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RAINFALL CORRELATES OF BIRD POPULATION FLUCTUATIONS IN A PUERTO RICAN DRY FOREST: A NINE YEAR STUDY

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Long-term studies on the population dynamics of Neotropical bird communities have been primarily limited to Panama (see Karr et al. [1982] for a mainland site and Willis [1974] for Barro Colorado Island). An earlier paper (Faaborg 1982a) contained the first long-term population measurements from a West Indian island, specifically a seasonally-dry forest site in southwest Puerto Rico. This 5-year study apparently spanned a population peak followed by drought conditions and a severe population decline. The effects of drought on total populations, membership in different foraging guilds, and winter resident densities were discussed.

We have continued these studies and here report on 9 years of banding and population monitoring activities in a single location. This allows us to expand our previous observations on relationships between rainfall patterns and population traits of guilds and species and expose the data to statistical analyses. We also document the attempted invasion of a new species (*Elaenia martinica*) into the Guanica Forest bird community. The possible meaning of these observations in terms of island equilibrium theory (MacArthur and Wilson 1967), long-term climatic patterns (Pregill and Olson 1981), and community structure studies (Faaborg 1982b) is discussed.

STUDY AREA AND METHODS

This study was done in seasonally dry scrub in the Guanica Forest of southwestern Puerto Rico (see Terborgh and Faaborg [1973] for detailed habitat description with photographs). This habitat occurs on a coraline limestone and contains sclerophyllous forest typical of such sites throughout the West Indies (Beard 1949).

Bird population characteristics were determined by mist netting as described earlier (Terborgh and Faaborg 1973). Here we report the results of a single line of 16 mist nets (each 12 m long and 2.6 m high, 36-mm mesh, NEBBA type ATX) placed contiguously and operated from dawn to dusk for 3 consecutive days. While regressions of capture rates can be used to predict total captures, here we use simple 3-day totals. In 1976 only 2 days of netting were completed. Since the third day of netting usually yields about 20% of the total captures (range 14.7%–23.4%), we have multiplied the birds caught in 2 days by 1.25 to get the 1976 totals. Faaborg (1982a) earlier reported on the results of two separate lines, but drought at the initial location turned three small clearings into large clearings. The line considered here was operated from 1973–1983 except for 1977 and 1979. Netting (sampling) was done from early January to early February. Captured birds were banded, measured, and released, with age and sex recorded when determined. Total number for a sample includes only the first capture of an individual in a sampling period. Recaptures are birds caught in one year but originally banded in a previous year. Bird nomenclature follows the A.O.U. Check-list (1983); common names are in the appendix.

Guild designations used are: gleaning insectivore, flycatching insectivore, nectarivore, and frugivore. (See Faaborg [1984] for a detailed rationale for these categories.) Although nearly all West Indian birds belong clearly to one of these guilds as adults, the extent that nectarivores or frugivores feed insects to their young affects our conclusions.

Because rainfall varies locally in southwestern Puerto Rico, we have used rainfall data from U.S. Weather Bureau stations at three sites surrounding Guanica. The Ensenada site is 6.4 km west of the study area, the Central San Francisco site 5 km east, and the Santa Rita site about 10 km northeast. Actual rainfall values reported in this study for Guanica were averaged across these three weather stations. Normal monthly rainfall values used were long-term averages as shown in Calvesbert (1970), and these values were also averaged across the three sites to provide normal rainfall values for the area. All precipitation variables reported as departures from normal (DFN) were calculated by comparing these representative actual and normal rainfalls in absolute values. The effect of DFN is essentially to rescale the data, based on the assumption that for bird populations adapted to a set of climatic conditions, the use of 10 for both a dry or wet year and 0 for a normal year might yield better correlations than using the actual rainfall measures. Thus, while we might expect positive correlations beween bird numbers and rainfall, we would expect negative correlations between bird numbers and DFN.

Spearman rank correlations were used to investigate the relationships between bird population levels and precipitation variables. *P*-values, the probability of obtaining a rank correlation coefficient at least as extreme as that actually observed if there is no association between the variables, are reported for all tests.

We chose several rainfall variables for correlation with the bird population data. We felt this necessary because of the highly seasonal nature of normal rainfall in the Guanica Forest (Fig. 1) and the observation that the majority of Greater Antillean birds of dry forest breed during the April–July period (Bond 1943, Diamond 1973, pers. obs.). Thus, breeding success for a year may be more closely associated with the occurrence and size of April–May rainfall than total yearly rainfall, much of which is accumulated during September and October (Faaborg 1982a). Total yearling rainfall undoubtedly affects vegetation growth and thus resource abundance for birds, but its effects may be both delayed and diffuse. Based on this rationale, we computed yearly rainfall totals both for the first 6-month period of the year (January–June) and the complete calendar year. Correlations were run between the bird population levels of a particular calendar year and total rainfall, DFN of total rainfall, 6-month rainfall, and DFN of 6-month rainfall for the current year, the previous year, the year 2 years previous, and the sum of the 2 previous years. Because of the large number of correlations computed from this data set, the probability of finding at least one significant correlation is fairly high. Thus, it is not simply the presence of a significant correlation that is important, but also the patterns of correlation between certain types of precipitation variables and the different bird guilds. In addition, we calculated correlations between bird populations sampled in January with rainfall occurring after the sample (i.e., rainfall in the current year) to test for spurious correlations; since none occurred these data are omitted here.

