ISLAND COLONIZATION BY LESSER ANTILLEAN BIRDS

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ABSTRACT.—We present an analysis of bird distribution in small islands in the northern Lesser Antilles colonized principally from Guadeloupe. In spite of great differences among the islands in soils, rainfall, and vegetation, their avifaunas are strikingly uniform.

We found that species inhabiting coastal scrub on the source island performed better as colonists than inhabitants of interior rainforest, suggesting that humid forests in the target islands would hold drastically impoverished bird communities. This proved not to be the case. Diversities in the small-island rainforest communities were compensated by the substitution of coastal scrub species for missing forest counterparts and the expansion of vertical foraging zones. In progressing from species-poor to species-rich communities in equivalent habitat, the number of trophic guilds remains constant, while the number of species per guild and the tightness of species packing increase. We conclude that the faunal uniformity of islands colonized from Guadeloupe results from nonuniform dispersal abilities coupled with ordering ecological constraints: versatility in habitat occupancy, trophic status and size in relation to guild neighbors.—*Department of Biology, Princeton University, Princeton, New Jersey 08540; Division of Biological Sciences, University of Missouri, Columbia, Missouri 60521; and Department of Zoology, University of Florida, Gainesville, Florida 32601.* Accepted 2 August 1976.

MODERN biogeography has enjoyed considerable success in accounting for the numbers of species of birds, lizards, and other taxa found on the islands of various archipelagoes. Nearly all the interisland variation in bird species numbers in the southwest Pacific, for example, can be explained by a simple empirical formula that takes into account each island's area, elevation, and distance from New Guinea, the ultimate source of colonists in that region (Diamond 1973). Equilibrium theory (MacArthur and Wilson 1963) maintains that insular faunas are stabilized by a dynamic balance of colonizations and extinctions, and suggests the statistical limits within which the number of species should vary on any given island. However, equilibrium theory tells us nothing about how different or how alike the faunas of two nearby islands should be. If they were totally different we should be surprised. We should also be surprised if they were totally alike, for the equilibrium model rests on random processes, limited to be sure by certain statistical constraints. To phrase the question in general terms, we ask whether the interaction of colonization and extinction leads to chaos, a rigidly ordered community structure, or to some more perplexing intermediate condition.

In at least one group of islands, the Lesser Antilles, the answer is clearly that the composition of insular avifaunas is highly deterministic. In a previous publication one of us (Terborgh 1973) showed by regression analysis that the species lists of both the smaller (<300 km^2) and larger (>300 but $<1,600$ km^2) islands were approximately 90% determined by their locations.

Another result of this analysis was that interisland differences in habitat in the Lesser Antilles exert such a minor influence on species composition that it is scarcely detectable. This was particularly astonishing in the case of the northern Lesser Antilles, a group of 10 islands lying to the north and northwest of Guadeloupe, and to the east of the Virgins (Fig. 1). These islands comprise 2 natural groups, an inner chain of 5 high, wet volcanic peaks covered with rainforest, and an outer chain of 5 low, dry coral platforms covered with xeromorphic scrub. Though the islands of the two chains are of very nearly the same size and within sight of one another, it is hard

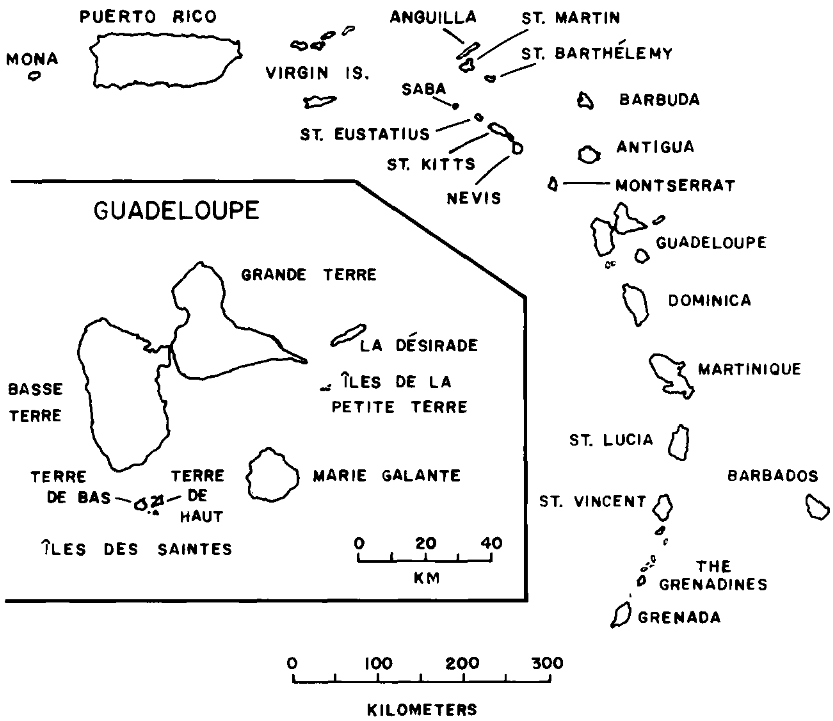

Fig. 1. Map of the Lesser Antilles with Mona, Puerto Rico and the Virgin Islands. Inset shows Guadeloupe and its satellites.

to imagine that they could be more different in topography, climate, and vegetation. Yet the wet and dry islands accommodate practically the same collections of bird species. This fact runs against the grain of our common sense and experience.

