



**Extinction-Mediated Competition: The Anolis Lizards and Insectivorous Birds of the West Indies**

S. Joseph Wright

*American Naturalist*, Volume 117, Issue 2 (Feb., 1981), 181-192.

---

Your use of the JSTOR database indicates your acceptance of JSTOR's Terms and Conditions of Use. A copy of JSTOR's Terms and Conditions of Use is available at <http://www.jstor.org/about/terms.html>, by contacting JSTOR at [jstor-info@umich.edu](mailto:jstor-info@umich.edu), or by calling JSTOR at (888)388-3574, (734)998-9101 or (FAX) (734)998-9113. No part of a JSTOR transmission may be copied, downloaded, stored, further transmitted, transferred, distributed, altered, or otherwise used, in any form or by any means, except: (1) one stored electronic and one paper copy of any article solely for your personal, non-commercial use, or (2) with prior written permission of JSTOR and the publisher of the article or other text.

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.

*American Naturalist* is published by University of Chicago Press. Please contact the publisher for further permissions regarding the use of this work. Publisher contact information may be obtained at <http://www.jstor.org/journals/ucpress.html>.

---

*American Naturalist*  
©1981 University of Chicago Press

JSTOR and the JSTOR logo are trademarks of JSTOR, and are Registered in the U.S. Patent and Trademark Office. For more information on JSTOR contact [jstor-info@umich.edu](mailto:jstor-info@umich.edu).

©2001 JSTOR

EXTINCTION-MEDIATED COMPETITION:  
THE *ANOLIS* LIZARDS AND INSECTIVOROUS  
BIRDS OF THE WEST INDIES

S. JOSEPH WRIGHT\*

Biology Department, University of California, Los Angeles, California 90024

*Submitted January 5, 1978; Accepted July 5, 1979*

Large, predatory mammals are rarely found on oceanic islands because they are poor overwater colonists (Carlquist 1965) and require large home ranges and so would be susceptible to extinction on islands. Evolutionary responses to the resulting ecological vacuum include the giant endemic raptors which once inhabited the Greater Antilles (Arredondo 1976) and the Gargano Peninsula (Ballmann 1973, 1976) and the Komodo dragon of the Lesser Sunda Islands (Carlquist 1965). Slight differences in persistence and colonization abilities might also affect the island distributions of competitors on an ecological time scale. The *Anolis* lizards and insectivorous birds of the Greater and Lesser Antilles present such a possibility.

Anoles are the most conspicuous component of the West Indian herpetofauna, and all anoles are diurnal insectivores. On the larger islands of the Greater Antilles, the member species of complex anole communities partition microhabitats and perch sites with the result that anoles are ubiquitous throughout the vegetation in all but the most xeric habitats (e.g., Rand 1964). On smaller islands with fewer anole species, ecological release has occurred and anoles are again ubiquitous (Lister 1976). Anoles can attain astronomical population densities in the West Indies. On seven islands anole densities in dense, sclerophyll scrub varied between 0.13 and 0.41 m<sup>-2</sup> (personal observation). On St. Croix 80 adult anoles were found in a single tree (Ruibal and Philibosian 1974), and on Abaco anole densities reach 0.97 m<sup>-2</sup> (Schoener and Schoener 1980).

On the other hand, insectivorous birds do poorly in the Greater and Lesser Antilles. In most habitats in the continental neotropics, insectivorous birds outnumber frugivorous birds. In the Antilles, the relative abundances of insectivorous and frugivorous birds are reversed (John Terborgh, personal communication; personal observation). It is tempting to suggest that the relative abundances of anoles and insectivorous birds are linked. Indeed, in central Panama, insectivorous lizards and birds affect one another's abundances through exploitation competition (Wright 1979). In this paper I will explore this possibility in the Antilles.

\* Present address: Smithsonian Tropical Research Institute, APDO 2072, Balboa, Republic of Panama.