RESULTS AND DISCUSSION

Rainfall correlates of population variation.—Total rainfall varied rather widely through the study period (Fig. 2), while 6-month rainfall was well

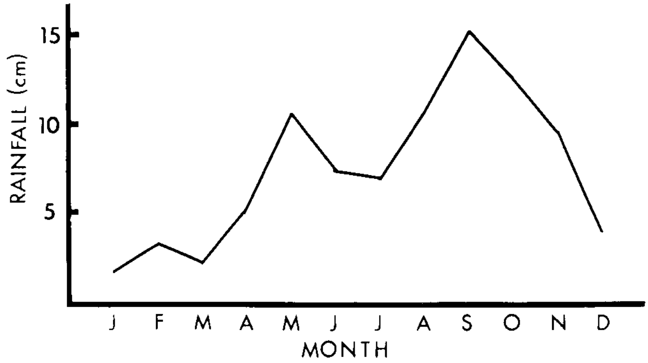

FIG. 1. Seasonal distribution of rainfall for the Guanica Forest taken as the average of the monthly averages of three nearby weather stations (Central San Francisco, Ensenada, and Santa Rita). Data are from Calvesbert (1970).

below normal from 1973–1978, but normal or above the rest of the time. The total number of resident birds captured generally was low during the middle of the sampling period with peaks in 1973 and 1982 (Fig. 3). The total number of winter resident birds did not vary as much over the years, although comparing their numbers with total resident captures obscures possibly important interactions (see below).

Dividing the resident population totals by guild membership shows varying patterns within these ecological groups (Fig. 4). Frugivore populations fluctuated substantially, with several high and low points during the study period. Nectarivores (primarily *Coereba flaveola*) declined sharply during 1974–1976 and have recovered only in recent years. The lowest capture rates for these guilds amount to less than one-third of the totals during peak years. In contrast, the relatively less abundant insectivores varied less dramatically in numbers. Gleaning insectivores showed fluctuations in numbers similar to those of frugivores but with relatively less variability, whereas flycatchers showed generally similar patterns each year with the exception of a population peak in 1976.

Most significant or near significant correlations were shown for bird populations and various measures of the rainfall occurring during the first 6 months of the year (Table 1). The single most important rainfall variable was the 6-month DFN from the previous year, which had one significant correlation (total birds, $r = -0.81$) and two strong trends: total insectivores ($r = -0.62$), and gleaning insectivores ($r = -0.61$). Two weaker trends were also shown for frugivores and nectarivores. The compound effects of low 6-month rainfall seem to be suggested by significant cor-

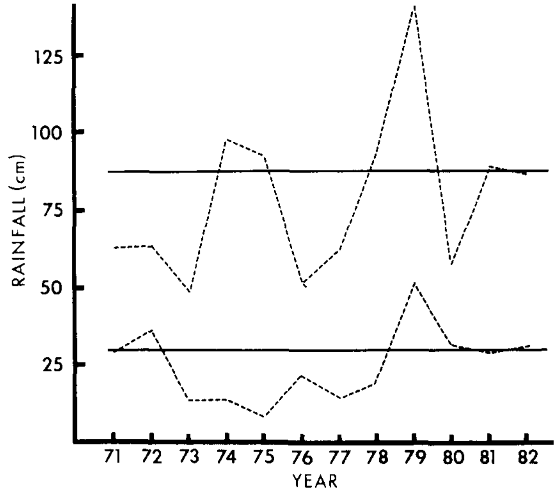

FIG. 2. Distribution of total yearly rainfall (top) and 6-month rainfall (January through June, bottom) for the period of study and two preceding years. Average values are shown as the solid flat lines. Data are averaged for the three stations as in Fig. 1.

relations between bird populations and (1) 6-month rains for 2 years previous to the sample (DFN), and (2) the sum of the 6-month rains during the 2 years previous to the birds sample (DFN). Total yearly rainfall showed no significant correlations with bird populations, although trends for the nectarivore guild and the sum of 2 previous years rainfall ($r = -0.60$) were demonstrated. However, three nearly significant correlations occur between total rainfall of the previous year and various categories

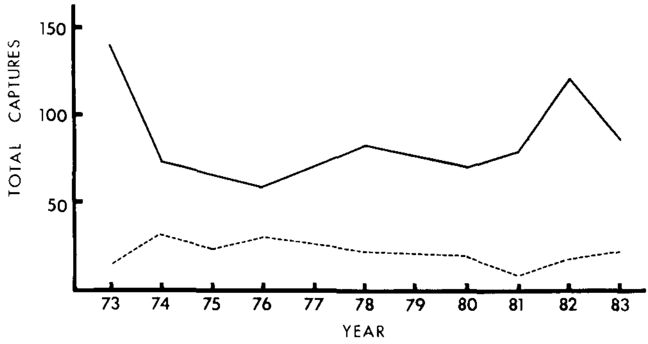

FIG. 3. Variation in the summer resident (solid line) and winter resident (dashed line) birds captured in the sampling periods during the period 1973–1983.

