TURNOVER AND ECOLOGICAL RELEASE IN THE AVIFAUNA OF MONA ISLAND, PUERTO RICO

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MODERN biogeographic theory states that the number of species in a class or other large taxonomic unit that inhabits an island is maintained within narrow bounds by a dynamic steady state between colonization and extinction[1] (MacArthur and Wilson 1967). Although a recent experimental test of the theory upheld most of its expectations (Simberloff and Wilson 1969), there remains a paucity of data on natural colonization and extinction rates from which to judge the time scale of faunal turnover on islands of varying geographic status. Two previous studies of avifaunal turnover on islands have come to our attention, one involving the California Channel Islands (Diamond 1969) and the other, Karkar, a volcanic island off the north coast of New Guinea (Diamond 1971c). Here we report on changes in the birdlife of Mona Island that have transpired since the turn of the century. Mona is especially well suited for the measurement of turnover for a number of reasons: its terrestrial avifauna consists of a very limited number of species, most of which are common; its topography and vegetation are extremely uniform, making unlikely the possibility that species have escaped detection in small pockets of habitat; it is large enough (24 square miles) to provide living space for numerically ample populations, yet small enough to cover on foot from end to end; it has suffered comparatively little disturbance by man; and its avifauna has been thoroughly surveyed on several prior occasions, first in 1901.

In having a fauna that is entirely composed of species found on the nearby western end of Puerto Rico, Mona also lends itself to a study of ecological release, an expansion in density, distribution, or behavior that is commonly observed when the performance of a species is recorded under high and low intensities of competition (Crowell 1961, 1962; Willis 1966; Diamond 1969, 1971a, 1971b; MacArthur et al. 1972). The presence of a gradient of habitat in Puerto Rico that extends from areas of high to low rainfall makes it possible to select a plot having almost any desired combination of structural characteristics. By comparing the censuses of matched plots, one obtains good control over at least some of the variables that potentially regulate faunal composition and density. The second part of the paper presents the results

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[1] The authors use this term loosely to include both extinction and extirpation.—Ed.

of such a comparison between Mona and Puerto Rico in which the resident and wintering bird populations were quantitatively sampled with mist nets.

Mona lies nearly midway between Puerto Rico and Hispaniola, being 42 miles from the former and 36 miles from the latter. Its structure consists entirely of Miocene and Pleistocene limestone, which forms a nearly level platform with a mean elevation of about 200 feet. On the north, east, and south it presents imposing vertical sea cliffs, pocked with cave entrances that boobies and tropicbirds use as nesting sites. On the west is a narrow coastal plain that carries the only soil on the island, and which consequently supports a comparatively robust vegetation that presently consists largely of planted mahogany (*Swietenia*) groves. About 90% of the island's surface is contained in a nearly featureless plateau covered by a thick, mostly evergreen, sclerophyll scrub. Over most of the plateau the tree stratum reaches a height of 15–20 feet, and includes as common components, mahogany, gumbo limbo (*Bursera*), and poisonwood (*Metopium*). A dense layer of 2–3 foot shrubs forms the understory, in which species in the Euphorbiaceae and Verbenaceae predominate. Along the exposed northern and eastern clifftops the tree layer drops out, leaving a nearly impenetrable shrubland punctuated in places by stands of arborescent cactus (*Cereus* sp. ?).

The results that follow were gathered by a party of five that visited the island from 31 January to 5 February 1972.

FAUNAL TURNOVER

Reports on the avifauna of Mona Island have appeared from time to time since 1892 when, according to the information available to us, the first collections were made (see Appendix for references and a list of species recorded for the island). Three of the surveys seem to have been exhaustive and are conveniently spaced in time. We have used these in addition to our own observations as the basis for estimating minimum colonization and extinction rates (Bowdish 1902; Struthers 1923, 1927; Barnés 1946). Table 1 lists the resident land birds each party recorded with qualitative estimates of abundances.

In estimating turnover we shall be concerned only with species believed to have established nesting populations. For this reason, three birds that breed elsewhere in the Greater Antilles but whose status on Mona is questionable have been deleted from consideration: (1) Mourning Dove (*Zenaida macroura*), known from a single sight record in 1944 that may pertain to vagrants; (2) Yellow-billed Cuckoo (*Coccyzus americanus*), a single specimen taken in August 1944 was probably a migrant; and (3) Purple Martin (*Progne subis*), recorded in small

TABLE 1

BREEDING LAND BIRDS OF MONA ISLAND: STATUS OF THE SPECIES IN FOUR SURVEYS

Species	Survey						
	1901[1]		1926[2]		1943–45[3]		1972
Falco sparverius					+[4]		++
Columba leucocephala	+++		+++		+++		*[5]
Columba squamosa	+++		+++		+++		*
Zenaida aurita	+++		+++		+++		+++
Zenaida asiatica					+		*
Columbina passerina	+++		+++		+++		+++
Geotrygon montana	+++		+				
Geotrygon chrysia	+						
Coccyzus minor	+++		+++		+++		+++
Crotophaga ani					++		+
Tyrannus dominicensis	++		++		+++		+++
Margarops fuscatus	+++		+++		+++		+++
Agelaius xanthomus	+++		+++		+++		+++
No. species	10		9		11		11
Extinctions		1		1		0	
Natural colonizations		0		3		0	

[1] Bowdish 1902.
[2] Struthers 1927.
[3] Barnés 1946.
[4] Crosses indicate subjective abundance: +, rare; ++, uncommon; +++, common.
[5] Asterisk indicates probable summer resident not found by our party.

numbers at various times of the year but not definitely known to breed.

