	Diet No. items/sample lizard	 frog	Feeding behaviour Prey size[a] (mm)	 Foraging stratum[b]	 Army ant[c]	Morphology Body mass (g)	 Body length (mm)	 Bill length (mm)
Falconidae									
Micrastur ruficollis	2	1	0	13.1	MS	R	165	355	14.8
Columbidae									
Leptotila cassinii	8	0	0	5.5	G	N	165	250	14.6
Geotrygon montana	9	0	0	2.5	G	N	110	223	11.7
Trogonidae									
Trogon rufus	7	0	0	10.9	MS	N	54	248	17.5
Momotidae									
Baryphthengus martii	8	0.13	0	17.2	MS	O	195	445	49.8
Furnariidae									
Xenops minutus	17	0	0	5.9	MS	N	12	119	14.1
Sclerurus guatemalensis	19	0.05	0.21	5.9	G	N	34	168	24.2
Dendrocolaptidae									
Dendrocincla fuliginosa	38	0.39	0.08	7.2	MS	F	42	210	29.7
Dendrocincla anabatina	2	0.5	0	7.5	MS	F	33	180	24.9
Dendrocincla homochroa	10	0.1	0.1	8.7	MS	F	46	190	26.9
Xiphorhynchus guttatus	18	0	0.39	11.5	MS	O	46	225	36.7
Formicariidae									
Thamnophilus punctatus	93	0.11	0.01	9.9	MS	R	23	145	20.9
Myrmotherula fulviventris	58	0	0.1	5.7	MS	N	11	98	15.3
Myrmotherula axillaris	14	0	0	5.2	MS	O	8	95	14.4
Cercomacra tyrannina	10	0	0.1	9.0	LU	N	16	133	17.9
Myrmeciza exsul	8	0.38	0.38	10.6	G	R	26	140	21.1
Hylophylax naevioides	44	0.16	0.23	5.0	G	F	17	113	17.2
Gymnopithys leucaspis	61	0.18	0.03	9.1	G	F	29	139	20.1
Phaenostictus mcleannani	14	0.29	0	13.0	G	F	50	195	23.1
Formicarius analis	15	0.4	0.47	7.4	G	R	58	175	21.9
Hylopezus perspicillatus	6	0	0.17	9.1	G	N	43	140	20.9

Table 1. (*cont.*)

Family Bird species	Diet			Feeding behaviour			Morphology		
	N	No. items/sample lizard	 frog	Prey size[a] (mm)	Foraging stratum[b]	Army ant[c]	Body mass (g)	Body length (mm)	Bill length (mm)
Tyrannidae									
Mionectes oleagineus	61	0	0	3.3	UU	N	10	135	15.7
Oncostoma olivaceum	39	0	0	3.7	MS	N	7	95	12.5
Cnipodectes subbruneus	9	0	0.22	7.3	UU	N	23	160	17.8
Rhynchocyclus olivaceus	8	0	0	6.8	MS	N	21	143	16.4
Platyrinchus coronatus	7	0	0	3.5	MS	O	9	85	12.3
Onychorhynchus coronatus	6	0	0	16.9	MS	N	35	163	24.9
Terenotriccus erythrurus	18	0	0	3.6	MS	N	7	95	9.9
Empidonax virescens	19	0	0	4.9	MS	O	12	133	15.2
Attila spadiceus	9	1.22	0.22	13.8	LU	O	37	178	24.3
Pipridae									
Schiffornis turdinus	29	0	0	23.5	LU	N	35	155	16.7
Troglodytidae									
Henicorhina leucostica	9	0	0	6.3	G	O	16	99	17.2
Cyphorhinus phaeocephalus	17	0	0.12	7.0	G	O	26	123	20.1
Muscicapidae (Turdinae)									
Catharus fuscescens	8	0	0	5.6	G	N	31	163	17.0
Catharus minimus	14	0	0.07	5.4	G	R	30	172	17.0
Catharus ustulatus	31	0	0	5.7	G	O	29	167	16.9
Emberizidae (Parulinae)									
Seiurus noveboracensis	10	0	0	2.6	G	N	16	130	13.2
Oporornis formosus	19	0.05	0	3.3	G	R	13	120	12.2
Emberizidae (Thraupinae)									
Eucometis penicillata	19	0.05	0	7.0	G	R	31	168	17.3
Tachyphonus luctuosus	11	0	0	8.7	MS	N	14	133	14.5
Habia fuscicauda	7	0	0	9.0	LU	O	37	186	19.4
Emberizidae (Cardinalinae)									
Cyanocompsa cyanoides	18	0	0	5.7	UU	N	29	156	20.4
Emberizidae (Emberizinae)									
Oryzoborus angolensis	10	0	0	2.5	LU	N	12	111	13.6

[a] Mean size of invertebrate prey taken.
[b] Foraging strata: G, ground; LU, low understorey; UU, upper understorey; MS, midstorey (D. Robinson, unpubl. data).
[c] Degrees of attendance at army-ant swarms: N, never; O, occasionally; R, regularly; F, frequently (Wetmore 1965, 1968, 1972; Wetmore *et al.* 1984).