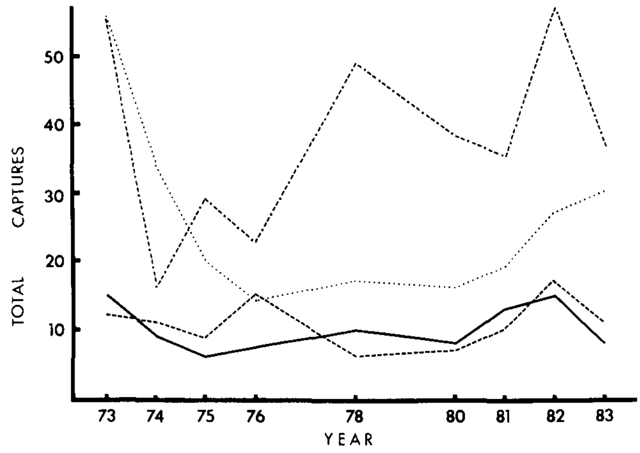

FIG. 4. Variation in captures by guild during the study. Frugivores are represented by dots and dashes, nectarivores by dots, gleaning insectivores by solid lines, and flycatching insectivores by dashes.

of insectivorous birds. The absence of a statistical relationship between yearly rainfall and bird populations may be a product of the variability (in both directions) of this rain and the fact that it is somewhat removed from directly effecting breeding success. It is apparent from these tests that Guanica Forest bird populations are very sensitive to the rainfall that ends the dry season at the start of their normal breeding period. Before we discuss this more fully, let us look at each guild in more detail.

Frugivores are notable for marked fluctuations in numbers. Earlier Faaborg and Terborgh (1980), and Faaborg (1982a) suggested that this may reflect the fact that harvesters of primary productivity face an immediate hardship with the onset of drought and cessation of production of seeds. Once those seeds on the ground are gone, food shortage may become limiting. Yet, seed production begins shortly after the rains start and the possibility for rapid population growth exists. Such a rapid population increase could occur because in the West Indies frugivores seem to have larger clutch-sizes than insectivores (Bond 1943). The only possible relationship between rainfall and frugivore numbers was a nonsignificant trend with 6-month rains for the previous year ($r = 0.62$). While this suggests frugivore dependence on April–May rains preceding their main breeding season, in several cases frugivore densities went up in years with low 6-month rainfall but high yearly rain (Fig. 5). There is some evidence (Bond 1943, Diamond 1973) that at least some West Indian frugivores may breed into August or September, although the situation

TABLE 1

P-VALUES FOR SPEARMAN RANK CORRELATIONS BETWEEN BIRD POPULATION LEVELS AND PRECIPITATION VARIABLES

Precipitation variable	Total birds	Frugivores	All insectivores	Gleaning insectivores	Flycatching insectivores	Nectarivores
Total, 1 year previous	0.2867	0.7324	0.1447	0.1407	0.9145	0.2054
Total, 1 year previous, DFN	0.4879	0.6059	0.5003	0.8291	0.1145	0.6682
6 month, 1 year previous	0.1705	0.0769	0.6989	0.2176	0.6816	0.7001
6 month, 1 year previous, DFN	0.0079*	0.1098	0.0738	0.0757	0.4751	0.1447
Total, 2 years previous	0.5165	0.3807	0.7640	0.7787	0.7466	0.3807
Total, 2 years previous, DFN	0.8984	0.8312	0.6989	0.3617	0.5874	0.9661
Six month, 2 years previous	0.1116	0.7324	0.0091*	0.0176*	0.4154	0.1544
Six month, 2 years previous, DFN	0.0159*	0.1544	0.1854	0.2081	0.2011	0.0358*
Total, sum of 2 previous years	0.2861	0.8312	0.4308	0.3251	0.7139	0.0876
Total, sum of 2 previous years, DFN	0.8984	0.7650	0.8305	0.4541	0.4288	0.7001
6 month, sum of 2 previous years	0.1875	0.2242	0.2624	0.0773	0.9829	0.5755
6 month, sum of 2 previous years, DFN	0.0159*	0.1116	0.1524	0.1561	0.3515	0.0769

* Significant at $P \leq 0.05$.