Known extinctions of established populations number three. (1) A weakly differentiated endemic race of the Hispaniolan Parakeet (*Aratinga chloroptera maugei*) disappeared suddenly sometime between 1892 and 1901. Local legend has it that the entire population departed en masse when blasting started for a guano mining operation, though hunting pressure almost certainly contributed to its demise. (2) The Ruddy Quail Dove (*Geotrygon montana*) was reported as plentiful by Bowdish in 1901, as scarce by Struthers in 1926, and has not been recorded since. Apparently the decline was gradual, if one accepts at face value these judgments on the abundance of a species difficult to observe. (3) The Key West Quail Dove (*Geotrygon chrysia*) was seen in 1901 by Bowdish. As this bird is inconspicuous at best, scarce over most of its range, and not known to migrate, it is probable that there was a resident population at that time.

An estimate of the rate at which extinctions occur, e, is given by: $e = 2E/t\ (I + F)$, where E is the number of recorded extinctions, t is the period of observation in years, and I and F are the initial and final numbers of species, respectively (cf. Diamond 1969). Since occasional surveys are likely to miss short-lived colonizations, the rate is a minimum one that pertains to well-established species, as will be discussed later.

The Mona data give an extinction rate of 0.29% of the fauna per year if the disappearance of the parakeet is judged to be a natural extinction, and 0.23% if only losses subsequent to the first thorough survey in 1901 are included. These values fall in the lower part of the range for the nine California Channel Islands (0.10–1.7%, Diamond 1969) and are close to that determined for Karkar near New Guinea (0.20%, Diamond 1971c). As extinction rates are expected to vary inversely with both island size and distance (MacArthur and Wilson 1967), one can predict the approximate rank order of extinction rates in a set of islands of varying size and distance. Direct comparison of the rates for tropical islands with those for the California Channel Islands is greatly complicated by the fact that the latter group lies along a major migratory flyway. Being exposed to greater immigration, these islands should, in general, show higher turnover rates than tropical islands of like size and distance, an expectation that is so far supported by the meager data now available. Even the outermost Channel Islands (61 miles) are so accessible to strong flying temperate migrants that the expected effect of distance on immigration is not discernible in the archipelago (Diamond 1969). Karkar differs from Mona in being near (10 miles) to a very rich source of colonists, in its larger area (142 square miles), and in having a much richer land bird fauna (53 spp.). Yet the equilibrium theory qualitatively anticipates similar extinction rates on small far islands and large near islands, a prediction that is gratifyingly upheld by these two tropical islands on opposite sides of the globe.

Since the beginning of the century, Mona has received at least five natural invasions and three introductions, the majority of which have met with little success. Of the natural invasions, two were first noted in 1935 and may have resulted from a furious hurricane that swept across the Dominican Republic in 1930 (Bond 1946). These are the Sparrow Hawk (*Falco sparverius*) and the Smooth-billed Ani (*Crotophaga ani*). The former now seems well-established, as we found pairs spaced at intervals of ½ to 1 mile over all parts of the island. On the other hand the ani, which prefers more open habitats elsewhere, has only barely survived to the present. Beatty (fide Bond, 1946) found two flocks numbering 20 birds in 1944, but our recent survey uncovered only a single cohort of 2–3 individuals, suggesting that the inappropriate habitat may be limiting the population. The White-winged Dove (*Zenaida asiatica*), which appears to be extending its range eastward in the Caribbean (Bond 1946), was found on Mona for the first time in 1944 by Barnés (1946), who estimated about 40 birds present, including a number of juveniles. Although we did not find this species, Barnés' account suggests that it may be a summer resident only, so we have not presumed its extinction. Our party encountered two additional species, the Sharp-shinned Hawk (*Accipiter striatus*) and Red-legged Thrush (*Mimocichla plumbea*). As we saw only single individuals of each, it seems best to regard them as vagrants rather than the vanguard of new populations.

Introductions have added three more species to the island's current fauna: the Bobwhite (*Colinus virginianus*), Red Jungle Fowl (*Gallus gallus*), and Bananaquit (*Coereba flaveola*). Members of the island's caretaker staff advised us that several small flocks of Jungle Fowl have occupied the central part of the plateau for many years. The Bobwhite derives from 100 pairs released in July 1971 (fide Dr. Felix Iñigo), but the status of the Bananaquit is somewhat problematical, there being unconfirmed reports of attempted introductions at various times since 1950 (fide Dr. Frank Wadsworth). The Bananaquit is one of the most successful colonists in the West Indian avifauna, having invaded nearly every available island (Cuba excepted) and habitat. In covering much of the island on foot, we located no more than four or five individuals, all living in close proximity near Uvaro. From this presumptive evidence one is tempted to surmise that the unexpected absence of the Bananaquit heretofore may not have been due to a lack of opportunity to colonize, but instead to the effect of some unrecognized component of the Mona environment that prevented its rapid increase and spread.

It is also curious in this connection to note the peculiar balance of Mona's avifauna. Of the 14 terrestrial species known to have been resident since 1892 (apart from introductions), 11 are nonpasserines, 9 of them pigeons and cuckoos. While the latter families are overrepresented in the West Indies generally (Terborgh 1973), communities with fewer than 50% passerine species are highly exceptional in the region, even on small islands. In this respect Mona's birdlife is decidedly atypical, though at present we have nothing concrete to offer by way of explanation.