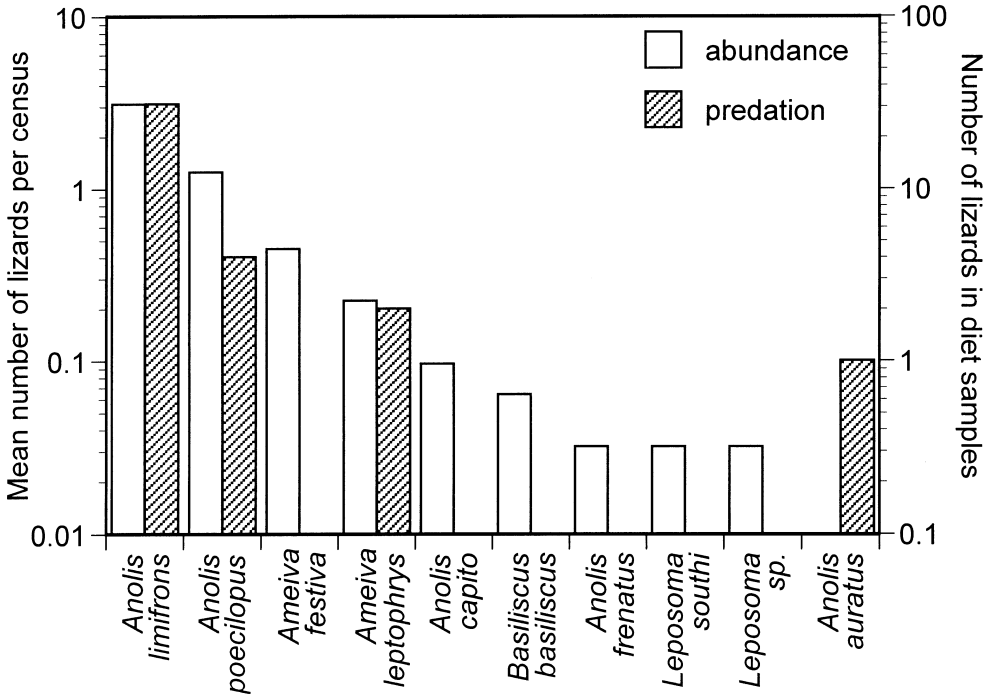

Figure 1. Comparison of bird predation and abundance of each lizard species in central Panama.

mm for *A. poecilopus* (Campbell 1973), only 13% (4/31) of the *Anolis* taken by birds were of adult size.

Frogs preyed upon by birds were relatively small (Figure 3). Estimated size of *Eleutherodactylus* found in the regurgitates averaged 14.5 mm SVL, ranging from 8.2 to 24.1 mm (n = 31). Size distribution of *Eleutherodactylus* in diet samples (Figure 3) did not differ from a normal distribution (G = 11.6, df = 6, ns). Based on a minimum adult SVL of 18 mm for *E. cerasinus*, 14.5 mm for *E. ridens*, 12 mm for *E. vocator*, and 25 mm for *E. fitzingeri*, it appears that 42% (13/31) of the frogs taken by birds were adult-sized individuals.

Predator attributes

Of the morphological and behavioural variables used in the multiple logistic regression analysis, intensity of attendance at army-ant swarms best explained the likelihood that a bird species preys upon lizards (regression coefficient = 2.53, P = 0.0005). This variable alone correctly classified 91% of the lizard-eating species (Figure 4). No other variable was added to the model because none of the remaining variables could explain a significant amount of the residual variance. Intensity of attendance at army-ant swarms was not significantly correlated with any other variables used in the model except bill length (r = 0.304, n = 43, P = 0.047). When attendance at army-ant swarms was removed

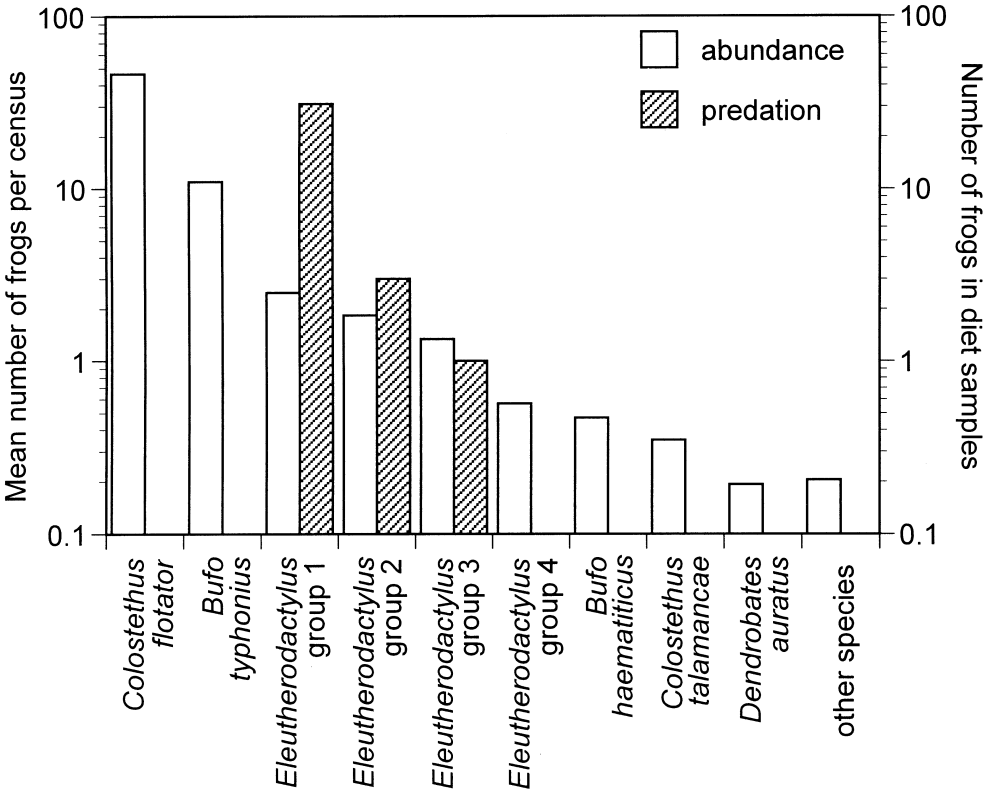

Figure 2. Comparison of bird predation and abundance of each frog species. *Eleutherodactylus* groups are defined in Methods.

from the analysis, no other variable or combination of variables could discriminate the lizard-eating birds with as much accuracy.