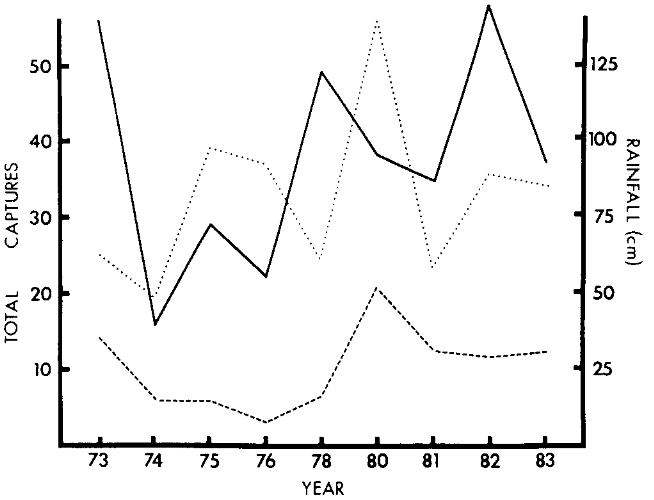

FIG. 5. Variation in the number of frugivores captured in each sample (solid line), total yearly rainfall for the calendar year preceding the sample (dotted line) and 6-month rainfall for the year preceding the sample (dashed line).

at Guanica vis-a-vis these species is unknown. Such an extended breeding season would allow frugivores to take advantage of more predictable late-season rains.

Resident insectivores (including both gleaners and flycatchers) did not show sharp fluctuations from year to year (Fig. 6). With the exception of a 1976 increase caused solely by an unusually large number of *Myiarchus antillarum,* resident insectivore numbers declined in 1974 and 1975 and remained low until increasing in 1981–1982. This pattern is not quite significantly correlated with the DFN for the first 6 months of the year previous to the sample ($r = -0.62$), but is significantly correlated with 6-month rain 2 years previous to sampling ($r = 0.80$). The numbers of gleaning insectivores showed the same general relationship plus one strong trend for the 6-month sum of the 2 previous years ($r = 0.61$). Flycatchers showed no significant correlations with rainfall and only one general trend thereto (DFN of total rain in previous year). The 1983 decrease in insectivorous birds did not correspond to the rainfall totals, probably because most of the 1982 rain fell in one downpour that was mostly lost to runoff (B. Cintron, pers. comm.). Population responses to changing climatic conditions seem to show a lag for insectivores, which may reflect the fact that insects have life cycles of their own and thus are a somewhat buffered resource for birds to use (Faaborg and Terborgh 1980, Faaborg 1982a). In addition, clutch-sizes of insectivores are generally small and,

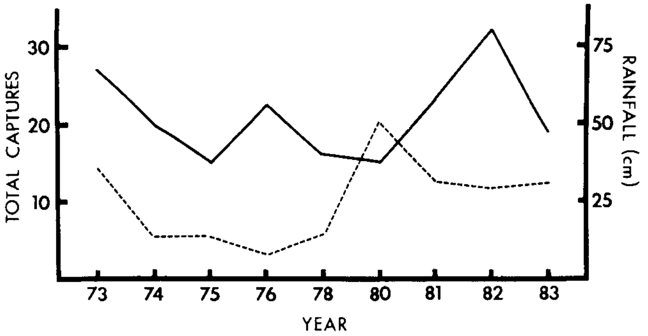

Fig. 6. Variation in the number of resident insectivores (both gleaners and flycatchers) captured (solid line) and 6-month rainfall for the period preceding the sample (dashed line).

as noted earlier, insectivorous species of birds appear to be restricted in Guanica to breeding during a few months. Thus, while wet season rains undoubtedly aid survivorship, the success of insectivore reproduction seems to be mostly dependent upon the length of the dry season and the occurrence of an adequate April–May rainy season.

Assessment of the effects of dry conditions on resident nectarivores in the Guanica Forest is based primarily on *Coereba flaveola.* The only common hummingbird (*Anthracothorax dominicus*) seemingly declined in numbers early in the study period and was not caught at all in 3 of the last 5 sampling years. No more than five individuals of this hummingbird were captured in any year. *Coereba* declined dramatically in the 1974–1976 interval, then leveled off until an increase in numbers began in 1981 (Fig. 4). A significant correlation occurred between nectarivore numbers and rainfall for one 6-month value (DFN of 2 years previous, $r = -0.70$) and trends occurred for summed DFN of the previous 2 years ($r = -0.62$) and the sum of the 2 previous years total rainfall ($r = 0.60$). The pattern for nectarivores resembles that of the insectivores except for a seemingly delayed response to rainfall and greater variation in numbers (*Coereba* alone nearly equaled the frugivores in 1973). Such variation in numbers is perhaps to be expected for a generalist like *Coereba,* which, in addition to nectar, takes soft fruits and gleans insects. Our observations and the absence of both fruits and flowers suggest that *Coereba* was primarily an insect gleaner during the aforementioned drought. While this species has been recorded breeding in all months of the year in other parts of Puerto Rico, we have never seen it breeding in winter in Guanica. A somewhat restricted breeding season may explain *Coereba*'s slow population increase, while its diverse diet may allow it to achieve high densities when conditions are favorable.