One of the distinctions it has been necessary to make in developing a theory of extinction on islands (MacArthur and Wilson 1967) is that between invasion and establishment. Mona provides examples that fall across the spectrum of possibilities from well-established species that have inexplicably vanished (the parakeet and two quail doves) to those that have invaded but apparently not succeeded in expanding to fill the habitat (ani, Bananaquit) to those that have dispersed in insufficient numbers to initiate a breeding population (Sharp-shinned Hawk, Red-legged Thrush). In the following discussion of faunal turnover, only species that fall into the first of these categories will be taken into account, for two reasons. First, infrequent surveys can be expected to provide reliable information on well-established species, but not on unsuccessful, ephemeral invasions. Second, as colonization and extinction are held in theory to be interactive processes, only when a well-dispersed species becomes extinct does its niche become susceptible to reinvasion by the same or a different species. Toehold populations such as the Bananaquit and ani now maintain on Mona can hardly influence the establishment of potential competitors.

If the extinction data for Mona are taken at face value, they can be extended to give a more interesting picture of turnover, provided one makes the admittedly unlikely assumption that all well-established species face an equal probability of extinction. Using the more conservative estimate of 0.23% of the fauna per year, survival can be computed as $(1\text{-}e)^n$ where e is the extinction rate and n is the number of years. Solving for survival of 0.5 and 0.1, we find that half the species present are expected to become extinct in 300 years and that only one should persist for more than 1,000 years. While these estimates may incorporate a certain degree of error, both in the measured extinction rate and in the assumption of equal likelihood of extinction, they nevertheless give an order of magnitude view of turnover that can be valuable for comparative purposes.

Indirect evidence led some years ago to the realization that turnover rates are a function of island size, or more explicitly of the average number of individuals in their populations (Mayr 1965). Accordingly only two islands in the Caribbean of less than 50 square miles (Montserrat and San Andrés) harbor endemic birds. Of the Mona residents, three have been described as subspecifically distinct (the parakeet, Ground Dove, *Columbina passerina*, and Yellow-shouldered Blackbird, *Agelaius xanthomus*), a degree of evolutionary divergence that seems compatible with residence times on the order of 500–1000 years (Selander and Johnston 1967). In contrast, the status of Mona's herpetofauna is quite revealing. Of the nine recorded species (1 frog, 3 snakes, and 5 lizards), all but one are regarded as endemic (Schmidt 1926, Weaver et al. 1961). In relation to the dispersal powers of these animals, Mona must be a great deal farther from the sources of colonists than it is for birds. Consequently one would expect a much reduced invasion rate and, concomitantly, a much lower extinction rate at equilibrium. The considerably extended residence time implied by this reasoning is in accord with the increased phylogenetic distinctness of Mona's herpetofauna.

TABLE 2
CHARACTERISTICS OF THE VEGETATION IN THE GUANICA AND MONA NETTING AREAS

	Guanica	Mona Island
Mean canopy height (feet)	17	18
Foliage density (relative units)		
0–2 feet	264	282
2–25 feet	644	887
$>$ 25 feet	0	0
Foliage height diversity	0.26	0.24
Plant species diversity ($1/\epsilon pi^2$)	7.9	7.3
Median illumination at 1 foot above ground (ft–c)	3200	2400

ECOLOGICAL RELEASE

Vegetation very similar to that covering the Mona Plateau occurs in the Guanica Forest in southwestern Puerto Rico. This portion of the paper undertakes a quantitative comparison of the bird populations inhabiting matched habitats on Mona and at Guanica. Similarity of the two study tracts with respect to appearance, height of the trees, foliage height diversity and plant species diversity can be judged from Figures 1 and 2 and Table 2.

Among the various Puerto Rico habitats that have been censused for resident birds, the semiarid scrub of the Guanica reserve has proved the richest, both in species and in the density of individuals (MacArthur et al. 1966; Kepler and Kepler 1970). The 40 or so species known to nest in the area include all the birds currently resident on Mona with the exception of the two introduced gallinaceous species. The Mona fauna thus constitutes a small subset of the Guanica fauna, a fact that permits a comparison of population structure that is uncomplicated by compositional differences.

The sampling technique is similar to that described by MacArthur et al. (1972). Mist nets are strung end to end in straight lines through the habitat and operated on successive days from dawn to dusk. It is assumed that they randomly capture birds within the nettable size range (ca. 3–150 g) that fly through the habitat at net height (0–2 m). This being so, a constant fraction of the previously unmarked population should be captured each day, and the number of new captures should decline exponentially. A measure of population density that can be used in comparing localities and habitats is obtained by regressing the log of the number of new captures each day against the cumulative net days of trapping effort (Figure 3). From the y-intercept one obtains an estimate of the capture rate for the unperturbed system. The capture rate at the end of the trapping period is easily computed by entering

