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AVIAN POPULATION FLUCTUATIONS DURING DROUGHT CONDITIONS IN PUERTO RICO

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Few long-term studies describe population dynamics of tropical avian communities during normal or abnormal periods. Karr et al. (1982) reported comparable measurements of bird density and community structure in Panamanian forest over a period of nearly a decade and Willis (1974) has long-term data for selected species on Barro Colorado Island, Panama. Although Diamond (1971) and Terborgh and Faaborg (1973) reported supposed cases of turnover (change in species composition over time without change in the equilibrium species number (see Diamond and May 1977) in island communities (cases which have been questioned [Lynch and Johnson 1974]), no one has examined the role of actual population fluctuations in the turnover process.

Here I report on the population dynamics of a West Indian bird community over a 5-year period that included severe drought conditions. The effects of these conditions on total populations, populations of foraging guilds, and winter resident populations are shown. Possible reasons for differences among species are discussed, along with the way that such "ecological crunches" (Wiens 1977) may have led to patterns found in the Guanica Forest bird community.

STUDY AREA AND METHODS

This study was done in seasonally dry scrub in the Guanica Forest of southwestern Puerto Rico (for detailed habitat description see Terborgh and Faaborg 1973). The vegetation is situated on a limestone platform and is generally short and sclerophyllous, with many arboreal cacti.

Population size was determined by mist netting, as described earlier (Terborgh and Faaborg 1973). Net lines were operated from dawn to dusk, usually for 3 days. This allowed us to construct regressions of the capture rate of birds over time and to predict a total capture. On a couple of occasions only 2 days of netting were done; thus 2-day totals are used. Addition of the third day only accentuates the difference between good and bad periods, as the third day of netting during drought periods often yielded fewer than 10 birds. In all cases, the number of unbanded birds netted declined throughout the sample period, suggesting a resident population; during the drought period drastic drops in capture rates often occurred after the first day.

One line of 16 nets was operated in January of 1972. In 1973 a second line was erected and both lines were operated subsequently in January or early February of each year. The area was visited and netted in June of 1973, but due to possible seasonal differences in territorial behavior, these data are not presented here. All birds captured were banded, measured and released (for longevity records see Faaborg and Winters 1979, 1980), and age and sex were recorded when possible.

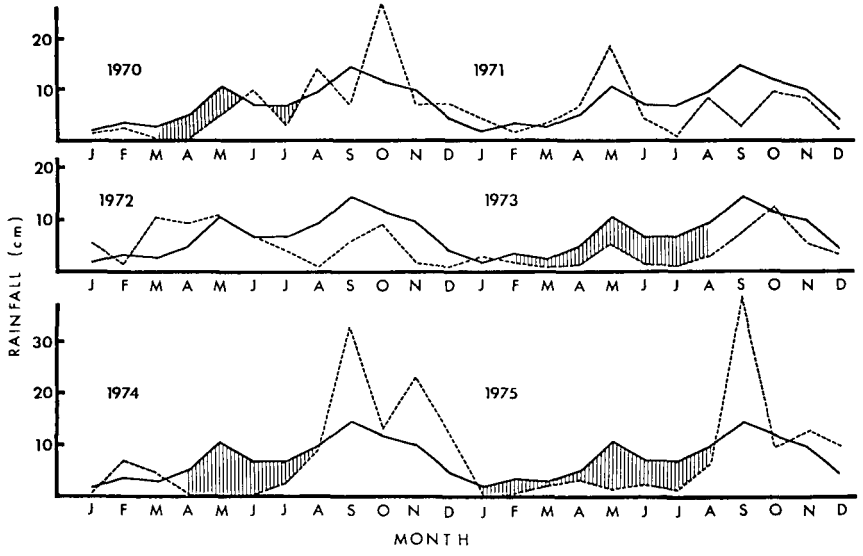

FIG. 1. Rainfall amounts for Ensenada for the period 1970–1975 (dashed line) with the normal amount (solid line). Shaded area designates a net deficit of rainfall during the first six months of a year. Data are from Calvesbert (1970 and supplements).