Am. Nat. 1981. Vol. 117, pp. 181-192.  
© 1981 by The University of Chicago. 0003-0147/81/1702-0004\$02.00

## METHODS

The relative abundances of anoles and insectivorous birds were obtained at sites on the following islands on the following dates: Puerto Rico, February 6–8, 1973; Mona, February 14–17, 1973; Guadeloupe, January 27–31, 1974; Desirade, January 18–22, 1974; Terre-de-Haute, January 13–17, 1974; Terre-de-Basse, January 13–17, 1974; and Bequia, July 14–17, 1975. Exact locations and further descriptions of study sites on Puerto Rico and Mona Island and in the Guadeloupean archipelago can be found in Terborgh and Faaborg (1973) and Terborgh et al. (1978), respectively. Bequia is in the Grenadines, and the Bequia study site was 200 m from the east end of Princess Anne Beach. North American migrants are nearly absent from the southern Caribbean (Terborgh and Faaborg 1980), and anole fecundity is aseasonal in the southern Caribbean (Licht and Gorman 1970). Therefore the population densities of anoles and insectivorous birds should show little seasonal change on Bequia which was visited during a different season than the remaining sites.

Each study site was located in thick, mostly evergreen, sclerophyll scrub. Vegetation structure was quantified by taking foliage height densities (MacArthur and MacArthur 1961), plant species diversities, and light meter readings. Plant species diversity was obtained for plants greater than 2.5 cm dbh in one 30 m  $\times$  30 m plot at each study site. Plant species diversity equals  $1/\sum P_i^2$ , where  $P_i$  is the proportion of individuals in the  $i$ th species. Light meter readings were taken at 20 points between 1,100 and 1,300 h on cloudless days and at a height of 30.5 cm.

*Population Estimates*

Birds were censused with mist nets. Between 10 and 20 nets (2 m  $\times$  12 m, 36-mm mesh) were erected end-to-end in a straight line at each site. Nets were opened from dawn to dusk for 3 or 4 consecutive days and population estimates for the entire avifauna were obtained with the regression technique of MacArthur et al. (1972). Population estimates were obtained for each bird species by multiplying the number of captured individuals of each species by the ratio of the population estimate for the entire avifauna to the total number of captures of all species. The method used to obtain a population estimate for each bird species involves no additional assumptions because the regression technique assumes that all individuals which forage below 2 m are equally likely to be captured (MacArthur et al. 1972). Mist nets effectively capture birds which weigh between 3 g and 150 g; all of the insectivorous bird species studied were in this range, and the assumption that all individuals which forage below 2 m are equally likely to be captured is valid. Inaccurate population estimates will be obtained for bird species which rarely forage below 2 m. The population size of only one insectivorous bird, *Tyrannus dominicensis*, is likely to have been underestimated for this reason, and *T. dominicensis* was rare at those study sites at which it was present.

A Lincoln index was used to census anoles in 15.25 m  $\times$  15.25 m plots. Ruibal and Philibosian (1974) have found that the Lincoln index gives accurate estimates of anole population densities. At each site two days were spent capturing anoles.

Each captured animal was marked dorsally between the hind legs with white paint and released at the capture site. On the third day each plot was censused with the aid of binoculars. Between 20% and 49% of the anoles in each plot were marked.

#### *Biomass Estimates*

Estimates of the arthropod portion of each bird species' diet were obtained from stomach content data for the birds of Puerto Rico (Wetmore 1916) and Guadeloupe (Danforth 1939). Data from conspecifics on Puerto Rico were used to approximate the diet of those Guadeloupean species for which Danforth sampled fewer than five stomachs. Stomach data for *Bequia* are not available. Therefore data for the nearest relative examined by Danforth or Wetmore were substituted. The diet of *Turdus nudigens* which does not have a congener on Guadeloupe or Puerto Rico was approximated by the diet of *Margarops fuscatus*, a confamilial of roughly similar habits. Hummingbirds were omitted from all analyses because of their low biomass and abundances, and unknown extent of insectivory. The diet of the remaining nectarivore, *Coereba flaveola*, was obtained from over 1,000 foraging observations compiled by Snow and Snow (1971) and Lack (1976).

The population estimate for each bird species was weighted by the proportion of its diet which consisted of arthropod prey and multiplied by the mass of the average individual of the species. This value summed over all the species netted at a site, excluding hummingbirds, will be referred to as the avian biomass dependent upon arthropod prey.

Between 96% and 100% of the items found in anole stomachs are arthropods (Wolcott 1924; Schoener 1968a; Schoener and Gorman 1968). Therefore the biomass of anoles which is supported by arthropod prey was obtained by multiplying the anole population estimate by the mass of the average individual.