The paper is organized into two major sections. The first inquires into the factors influencing the colonization of the 10 northern Lesser Antillean islands. In particular, we focus on the rainforest communities of these islands, because the paucity of forest birds in their faunas suggested that their forests should be strikingly impoverished in relation to those of larger source islands to the south. The second section examines the constancy of the colonization process in the Guadeloupe satellite islands of the Îles des Saintes, Desirade, and Marie Galante. The locations of these islands, nearly equidistant from Guadeloupe and closer to it than to each other, suggest that they have been colonized independently. Together they constitute a replicated "natural experiment" of islands colonized from a common source.

Localities and Methods

One or another of us visited 11 Lesser Antillean islands in the course of this research. Intensive studies, including netting and species censuses, were undertaken at 9 sites on 8 islands. Four of the 9 sites were in montane rainforest and 5 in coastal scrub. Details follow below.

Rainforest sites.—The vegetation at each of these consisted of very old or virgin montane evergreen forest dominated by the typical association of *Dactryodes* and *Sloanea*. Canopy height varied somewhat between localities from 20 to 30 m depending on the degree of slope and exposure. It was greatest in Dominica, only slightly less in Guadeloupe, and least on Montserrat.

Dominica, 26 January to 30 January 1971, elev. 280 m in Brown's River watershed ca. 1 km S of the road to Rosalie Bay.

Guadeloupe (Basse Terre), 24 January to 28 January 1974, elev. 350 m, 1 km W of the Grand Etang.

Montserrat, 14 January to 18 January 1975, elev. 425 m, 1 km S of the Dannenborg Farm on the road between Blackburne Field and Plymouth.

St. Kitts, 8 February to 13 February 1972, elev. 500 m on the northeast facing slope of the South East Range in the upper part of the Lodge Estate.

Coastal scrub sites.—All of these were on Gaudeloupe and its satellites. In its natural state, the xeromorphic scrub vegetation of the Antilles consists of two usually well separated layers, a tree canopy 4–5 m high of legumes, *Bursera*, *Tabebuia*, etc., and a 1–2 m understory of *Croton*, *Hematoxylon*, and other shrubby sclerophylls. Very little of this remains in anything resembling its original condition. Of our 5 sites, only the one on Terre de Haut (Îles des Saintes) could be considered undisturbed; the rest were in various states of degradation, as explained later. Charcoal making followed by heavy grazing by cattle and goats convert natural scrub to nearly impenetrable spiny thickets of *Acacia* and *Opuntia*. This has happened throughout the Guadeloupe archipelago except on the Îles des Saintes where it is only starting. Our sites represent the best habitat available on each island.

Îles des Saintes (Terre de Bas), 13 January to 17 January 1974, 1 km SW of Grand Anse.

Îles des Saintes (Terre de Haut), 13 January to 17 January 1974, 1.5 km WSW of Terre de Haut.

Desirade, 18 January to 22 January 1974, 1 km NW of Grand Anse.

Marie Galante, 19 January to 23 January 1974, 2 km N of Pointe des Basses.

Guadeloupe (Grande Terre), 27 January to 31 January 1974, 5 km NNE of Saint François.

We also briefly visited Nevis, Antigua, and Barbuda.

At each study site we set up a camp where we remained for 5–6 days. During this time we censused the local birdlife, taking notes on diets, foraging behaviors, etc., and operated mist nets to capture a sample of the birds using the airspace from 0.1 to 2 m above the ground. The nets (12 m, 36-mm mesh) were strung in a long, nearly continuous line and operated from dawn to dark for a succession of 3 or 4 days. Birds were banded, measured (wing, occasionally bill or tarsus), weighed, and released. The data presented in the tables refer to resident species only. North American migrants were excluded on the grounds that they are a transient and insignificant component of the fauna (8 out of a total of 1,340 individuals captured).

Daily net catches invariably declined over the 3–4-day periods to half or less of the initial levels. Estimates of the total nettable population (referred to as the projected population per net) at each site were obtained from $[N/n]/[1 - (C_f/C_0)]$, where N = the total number of different individuals captured, n = the number of nets used, C_f = the final and C_0 the intial catch rates. The latter two values are taken from the log-linear regression of daily catch rate against the cumulative number of net days of trapping. For further details see Terborgh and Faaborg (1973).

Faunal Homogeneity of the Northern Lesser Antilles

The faunal homogeneity of the wet and dry northern Lesser Antillean islands would not seem so paradoxical if we could attribute it to stepping-stone colonization. This is a plausible suggestion, and there is evidence to support it. The two islands nearest to Guadeloupe, the presumptive source, are Montserrat, a wet island, and Antigua, a dry island (Fig. 1). Each has more species than any other in its respective chain. As Montserrat and Antigua are nearly as close to Guadeloupe (56 and 60 km) as they are to each other (38 km), it is reasonable to suppose that in the main they were colonized independently. Yet, surprisingly, 20 out of the 24 species known to occur naturally on Antigua (83%) also inhabit Montserrat (Table 1). Thus, while stepping-stone filtering may result in somewhat reduced species densities in the most distal islands of the two arcs, it does not convincingly account for the strikingly similar communities of the wet and dry islands. Instead we must conclude, first, that the faunal homogeneity of the northern Lesser Antilles is due to a very uneven distribution of colonizing ability among the species constituting the source fauna (i.e. certain species have colonized many small islands, others few or none), and second, that colonizing ability in most instances overrides the effects of habitat on the recipient island.