Rainfall data are from the U.S. Weather Bureau station at Ensenada, a coastal community 4 miles west of the study area. Average rainfall for this area is characterized by a small peak during May and a much larger peak in September and October. A dry season usually occurs from December to April.

The winter bird community can be separated into a permanent resident and winter resident component. The majority of breeding by permanent resident species, plus a few summer residents, occurs from late April to June (Wetmore 1916, Bond 1943), although a few species (mostly frugivores and nectarivores) breed at other times. Most non-breeding species arrive in September and stay until April, a period that encompasses both the wettest and driest parts of the year. Virtually all of these winter residents are gleaning insectivores (Faaborg and Terborgh 1980). Permanent residents were divided into the simple foraging guilds of frugivore (including both fruits and seeds), flycatching insectivore, gleaning insectivore, and nectarivore based upon known diets and foraging habits (Wetmore 1916).

RESULTS

Drought conditions.—Monthly rainfall totals for 1970–1975 are shown graphically in Fig. 1 along with the normal monthly amounts. One year was near normal, three were below normal (one nearly 40 cm below), and two were above normal in annual rainfall. However, annual rainfall may not be the best way to understand the effect of climate on bird populations in a habitat such as this, one in which potential evapotranspiration nearly always exceeds rainfall. Rather, the length and severity of the dry season

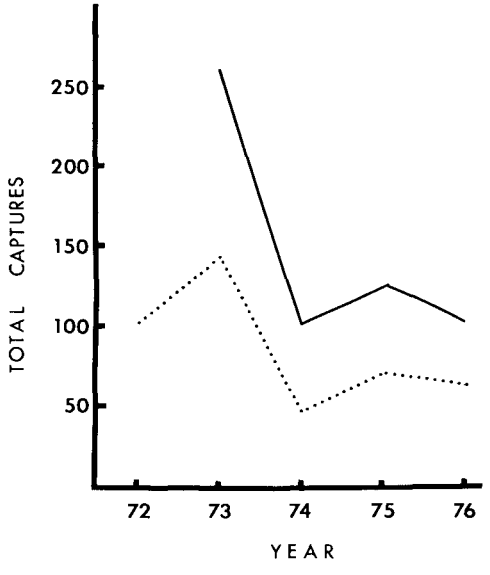

FIG. 2. Population fluctuations of the total resident bird population for 16-net, two-day samples over five years (dotted line) and 32-net, two-day samples over four years (solid line).

and the occurrence of rains before and during the breeding season may be critical. The yearly totals are greatly affected by heavy autumn rains occurring after the breeding season and often associated with tropical storms.

As shown in Fig. 1, the period 1970–1972 was characterized by normal or above normal precipitation before and during the breeding season. The fall rains did not occur to any extent in 1972 and the dry season started over a month early. Below normal rainfall characterizes 10 months of 1973, with the first 6 months running less than one-half the normal amount (13.54 cm vs 29.90 cm). While the fall of 1973 was about normal, the first 6 months of 1974 were drier than 1973 (12.17 cm). The drought was broken by heavy rains in the fall of 1974 and again in the fall of 1975, although the first 6 months of 1975 were very dry (7.85 cm). Thus, after three relatively normal years, the breeding seasons of 1973 through 1975 were characterized by drought conditions, while the dry seasons of 1972–73 and 1973–74 were relatively severe.