Avian predation on frogs was best explained by successively selecting two morphological variables, bill length (regression coefficient = 0.51, P = 0.0020) and body length (regression coefficient = –0.05, P = 0.0037). Together they correctly classified 88% of the frog-eating species (Figure 5). When these two variables were included in the model, none of the remaining variables could explain a significant amount of the residual variance. Body length was strongly correlated with body mass ($r = 0.904$, $n = 43$, $P < 0.001$), and bill and body lengths were both correlated with the proportion of invertebrate-prey larger than 5, 10, 15 and 20 mm ($r = 0.362$ to 0.529, $n = 43$, all $P < 0.05$) and with mean invertebrate-prey size ($r = 0.542$ and 0.490, $n = 43$, both $P < 0.001$). However, when bill and/or body length were removed from the model, no other variable or combination of variables provided as good a classification of frog-eating birds.

Seasonality of predation

Frog and lizard intake by birds peaked in the dry season, decreased sharply in April (frog) or May (lizard), and increased again in August and September

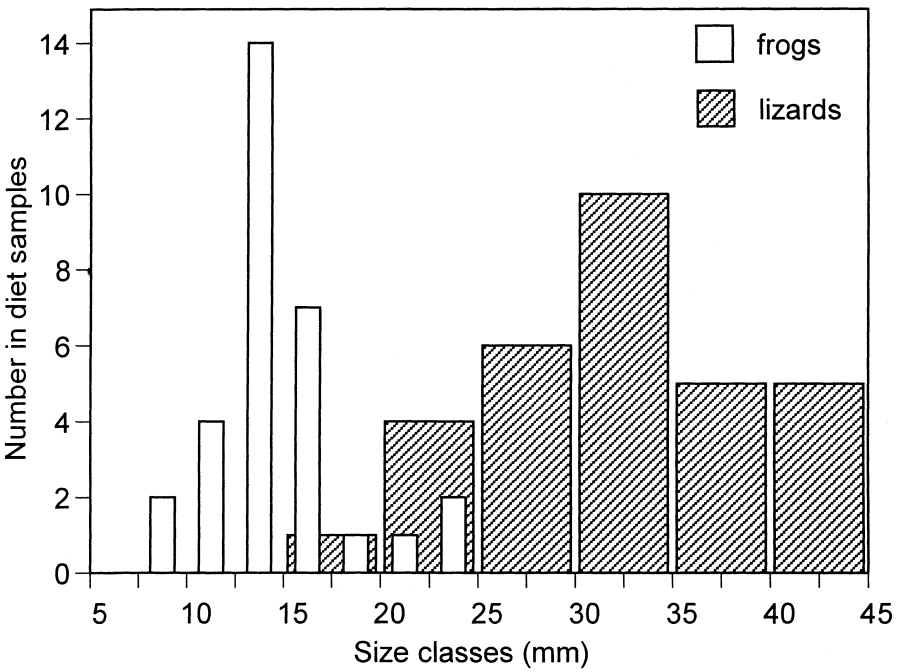

Figure 3. Size distribution of *Anolis* (n = 31) and *Eleutherodactylus* (n = 31) found in the birds' regurgitates.

(Figures 6 and 7). Bird predation upon frogs and lizards dropped in October of both years. In the multiple regression analysis, intensity of avian breeding (regression coefficient = −1.29, P = 0.0026) and arthropod availability (regression coefficient = −1.48, P = 0.0319) were successively selected as explanatory variables of the seasonal variation in lizard intake, and together accounted for 66% of the variance observed. After these variables were selected, none of the remaining variables explained a significant amount of the residual variance. When avian breeding was removed, no other variable explained a significant amount of the observed variance. When arthropod availability was removed, no other variable explained a significant amount of the observed variance. Lizard predation varied positively with arthropod availability except during the breeding season when lizard intake decreased and arthropod availability remained high (Figure 6).

The index of frog availability was the only variable selected in the multiple stepwise regression analysis on seasonal variation in frog predation (regression coefficient = 26.8, P = 0.0162). This factor varied similarly to the seasonality in frog intake by birds (Figure 7), and accounted for 45% of the variance observed. When this variable was removed, no other variable was selected. However, the index of frog availability was inversely related to the index of arthropod availability, when considering both all arthropods and large ones only (r = −0.647 and −0.661 respectively, df = 10, $P < 0.05$).