#### *Diet Overlaps*

The taxonomic distributions of the arthropod prey taken by Puerto Rican anoles and insectivorous birds were used to compute diet overlaps. If at least 75% of a bird species' stomach contents consisted of arthropod prey, that species was included in the diet analysis. Nonarthropod prey items did not contribute to diet overlaps. Swallows and swifts were not included in the analysis because they forage above rather than within the vegetation. The diets of nine insectivorous birds (Wetmore 1916) and six anoles (Wolcott 1924) were compared. Prey were identified to order within the class Insecta and to class within the remainder of the phylum Arthropoda. Diet overlaps,  $\alpha_{ij}$ , were computed with the following formula:  $\alpha_{ij} = \sum(P_{ih}P_{jh})/\sum P_{ih}$ , where  $P_{ih}$  equals the proportion of species  $i$ 's diet composed of arthropod taxon  $h$  (Levins 1968).

#### *Insectivory in the West Indian Avifauna*

The importance of insectivory to the terrestrial avifauna was assessed for the following islands: Saba, St. Eustatius, Anguilla, Nevis, Montserrat, St. Kitts, St.

Vincent, Guadeloupe, Puerto Rico, and Jamaica. The terrestrial avifauna includes all species in the Falconiformes and the orders Columbiformes through Passeriformes excepting the Alcedinidae. Distributional data were obtained from Terborgh et al. (1978) for the northern Lesser Antilles, from Lack (1976) for Jamaica, and from Bond (1971) for Guadeloupe, St. Vincent, and Puerto Rico. Food habits of the closest relative studied by Danforth (1939), Lack (1976), or Wetmore (1916) were used to estimate the proportion of each bird species' diet which consisted of arthropods. These proportions were summed for all of the terrestrial bird species which bred on each island. This sum was divided by the number of terrestrial bird species which bred on the island to obtain the proportional contribution of insectivory to the terrestrial avifauna.

#### RESULTS

All sites had nearly identical foliage height profiles (table 1). Plant species diversity was low at the Terre-de-Basse site which may reflect the relatively high level of human disturbance at this site; otherwise, the habitat structures of the seven study sites were very similar (table 1).

Frequency distributions of overlap values which were generated by comparisons between the taxonomic composition of the prey taken by pairs of anole species, pairs of bird species, and one anole and one bird species are presented in figure 1. All prey records are from Puerto Rico. The average diet overlap between pairs of anole species is greater than both the average diet overlap between pairs of bird species ( $t = 5.21$ ,  $P < .001$ ) and the average diet overlap between pairs consisting of one anole species and one bird species ( $t = 6.09$ ,  $P < .001$ ). The mean diet overlap between pairs of bird species and the mean diet overlap between pairs consisting of one anole and one bird species are nearly identical ( $t = 0.29$ ,  $P < .50$ ). With respect to the taxonomic distributions of their prey, insectivorous birds cannot be distinguished from anoles.

If two taxa compete for their prey they must utilize the same taxa and the same size distributions of prey items. Correlations between the size and taxa of the prey taken by different insectivorous bird species indicate that prey size and prey taxa are not independent niche dimensions (Hespenheide 1971, 1975). Moreover, anoles have indeterminate growth, and different size classes of anoles take mean prey sizes of between 2.0 mm and 19.3 mm (Schoener 1968a; Schoener and Gorman 1968). Size distributions are not available for the arthropod prey taken by West Indian birds, but 22 bird species of North and Central America take mean arthropod prey sizes of between 1.4 mm and 14.7 mm (Root 1967; Hespenheide 1971, 1975). By inference the prey sizes taken by West Indian birds must overlap the broad range of prey sizes taken by West Indian anoles.

The biomass of anoles at a site varied between 0.18 g/m<sup>2</sup> and 1.79 g/m<sup>2</sup> (table 2). The biomass of birds dependent upon arthropod prey varied between 146 g/10 mist nets and 909 g/10 mist nets (table 2). Avian abundances could not be converted to density measures because the area censused by a mist net is not known. The biomass of anoles at a site and the biomass of birds dependent upon arthropod prey are negatively correlated (fig. 2.,  $r = -.72$ ,  $P < .05$ , one-tailed  $t$ -test). A

TABLE 1  
VEGETATION CHARACTERISTICS

	Puerto Rico	Guadeloupe	Mona	Desirade	Terre-de-Basse	Terre-de-Haute	Bequia
Percentage of foliage between							
0-0.61 m .....	29	27	24	22	...	12	11
0.61-7.62 m .....	71	73	76	78	...	84	80
above 7.62 m .....	0	0	0	0	...	4	9
Foliage height diversity ( $-\sum P_i \ln P_i$ ) .....	.60	.58	.55	.53	...	.54	.63
Plant species diversity ( $1/\sum P_i^2$ ) .....	7.9	5.3	7.3	...	2.6	4.6	4.8
Median illumination at 30.5 cm (ft-c) .....	3,200	1,800	2,400	1,800	2,100	2,400	...