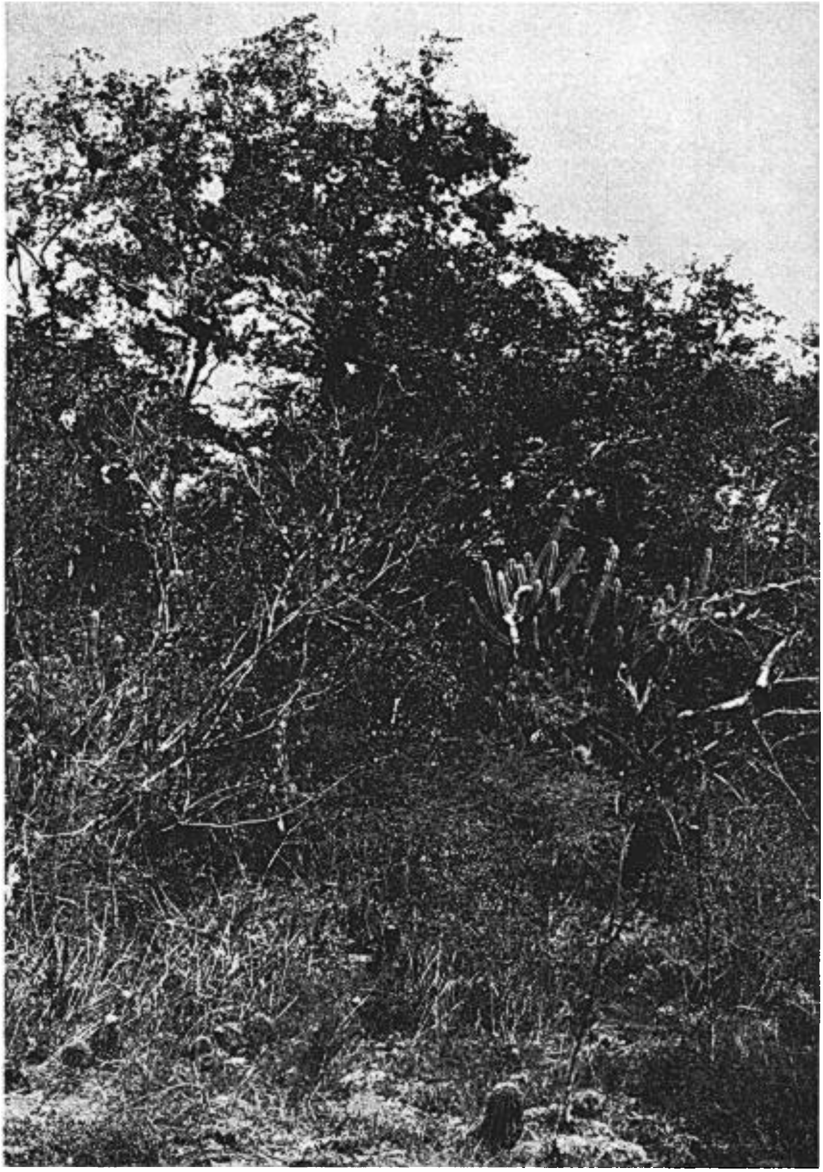

Figure 1. Limestone sclerophyll scrub adjacent to the net line in Guanica State Forest, southwestern Puerto Rico.

Figure 2. Limestone sclerophyll scrub on Mona Island, Puerto Rico. Net line passes through center of photo.

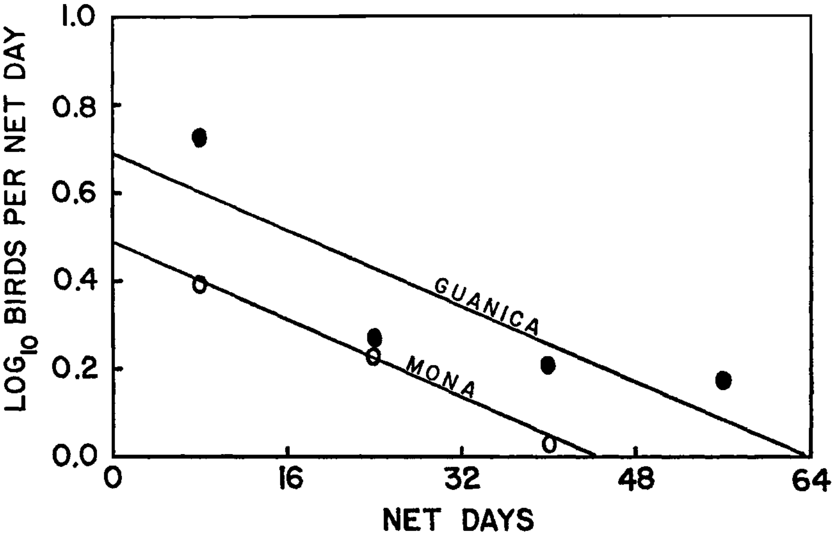

Figure 3. Regressions of log catch rate against accumulated net days for Guanica and Mona net samples. Sixteen nets were strung end to end at both localities and operated daily from dawn to dusk. Catch rates include only previously unmarked birds adjusted to a per net-day base.

the appropriate number of net-days into the regression equation. If f is defined as the final over the initial capture rate, 1-f then equals the proportion of the trappable population that was marked and released over the period. The total number of individuals marked and released divided by 1-f then gives an estimate of the size of the trappable population, a quantity we shall call the projected population. It must be understood that the trappable component of the local avifauna may be small or large depending upon the height of the vegetation and the vertical foraging behavior of the species present (Terborgh and Weske 1969). Nevertheless the netting technique does provide a good measure of relative intensity of use of the understory and is particularly appropriate for comparing habitats of similar structure (Diamond 1971b).