Population fluctuations of resident birds.—Fig. 2 shows population fluctuations for the total sampled community for the single netline (1972–1976) and the combined netlines (1973–1976). (Capture data by species and guild are listed in the Appendix.) Total populations were high in 1972 and

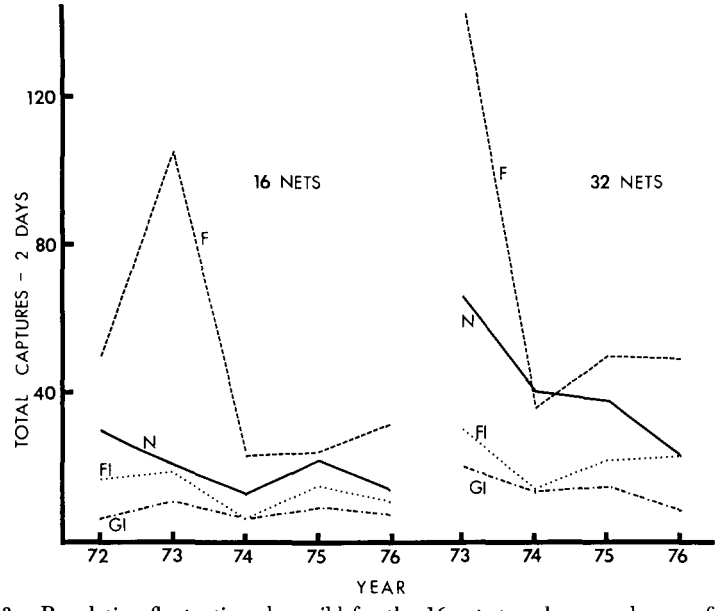

FIG. 3. Population fluctuations by guild for the 16-net, two-day sample over five years (left side) and the 32-net, two-day sample over four years (right side). F is frugivore, N is nectarivore, FI is flycatching insectivore and GI is gleaning insectivore.

peaked in 1973. Observations during June of 1973 revealed no active breeding; by January of 1974 the total population had declined sharply to less than 40% of its peak. The 1974 sample showed only about 6% juvenile birds and a high recapture rate of previously banded birds. A slight population increase occurred in 1975 followed by a slight reduction in 1976.

Fig. 3 shows the population fluctuations of resident birds by guild. The largest decrease occurred with frugivores, which also showed the greatest increases in 1973 and 1975. Resident gleaning insectivores declined relatively slowly from the 1973 peak, while flycatching insectivores declined sharply in 1974 but recovered somewhat in 1975 and 1976. Captures of nectarivores (the Bananaquit and two hummingbirds) decreased in 1973, probably as a result of a lack of flowers resulting from the early dry season. This decline continued throughout the remainder of the study. Hummingbirds had virtually disappeared from the Guanica Forest by 1975 and Bananaquits behaved largely as a gleaning insectivore during the drought.

The greatest single-species declines were also shown by frugivores. The Common Ground Dove fluctuated from 54 to 2 individuals during the crash while Puerto Rican Bullfinches dropped from 49 to 16 and the Black-faced

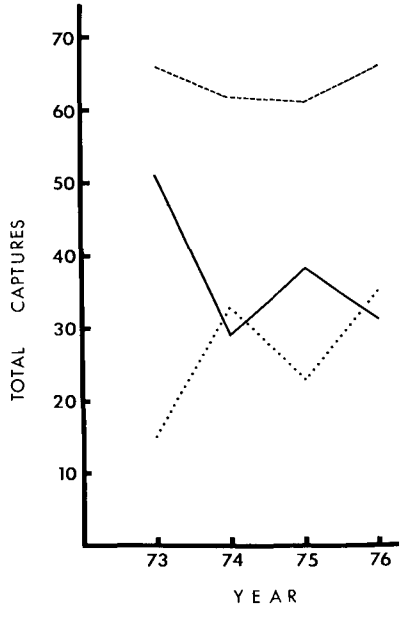

FIG. 4. Population fluctuations of winter residents (dotted line) and permanent resident insectivores (gleaners and flycatchers, solid line) with the total density of wintering insectivores (dashed line).

Grassquit from 29 to 6. Two of the largest frugivores (the Pearly-eyed Thrasher and Red-legged Thrush) actually increased in numbers during the severest part of the drought.