Thus, in the seasonal conditions of the Guanica Forest, the occurrence and size of early wet season rains is seemingly correlated with population sizes of all avian guilds. Since these rains follow a 4-month long dry season, they are critical to the nesting success of birds that breed during the April–July period. The question that arises at this point is: Given a more predictable August–November wet season, why do most, if not all, species confine their breeding to the April–July period? There is some evidence that arthropods are plentiful at this time (Kepler 1972, Diamond 1973, Janzen 1973), although these studies were based on the use of a variety of techniques of resource assessment applied in different habitat types. Any increase in insect numbers depends upon the rains which signal the beginning of the wet season, thus, in terms of resource availability it is less apparent why birds don't initiate breeding in August or September if rains are delayed until then. We believe that another important factor relates to the presence of high densities of winter residents that are primarily insectivores, including some which flycatch (Bennett 1980). These wintering migrants may be sufficiently numerous to have effects upon resident insectivores and, to the extent that these birds feed their young insects, even frugivores and nectarivores.

While Fig. 3 shows that winter resident numbers did not fluctuate as greatly as those of permanently resident species, a closer look at winter resident numbers and resident insectivore (including *Coereba*) totals, shows the potential for interaction among these groups (Fig. 7). In many years, the number of winter resident insectivores exceeds that of resident gleaners and flycatchers, a fact that at the least must affect the breeding season of Guanica's warbler and vireo, if not other species. Although no statistical correlations between the numbers of these groups were found, in several cases an increase by one group has been accompanied by a decrease in the other, suggesting some sort of competitive interaction. While a detailed discussion of interactions among the insectivores and *Coereba* is difficult without some measure of the effects of drought on insect numbers, we can look at how the total number of insectivores varied over the study to get some idea of habitat carrying capacity for insectivores. This density was at its peak in 1973 (although many of *Coereba* at this time must have been highly nectarivorous), occurring after at least two wet breeding seasons, even though those 2 years had below-normal yearly rainfalls. The lowest insectivore totals occurred in 1980 and 1981, even though 1979 was one of the wettest years in the study, both before and after July. This lag in the recovery of insectivore populations may well reflect a lag in population growth of insects following the end of the drought, coupled with the effects of small clutch-size and limited breeding season in Guanica birds.

While it is perhaps not surprising that all resident and winter resident

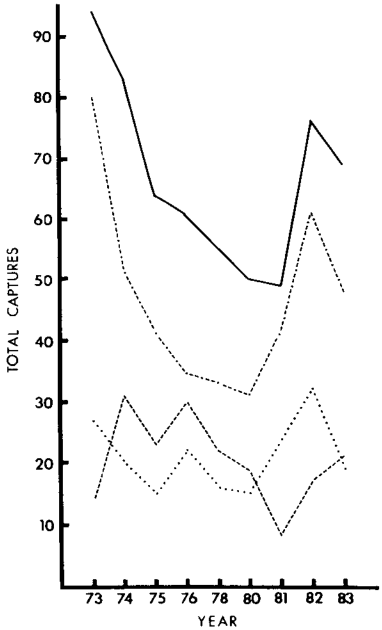

FIG. 7. Variation in insectivores captured throughout the study. The dashed line shows winter resident numbers, the dotted line resident insectivores (gleaners and flycatchers), the dash-dot line resident insectivores plus *Coereba,* and the solid line all insectivores (residents and winter residents).

insectivores reached their lowest levels at the same time, the fluctuations of these groups before this sharp reduction in numbers are of interest. Except for the drought, winter residents showed lowest densities when resident insectivores had their highest, and as the drought caused resident insectivore numbers to decline, winter resident populations actually climbed and stayed high until resource limitation apparently occurred. The winter residents have the advantages of using the Guanica Forest only for survival during their winter tenure, obtained by arriving during the more resource stable season, and by having more flexibility in choice of specific sites at which to winter. We suggest that when resident insectivore numbers are reduced due to a dry breeding season, winter residents can respond to the decrease by increasing their numbers to the extent made possible by rainy season conditions. In contrast, when resident insectivore populations are high, in turn they may limit the number of winter residents in the Guanica Forest. The specific traits of these winter residents are discussed elsewhere (Faaborg and Arendt 1984); suffice to say we see two types of winter residents. One type is present in the Guanica Forest each winter and generally shows a high degree of wintering philopatry; populations of these vary somewhat but do not correspond to any of the weather patterns. A second set of warblers, seemingly much more opportunistic, was more abundant when resident numbers were low. The Cape May (*Dendroica tigrina*) and Prothonotary (*Protonotaria citreria*) warblers were found only when resident numbers were low while the American Parula (*Parula americana*) and Prairie Warbler (*Dendroica discolor*) were commonest at this time.

Certainly more data on bird and resource populations are needed to understand any effects of competition in this situation. Assessing competition is complicated by the need to intepret import of several species that occur in the Greater Antilles only during the breeding season (Faaborg and Terborgh 1980). Perhaps as well as any other, this situation exemplifies the complexity of potential competitive interactions and the fact that they do not always involve simple exclusions or the responses to "ecological crunches." In this case, one set of competitors (winter residents) seems to restrict the other set (resident insectivores) to a relatively short breeding season. Whether or not the winter residents "win" is seemingly a function of the climatic conditions at the time the residents breed. Thus, a critical determinant of the outcome of a competitive interaction occurs when the competing groups are thousands of miles apart. The extent that frugivores feed their young insects adds to the complexity of this situation; we hope to study this in more detail in the future.