The regression method does not give an estimate of absolute population density, but rather a figure that is a product of the population density and a factor that expresses the mean foraging radius of the captured species. By way of illustration, consider a line of nets running through two habitats of similar structure and containing equally dense bird populations. Now, let the individuals in one habitat be territorial in the strictest sense of nonoverlapping foraging ranges, and let the individuals in the second habitat have much broader, freely overlapping home ranges. The measured density will be less in the first instance and, in general, we can expect a more rapid decline in new captures with time. Comparisons between habitats are thus subject to the assumption of a like degree of intraspecific overlap in foraging range, a population characteristic that is correlated with the slope of the regression line. As the slopes given by the Mona and Guanica populations are very nearly the same, we will consider that this assumption is valid.

Comparison of the netting results (Table 3) leads to several conclusions. (1) The number of resident species using the airspace between 0 and 6 feet on Mona is only a small fraction of that at Guanica (3 vs. 15). (2) The density and diversity of wintering birds are about the same in both localities. (3) For resident species the density of individuals is greater at Guanica, while (4) more biomass is carried on Mona. (5) The two abundant species on Mona, the Ground Dove and Pearly-eyed Thrasher (*Margarops fuscatus*) are, respectively, 11 and 6 times more numerous there than at Guanica.

Of these findings, the last is especially interesting for what it suggests about niche overlap and interspecific competition. Although the contrasts are large, they cannot be evaluated even qualitatively without making assumptions about how the populations are limited in the two localities. Three classes of potential limiting factors seem relevant to the case at hand: productivity (carrying capacity) of the habitat, a quantity that may contain complications in the form of seasonal patterns of relative abundance, and scarcity (Smythe 1970); predation; and interspecific competition. We will consider pertinent information on each of these in turn.

Productivity.—Most of the techniques for estimating the annual productivity of vegetation require repeated or long-term measurements (e.g. Whittaker and Woodwell 1969) or are inapplicable in the tropics (e.g. measurement of incremental growth). Anything done hastily or indirectly is bound to be crude, but may suffice to discriminate coarse differences. For example Rosensweig (1968) has shown that within world extremes a high correlation exists between evapotranspiration and net annual productivity. By this criterion Mona should be similar to the extent that this can be judged from the scanty climatic information available (Walter and Leith 1960).

Under these circumstances a more reliable indication of productivity may be obtained by measuring the amount of light penetrating the foliage. Following this approach, we took 55 and 62 readings with a Weston photographic lightmeter near noon on clear days at Mona and Guanica, respectively, at 3-foot intervals beside the net lines. The median reading at 1 foot above the ground was 2,400 ft-c at Mona and 3,200 ft-c

TABLE 3

COMPARISON OF NUMBERS, WEIGHTS, BIOMASS, AND METABOLIC DEMAND OF GUANICA AND MONA BIRD POPULATIONS[1]

Species	No. captured		Projected population		Mean weight (g)		Biomass of projected population (g)		Metabolic demand of projected population (kcal/day)	
	G	M	G	M	G	M	G	M	G	M
Fruit and seed eaters										
Columbina passerina	5	49	6.2	68.7	35.4	27.0	220.5	1855.8	48.5	437.2
Mimus polyglottos	2		2.5		45.5		113.3		41.2	
Margarops fuscatus	4	23	5.0	32.3	94.9	101.2	473.0	3265.1	129.8	875.0
Mimocichla plumbea	5		6.2		73.9		460.2		139.0	
Spindalis zena	1		1.2		28.5		35.5		15.4	
Loxigilla portoricensis	36		45.7		32.3		1474.3		608.8	
Tiaris bicolor	17		21.6		9.5		204.7		134.8	
Total fruit and seed eaters	70	72	88.4	101.0			2981.5	5120.9	1117.5	1312.2
Resident nectar and insect eaters										
Chlorostilbon maugaeus	1		1.2		2.5		3.1		1.3	
Anthracothorax dominicus	10		12.7		5.4		67.9		24.0	
Todus mexicanus	6		7.7		5.6		42.7		14.9	
Myiarchus stolidus	19		24.1		23.0		554.4		260.8	
Vireo latimeri	2		2.5		12.2		30.4		18.2	
Dendroica adelaidae	3		3.7		6.7		25.2		18.9	
Coereba flaveola	33	1	41.7	1.4	9.4	9.8	393.5	13.7	259.8	8.9
Icterus icterus	4		5.0		72.0		358.7		109.4	
Total resident nectar and insect eaters	78	1	98.6	1.4			1475.9	13.7	707.3	8.9
Wintering North American migrants										
Sphyrapicus varius		1		1.4		40.0		55.9		12.0
Mniotilta varia	6		7.7		9.5		72.6		47.9	
Parula americana	4	1	5.0	1.4	6.7	7.4	37.5	10.5	27.0	7.6
Dendroica tigrina		2		2.8		9.1		25.4		17.0
Dendroica coronata		1		1.4		8.9		12.4		8.4
Dendroica discolor	4	4	5.0	5.6	6.9	6.9	34.0	38.1	25.4	28.4
Setophaga ruticilla	2	1	2.5	1.4	7.4	7.0	18.0	10.1	13.1	7.4
Total wintering migrants	16	10	20.2	14.0			162.1	152.4	113.4	80.8
GRAND TOTALS	164	83	207.2	116.4			4619.5	5287.0	1938.2	1401.9

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[1] Estimated from netted and projected samples.

at Guanica. When these values are contrasted with figures obtained with the same meter for evergreen rainforest (120–320 ft-c) and desert (full sun), vegetation types that differ widely in productivity, it can be appreciated that they fall together in an intermediate range.