\* Data not available.

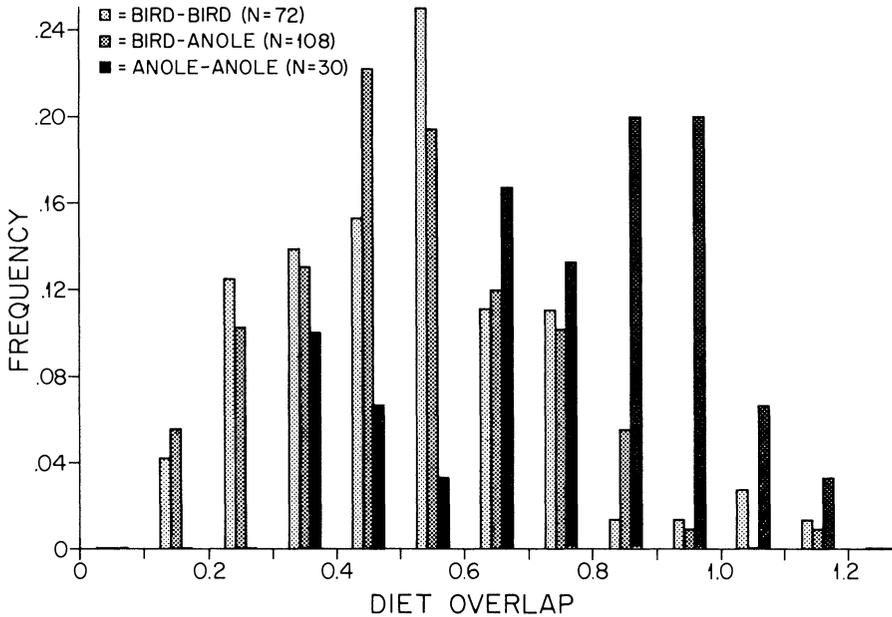


FIG. 1.—Frequency histograms of diet overlap values between pairs of insectivorous bird species, pairs of anole species, and pairs consisting of one anole and one insectivorous bird species. All species are from Puerto Rico. Diet overlaps were computed from the taxonomic distributions of the arthropod prey items found in the guts of each species.

one-tailed *t*-test was used to ascertain the significance of this correlation because there is an a priori expectation that the biomasses of competing taxa are negatively correlated.

The effect of island area on the outcome of the competitive interaction between anoles and birds was explored. Study sites were ranked by island area and by the ratio of anole biomass to bird biomass dependent upon arthropod prey (table 2). A Spearman rank correlation indicates that this ratio has low values on large and

TABLE 2  
ISLAND AREAS, CENSUS RESULTS, AND RATIO OF ANOLE BIOMASS  
TO BIRD BIOMASS DEPENDENT UPON ARTHROPOD PREY

	Area (km)	Anole Biomass: Bird Biomass	Anole Biomass (g/233 m <sup>2</sup> )	Bird Biomass* (g/10 mist nets)
Puerto Rico . . . . .	8776	.07	64	909
Guadeloupe . . . . .	1525	.18	93	530
Mona . . . . .	62.1	.27	172	627
Desirade . . . . .	27.1	.40	227	566
Bequia . . . . .	18.3	.37	228	613
Terre-de-Basse . . . .	6.5	.98	416	425
Terre-de-Haute . . . .	4.1	2.23	326	146

\* Bird biomass dependent upon arthropod prey.