Species responses to drought.—The decline of captures of a species may reflect actual mortality of local residents, movement from the sampling area, or net shyness of birds previously captured. Because our net samples were a year apart, often included a high percentage of recaptures, and showed some of the lowest totals after 2-year intervals, we doubt that net-shyness is of great importance. Looking at the fluctuations of each species through this 10-year period, along with measurements on the rate of recapture of banded birds and measurements of longevity (Table 2) gives us some idea of the range of strategies used by individual species to survive these conditions. It should be noted that the highest rate of recapture of all individuals (the proportion of birds in a sample banded in previous studies) was about 50%, suggesting a fairly high rate of local turnover at all times.

As the most complex guild, it is not surprising that frugivores show the greatest variety of responses to drought conditions. With the exception of the large doves that are not easily captured, *Euphonia musica,* an erratic wanderer that feeds on mistletoe, and *Spindalis zena,* none of the frugivores was ever absent for more than two sampling periods and all pop-

TABLE 2

INFORMATION ON RECAPTURES OF GUANICA FOREST BIRDS BETWEEN SAMPLING PERIODS

Species	Total captures[a]	No. recaptures	Mean duration[b]	Longest[c]
Columbina passerina	41	2	1, 6	2, 0
Todus mexicanus	26	4	4, 6	8, 11
Melanerpes portoricensis	7	1	1, 0	1, 0
Myiarchus antillarum	50	14	3, 3	9, 6
Elaenia martinica	18	4	1, 3	1, 11
Margarops fuscatus	74	9	2, 8	6, 0
Turdus plumbeus	39	11	2, 10	6, 6
Vireo latimeri	18	6	1, 9	4, 1
Dendroica adelaidae	45	10	2, 9	7, 0
Coereba flaveola	242	31	2, 0	5, 0
Spindalis zena	18	1	1, 0	1, 0
Icterus dominicensis	4	2	1, 6	2, 0
I. icterus	14	1	2, 0	2, 0
Loxigilla portoricensis	131	18	1, 5	3, 0

[a] Number of new captures in each sample summed for the nine samples.
[b] In years, months.
[c] Longest time between recaptures.

ulations increased with the amelioration of "unfavorable" conditions. The smaller frugivores showed the greatest fluctuations. *Columbina passerina* dropped from 16 captures to 1 capture in just a year and has been of spotty occurrence in recent years; *Tiaris bicolor* dropped from six to zero individuals during the same period. Both of these species prefer clearings for feeding and appear to be the most nomadic of the frugivores, as we recaptured no grassquits and just 2 of 41 ground doves (Table 2). *Loxigilla portoricensis* also declined dramatically (from 22–6 captures) but it showed a 14% recapture rate overall and 37% rate at the lowest population levels.

The two large but common frugivores fluctuated less than the small species and actually increased during and following the severest drought period. *Margarops fuscatus* showed a 12% recapture rate overall, with most of the recaptures late in the study when the numbers of this species had increased. Although *Turdus plumbeus* was not netted in the abbreviated 1976 sample, it too generally showed no decline during the drought and an early increase after it. Both species had long-lived individuals, with thrushes recaptured at up to 6.5-year intervals. The apparent immunity of these larger frugivores to severe conditions is in accord with arguments suggesting they have higher survival capacities than small birds on islands (Grant 1968, Wilson 1975), perhaps because they feed on more animal matter (either insects or lizards) than the other frugivores.

Two nectarivores showed distinct declines during the drought. *Anthra-*

cothorax dominicus declined from a high of three individuals to two in 1976, then was captured again only once until 1983. *Coereba* dropped from 53–11 captures in a 3-year period and was seemingly fairly sedentary, with a 13% recapture rate overall and yearly rate up to 38% during the decline. The oldest recapture for this species was 5 years with a mean recapture time of 2 years.

Only four resident insectivores could be effectively sampled by nets throughout the study. *Tyrannus dominicensis* was common but stayed above the canopy at Guanica, while the cuckoos were both uncommon and large enough that netting was a poor sampling tool. All the nettable insectivores showed declines. *Myiarchus antillarum* fluctuated between 11 and 2 individuals, while the tiny flycatching *Todus mexicanus* ranged from one to six individuals. Both of these species showed high overall recapture rates and both have longevity records approaching 10 years (8.9 years for the tody and 9.5 years for the flycatcher). The two small permanent resident gleaners include *Dendroica adelaidae* which varied from one to eight individuals and *Vireo latimeri* which ranged from four to zero captures. *Dendroica* showed a 22% overall recapture rate while *Vireo* had a 33% rate; both had individuals that lived through much of the drought. The Black-whiskered Vireo (*Vireo altiloquus*) breeds at Guanica but has never been captured in the dry season because it winters in South America.