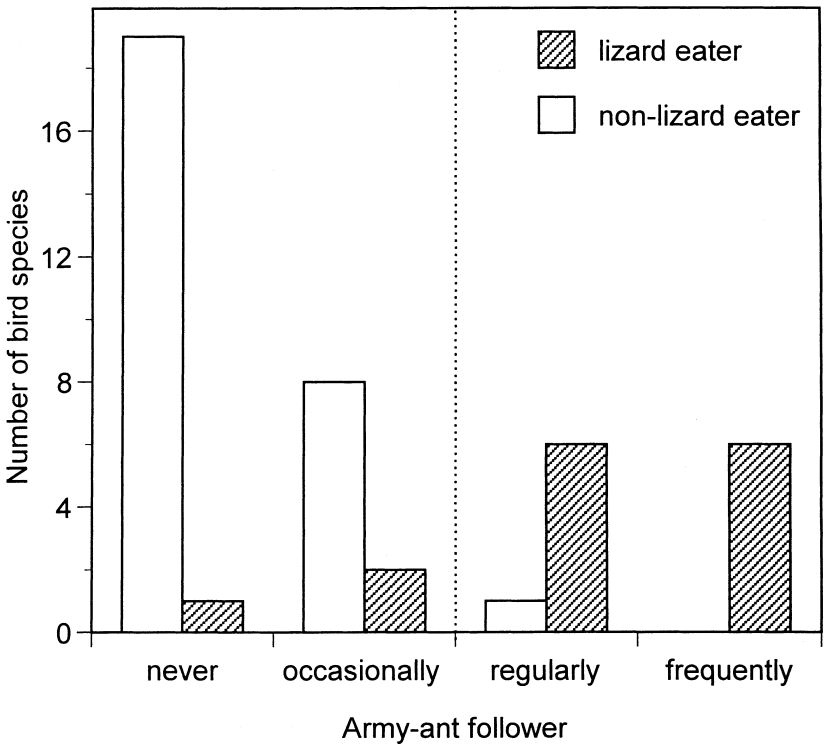

Figure 4. Degree of attendance at army-ant swarms by the 43 bird species. Species classified as lizard eaters by the logistic regression analysis are on the left side of the vertical line, while species classified as non-lizard eaters are on the right side.

DISCUSSION

The number of bird species that fed on frogs and/or lizards was surprisingly high (n = 22), representing more than half of the common insectivorous species in the forest understorey. These birds were distributed among nine families and differed in several aspects. They typically foraged from the ground-level to the midstorey strata, and fed on invertebrate prey averaging from 3.3 to 17.2 mm in length. Their body mass varied from 11 to 195 g, and their bill length from 12.2 to 49.8 mm. In contrast to our expectations, we did not find any relationship between vertebrate intake and predator size and/or invertebrate-prey size.

Prey selection

Birds preyed upon five lizard species, but primarily upon *Anolis limifrons* which is the most common anole in lowland forests of central Panama (Rand & Myers 1990). While birds seem to prey opportunistically on the different lizard species, they showed a strong selection for prey size. During a 10-y census on Barro Colorado Island in Panama (Andrews & Rand 1982), over 60% (665/

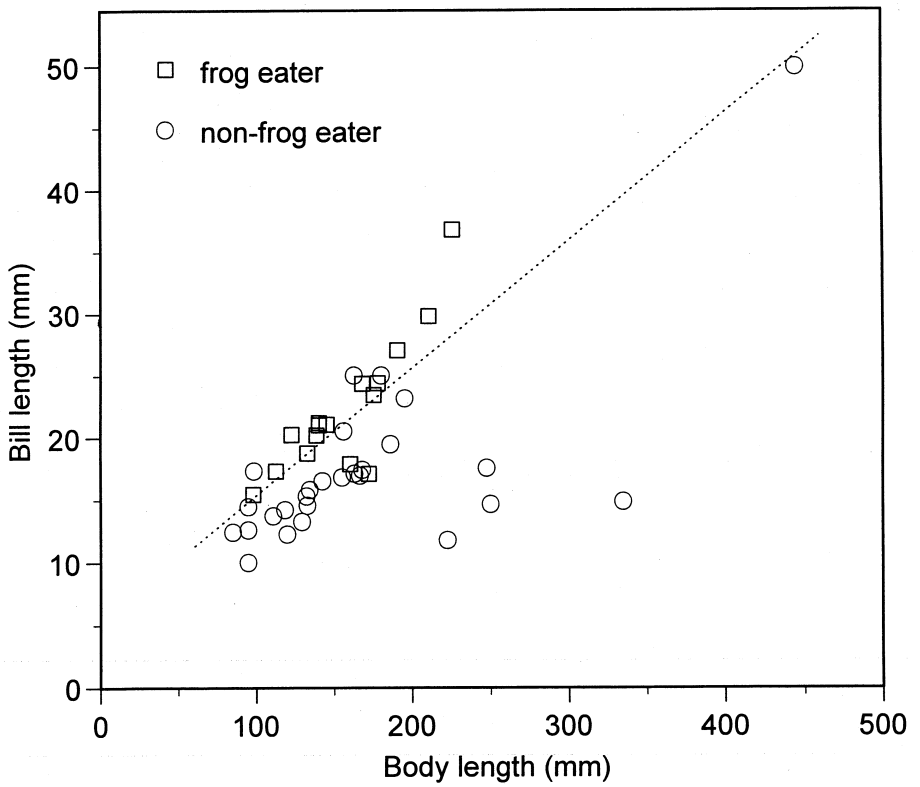

Figure 5. Relationships between bill and body lengths among the 43 bird species. Species classified as frog eaters by the logistic regression analysis are above the diagonal line, while species classified as non-frog eaters are below the diagonal line.

1085) of the *Anolis limifrons* observed were adults, in contrast to 13% in our diet samples. The high proportion of juvenile *Anolis* in the birds' diet is unlikely to reflect prey inexperience because old juveniles (30–39 mm) were taken more frequently than younger individuals (20–29 mm). Although seasonal abundance of *Anolis limifrons* varies according to age classes (Andrews *et al.* 1983), there was no consistent temporal trend in prey size within our diet samples. The predominance of juvenile *Anolis* in the birds' diet is probably a consequence of predator/prey size limitation since our diet samples suggest an optimal prey size below that of adult *Anolis*. This factor also probably explains why the larger *Anolis* species such as *A. capito* (SVL 50–90 mm, Taylor 1956) and *A. frenatus* (SVL 111–137 mm, Savage & Talbot 1978) were not taken by birds. *Ameiva*, which is a large lizard in comparison with most *Anolis*, was taken only by raptors (*Micrastur*) at our study site.