The latter conclusion would offer an easy solution of the paradox if it turned out that the species that have successfully invaded the northern Lesser Antilles are

TABLE 1

LAND BIRDS OF THE NORTHERN LESSER ANTILLES AND THEIR SOURCES[1]

	Wet islands[2]					Dry islands[3]					Source of race (or species)	Source habitat
	Mo	Ne	SK	SE	Sa	Ant	Ba	SB	SM	Ang		
Buteo jamaicensis	r[4]	+	+	+	+				r		GA[5]	B[6]
Buteo platypterus						E					[W]	B
Falco sparverius	+	+	+	+	+	+	+	+	+	+	LA, GA	C
Columba leucocephala	r					+	+	r	r	r	W	C
Columba squamosa	+	+	+	+	+	+	+		+		W	B
Zenaida aurita	+	+	+	+	+	+	+	+	+	+	LA	C
Columbina passerina	+	+	+	+	+	+	+	+	+	+	LA, VI	C
Geotrygon mystacea	+	+	+	+	+	+	+				LA, VI	C
Coccyzus minor	+					E	E		r		LA	B
Crotophaga ani	+			+							W	O
Speotyto cunicularia		X	X			X					[W]	O
Cypseloides niger	+		+								LA, GA	M
Eulampis jugularis	+	+	+	+	+	+	r				LA	M
Sericotes holosericeus	+	+	+	+	+	+	+	+	+	+	LA, VI	C
Orthorhynchus cristatus	+	+	+	+	+	+	+	+	+	+	LA, VI	C
Tyrannus dominicensis	1	2	2	2	2	1	1	2	2	2	1LA, 2GA	C
Myiarchus oberi[7]		E	E				E				LA	M
Elaenia martinica	1	1	1	1	1	2	2	2	2	2	1LA, 2VI	C
Progne subis	+		+	+	+	+	+		+		LA, GA	C
Margarops fuscus	+	+	+	+	+	+	+				LA	B
Margarops fuscatus	1	2	2	2	2	2	2	2	2	2	1LA, 2GA	B
Cinclocerthia ruficauda	E	E	E	E	E						[LA]	M
Cichlherminia l'herminieri	E										[LA]	M
Vireo altiloquus	+	+	+	+		+	+	+	+	+	LA, VI	B
Dendroica petechia	E	E	E	E		E	E	E	E	E	[W]	C
Dendroica adelaidae							E				[LA, GA]	C
Coereba flaveola	+	+	+	+	+	E	E	E	E	E	LA	B
Euphonia musica	+				+	+	+	+			LA	C
Molothrus bonariensis						+					W	O
Quiscalus lugubris	+		I			I	I				LA	O
Icterus oberi	E										—	—
Loxigilla portoricensis			X								[GA]	B
Loxigilla noctis	E_1	E_1	E_1	E_1	E_1	E_2	E_2	E_2	E_2	E_2	[LA]	B
Tiaris bicolor	+	+	+	+	+	+	+	+	+	+	W	C
Totals[8]	26	21	24	21	19	24	22	14	15	13		

[1] From Bond 1956, 1971, 1956–1974.
[2] Mo = Montserrat, Ne = Nevis, SK = St. Kitts, SE = St. Eustatius, Sa = Saba.
[3] Ant = Antiqua, Ba = Barbuda, SB = St. Barthélemy, SM = St. Martin, Ang = Anguilla.
[4] + = resident, E = endemic race or species, r = recorded, X = extinct.
[5] LA = Lesser Antilles, GA = Greater Antilles, VI = Virgin Islands, W = Widespread.
[6] C = coastal scrub, M = montane rainforest, B = both of preceding, O = openings, fields, etc.
[7] Classified by Lanyon (1967) as belonging to an endemic Lesser Antillean species.
[8] Includes extinct populations but not introductions or isolated records.

habitat generalists. In order to examine this possibility we must first identify the source of colonists and then determine the habitat affinities of the species in question in the source region.

Source of colonists.—Table 1 shows the distributions of the 34 living or recently extinct species of land birds known to inhabit the northern Lesser Antilles. Among these 34 species, 31 (91%) occur on the larger Lesser Antillean islands, 28 of them on Guadeloupe. At the racial level the affinities of the northern Lesser Antillean fauna are also clearly with the islands to the south.

Habitat affinities in the source region.—Several distinct vegetation formations occur on each of the 6 principal islands of the main Lesser Antillean chain (Grenada through Guadeloupe). These include elfin forest near the summits of the windswept volcanic peaks, montane rainforest on the steep slopes, semideciduous to xerophytic scrub along the leeward coasts, savannah and mangroves (Beard 1949, Hodge 1954).