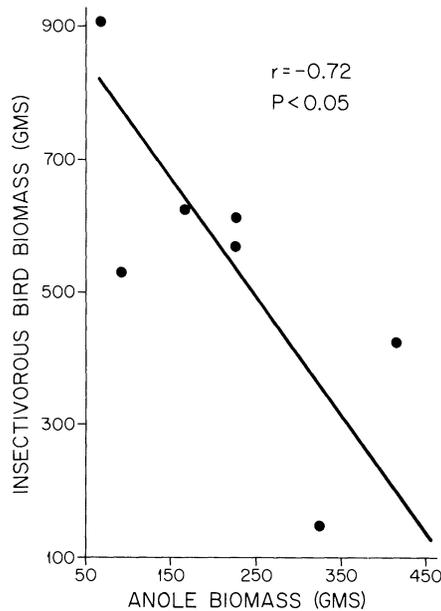


FIG. 2.—Abscissa, anole biomass at a site; ordinate, avian biomass dependent upon arthropod prey at the site. The solid line was fitted by least-squares regression. The significance level was determined with a one-tailed  $t$ -test because there is an a priori prediction that the biomasses of competing taxa should be negatively correlated.

high values on small islands ( $r_s = .96$ ,  $P < .001$ ). Thus birds are relatively important arthropod predators on large islands and anoles are relatively important arthropod predators on small islands.

Anole biomass and log island area are negatively correlated ( $r = -.89$ ,  $P < .01$ ). Release from predation might explain the high anole biomasses which are typical of small islands (table 2), and thereby might, at least in part, explain the correlation between island area and the ratio of anole biomass to bird biomass dependent upon arthropod prey. Birds and snakes are the only potential predators of anoles in dry, sclerophyll scrub in the West Indies. On Puerto Rico three snake species, *Alsophis portoricensis*, *Arrhyton exiquum*, and *Epicrates inornatum*, may prey upon anoles, and two of these species are represented by conspecifics or endemic congeners on Mona Island (MacLean et al. 1977). On Guadeloupe two snake species, *Alsophis antillensis* and *Dromicus juliae*, may prey upon anoles, and one of these species is present on the Iles des Saintes (MacLean et al. 1977). Only four bird species which frequent dry, sclerophyll scrub on Puerto Rico and/or Guadeloupe are significant anole predators. These four and the proportion of their stomach contents (by volume) composed of anoles are: *Falco sparverius* (40%), *Saurothera vielloti* (79%), *Tyrannus dominicensis* (3.6%), and *Mimocichla plumbea* (<8.4%; Wetmore 1916; Danforth 1939). The sparrowhawk was present at each study site, and *T. dominicensis* was present at all sites except Terre-de-Basse and Terre-de-Haute. *Saurothera vielloti* is endemic to Puerto Rico where it

is rare, and of the seven study islands *Mimochichla plumbea* occurs only on Puerto Rico. Anoles constitute no more than 1% of the stomach contents (by volume) of the other bird species observed at the seven study sites (Wetmore 1916; Danforth 1939). Hence, avian predators are probably not a significant cause of mortality among anoles in dry, sclerophyll scrub in the Greater and Lesser Antilles. Moreover, the distributions of predators do not suggest that anoles experience lower predation pressure on small islands than on large islands in the Antilles.

The proportion of an island's terrestrial avifauna which is composed of insectivorous species varied between 19% on Saba and 46% on Jamaica. The proportion of the terrestrial avifauna which is composed of insectivorous species and log island area are positively correlated (fig. 3,  $r = .86$ ,  $P < .01$ ).

#### DISCUSSION

Exploitation competition might occur between two taxa if they contest a common, limiting resource. West Indian anoles are food-limited (Licht 1974; Andrews 1976; Schoener and Schoener 1978), and there is a high degree of overlap between the diets of West Indian anoles and insectivorous birds (fig. 1). Reciprocal changes in the biomasses of anoles and insectivorous birds on islands of different area (fig. 2) provide further evidence that these taxa compete for their arthropod prey.

Similar results were obtained at a series of six island and two mainland sites in the vicinity of Lake Gatun, Panama (Wright 1979). Comparative and correlative evidence indicated that: (1) The numerically dominant lizard in central Panama, *Anolis limifrons*, is food-limited; (2) there is broad overlap between the diets of a representative insectivorous bird and *A. limifrons*; (3) avian insectivores have a major impact on arthropod abundances; (4) avian abundance influences the physi-