The flycatching Puerto Rican Tody declined steadily and the Stolid Flycatcher decreased by half in 1974 but recovered in 1975 and 1976. Among gleaning insectivores, only the Puerto Rican Vireo showed a substantial drop (7 to 2), while others declined slowly. The Bananaquit and Antillean Mango demonstrated similar decreases in 1974, but the hummingbird continued to decline in subsequent years, whereas the more generalized Bananaquit remained relatively stable in numbers.

Winter resident population fluctuations.—Populations of winter residents fluctuated in the opposite direction of resident bird populations (Fig. 4). The total of resident insectivores (flycatchers and gleaners) and winter residents indicates an almost constant population of insect eating birds. Combining resident flycatchers and gleaners and comparing them with the winter residents is not unreasonable, as several of the winter residents, particularly the American Redstart, also flycatch; some overlap in resource use must occur. (Adding the partially insectivorous Bananaquit to

this group would give combined densities of 121, 96, 97 and 87 for 1973–1976, a particularly stable figure for the last 3 years when nectarivory could not have been a major factor for the Bananaquit.)

Numbers of the five dominant winter resident species (Parula Warbler, Prairie Warbler, Black-and-white Warbler, American Redstart and Ovenbird) fluctuated considerably from year to year. During the last 2 years of the study when resident populations were lowest, five more species were netted. While the Prothonotary Warbler, Hooded Warbler and Northern Waterthrush were netted only once, 10 Cape May Warblers were caught in 1975 and 1976 and five Indigo Buntings were captured in 1976. Neither of these species had been previously seen in the Guanica Forest.

DISCUSSION

With the observation that most Puerto Rican birds breed during the May–June rainy season, it is not difficult to see how lack of rainfall during the first half of the year could drastically affect breeding success and thus population levels. The occurrence of autumn rainfall, even if heavy, may be of relatively little consequence if breeding season conditions are poor. Of course, an extended dry season can have an effect on survivorship, but good conditions in autumn will not help recruitment to the population.

The data suggest that the insectivorous guilds, particularly gleaning insectivores, are least affected by drought conditions, while the frugivores, although able to attain high densities in good conditions, are very sensitive to drought. This difference could be explained by the resources involved. Frugivores feed upon what is basically the yield of primary productivity; with the absence of water there is probably an almost immediate decline in the amount of fruit and seeds produced. In contrast, insectivores feed upon the yield of secondary productivity; even in years when few seeds are produced there are leaves on which insects can feed. Insects may emerge from pupae or hatch in dry conditions following favorable periods and they may linger after conditions become unfavorable. While little is known about island insect densities (Janzen 1973), during the dry season in Costa Rica even the driest locations maintained moderate densities of insects (Janzen and Schoener 1968). Thus, although insects may be relatively scarce, they may be somewhat buffered from climatic fluctuations and birds feeding on insects may show more stable populations than frugivores or nectarivores.

This difference between fluctuations in insectivorous and non-insectivorous guilds has been used to explain the almost total dominance of gleaning insectivores among winter resident species (Faaborg and Terborgh 1980). A bird population attempting to winter within the confines of an island must have a predictable resource. While the availability of fruits,

seeds and flowers may be too variable, the insect resource is stable enough to support winter residents.

Variations in the time required by the different resources to respond to the onset of the wet season could accentuate the differences between guild characteristics. While many plants may flower and fruit rather rapidly after rains (often using stored energy), many insects may require a longer period of time to go through life-cycles and achieve larger sizes and higher densities. Janzen and Schoener (1968) found reduced proportions of subadult insects in the driest sites sampled during the dry season in Costa Rica. Fewer young insects during this period must delay insect population growth during favorable conditions.