TABLE 2

HABITAT AFFINITIES OF THE LAND BIRDS OF DOMINICA AND GUADELOUPE AND THEIR SUCCESS IN COLONIZING THE NORTHERN LESSER ANTILLES

Major habitat	No. of species in Dominica and Guadeloupe	No. of species reaching northern Lesser Antilles (%)	Mean no. of islands colonized per species
Montane rainforest	16	5 (31)	3.4
Coastal scrub	15	13 (87)	8.4
Both of above	8	8 (100)	7.3
Openings, fields, etc.	5	3 (60)[1]	3.0
Total or weighted mean	44	29 (66)	6.7

[1] Includes 3 extinct populations of *Speotyto* and 4 probably introduced populations of *Quiscalus lugubris*.

Only two of these, montane rainforest and coastal scrub, are of major importance to birdlife, as none of the others covers more than a few percent of the surface of any of these islands. Moreover, nearly all of the land birds that occur in the Lesser Antilles occupy one or the other or both of these vegetation types. The few that today preferentially inhabit pastures, gardens and other open areas were probably of restricted occurrence when the islands were in a pristine state (*Speotyto cunicularia*, *Crotophaga ani*, *Mimus gilvus*, *Quiscalus lugubris*), or are recently introduced species that have been rapidly expanding their ranges (*Molothrus bonariensis, Sicalis luteola*).

To establish the habitat affinities of the birds present in the principal source region for the northern Lesser Antilles, we conducted systematic 2-week surveys of Guadeloupe and its neighbor, Dominica, visiting each major habitat and censusing its birdlife. We surveyed Dominica to be sure that the distributions we observed in Guadeloupe were typical of the whole source region, and because it harbors a number of species that do not occur on Guadeloupe.

Colonization in relation to habitat utilization.—Now we may examine the performance of the birds of Guadeloupe and Dominica as colonists in relation to their habitat affinities. Of the 44 land birds present on these two islands, 29 have established one or more populations in the northern Lesser Antilles (Table 2). The most successful species, as judged either by the incidence of colonizing ability or the number of islands colonized, are those that inhabit coastal scrub or are habitat generalists (both scrub and rainforest). Although the 8 habitat generalists were uniformly successful, they account for only 28% of the proved colonists in the source

TABLE 3

SUMMARY OF INSULAR CHARACTERISTICS AND NETTING RESULTS AT FOUR RAINFOREST SITES

	Dominica	Guadeloupe	Montserrat	St. Kitts
Area of island (km^2)	790	1,510	98	176
No. of species present on island[1]	40	33	26	23
No. of species present in habitat[2]	19	17	14	13
No. of species captured in nets	10	10	11	11
Diversity of net samples[3]	8.4	5.8	7.6	7.1
Netting effort (no. net-days)	51	60	57	80
No. individuals captured	48	60	208	107
Projected population per net[4]	4.0	4.1	19.1	8.0

[1] Land birds only; includes introduced species; does not include recently extinct species.
[2] Number of species recorded in our surveys of the areas sampled by the net lines.
[3] The number of equally common species contained in the samples, computed as $\exp - \Sigma\, p_i \ln p_i$, where p_i is the proportion of the ith species in the sample.
[4] See methods for details.

TABLE 4

NETTING RESULTS AT FOUR LESSER ANTILLEAN RAINFOREST SITES

Species	Projected population for 16 nets[1]				Relative abundance (%)				Mean weight (g)
	Dom.	Guad.	Mont.	St. Kitts	Dom.	Guad.	Mont.	St. Kitts	
Buteo jamaicensis	a[2]	a	a	1	–	–	–	1	–
Buteo platypterus	1	a	a	a	2	–	–	–	>400
Geotrygon montana	12	pu	a	a	19	–	–	–	148
Geotrygon mystacea	c	c	4	6	–	–	1	5	224.5
Cyanophaia bicolor	9	a	a	a	15	–	–	–	4.4
Eulampis jugularis	4	4	21	7	6	7	7	6	8.7
Orthorhynchus cristatus	c	8	7	5	–	12	2	4	2.8
Melanerpes l'herminieri	a	1	a	a	–	2	–	–	98.5
Myiarchus tyrannulus	pc	pc	a	4	–	–	–	3	32.5
Contopus latirostris	pc	2	a	a	–	3	–	–	11.2
Elaenia martinica	c	c	3	1	–	–	1	1	21.0
Troglodytes aedon	4	e	a	a	6	–	–	–	11.9
Margarops fuscus	pc	3	52	21	–	5	17	17	72.0
Margarops fuscatus	pc	pc	60	5	–	–	20	4	105.0
Cinclocerthia ruficauda	5	2	38	12	8	3	13	9	52.0
Cichlherminia l'herminieri	pu	6	28	a	–	10	9	–	103.0
Myadestes genibarbis	4	a	a	a	6	–	–	–	26.0
Dendroica plumbea	12	31	a	a	19	48	–	–	10.2
Coereba flaveola	3	4	69	32	4	7	23	25	10.0
Icterus oberi	a	a	1	a	–	–	1	–	39
Loxigilla noctis	9	2	22	33	15	3	7	26	17.5
Total	63	63	305	127					

[1] Projected population per net times 16, the modal number of nets used. See methods for further details.