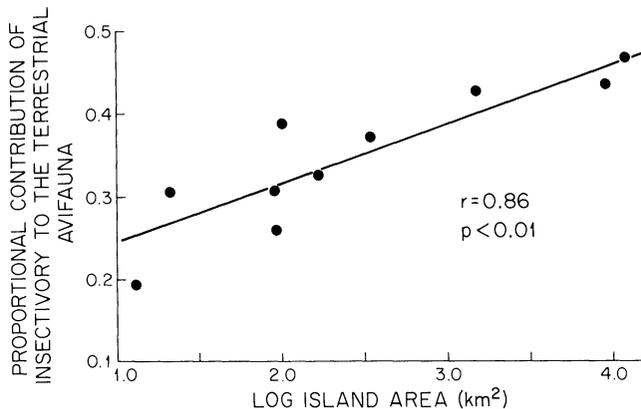


FIG. 3.—Abscissa, log island area; ordinate, the proportion of the resident terrestrial avifauna which is composed of insectivorous species. The solid line was fitted by least-squares regression.

ological condition of *A. limifrons*; and (5) there are reciprocal between-site changes in the abundances of birds and insectivorous lizards. In the Lake Gatun area, the number of bird species at a site accounted for 96% of the between-site variation in avian abundance. Bird species number is controlled by biogeographic processes, i.e., extinction and immigration, which act independently of the bird-lizard interaction. Bird species number and avian abundance were relatively high on the Panamanian mainland and on large islands and relatively low on small islands. Consequently, insectivorous lizards experienced ecological release on small islands and were more abundant on small islands than on the mainland and large islands.

The same pattern occurs in the Antilles. The relative abundance of insectivorous birds and anoles shifts toward anoles as island area declines (table 2, cols. 1, 2). As mentioned previously, there is very little difference in the number of potential anole predators on the study islands. Therefore differences in predation pressure cannot explain the increased abundance of anoles on small islands. Rather, their low metabolic rates and potentially great population densities may preadapt anoles to an island existence.

The expected time until an island population becomes extinct increases as the size of the population increases (MacArthur and Wilson 1967; Abbott and Grant 1976; Jones and Diamond 1976). Birds and lizards should experience different island extinction rates because lizards can maintain much greater population densities than can birds. Free-ranging insectivorous birds require 35 times more energy per day than do free-ranging iguanid lizards of equal body weight (Bennett and Nagy 1977). Therefore birds require much larger home ranges than do lizards of equal body weight (Schoener 1968*b*; Turner et al. 1969), and, within the confines of an island, lizards should maintain larger populations than do birds of equal body weight.

The disparity between the island-wide population sizes of anoles and insectivorous birds will be increased by differences in their body weights. The mean body weight of sexually mature males of the anole species studied varied between 2.4 g and 8.3 g, and the mean body weights of the bird species studied varied between 8.9 g and 107.6 g. Hence, the body weights of the bird species studied are between 1.1 and 44.8 times greater than the body weights of the anole species studied, and birds require 35 times more energy per unit body weight than do anoles. If only metabolic demands are considered, anoles should be able to support populations which are 40 to 1,500 times larger than the populations of their avian competitors, and anoles should experience concomitantly lower extinction rates.

The relative avian and saurian extinction rates predicted from energetic considerations have been verified empirically. Since the Miocene inundation of the West Indies, the fossil record suggests that many West Indian bird species have become extinct (Olson 1978), while at most a single anole population has become extinct (Williams 1969). During the twentieth century the sole extinction of a West Indian anole, *A. watsi* on Anguilla, was caused by human habitat destruction (Lazell 1972). By way of contrast, two of the 10 bird species present on Mona

Island in 1901 had become extinct by 1971 (Terborgh and Faaborg 1973), and avian extinctions are an ongoing phenomenon throughout the West Indies (Ricklefs and Cox 1972). Avian extinction rates are higher than saurian extinction rates on Mona Island (Terborgh and Faaborg 1973), on islands in the Gulf of California (Case 1975), and on islands in Lake Gatun, Panama (Wright 1979).

A mechanism to explain the relationship between island area and the relative abundances of insectivorous birds and lizards will now be proposed. If lizards and birds compete for their arthropod prey, resident lizards might experience ecological release after the extinction of an avian insectivore. In the West Indies, bird populations become extinct more frequently on small islands than on large islands (Ricklefs and Cox 1972) while anole populations are largely immune to extinction (Williams 1969; Lazell 1972). Therefore anoles might experience ecological release more frequently on small islands than on large islands, and, as a result, anoles should be relatively more abundant on small islands, and the bird species which compete with anoles should be relatively more abundant on large islands. This is exactly the case in the West Indies (table 2) and on islands in Lake Gatun, Panama (Wright 1979). In addition, by compensating for the density of a recently extinct avian competitor and minimizing postextinction increases in resource abundances, anoles may increase the expected time between the extinction of the avian competitor and the successful recolonization of the island by another avian insectivore.