As we hypothesized, discrepancies between local abundance and predation rates revealed a stronger prey selection among frog than lizard species. The two most common anurans, *Colostethus flotator* and *Bufo typhonius*, were totally absent from the birds' regurgitates, with only *Eleutherodactylus* frogs being taken

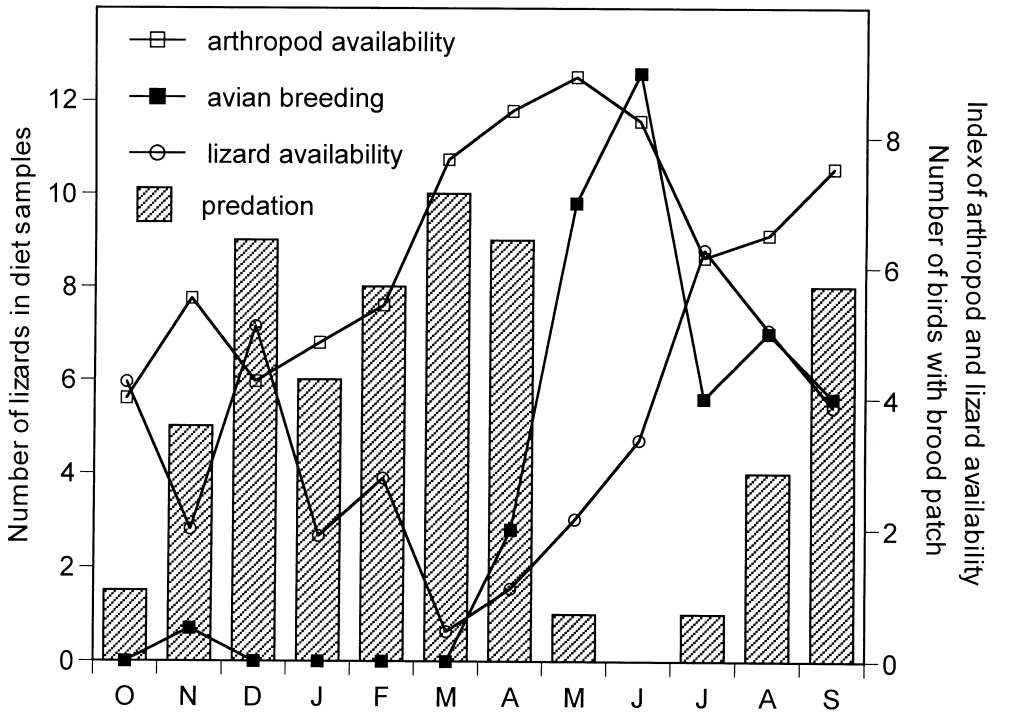

Figure 6. Temporal variation in lizard intake by birds in relation to avian breeding and availability of lizards and arthropods.

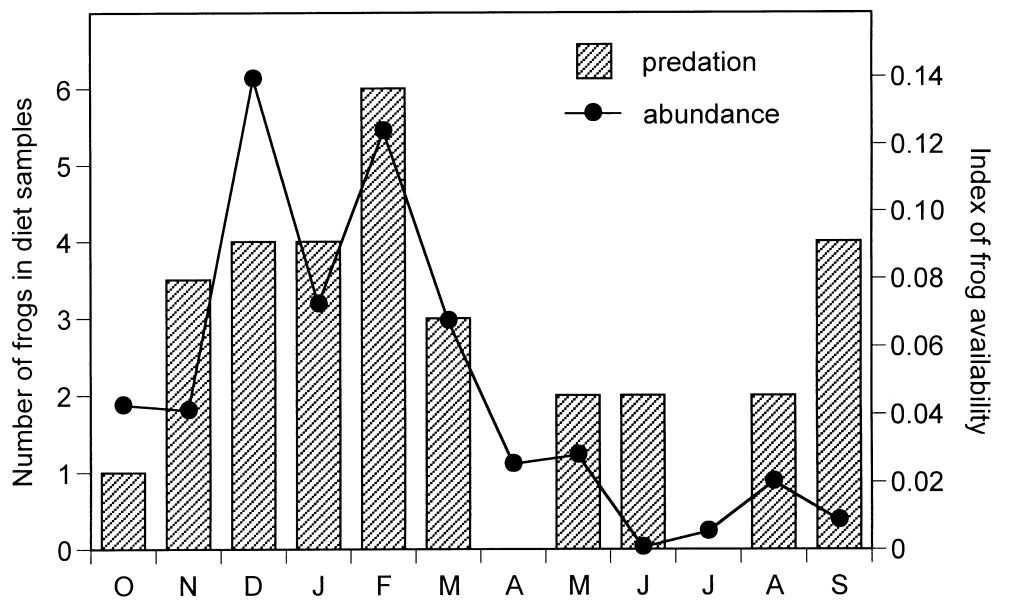

Figure 7. Temporal variation in frog intake by birds in relation to frog availability.