[2] a = absent on island, c = exclusively coastal scrub, e = extinct, pc = present in forest canopy, pu = present in forest understory but not captured.

fauna. Thus only a part of the faunal homogeneity of the northern islands can be accounted for by preferential colonization by ecologically versatile species. Surprisingly, open country species have made a relatively poor showing, though four of them have been extending their ranges and may continue to spread into the abundant man-made habitat that awaits them (*Crotophaga ani*, *Mimus gilvus*, *Molothrus bonariensis*, and *Sicalis luteola*). Birds that inhabit rainforest exclusively are clearly the poorest colonists. This could be due either to inherent sedentary tendencies or to the fact that the tall trees of their habitat afford better shelter against the heavy winds that frequently buffet these islands. Of the 15 species that have not reached the northern Lesser Antilles, 11 are rainforest inhabitants and 7 do not occur on Guadeloupe, the most likely point of departure.

It is now apparent that the faunal homogeneity of the wet and dry chains results mainly from a poor representation of rainforest species on the wet islands. Judging from the species lists of these islands one would anticipate that their montane forests would harbor impoverished bird communities. Yet this expectation is not borne out by our results.

Comparison of rainforest sites.—We compared four rainforest sites, one each in Dominica, Guadeloupe, Montserrat, and St. Kitts (see Localities section for further details). These were all situated in undisturbed, middle elevation (>280 but <500 m) humid montane forest. In all cases our sampling and censusing activities were confined to the forest interior, at least 200 m from the nearest edge.

First, we note that the four islands vary over a factor of nearly 2 in the number of species they contain (Dominica 40, St. Kitts 23; Table 3). But species densities at the four localities we studied varied over only a 1.5-fold range. Already this suggests that the smaller faunas have undergone some form of internal adjustment. Such a trend is abundantly clear in the netting results. As many species were captured on the two target islands as on the richer source islands. This holds even if we discount the larger catches made on the two small islands by truncating the samples to equal netting efforts or to equal numbers captured. The maintenance of constant diversity over a gradient in insular species numbers requires the operation of compensating mechanisms. What are they?

They are two: one that operates between habitats and one that operates within habitats. The first we can call ecological substitution, the replacement of missing species by trophically equivalent ones that invade from other habitats. The second entails adjustments in the vertical foraging ranges of the species present so as to maintain nearly constant within-layer diversity. Diamond (1971a) recorded both these forms of ecological release from competition in the bird faunas of islands in the southwest Pacific.

Ecological substitutions.—The results illustrate three instances (Table 4): in quail-doves (*Geotrygon*), hummingbirds (*Cyanophaia*, *Orthorhynchus*), and flycatchers (*Contopus*, *Elaenia*). Dominica and Guadeloupe each have two quail-doves, *G. mystacea* which lives in dry coastal forest, and *G. montana* which inhabits the rainsoaked montane forests of the interior. Only *G. mystacea* has colonized the northern Lesser Antilles where it inhabits both wet and dry forests. It occurred in the montane forests of Montserrat and St. Kitts at lower density than its counterpart, *G. montana* did on Dominica. The scarcity of *G. montana* on Guadeloupe may simply be an accident of sampling, or may be due in part to the presence of the mongoose and heavy hunting pressure there.

The Lesser Antillean hummingbirds provide a particularly fine example of competitive release. Dominica has four, a large (*Sericotes*) and small (*Orthorhynchus*) pair that live in coastal scrub and a large (*Eulampis*) and small (*Cyanophaia*) pair that inhabit montane forest. The large forest species (*Eulampis*) is widespread in the eastern Caribbean and was present at nearly constant relative density at all four of the localities we studied. On the other hand, the small forest species (*Cyanophaia*) is absent from Guadeloupe, Montserrat, and St. Kitts, where the small coastal species (*Orthorhynchus*) takes its place in montane forest at reduced density.

Flycatchers present a parallel situation. The source islands each possess two large-small pairs, one (*Tyrannus-Elaenia*) in coastal scrub, and one (*Myiarchus-Contopus*) in montane forests, though all four species can occasionally be found together around clearings in the interior. The large forest species (*Myiarchus*) is present on all the islands we studied except Montserrat, while the smaller species (*Contopus*) is present only on the two source islands. Again, the coastal scrub species (*Elaenia*) has moved into montane forest where the latter is missing, and also at apparently reduced density, though the catch rates for these canopy dwellers are only weak indicators of their true abundances.

No additional coastal scrub species have invaded the rainforests of Montserrat and St. Kitts. There were two instances in which a scrub species failed to replace a missing forest counterpart: *Dendroica petechia* and *Tyrannus dominicensis* do not enter forest in the absence respectively, of *D. plumbea* on Montserrat and St. Kitts and of *Myiarchus oberi* on Montserrat.

All three cases of ecological substitution conform to the same simple pattern; replacement of a missing forest species at reduced density by an ecologically similar coastal scrub counterpart. If the scrub habitat of these species on the source islands is taken as typical, i.e. the one for which the species are best adapted, then their reduced densities in rainforest (relative to missing counterparts) can be interpreted as reflecting their lower efficiencies, hence inferior competitive status, in an atypical habitat.