Predation.—In the literature on bird populations, the importance of predation in limiting numbers of adults is a will-o'-the-wisp. At best we can inspect the two localities for possible differences. As regards avian and reptilian predators, the match is good. Sparrow Hawks are moderately common in both places, the Sharp-shinned Hawk is absent or casual, and each island has three snakes, at least one of which is primarily arboreal and probably raids nests. Rats and feral house cats are conspicuously present in both localities, and Puerto Rico in addition hosts the mongoose which, by presumptive evidence, appears to be comparatively scarce at Guanica (Kepler 1970). Although the mongoose is suspected of contributing to the scarcity or extinction of certain ground nesting birds in the West Indies (Bond 1971), comparisons of bird densities on islands where the mongoose is present or absent have shown no discernible differences (Terborgh, MS). Hence there is little reason to suppose that predation may affect the Mona and Guanica populations differently.

Competition.—Species that share portions of a pool of limiting resources are expected to influence each other's abundances reciprocally to the extent of their overlap in the use of the resource (Gause 1964). In general the productivity of the habitat will determine the supply of resources, which in turn must impose an upper limit on the number of organisms harvesting the resources. Given that two habitats provide an equal array of resources harvestable by birds (as fruit, nectar, seeds, insects, vertebrate prey, etc.), and given that these bird populations are resource-limited, the total biomass of birds living in the habitats may differ for two reasons: (1) The communities may possess different average efficiencies in harvesting the resources, and (2) the species present may differ in their average size and hence in their metabolic demand per unit of biomass, larger species requiring fewer calories per gram of body weight for maintenance (Kendeigh 1972).

Whether by coincidence or unknown cause, the two common nettable birds of Mona are both large. In order to compare the metabolic demand of Mona and Guanica bird populations on their respective habitats, it is necessary to multiply the number of each species by the caloric intake required for normal activity. Estimates of the latter for passerine and nonpasserine species of any weight can be obtained using regression equations given by Kendeigh (1970). Following this procedure, and summing over all the netted species in each locality, one finds that the metabolic demand of the Guanica population is greater by about 38 percent (Table 3).

In seeking to interpret this result, we must take into account the functional differences between the two communities. Several of the Guanica species employ foraging techniques (e.g., hovering, hawking) and utilize food resources (nectar, small insects) that would not be expected for either of the abundant Mona species. To obtain a rough correction for this, we have used stomach content data from Wetmore (1916) and our own observations to classify each species according to its principal food resource (Table 3). As judged from the stomachs of Puerto Rican specimens, the diet of the two common Mona species is as follows (Wetmore 1916): Ground Dove, 99.8% seeds; Pearly-eyed Thrasher, 13% animal, 87% vegetable (mostly fruit). By removing from the Guanica population the eight species that feed mainly or exclusively on insects or nectar, one can compute a maximum figure for the metabolic demand for fruits and seeds by the remaining species, given the generous assumption that their entire food intake consists of these products.

We now find that the two Mona species harvest ca. 17% more energy as fruits and seeds than do the seven species at Guanica. As it is unlikely that this is due to a greater harvesting efficiency on the part of the Mona community, we conclude that the carrying capacity of the Mona vegetation for fruits and seeds is at least 17% greater. Differences this large could arise in two distinct ways, even in plots having the same net photosynthetic productivity. One habitat could contain a higher proportion of plant species that furnish fruits and seeds to birds, or it could supply these foods with less seasonal variance. Our present knowledge of the two localities affords no means of discriminating between these possibilities.

If we now concede that the carrying capacities of the Mona and Guanica habitats with respect to fruits and seeds are not grossly different, let us say within a factor of 2, the next question to consider is the disparity in the abundances of the Ground Dove and Pearly-eyed Thrasher. The possibilities fall into two categories. First the resource spectra offered by the habitats could differ in such a way that the bulk of fruit and seeds supplied by the Mona vegetation was of types normally utilized by the two species present (i.e., little niche expansion). Or second the habitats could provide roughly equal resource spectra and, in the absence of competitors, the Mona populations could have increased to fill most of the void (niche expansion).

If the first of these alternatives were true, one would expect to find irregular variation in the abundance of consumer species along a habitat

TABLE 4
BIRDS RECORDED ON MONA ISLAND, 1892–1972[1]