by birds. *Bufo typhonius*, as well as members of the Dendrobatidae (e.g. *Colostethus* and *Dendrobates*) are active during daytime (Jaeger & Hailman 1981, Myers & Daly 1983), which should make them more vulnerable to diurnal avian predators. However, most *Dendrobates* and *Bufo* are toxic (Daly & Myers 1967, Daly *et al.* 1987, 1994), which probably explains their avoidance by birds. This is not the case of most *Colostethus* (Myers & Daly 1983), including *C. flotator*, which are free of toxins and dendrobatid-type alkaloids (J. W. Daly, *pers. comm.*). The fact that this latter species is not preyed upon by birds is puzzling considering that: (1) these frogs are the most abundant in the area; (2) they are active foragers (Toft 1981) concentrating their activities in early morning and late afternoon (Jaeger *et al.* 1976) when avian foraging activities are highest; (3) they are relatively slow-moving frogs which escape through a series of short hops (Duellman & Trueb 1986); and (4) their mean size (15.2 mm) lies within the range of the frogs taken by birds in this study. In comparison, *Eleutherodactylus* are predominantly nocturnal, sit-and-wait predators that forage on large insects (Toft 1981). In addition to being much less numerous and presumably less conspicuous than *Colostethus*, *Eleutherodactylus* have long legs which allow them to escape at a higher speed through single, long leaps (Duellman & Trueb 1986). Despite the fact that *Eleutherodactylus* represented less than 10% of all frogs observed during the censuses, the different groups of *Eleutherodactylus* species were taken in the same rank order as their relative abundance. The low proportion of *Eleutherodactylus* of adult size observed during the census (65 out of 418 individuals measured) suggests that birds select for the largest individuals in the forest.

Terrestrial eggs of frogs and anoles are most commonly preyed upon by large invertebrates (Andrews 1982, Duellman & Trueb 1986). *Leptotila cassinii* is a ground-foraging dove that searches for fruits and arthropods by pushing aside fallen leaves with its bill (Stiles *et al.* 1989). This searching tactic probably allowed the bird to find frog and lizard eggs hidden in the litter. Although ground-foraging birds are considered as potential predators, this study provides the first reports of avian predation on *Eleutherodactylus* and *Anolis* eggs to our knowledge.

Predator attributes and seasonality of predation

Lizard intake was not associated with any morphological traits of avian predators, but rather with the frequency of foraging at army-ant swarms, a behaviour present in many tropical birds although attendance rates are variable among species (Willis & Oniki 1978). During his intensive study, Willis (1967, 1972a, b; 1973) observed various bird species feeding on lizards while attending army-ant swarms, but not when foraging away from the ants. Similarly, small vertebrates have been reported as occasional food items in the diet of various army-ant following birds (Chapman & Rosenberg 1991, Chesser 1995). With the exception of *Attila spadiceus*, which probably foraged actively upon lizards in a fashion similar to canopy dwellers, most

birds in the forest understorey appear to be opportunistic lizard-eaters. Our analyses suggest that predation risks for *Anolis* are highest when they are disturbed by ant swarms and that most army-ant followers in tropical mainland humid forests are potential lizard predators. While we predicted social behaviour to contribute to vertebrate predation, we did not expect ant-following to be the main explanatory variable of lizard intake. Seasonality of swarming behaviour, however, cannot account for the variation observed in lizard predation rates since *Eciton burchelli* swarms are aseasonal and those of *Labidus praedator* decrease during the dry season (Willis 1967) when lizard predation is highest. In contrast to our expectations, lizard intake decreased sharply during the early avian breeding season and subsequently varied similarly to arthropod availability. The low intake of lizards during avian nesting activities is probably related to a decrease in foraging at army-ant swarms during that period, a behaviour that characterizes most species, even the most frequent army-ant followers (Willis 1967, 1972a, b). The fact that lizard intake varies similarly to arthropod availability, suggests that lizards are not just an alternate food type to these primarily insectivorous birds.

Frog predation on the other hand was closely related to the birds' morphological characters, more specifically bill and body lengths. For any particular body length, birds with longer bills were more likely to feed on frogs. These two variables were strongly correlated ($r = 0.858$, df = 14, $P < 0.00005$) among frog-eating birds, and showed a fairly constant 1:7 ratio (as opposed to a mean but highly variable 1:10 ratio in birds not known to eat frogs). Longer bills allow more rapid movements of the tip of the bill, facilitating the capture of fast-moving prey (Ashmole 1968). Long tails are likely to be prejudicial to bird motility in ground or vegetation sallies, and this is probably why bill length is more closely related to body length (strongly influenced by tail length) than to body mass in frog-eating birds. *Eleutherodactylus* are fast moving, long-legged frogs, and presumably the hardest ones to catch in the forest. Our results suggest that short-tailed and long-billed birds are at a strong advantage to successfully prey upon them. In contrast to lizards, there was no evidence of social foraging contributing to avian predation on frogs.

Among the dependent variables selected, only frog availability accounted for the seasonal variation observed in frog predation. Concurrent variations in indices of frog and arthropod availability suggest that birds feed opportunistically on frogs, especially when invertebrates are less abundant. While this finding is in accordance with our third hypothesis, over 50% of the temporal variation in frog intake remains unexplained, suggesting that other factors are potentially involved. Jaeger (1981) observed that birds foraging in the litter were less efficient in capturing salamanders during the wet season because of the birds' inability to separate wet leaves. Differences in abundance pattern among age classes could also affect predation rates since birds preyed proportionally more on adult-sized frogs.