Vertical foraging ranges.—Adjustments in vertical foraging ranges constitute the second compensatory mechanism. In these instances the response to a missing species is a downward expansion of the foraging range of a canopy-dwelling species to include the understory. (Obviously the netting technique would not detect upward expansions.)

Dominica has four forest understory species that are absent from the northern Lesser Antilles. These fall into two trophic categories: insectivorous foliage gleaners (*Troglodytes aedon* and *Dendroica plumbea*) and frugivores (*Cichlherminia l'herminieri* and *Myadestes genibarbis*). (*Cichlherminia* was uncommon in the vicinity of our Dominica camp and failed to enter the nets.) Guadeloupe lacks two of these species: *Troglodytes* which became extinct more than 100 years ago and *Myadestes*; Montserrat has only *Cichlherminia*; and St. Kitts lacks all of them.

On Guadeloupe where *Troglodytes* is extinct, the other understory insectivore (*D. plumbea*) is extraordinarily common (Table 4). On Montserrat and St. Kitts where neither of these birds occur, the Bananaquit (*Coereba*) is plentiful in the forest understory. It is also common in the forests of Dominica and Guadeloupe, but on these islands lives principally in the canopy and is only occasionally captured near the ground in nets.

Ecological relationships are more complex in the large frugivore trophic guild and, accordingly, the results are less easily interpreted. *Cichlherminia* was scarce at our Dominica site where *Myadestes* was common, and was relatively more common on Guadeloupe and Montserrat where *Myadestes* is absent. However, the two thrashers, *Margarops fuscus* and *M. fuscatus* are far more abundant on St. Kitts and Montserrat than their putative understory counterparts on Dominica and Guadeloupe. Both these birds are present in the forest canopy of the latter two islands where, like the Bananaquit, they rarely descend to the level of nets. Why are they so common in nets on the two smaller islands? We can offer two explanations. One, which is not easily tested, is that the fruit-eating guild as a whole is overrepresented on the smaller islands, a condition that could result from unknown differences in the trophic bases of the communities.

The second possibility is more interesting because it sheds light on the mechanism of "overcompensation," a feature of competitive release that has received a good deal of attention in the recent literature (MacArthur et al. 1972, MacArthur 1972, Diamond, 1974). These authors report several studies in which the bird communities of species-rich islands or mainlands and species-poor islands are compared with netting techniques similar to ours. The most striking feature of their results has been the finding that bird populations are often more dense (in numbers of individuals, biomass, etc.) in species-poor communities, a phenomenon they have termed overcompensation. Their publications suggest several alternative interpretations (overexploitation of prey in rich mainland faunas, release from predation, more productive successional vegetation on small islands, etc.), but the data at hand were inadequate to rule out any of the possibilities. One explanation they did not consider is that overcompensation may be an artifact of using nets to conduct the censuses.

Consider the simplest case of an interactive species pair that segregates vertically in the vegetation of a species-rich locality. If the vegetation is tall (>10 m), nets

TABLE 5
INSULAR CHARACTERISTICS AND NETTING RESULTS AT FIVE COASTAL SCRUB SITES IN THE GUADELOUPE ARCHIPELAGO

				Îles des Saintes	
	Guadeloupe (Grande Terre)	Marie Galante	Desirade	Terre de Bas	Terre de Haut
Area of island (km^2)	1,510	155	20.5	6.8	4.6
Distance from Guadeloupe (km)	—	26	10	10	11
No. species present on island[1]	34	23	19	15	17
No. species present in habitat[2]	18	14	14	11	12
No. species captured in nets	14	10	14	9	8
Diversity of net samples[3]	6.8	3.4	5.1	6.4	5.7
Netting effort (no. net-days)	48	36	60	42	30
No. individuals captured	323	133	445	264	62
Projected population per net[4]	23.1	21.6	30.4	27.2	10.6

[1] Land birds only; includes all birds reported in the literature and found by us on each island. The species totals for the smaller islands (Desirade and Îles des Saintes) are almost certainly too high, for we were not able to find a number of species that had been recorded by previous observers. This was in spite of the facts that we searched each island thoroughly and invested more man-hours in the surveys than did earlier exploring parties. Because such data are relevant to the problem of insular species turnover, we record here apparent absences and species not previously reported for each island. Species recorded for Desirade but not found by us: *Geotrygon mystacea*, *Coccyzus minor*, *Eulampis jugularis*, *Progne subis* (may not have returned from wintering grounds); found by us, and reported in 1963 but not previously: *Crotophaga ani*. Species recorded for the Îles des Saintes but not found by us (Vaurie 1961): *Columba squamosa*, *Geotrygon mystacea*, *Coccyzus minor*, *Eulampis jugularis*, *Progne subis* (on wintering grounds?), *Dendroica plumbea*; found by us but not reported previously: *Euphonia musica* on Terre de Haut. In addition, the 5 *Eulampis jugularis* we captured on Marie Galante apparently constitute a new record for that island. While we recognize that absences are not easily proved (Lynch and Johnson 1974), the considerable numbers of them in our surveys, plus the new records, suggest an appreciable species turnover on these islands.