If the hypothesized mechanism accounts for the relation between island area and the relative abundances of anoles and insectivorous birds, one additional prediction is possible. Lizards have been hypothesized to interfere with the colonization of small islands by insectivorous birds. Therefore insectivorous birds should account for a progressively smaller proportion of the resident avifauna on progressively smaller islands. This is the case in the West Indies (fig. 3), and insectivorous birds are also underrepresented on small islands in Lake Gatun, Panama (Wright 1979).

#### SUMMARY

Three lines of evidence suggest that West Indian *Anolis* lizards and insectivorous birds compete for their arthropod prey: (1) Extensive diet overlaps exist between anoles and insectivorous birds; (2) West Indian anoles are food-limited; (3) there are reciprocal changes in the population densities of anoles and insectivorous birds on islands of different area. On small islands anoles are relatively abundant and on large islands insectivorous birds are relatively abundant. Differences in extinction rates may account for this pattern. West Indian anoles are apparently immune to extinction, but avian extinctions are a regular phenomenon and occur most frequently on small islands. Therefore, if anoles experience ecological release after the extinction of an avian insectivore, anoles should be progressively more abundant on progressively smaller islands. Concomitantly insectivorous birds should be progressively more abundant on progressively larger islands, as is the case.

## ACKNOWLEDGMENTS

John Terborgh provided the initial stimulus for this study and supplied encouragement and constructive criticism until its completion. Much of the field work would not have been possible were it not for John Faaborg's intimate knowledge of the West Indies, and much of the data from the Guadeloupean archipelago could not have been collected without the aid of the students in Princeton University's 1974 tropical ecology course. Henry Hespdenheide, Martin Cody, Tom Sherry, and Todd Shelly made helpful criticisms of drafts of the manuscript. Funding was received from a National Science Foundation Undergraduate Participation Program grant and Princeton University.

## LITERATURE CITED

- Abbott, I., and P. R. Grant. 1976. Nonequilibrium bird faunas on islands. *Am. Nat.* 110:507-528.
- Andrews, R. M. 1976. Growth rate in island and mainland anoline lizards. *Copeia* 1976:477-482.
- Arredondo, O. 1976. The great predatory birds of the Pleistocene of Cuba. Pages 169-187 in S. L. Olson, ed. *Collected papers in avian paleontology honoring the 90th birthday of Alexander Wetmore*. Smithsonian. *Contrib. to Paleobiol.*, No. 27.
- Ballmann, P. 1973. Fossile vögel aus dem neogen der halbinsel Gargano (Italien). *Scripta Geologica* 17:1-75; 38:1-59. Cited in Olson, S. L. 1978. A paleontological perspective of West Indian birds and mammals. Pages 99-188 in F. B. Gill, ed. *Zoogeography of the Caribbean*. Acad. Nat. Sci. Philadelphia Spec. Publ. No. 13.
- Bennett, A. F., and K. A. Nagy. 1977. Energy expenditure in free-ranging lizards. *Ecology* 58:697-700.
- Bond, J. 1971. *Birds of the West Indies*. 2d ed. Houghton Mifflin, Boston, Mass.
- Carlquist, S. 1965. *Island life*. Natural History Press, New York.
- Case, T. J. 1975. Species numbers, density compensation, and colonizing ability of lizards on islands in the Gulf of California. *Ecology* 56:3-18.
- Danforth, S. T. 1939. Birds of Guadeloupe and adjacent islands. *J. Agric. Univ. P. R.* 23:9-46.
- Hespdenheide, H. A. 1971. Food preference and the extent of overlap in some insectivorous birds with special reference to the Tyrannidae. *Ibis* 113:59-72.
- . 1975. Prey characteristics and predator niche width. Pages 158-180 in M. L. Cody and J. M. Diamond, eds. *Ecology and evolution of communities*. Belknap, Cambridge, Mass.
- Jones, H. L., and J. M. Diamond. 1976. Short-time-basis studies of turnover in breeding bird populations on the California Channel Islands. *Condor* 78:526-549.
- Lack, D. 1976. *Island biology*. Blackwell Scientific, Oxford.
- Lazell, J. D., Jr. 1972. The anoles (Sauria, Iguanidae) of the Lesser Antilles. *Bull. Mus. Comp. Zool.* 143(1):1-115.
- Levins, R. 1968. *Evolution in changing environments*. Princeton University Press, Princeton, N.J.
- Licht, P. 1974. Response of *Anolis* lizards to food supplementation in nature. *Copeia* 1974:215-221.
- Licht, P., and G. C. Gorman. 1970. Reproductive and fat cycles in Caribbean *Anolis* lizards. *Univ. Calif. Publ. Zool.* 95:1-52.
- Lister, B. C. 1976. The nature of niche expansions in West Indian *Anolis* lizards. I. Ecological consequences of reduced competition. *Evolution* 30:659-676.
- MacArthur, R. H. 1972. *Geographical ecology*. Harper & Row, New York.
- MacArthur, R. H., J. M. Diamond, and J. R. Karr. 1972. Density compensation in island faunas. *Ecology* 53:330-342.
- MacArthur, R. H., and J. W. MacArthur. 1961. On bird species diversity. *Ecology* 42:594-598.
- MacArthur, R. H., and E. O. Wilson. 1967. *The theory of island biogeography*. Princeton University Press, Princeton, N.J.