Predator attributes differed importantly between frog- and lizard-eaters. Moreover, frog-eating birds were not more likely to feed on lizards than birds not known to eat frogs, and *vice versa*. Frogs are certainly as likely as lizards to be disturbed by army-ant swarms, but only lizards flee by climbing up stems where most army-ant following birds forage (Willis & Oniki 1978). This distinction in escaping behaviour might well account for the differences observed since *Formicarius analis* and *Myrmeciza exsul*, which are some of the few army-ant followers that typically forage on the ground, fed extensively on frogs as well. Similarly, long bills should be advantageous for capturing fast-moving prey such as *Anolis*. However, unless they have evolved a stronger musculature, longer beaks are proportionally weaker (Ashmole 1968), and therefore less efficient for handling lizards as they writhe strenuously after being caught.

Frogs and lizards appear to be a regular food source for several bird species at our neotropical forest site. Attributes of frog-eating birds suggest that simple morphological characters can segregate members of a guild even though a minor prey item is involved. Attributes of lizard-eating species suggest that social feeding can contribute importantly to diet composition and not only to foraging success. It is noteworthy that so few factors could discriminate the lizard- and frog-eating birds almost perfectly from a subset of 43 species exhibiting a great diversity of physiological, morphological and behavioural traits. While this study highlights the potential complexity of food webs, it also raises questions about their fragility and recurrence among habitats and seasons. What are the attributes of lizard-eating birds within tropical dry forests lacking swarms of army ants? How would a decrease in *Eleutherodactylus* populations affect the abundance of birds for which frogs represent an important alternate food when arthropods are scarce?

Several of the bird species in this study are reported to feed on frogs and/or lizards for the first time, confirming that many trophic links have yet to be described. Food webs have become a theoretical field based on an oversimplified and often inaccurate understanding of trophic interactions within communities (Goldwasser & Roughgarden 1993, 1997; Polis 1991). We hope that this contribution will encourage community-wide investigations of diets, which are a necessary step if we wish to understand empirical patterns and construct food web models reflecting real processes within natural communities.

ACKNOWLEDGEMENTS

This study was supported by the Natural Sciences and Engineering Research Council of Canada (postdoctoral grant to B. Poulin), the National Science Foundation (Grant DEB-9200081 to R. Ibáñez), and the Smithsonian Tropical Research Institute (short-term fellowship to C. Hernández). We are indebted to Douglas Robinson for kindly providing his unpublished data on the vertical distribution of avian foraging, and to James Coronado and Iván Domínguez for their assistance during the frog and lizard censuses. We are grateful to the

Smithsonian Tropical Research Institute for providing logistical support and to INRENARE for issuing the research permits to work in Soberanía National Park.

LITERATURE CITED

ANDREWS, R. M. 1982. Spatial variation in egg mortality of the lizard *Anolis limifrons*. *Herpetologica* 38:165–171.

ANDREWS, R. M. & RAND, A. S. 1982. Seasonal breeding and long-term population fluctuations in the lizard *Anolis limifrons*. Pp. 405–411 in Leigh, E. G. Jr., Rand, A. S. & Windsor, D. M. (eds). *The ecology of a tropical forest: seasonal rhythms and long-term changes*. Smithsonian Institution Press, Washington, DC.

ANDREWS, R. M., RAND A. S. & GUERRERO, S. 1983. Seasonal and spatial variation in the annual cycle of a tropical lizard. Pp. 441–454 in Rhodin, A. G. J. & Miyata, K. (eds). *Advances in herpetology and evolutionary biology*. Museum of Comparative Zoology, Cambridge.

ASHMOLE, N. P. 1968. Body size, prey size, and ecological segregation in five sympatric tropical terns (Aves: Laridae). *Systematic Zoology* 17:292–304.

BENNETTS, R. E. & DREITZ, V. 1997. Possible use of wading birds as beaters by snail kites, boat-tailed grackles, and limpkins. *Wilson Bulletin* 109:169–173.

BRANDL, R., KRISTIN, A. & LEISLER, B. 1994. Dietary niche breadth in a local community of passerine birds, an analysis using phylogenetic contrasts. *Oecologia* 98:109–116.

CAMPBELL, H. W. 1973. Ecological observations on *Anolis lionotus* and *Anolis poecilopus* (Reptilia, Sauria) in Panama. *American Museum of Natural History, Novitates* 2516:1–29.

CHAPMAN, A. & ROSENBERG, K. V. 1991. Diets of four sympatric Amazonian woodcreepers (Dendrocolaptidae). *Condor* 93:904–915.

CHESSER, R. T. 1995. Comparative diets of obligate ant-following birds at a site in northern Bolivia. *Biotropica* 27:382–390.

CROAT, T. B. 1978. *Flora of Barro Colorado Island*. Stanford University Press, Stanford. 943 pp.

DALY, J. W., GUSOVSKY, F., MYERS, C. W., YOTSU-YAMASHITA, M. & YASUMOTO, T. 1994. First occurrence of tetrodotoxin in a dendrobatid frog (*Colostethus inguinalis*), with further reports for the bufonid genus *Atelopus*. *Toxicon* 32:279–285.

DALY, J. W. & MYERS, C. W. 1967. Toxicity of Panamanian poison frogs (*Dendrobates*): some biological and chemical aspects. *Science* 156:970–973.

DALY, J. W., MYERS, C. W. & WHITTAKER, N. 1987. Further classification of skin alkaloids from Neotropical poison frogs (Dendrobatidae), with a general survey of toxic/noxious substances in the Amphibia. *Toxicon* 25:1023–1095.

DUELLMAN, W. E. & TRUEB, L. 1986. *Biology of amphibians*. McGraw-Hill Book Company, New York. 670 pp.

EVANS, H. E. 1947. Notes on Panamanian reptiles and amphibians. *Copeia* 1947:166–170.