[2] These figures refer to the numbers of species found by us in uniform habitat in the vicinity of the net lines.

[3] The number of equally common species contained in the samples, computed as $\exp - \Sigma\, p_i \ln p_i$, where p_i is the proportion of the ith species in the sample.

[4] See methods for details.

would normally capture only the species that foraged lower. Now let us suppose that one of the species is missing at a species-poor locality. If the one that is present undergoes ecological release, by expanding its foraging zone to include that of its missing competitor, and proportionately increases its population density, nets would capture up to twice as many individuals per unit area. Hence one must be extremely cautious in drawing conclusions about avian densities from netting data.

In the present study, we think it likely that the high population densities recorded on Montserrat and St. Kitts, especially those of *Coereba* and the two *Margarops* thrashers, are due to the mechanism just described. This plus the fact of taller forests on Dominica and Guadeloupe may be all that is necessary to account for the large disparities in the net yields obtained at the four localities. It is because of these uncertainties that we have stressed relative rather than absolute abundances.

COLONIZATION OF THE GUADELOUPE SATELLITE ISLANDS

We now report on a second set of results that in many ways parallel and complement the ones presented above. The object was to examine a set of coastal scrub communities that differed systematically in their avian species densities. We did this by carrying out similar netting and survey operations on each of the Guadeloupe satellites.

These islands all lie within sight of Guadeloupe to the southwest (Îles des Saintes), south (Marie Galante) and southeast (Desirade), each being as close or closer to the main island than to any of the others, except for the twin islands Terre de Haut and Terre de Bas of the Îles des Saintes. Thus we can presume that each was independently colonized from Guadeloupe. Together they form a graded series of island sizes and, concomitantly, of species densities. Relatively intact natural vegetation can still be found on the Îles des Saintes, while the habitat at our Desirade and main island

TABLE 6

NETTING RESULTS AT FIVE COASTAL SCRUB SITES IN THE GUADELOUPE ARCHIPELAGO[1]

Guild	Mean weight (g)	Îles des Saintes: Terre de Bas	Îles des Saintes: Terre de Haut	Desirade	Marie Galante	Guadeloupe (Grande Terre)
Raptors						
Falco sparverius	95.3[2]	2[3]	p[4]	3	p	p
Nectarivores						
Orthorhynchus cristatus	2.8	26	p	11	3	8
Sericotes holosericeus	6.0	p	3	4		2
Eulampis jugularis	7.7				5	
Coereba flaveola	10.6	117	30	236	200	116
Hawking insectivores						
Elaenia martinica	21.5	76	49	27	94	114
Tyrannus dominicensis	49.5			1	p	p
Gleaning insectivores						
Dendroica petechia	9.6	13	6	12	5	13
Vireo altiloquus	19.8	5	8	2	18	18
Coccyzus minor	61.8[5]					p
Fruit and/or seed eaters						
Tiaris bicolor	10.3	76	47	117	5	16
Euphonia musica	15.8		p			10
Loxigilla noctis	17.3	64	11	20	3	31
Columbina passerina	34.8	56	16	21	p	22
Saltator albicollis	52.4					13
Margarops fuscus	65.3			10	10	5
Margarops fuscatus	92.5			21	3	1
Zenaida aurita	173	p	p	1	p	p
Geotrygon mystacea	228					1
Total		435	170	486	346	370

[1] Only those species found by us at the study sites are listed.
[2] Mean weights for coastal scrub populations were taken from the Grande Terre sample unless the number of individuals was fewer than 5, then taken from the largest catch available.
[3] Projected population per net times 16, the modal number of nets used. See methods for further details.
[4] p = present at the site but not captured.
[5] Mean of 12 individuals captured on Mona Island.

control sites was partially degraded, and that on Marie Galante was entirely secondary.

Species numbers in the Guadeloupe archipelago vary from 15 on the Îles des Saintes to 34 on Guadeloupe itself, a difference of 2.3-fold (Table 5). As was true of the rainforest sites, local species numbers varied over a reduced range (1.7-fold) and the diversity of the net samples over a still smaller range (1.3-fold if we disregard the spurious results from Marie Galante which may be an artifact of the poor quality of the vegetation there). Netting yields at the five stations varied from 11 to 30 birds/net. The pattern of variation affords no obvious interpretation. There may be some effect of reduced vertical stratification on the smaller islands where up to 100% of the species present in the habitat were captured (Desirade) vs. 67% on Marie Galante and 74% on Guadeloupe. This effect is certainly much weaker than in rainforest where the vegetation is 10 or 15 times, rather than 2 or 3 times taller than the nets. Thus, though measured bird densities averaged 2.5 times greater in the coastal scrub localities than they did at the rainforest stations, the actual densities in the two types of habitat are undoubtedly much more nearly equal.