- MacLean, W. P., R. Kellner, and H. Dennis. 1977. Island lists of West Indian amphibians and reptiles. *Smithson. Herpetol. Info. Serv.* No. 40.
- Olson, S. L. 1978. A paleontological perspective of West Indian birds and mammals. Pages 99–118 in F. B. Gill, ed. *Zoogeography of the Caribbean*. Acad. Nat. Sci. Philadelphia Spec. Publ., No. 13.
- Rand, A. S. 1964. Ecological distribution in anoline lizards of Puerto Rico. *Ecology* 45:745–752.
- Ricklefs, R. E., and G. W. Cox. 1972. Taxon cycles in the West Indian avifauna. *Am. Nat.* 106:195–219.
- Root, R. B. 1967. The niche exploitation pattern of the blue-gray gnatcatcher. *Ecol. Monogr.* 37:317–350.
- Ruibal, R., and R. Philibosian. 1974. The population ecology of the lizard *Anolis acutus*. *Ecology* 55:525–537.
- Schoener, T. W. 1968a. The *Anolis* lizards of Bimini: resource partitioning in a complex fauna. *Ecology* 49:704–726.
- . 1968b. Sizes of feeding territories among birds. *Ecology* 49:123–141.
- Schoener, T. W., and G. C. Gorman. 1968. Some niche differences in three Lesser Antillean lizards of the genus *Anolis*. *Ecology* 49:819–830.
- Schoener, T. W., and A. Schoener. 1978. Estimating and interpreting body-size growth in some *Anolis* lizards. *Copeia* 1978:390–405.
- . 1980. Densities, sex ratios, and population structure in four species of Bahamian *Anolis* lizards. *J. Anim. Ecol.* 49:19–53.
- Snow, B. K., and D. W. Snow. 1971. The feeding ecology of tanagers and honeycreepers in Trinidad. *Auk* 88:291–322.
- Terborgh, J., and J. Faaborg. 1973. Turnover and ecological release in the avifauna of Mona Island, Puerto Rico. *Auk* 90:759–779.
- . 1980. Factors affecting the distribution and abundance of North American migrants in the Eastern Caribbean region. In E. S. Morton and A. Keast, eds. *The proceedings of the migrant bird symposium*. National Zoological Park, Washington, D.C.
- Terborgh, J., J. Faaborg, and H. J. Brockmann. 1978. Island colonization by Lesser Antillean birds. *Auk* 95:59–72.
- Turner, F. B., R. I. Jennrich, and J. D. Weintraub. 1969. Home range and body size of lizards. *Ecology* 50:1076–1081.
- Wetmore, A. 1916. Birds of Puerto Rico. U.S. Dep. Agric. Bull. 326:1–140.
- Williams, E. E. 1969. The ecology of colonization as seen in the zoogeography of anoline lizards on small islands. *Q. Rev. Biol.* 44:345–389.
- Wolcott, G. N. 1924. The food of Puerto Rican lizards. *J. Dep. Agric. P.R.* 7(4):1–43.
- Wright, S. J. 1979. Competition between insectivorous lizards and birds in central Panama. *Am. Zool.* 19:1145–1156.