GOLDWASSER, L. & ROUGHGARDEN, J. 1993. Construction and analysis of a large Caribbean food web. *Ecology* 74:1216–1233.

GOLDWASSER, L. & ROUGHGARDEN, J. 1997. Sampling effects and the estimation of food-web properties. *Ecology* 78:41–54.

GREENE, H. W. 1988. Antipredator mechanisms in reptiles. Pp. 1–152 in Gans, C. & Huey, R. B. (eds). *Biology of the Reptilia*. Volume 16. *Ecology B. Defense and life history*. Alan R. Liss Inc., New York.

JAEGER, R. G. 1981. Birds as inefficient predators on terrestrial salamanders. *American Naturalist* 117:835–837.

JAEGER, R. G. & HAILMAN, J. P. 1981. Activity of Neotropical frogs in relation to ambient light. *Biotropica* 13:59–65.

JAEGER, R. G., HAILMAN, J. P. & JAEGER, L. S. 1976. Bimodal diel activity of a Panamanian dendrobatid frog, *Colostethus nubicola*, in relation to light. *Herpetologica* 32:77–81.

LEDERER, R. J. 1975. Bill size, food size, and jaw forces of insectivorous birds. *Auk* 92:385–387.

MYERS, C. W. & DALY, J. W. 1983. Dart-poison frogs. *Scientific American* 248:120–133.

POLIS, G. A. 1991. Complex trophic interactions in deserts: an empirical critique of food-web theory. *American Naturalist* 138:123–155.

POULIN, B. & LEFEBVRE, G. 1995. Additional information on the use of emetic in determining the diet of tropical birds. *Condor* 97:897–902.

POULIN, B. & LEFEBVRE, G. 1997. Estimation of arthropods available to birds: effect of trapping technique, prey distribution, and bird diet. *Journal of Field Ornithology* 68:426–442.

RAND, A. L. 1954. Social feeding behavior of birds. *Fieldiana-Zoology*. 36:1–71.

RAND, A. S. & MYERS, C. W. 1990. The herpetofauna of Barro Colorado Island, Panama: an ecological summary. Pp. 386–409 in Gentry, A. H. (ed.). *Four Neotropical rainforests*. Yale University Press, New Haven.

RIDGELY, R. S. & GWYNNE, J. A. 1989. *A guide to the birds of Panama with Costa Rica, Nicaragua, and Honduras*. Princeton University Press, Princeton. 534 pp.

SAVAGE, J. M. & TALBOT, J. J. 1978. The giant anoline lizards of Costa Rica and western Panama. *Copeia* 1978:480–492.

SEXTON, O. J., ORTLEB, E. P., HATHAWAY, L. M., BALLINGER, L. E & LICHT, P. 1971. Reproductive cycles of three species of anoline lizards from the isthmus of Panama. *Ecology* 52:201–215.

STILES, F. G., SKUTCH, A. F. & GARDNER, D. 1989. *A guide to the birds of Costa Rica*. Cornell University Press, Ithaca. 511 pp.

TAYLOR, E. H. 1956. A review of the lizards of Costa Rica. *University of Kansas Science Bulletin* 38:1–322.

TOFT, C. A. 1981. Feeding ecology of Panamanian litter anurans: patterns in diet and foraging mode. *Journal of Herpetology* 15:139–144.

WETMORE, A. 1965. *The birds of the Republic of Panamá. Part 1. Tinamidae (Tinamous) to Rynchopidae (Skimmers)*. Smithsonian Miscellaneous Collections, Volume 150. Smithsonian Institution Press, Washington, DC.

WETMORE, A. 1968. *The birds of the Republic of Panamá. Part 2. Columbidae (pigeons) to Picidae (woodpeckers)*. Smithsonian Miscellaneous Collections, Volume 150. Smithsonian Institution Press, Washington, DC.

WETMORE, A. 1972. *The birds of the Republic of Panamá. Part 3. Passeriformes: Dendrocolaptidae (woodcreepers) to Oxyruncidae (sharpbills)*. Smithsonian Miscellaneous Collections, Volume 150. Smithsonian Institution Press, Washington, DC.

WETMORE, A, PASQUIER, R. F. & OLSON, S. L. 1984. *The birds of the Republic of Panamá. Part 4. Passeriformes: Hirundinidae (swallows) to Fringillidae (finches)*. Smithsonian Miscellaneous Collections, Volume 150. Smithsonian Institution Press, Washington, DC.

WILBUR, H. M. 1997. Experimental ecology of food webs: complex systems in temporary ponds. *Ecology* 78:2279–2302.

WILLIS, E. O. 1967. The behavior of bicolored antbirds. *University of California Publications in Zoology* 79:1–132.

WILLIS, E. O. 1972a. The behavior of plain-brown woodcreepers, *Dendrocincla fuliginosa*. *Wilson Bulletin* 84:377–420.

WILLIS, E. O. 1972b. The behavior of spotted antbirds. *American Ornithologists' Union Monographs* 10:1–162.

WILLIS, E. O. 1973. The behavior of ocellated antbirds. *Smithsonian Contributions to Zoology* 144:1–57.

WILLIS, E. O & ONIKI, Y. 1978. Birds and army ants. *Annual Review of Ecology and Systematics* 9:243–263.

WUNDERLE, J. M. 1981. Avian predation upon *Anolis* lizards on Grenada, West Indies. *Herpetologica* 37:104–108.

ZUG, G. R. 1993. *Herpetology: an introductory biology of amphibians and reptiles*. Academic Press, New York. 527 pp.