The above climatic and resource patterns suggest that it might be best to breed later in the year as rains are then more predictable. This may not be possible due to the high densities of winter resident insect gleaners that arrive in September. Attempting to compete with these winter residents and breed may be impossible, so residents must use the early wet period when conditions are more variable but competition is reduced (see Keast and Morton [1980] for more evidence of this type). Following this logic, frugivores and nectarivores should not be as constrained and the data from Wetmore (1916) suggest this is so. The extent to which these latter species feed insects to their young may put some constraints on their breeding season. A final complexity to the above situation is added by the fact that three other insectivorous species (the Black-whiskered Vireo [*Vireo altiloquus*], Yellow-billed Cuckoo [*Coccyzus americanus*] and Common Nighthawk [*Chordeiles minor*]) breed in the Guanica Forest at the same time as the permanent residents. This complex set of seasonal movements suggests many interesting questions, but more data on resource distributions, philopatry of migrants, and other factors will be needed before any answers can be offered.

Although many resident species declined sharply, no regular member of the Guanica Forest bird community disappeared during this drought. So, while the above data show some interesting responses to severe conditions, this "ecological crunch" was not sufficiently severe to cause even the local extinction of a regular community member. Perhaps it is the occurrence of droughts and other climatic variations such as this or worse that (1) has selected for the proper family composition on these islands (Terborgh 1973), (2) has dictated a level of species saturation in each habitat (Terborgh and Faaborg 1980) and (3) has resulted in rules for structuring the guilds composing these communities (Faaborg 1982). In view of the presumed antiquity of most Puerto Rican residents, it would have been surprising to find local extirpation caused by a 3-year drought. A few uncommon species that are common in other habitats on the island (Puerto

Rican Emerald, Stripe-headed Tanager) did seemingly disappear, but it appears that previous climatic and resource factors have selected a set of species that can coexist through these stress periods when resources are limited and competition is important (Wiens 1977, MacArthur 1972:21). During more favorable conditions, each species may increase in density in response to the types of resources it best uses, probably with less interaction with other community members. During these periods species from other habitats may temporarily invade the Guanica Forest and winter residents may face increased competition from resident insectivores. The members of this community seem well adapted to such severe conditions, thus island turnover must in fact be a rare event in the West Indies.

SUMMARY

The fluctuations of a Puerto Rican dry forest bird population were sampled by netting over a 5-year period that included drought conditions. The absence of normal May and June rains most affected the resident bird populations that breed during this period. Frugivorous species declined most sharply, while gleaning insectivores declined least. Winter resident gleaning insectivores actually increased as resident insectivores declined. It is suggested that insects may provide a scarce, but predictable, resource that attracts winter residents, and thus, in turn, restricts the breeding season of resident insectivores. Such restriction exposes breeding birds to variable early wet season conditions. The relative unpredictability of the fruit, seed and flower resource seems to limit winter residents that use these foods and releases resident members of these guilds from some of the restrictions in breeding. Despite pronounced population declines, no regular member of the Guanica Forest bird community disappeared during the drought.

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APPENDIX

TWO-DAY CAPTURE TOTALS BY SPECIES AND GUILD FOR THE COMBINED 32 NETS 1973–1976 AND THE 16 NET LINE 1972–1976 (IN PARENTHESES)[a]