While we did not catch a few species in some samples, in all cases these species were observed in the Guanica Forest area during the sampling period. Only the hummingbird and *Spindalis* (which may not breed at Guanica) were not seen somewhere in the forest each sampling period. While a few species seemed to be somewhat nomadic on a local scale, most appeared fairly sedentary. A preliminary analysis of our weight measurements (Arendt and Faaborg, unpubl.) has shown no changes in mean weights during the drought, suggesting that maintenance of adult birds may not be as difficult as successful reproduction seems to be. All the species seemed well-adapted to exceptionally harsh conditions in an always harsh environment.

The attempted invasion of the Caribbean Elaenia.—Although none of the species present before the onset of drought disappeared from Guanica, an apparent temporary invasion of the Caribbean Elaenia into this area did occur. This species was not recorded in the forest until an individual was captured in the initial netline in 1975, after at least 1000 individuals of other species had been netted. No additional elaenias were netted until 1980. Then the capture rate increased to six in 1981 and nine in 1982, of which three were recaptures. Only two, however, were netted in 1983, one of these a recapture from 1981.

Although the Tyrannidae are generally thought of as insectivores, *Elaen-*

ia spp. are well known for their fruit-eating preferences (Crowell 1968). Nonetheless *E. martinica* regularly hawks insects; Faaborg (unpubl.) found its insectivorous habits to predominate during the drought of 1973 on Vieques Island. In assigning guilds, we attemped to go by the foods or feeding technique critical to a species during stress periods. For this reason we grouped *Elaenia* with the other flycatchers, many of which eat fruit when it is available.

The range of *E. martinica* in the West Indies suggests that it could be categorized as a "tramp" following Diamond (1975). It is found from Aruba, Providencia, and St. Andrews, northward throughout the Lesser Antilles and islands east of Puerto Rico, and on the Cayman Islands, the only place where it coexists with a similar-sized tyrannid. (Johnston [1975] felt this coexistence was possible because *Elaenia* ate so much fruit, but that explanation does not seem to apply elsewhere.) It is only patchily distributed on Puerto Rico and absent from the other Greater Antilles. The combined characteristics of wide range but absence on larger islands with higher species numbers fit the tramp designation perfectly. Following the logic of Diamond (1975), we can look at this species as one that is a poor competitor that cannot survive on large islands but an excellent disperser and generalist that excels on small islands.

If true, how will these traits affect *E. martinica*'s chances of becoming permanently established in the Guanica Forest bird community—one of the most complex in the Caribbean? First, it should be noted that *E. martinica* is about the size of the resident flycatcher (*Myiarchus antillarum*). Only on the Cayman Islands do two like-sized flycatchers coexist, so this appears to be an unstable situation in which competitive exclusion of one or the other species may occur. *Myiarchus* sp. and *Elaenia* sp. do coexist on some Lesser Antillean islands, but on these islands the large *Myiarchus* sp. is usually not found with a large (45 g) kingbird (*Tyrannus* sp.), as is the case at Guanica. There *Myiarchus* may have an advantage as an established resident, but in turn the broader diet of *E. martinica* may be of advantage to it. It should be noted again that *Elaenia* appeared and increased at the time of general increase in most populations following cessation of the drought. This would have been a period when food levels were relatively high while competitors were few, a seemingly excellent time for an "invasion" attempt. The overall decline in populations found in 1983 was particularly hard on this species, perhaps because resources had once again become limited and competition was having its effects. Should *E. martinica* ultimately be excluded, it would lend support to the contention that it is a poorly competing tramp species using an "in-and-out" strategy of attempted colonization.

Saturation and stability in the Guanica Forest bird community.—The overriding conclusion from our data seems to be that the Guanica Forest supports a set of resident species which can coexist during severe drought conditions without any loss of species. While many species reached low levels in our net samples, they were widespread throughout the forest and did not face threat of extinction. Perhaps a competition among these species in the drought and in previous "ecological crunches" (Wiens 1977) has led to the fairly simple and conservative patterns of structure we find in West Indian bird communities (Terborgh and Faaborg 1980; Faaborg 1982b, 1984). In as much as colonization rates are very low on these islands, intervals are not long enough between stress periods for high turnover of species. Thus, the apparent results of competition in determining the component species on these islands are everpresent, while actual species densities may fluctuate somewhat independently in response to the specific resources available to a species. Pregill and Olson (1981) pointed out that dry forest vegetation such as that found at Guanica was much more common in the West Indies during Pleistocene dry periods; thus, we may be seeing super-saturated communities in this habitat today. While we think their observation is important in explaining the difference in species densities between wet and dry forests in the West Indies today, the observed stability of this community through severe conditions suggests it is quite resistant collectively to extinction. On the other hand, the difficulty that *E. martinica* appears to be having and the fact that none of the many introduced species common in Puerto Rico (Raffaele 1983) has been seen in the forest suggests that the Guanica Forest bird community is resistant to the successful invasion of new species.