Puffinus lherminieri	O[2]	*Columbina passerina*	CP
Oceanodroma leucorhoa	O	*Geotrygon montana*	E
Phaethon lepturus	CP	*Geotrygon chrysia*	E
Pelecanus occidentalis	O	*Aratinga chloroptera*	E
Sula leucogaster	CP	*Coccyzus minor*	CP
Sula sula	UP	*Coccyzus americanus*	RM
Fregata magnificens	CP	*Crotophaga ani*	RP
Bubulcus ibis	O	*Caprimulgus carolinensis*	UW
Nyctanassa violacea	UP	*Chordeiles minor*	RM
Anas discors	O	*Ceryle alcyon*	UW
Accipiter striatus	O	*Sphyrapicus varius*	UW
Pandion haliaetus	UW	*Tyrannus dominicensis*	CP
Falco peregrinus	O	*Progne subis*	US
Falco sparverius	CP	*Petrochelidon* sp.	O
Gallus gallus	I	*Hirundo rustica*	UM
Colinus virginianus	I	*Mimus polyglottos*	O
Porzana carolina	O	*Margarops fuscatus*	CP
Charadrius vociferus	UW	*Mimocichla plumbea*	O
Squatarola squatarola	O	*Vireo griseus*	RW
Arenaria interpres	O	*Mniotilta varia*	UW
Himantopus himantopus	O	*Parula americana*	CW
Actitis macularia	UW	*Dendroica magnolia*	RW
Tringa solitaria	O	*Dendroica tigrina*	UW
Tringa melanoleuca	RW	*Dendroica caerulescens*	RW
Tringa flavipes	UW	*Dendroica coronata*	CW
Calidris minutilla	O	*Dendroica dominica*	UW
Calidris pusilla	O	*Dendroica castanea*	OM
Crocethia alba	UW	*Dendroica discolor*	CW
Micropalama himantopus	O	*Dendroica palmarum*	UW
Larus atricilla	US	*Seiurus aurocapillus*	UW
Sterna anaethentus	CP	*Seiurus noveboracensis*	UW
Sterna fuscata	UP	*Seiurus motacilla*	RW
Thalasseus maximus	UW	*Oporornis agilis*	OM
Anous stolidus	CP	*Geothlypis trichas*	RW
Columba leucocephala	CS	*Wilsonia citrina*	RW
Columba squamosa	CS	*Setophaga ruticilla*	UW
Zenaida macroura	O	*Coereba flaveola*	I
Zenaida aurita	CP	*Piranga olivacea*	OM
Zenaida asiatica	US	*Agelaius xanthomus*	CP
		Guiraca caerulea	OM

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[1] Taken from Cory (1892), Bowdish (1902, 1903), Struthers (1923, 1927), Danforth (1936), Barnés (1946), Bond (1946, 1956, 1963, 1968), Weaver et al. (1961), and the observations of the authors.

[2] Abbreviations: C, common; E, extinct; I, introduced; M, migrant; O, occasional; P, permanent resident; R, rare; S, summer resident; U, uncommon; W, winter resident.

gradient as different preferred food plants entered and dropped out of the vegetation. Where the responses of bird populations to smooth environmental gradients have been examined it is generally observed that each species has an optimum position on the gradient, away from which its abundance decreases steadily to zero (Terborgh 1971). This result implies that environmental control of abundance is mediated more through broad gradients in climate and habitat structure than through local variations in the species composition of the vegetation. The abundance of the Ground Dove in the Dominican Republic, for example, closely tracks an environmental moisture gradient, ranging from zero in rain forest to ca. 0.5 pair per acre in evergreen limestone scrub similar to that on Mona, to a maximum of 0.9 pair per acre in desert dominated by arborescent cacti (Terborgh, MS). One concludes that the environmental optimum for this species in the presence of a wide array of potential competitors is in habitats that are more open and arid than those found on Mona. Avaliable data for Puerto Rico concur in showing maximum abundance of the Ground Dove in the comparatively dry Guanica region (MacArthur et al. 1966, Kepler and Kepler 1970). In contrast the Pearly-eyed Thrasher is most numerous in rainforest. Line censuses of singing birds indicated 4.3 per km in the wet Luquillo forest and only 1.0 per km at Guanica (Kepler and Kepler 1970).

Judging from the performance of the two species on adjacent islands, neither appears to be at its environmental optimum on Mona. Moreover in species-rich communities, neither appears to attain densities as high as those measured on Mona, even in habitats representing their respective environmental optima. These arguments strongly imply that the Ground Dove and Pearly-eyed Thrasher have undergone considerable niche expansion on Mona, explicitly in response to the paucity of competitors.

Previous studies have noted that the ecological responses of birds to species-poor insular environments fall into a number of categories: increase in abundance (Crowell 1962, MacArthur et al. 1972), use of a greater range of habitats or new habitats (Diamond 1971a), expansion of distributions with respect to environmental gradients (Diamond 1971a), broadening of foraging behavior (Keast 1970; Diamond 1971a), and expansion or shift in food spectrum (Grant 1966, Diamond 1971a). In the present instance we are concerned with a major increase in abundance that seems to have resulted from an invasion of other species' niches. The missing species in order of their metabolic demand on the Guanica habitat are: Puerto Rican Bullfinch (*Loxigilla portoricensis*), Red-legged Thrush, Black-faced Grassquit (*Tiaris bicolor*), Mockingbird (*Mimus polyglottos*), and Stripe-headed Tanager (*Spindalis zena*), the latter two being comparatively unimportant (Table 3).

Note that the first three of these are in different families from either of the two common Mona species. One would like to know in what ways the Mona populations could be utilizing the resources that are harvested by these other birds at Guanica. On Mona the Ground Doves forage mainly on the ground and the Pearly-eyed Thrashers in the crowns of trees, much as they do elsewhere. Thus more varied foraging behavior does not seem to be at the root of the expansion.