Species	$\bar{x}$ weight (g)	Yearly captures				
		1972	1973	1974	1975	1976
Frugivores						
Zenaida Dove (*Zenaida aurita*)	153.0	—	—	1 (1)	—	—
Common Ground Dove (*Columbina passerina*)	35.4	(5)	54 (40)	2 (1)	7 (2)	14 (10)
Northern Mockingbird (*Mimus polyglottos*)	43.8	—	1 (1)	—	—	—
Pearly-eyed Thrasher (*Margarops fuscatus*)	100.7	(4)	3 (1)	5	9 (1)	10 (5)
Red-legged Thrush (*Mimocichla plumbea*)	74.5	(4)	2 (1)	5 (3)	8 (3)	—
Blue-hooded Euphonia (*Euphonia musica*)	15.7	—	—	—	—	1
Stripe-headed Tanager (*Spindalis zena*)	29.7	—	7 (2)	1	—	—
Puerto Rican Bullfinch (*Loxigilla portoricensis*)	32.1	(27)	49 (36)	16 (12)	15 (7)	8 (2)
Black-faced Grassquit (*Tiaris bicolor*)	9.7	(10)	29 (24)	6 (6)	11 (11)	15 (14)
Yellow-faced Grassquit (*Tiaris olivacea*)	7.0	—	—	—	—	1 (1)
Total frugivores	—	(50)	145 (105)	36 (23)	50 (24)	49 (32)
Flycatching insectivores						
Puerto Rican Tody (*Todus mexicanus*)	5.4	(3)	12 (6)	5 (1)	2 (1)	2 (1)
Stolid Flycatcher (*Myiarchus stolidus*)	22.9	(14)	18 (13)	10 (5)	19 (12)	21 (10)
Caribbean Elaenia (*Elaenia martinica*)	22.0	—	—	—	1 (1)	—
Grey Kingbird (*Tyrannus dominicensis*)	47.6	—	—	—	1 (1)	—
Total flycatchers	—	(17)	30 (19)	15 (6)	23 (15)	23 (11)
Gleaning insectivores						
Puerto Rican Lizard Cuckoo (*Saurothera vieilloti*)	77.1	—	2 (1)	—	—	1 (1)

APPENDIX
CONTINUED[a]

Species	$\bar{x}$ weight (g)	Yearly captures				
		1972	1973	1974	1975	1976
Puerto Rican Vireo (*Vireo latimeri*)	11.2	—	7 (3)	2	2 (1)	—
Adelaide's Warbler (*Dendroica adelaidae*)	6.7	(3)	7 (5)	9 (4)	3 (2)	3
Black-cowled Oriole (*Icterus dominicensis*)	37.2	—	1	1	2	—
Troupial (*Icterus icterus*)	72.2	(3)	4 (2)	2 (2)	8 (6)	4 (4)
Total gleaning insectivores	—	(6)	21 (11)	14 (6)	15 (9)	8 (7)
Nectarivores						
Puerto Rican Emerald (*Chlorostilbon maugaeus*)	2.8	(1)	—	—	—	—
Antillean Mango (*Anthracothorax dominicus*)	5.4	(8)	11 (8)	6 (5)	2 (2)	2 (2)
Bananaquit (*Coereba flaveola*)	9.4	(21)	55 (13)	34 (8)	36 (21)	21 (12)
Total nectarivores	—	(30)	66 (21)	40 (13)	38 (23)	23 (14)
Winter residents						
Black-and-white Warbler (*Mniotilta varia*)	9.7	(5)	6 (2)	7 (2)	2	4
Prothonotary Warbler (*Protonotaria citrea*)	13.0	—	—	—	—	1
Parula Warbler (*Parula americana*)	7.4	(2)	—	5	4 (1)	8 (1)
Cape May Warbler (*Dendroica tigrina*)	10.0	—	—	—	7	3
Prairie Warbler (*D. discolor*)	6.9	(3)	2 (2)	11 (4)	7 (5)	6 (4)
Ovenbird (*Seiurus aurocapillus*)	18.7	—	2	3	1	1
Northern Waterthrush (*S. noveboracensis*)	15.0	—	—	—	—	1 (1)
Hooded Warbler (*Wilsonia citrina*)	11.0	—	—	—	1	—
American Redstart (*Setophaga ruticilla*)	7.2	(1)	5	7	1 (1)	6
Indigo Bunting (*Passerina cyanea*)	13.2	—	—	—	—	5 (5)
Total winter residents	—	(11)	15 (4)	33 (6)	23 (7)	35 (11)
Total captures	—	(114)	277 (160)	138 (54)	149 (78)	138 (75)

[a] Nomenclature is from Bond (1971) and weights are from Faaborg and Winters (1979) who list statistical data.