SUMMARY

Possible interactions between bird population fluctuations and rainfall patterns are discussed using data gathered over 9 years in the period 1973–1983 (no netting was done in 1977 or 1979) in a Puerto Rican dry forest. Bird populations were assayed using a 16-net line of mist nets operated from dawn to dark for 3 consecutive days in January or early February of each year. Total captures were divided by resident or winter resident status and the residents divided into four guilds based on foods and/or foraging behavior. The rainfall data used were an average of measurements from three weather stations within 10 km of the study site. Average monthly rainfall at these sites was added both for yearly totals and for a 6-month total covering the period January–June, a potentially critical value as April and May rains seem to be necessary to end the effects of the dry season at the start of the normal April–July bird breeding season. Spearman rank correlations were used to assess the relationships between bird population levels and precipitation variables.

Total yearly rainfall varied widely throughout the study while 6-month rain totals were below normal for the period 1973–1978. Total bird populations peaked in 1973 and 1982 and were lowest in 1976. Virtually all the significant correlations that occurred were between bird population levels and measures of the 6-month rainfall. It is suggested that without ample totals from these rains, local birds cannot successfully rear young during their normal April–July breeding period. We further suggest that the resident birds do not delay their

breeding season until the more predictable rains of August–November because of the relatively large influx of winter resident insectivores that appear at this time. Winter resident densities often exceed those of resident insectivores, a fact which must affect selection for resident insectivore breeding seasons and would affect frugivores to the extent that the latter feed insects to their young.

Some further possible interactions between resident and non-resident birds are discussed. Some of the characteristics of longevity and site-fidelity of the resident species are described. Also documented is the invasion of the Caribbean Elaenia (*Elaenia martinica*), a species not recorded in Guanica Forest until 1980, whose numbers peaked in 1982, and now has apparently only a tenuous hold within the study area. The facts that no species was extirpated during the severe drought and neither *E. martinica* or any introduced species have successfully colonized the Guanica Forest community suggest it is at equilibrium.

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APPENDIX

NUMBER OF NEW CAPTURES OF INDIVIDUALS OF EACH SPECIES DURING EACH SAMPLING PERIOD

Species	1973	1974	1975	1976[a]	1978	1980	1981	1982	1983
Frugivores									
Zenaida Dove (*Zenaida aurita*)	—	—	—	—	1	—	—	—	—
Common Ground Dove (*Columbina passerina*)	16	1	7	4	6	—	4	—	3
Key West Quail-dove (*Geotrygon chrysia*)	—	—	—	—	2	1	—	—	1
Pearly-eyed Thrasher (*Margarops fuscatus*)	4	5	8	5	11	8	8	16	9
Red-legged Thrush (*Turdus plumbeus*)	2	2	5	—	4	10	5	6	6
Antillean Euphonia (*Euphonia musica*)	—	—	—	1	—	—	—	—	—
Stripe-headed Tanager (*Spindalis zena*)	6	2	1	—	1	2	1	5	—
Puerto Rican Bullfinch (*Loxigilla portoricensis*)	22	6	8	6	18	13	16	29	13
Yellow-faced Grassquit (*Tiaris olivacea*)	—	—	—	1	—	—	—	—	—
Black-faced Grassquit (*Tiaris bicolor*)	6	—	—	1	6	4	1	2	5
Gleaning Insectivores									
Mangrove Cuckoo (*Coccyzus minor*)	—	—	—	—	—	2	—	1	—
Puerto Rican Lizard-cuckoo (*Saurothera vieilloti*)	1	—	—	1	—	1	2	1	—
Puerto Rican Vireo (*Vireo latimeri*)	4	2	1	—	2	2	4	3	—
Adelaide's Warbler (*Dendroica adelaidae*)	5	6	1	1	7	3	7	8	7
Black-cowled Oriole (*Icterus dominicensis*)	1	1	2	—	—	—	—	—	—
Troupial (*Icterus icterus*)	4	—	2	4	1	—	—	2	1
Nectarivores									
Antillean Mango (*Anthracothorax dominicus*)	3	1	2	2	—	—	1	—	1
Bananaquit (*Coereba flaveola*)	53	33	18	9	17	16	18	27	29
Flycatching Insectivores									
Gray Kingbird (*Tyrannus dominicensis*)	—	—	—	—	1	—	—	—	—
Puerto Rican Flycatcher (*Myiarchus antillarum*)	6	5	8	11	4	2	3	5	6

APPENDIX
CONTINUED

Species	1973	1974	1975	1976[a]	1978	1980	1981	1982	1983
Caribbean Elaenia (*Elaenia martinica*)	—	—	—	—	—	1	6	9	2
Puerto Rican Tody (*Todus mexicanus*)	6	6	1	1	1	4	1	3	3
Miscellaneous Species									
American Kestrel (*Falco sparverius*)	1	—	—	—	—	—	—	—	—
Puerto Rican Woodpecker (*Melanerpes portoricensis*)	—	3	—	—	—	—	1	3	—
Puerto Rican Screech-owl (*Otus nudipes*)	—	—	1	—	—	—	1	—	—
Total resident individuals	140	73	65	47	82	69	78	120	86
Total winter residents	14	31	23	24	22	19	8	17	21
Grand total captures	154	104	89	71	104	88	86	137	107

[a] Because only 2 days of netting were done, these totals were multiplied by 1.25 to get a projected total for 3 days when graphing patterns in Figs. 1–7.