Bullfinches and grassquits obtain much of their food directly from plants, while Ground Doves must wait until it drops. The latter thus stands to gain directly from the absence of arboreal seed eaters, to the extent that the crop is free from decay and insect depredation. At least some of the fruits commonly eaten by Mockingbirds, Red-legged Thrushes, and bullfinches are also taken by Pearly-eyed Thrashers (e.g. *Bursera*), but the extent of overlap on other types of fruit has not been studied. By being large, the thrasher is able to exploit a broader range of fruit sizes than a smaller bird, and thus is able to undergo a greater expansion in abundance when released from competition (Schoener 1969; Terborgh and Diamond 1970).

A final comment concerns the evolutionary course that the Ground Dove and Pearly-eyed Thrasher appear to be taking on Mona. Stomach content analyses of Puerto Rican birds indicate that they normally consume different resources there (Wetmore 1916) and, moreover, one is terrestrial and the other strictly arboreal. Taken together these observations imply that the potential for niche overlap between them is minimal. Nevertheless our weight data show that the two Mona populations have diverged in size with respect to their Guanica counterparts (Table 3). The difference is highly significant for the Ground Doves, which are considered separate subspecies, and just significant ($P = 0.05$) for the Pearly-eyed Thrashers, which may have invaded the region in comparatively recent times.

While it is possible that the ecological expansion of both species in the absence of other competitors could have brought them into competition enough to produce character divergence, it seems more likely that each has independently evolved in the direction that confers the greatest adaptive advantage on Mona. In the case of the Ground Dove, a decrease in size is the expected consequence of expansion into the niches of the bullfinch and Black-faced Grassquit, the two commonest seed-eating species at Guanica, both of which are smaller than the Ground Dove of Puerto Rico. It is less obvious why the Pearly-eyed Thrasher has increased, unless the mean size of fruits provided by the Mona habitat is somewhat larger.

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SUMMARY

Mona Island, in the strait between Puerto Rico and Hispaniola, is unusual among West Indian islands of its size (24 square miles) in

having been little disturbed by human activities and in having been the subject of repeated ornithological investigations. Several thorough surveys of its birdlife have made possible the determination of extinction and immigration rates for the interval of 1892 to the present. During this period there have been three extinctions, three natural colonizations, and three introductions plus several records of vagrant individuals of potentially resident species. The measured extinction rate of 0.23% of the fauna per year is in close agreement with the only other available figure for a tropical insular avifauna (0.20% per year: Diamond 1971c) and both are lower than the values for all but one of the nine California Channel Islands (Diamond 1969), in accordance with theoretical expectation.

A second part of the paper compares netted samples of birds captured in matched habitats on Mona and in the Guanica Forest Reserve in southwestern Puerto Rico. The vegetation on the two sites was quantitatively similar in the following measures: canopy height, foliage density, foliage height diversity, plant species diversity and light penetrating to the ground. All bird species present on Mona, with the exception of two introduced game birds, also occur commonly at Guanica. The sample of birds netted on Mona included only three resident species of which two, the Ground Dove and Pearly-eyed Thrasher, comprised over 99% of the biomass and were respectively, 11 and 6 times more abundant than at Guanica. Arguments are developed strongly implying that most of the increased abundance of these two species on Mona is due to expansion into the food niches of five trophically similar species present at Guanica.

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APPENDIX

Table 4 lists the birds recorded on Mona Island since 1892, with a qualitative evaluation of the current status of each. Our expedition added 13 species to the 66 mentioned in previous reports for a total of 79. Particulars for these new records are given below.

Cattle Egret (*Bubulcus ibis*): One seen flying over the costal plain near Sardinera 5 February.

Sharp-shinned Hawk (*Accipter striatus*). An immature was carefully observed near Sardinera 5 February.

Red Jungle Fowl (*Gallus gallus*): Crewmembers of the island's two manned stations told us that domestic fowl had been present on the island for many years and that several flocks currently inhabit the dense growth in the central part of the plateau.

Bobwhite (*Colinus virginianus*): We flushed one from the grassy clearing at Sardinera on 1 February. Dr. Felix Iñigo has kindly informed us that 100 pairs were released 14 July 1971 by the Fish and Wildlife Division of the Puerto Rican Department of Agriculture.

Yellow-bellied Sapsucker (*Sphyrapicus varius*): Borings were conspicuous in wooded portions of the plateau and coastal plain, especially in mahogany (*Swietenia*) trees. One was captured on 4 February and another seen on the plateau the day before. Apparently it is an uncommon but regular winter resident.

Red-legged Thrush (*Mimocichla plumbea*): A lone bird was seen twice by several members of the party near Sardinera on 31 January. Although the habitat on Mona is appropriate for the species, the lack of any further sightings suggests that the bird was probably a vagrant.

White-eyed Vireo (*Vireo griseus*): One sang daily in an Acacia thicket near our camp at Uvaro.

Magnolia Warbler (*Dendroica magnolia*): Several immature birds were seen foraging in tree crowns on the coastal plain.

Cape May Warbler (*Dendroica tigrina*): Two were caught in mist nets on the plateau.

Black-throated Blue Warbler (*Dendroica caerulescens*): A full-plumaged male was seen near Sardinera 5 February.

Common Yellowthroat (*Geothlypis trichas*): A male was netted on the coastal plain 3 February.

Hooded Warbler (*Wilsonia citrina*): A male was netted on the coastal plain 3 February.

Bananaquit (*Coereba flaveola*): A single bird was taken twice in our plateau nets, while at least two others were seen and heard repeatedly in some large flowering *Guaiacum* trees just below the rim of the plateau.