Ecological screening of potential colonists arriving randomly on the Guadeloupe satellite islands produced astonishingly nonrandom results. Marie Galante, Desirade, and the Îles des Saintes, in descending order of size, contain perfectly nested subsets of the source fauna. That is, all the species that are on the Îles des Saintes occur also on all the larger islands; the same is true of Desirade and Marie Galante. The only exceptions to this regularity are: records of *Dendroica plumbea* (Vaurie 1961) and *Euphonia musica* on Terre de Haut, and the apparent absence of *Coccyzus minor* on Marie Galante. Both the Terre de Haut records were of a small number of individuals seen at one spot on the island. They may represent unsuccessful attempts at colonization; this is very likely the case for *D. plumbea* whose presence we were unable to confirm, even though we searched the western end of the island where Vaurie found it. If *Coccyzus minor* is really missing on Marie Galante, it constitutes an exception to an otherwise orderly nesting of faunas on progressively smaller islands.

The most rudimentary community is that found on Terre de Bas (Table 6). It consists of 1 small raptor, 3 nectarivores (small, medium, and large—here we include the Bananaquit as a nectarivore), 1 small flycatcher, 2 foliage gleaners (small and medium), and 4 frugivores that range in weight from 10.3 to 173 g. Each bird differs in weight from other members of its guild by very nearly a factor of 2, in conformity with a recurrent pattern in ecology (Hutchinson 1959, Diamond 1973). There is only one gap, and that is between the ground dove (34.8 g) and the Zenaida Dove (173 g). This gap is filled by the two *Margarops* thrashers in the next larger community (Desirade), which also includes a large flycatcher. The only bird inhabiting Desirade and the Îles des Saintes that does not inhabit scrub vegetation is the Smooth-billed Ani, which forages in pastures and around habitations.

Indeed, it seems to be a consistent feature of small islands that all or practically all of the species present co-occur in the prevalent vegetation type, as has been documented also for Mona Island (Terborgh and Faaborg 1973) and St. John (Robertson 1962). This pattern appears to hold on Caribbean islands containing up to about 20 species. Where more are present we begin to notice an appreciable degree of sorting into distinct habitats. This is clearly the case on Marie Galante, which is more than 7 times larger than Desirade and is reported to have 23 land birds. Five species on Marie Galante, in addition to the ani, occupy habitats other than coastal scrub: *Speotyto cunicularia* (now extinct), *Molothrus bonariensis* (a recent invader, first reported in 1962, Bond 1956, Suppl. VII) and *Quiscalus lugubris* in openings, pastures, etc.; *Eulampis jugularis* and *Dendroica plumbea* in shady interior forests. These account for the entirety of the increased species number on Marie Galante compared with Desirade. That the extra species are mainly going into other habitats on Marie Galante is also indicated by the identical number of species (14) present at our study sites on the two islands, though it is probable that we would have found one or two additional species on the larger island had better quality habitat been available.

Guadeloupe contains 11 more species than Marie Galante, but only 4 of these, 3 of them frugivores, add to the scrub community (*Geotrygon mystacea*, *Coccyzus minor*, *Euphonia musica*, and *Saltator albicollis*: Table 6). Most of the remaining species occupy montane rainforest.

In North American bird communities, one finds the most confusing arrays of closely related species among the insectivorous guilds (MacArthur 1958). In sharp contrast, frugivorous birds predominate in the West Indies, and it is in this guild that we find the closest species packing. Comparing the scrub communities of Terre de Bas and Guadeloupe, we note the following. All guilds represented in the 18-member community of Guadeloupe are also present in the 11-member community of Terre de

Bas. Of the additional 7 species in the Guadeloupe community, 5 are members of the fruit- and seed-eating guild. On Guadeloupe this guild includes 9 members that differ from each other in size by a (geometric) mean factor of 1.5. The fruit and seed eaters inhabiting Terre de Bas are less crowded in an ecological sense, and differ by a mean factor of 2.6, while mean values for the other islands are intermediate. The other 4 guilds remain uncrowded throughout with mean weight differences $\geqslant 2.0$.

DISCUSSION

Density compensation in island avifaunas.—Several years ago when we embarked on these studies we hoped it would be possible to discover a threshold species number below which density compensation would fail. As long as the members of a community have broadly overlapping niches, the addition or deletion of a few species should have a minimal impact on the total biomass or density of individuals, because such perturbations will be met with by compensatory internal adjustments in the community. Nevertheless, we reasoned, it should be possible, by working down a gradient of island size, to locate communities that are so rarified that niche overlap between the species is negligible. At this point density compensation should fail. In even poorer communities the mean abundance per species should remain constant, but the biomass or aggregate density should fall off in proportion to the number of species present. Diamond (1971b) in fact reported just such a result from a group of islands near New Guinea. His data show a strong proportionality between netting yield and the locally available number of species over a range (27–132 species) that lies well on the high side of that in the studies we report here. Although we netted birds on 13 Caribbean islands ranging in size from Hispaniola down to the Îles de Saintes, we can find no evidence for such an effect. Even on Mona Island where only 2 frugivorous species regularly enter nets, the avian biomass equals that achieved by 7 frugivorous species in a control locality in Puerto Rico (Terborgh and Faaborg 1973). The measurements we report here show no indication that bird population densities vary in any systematic way with the number of species locally present, whether in rainforest or coastal scrub. Moreover the net yields we recorded are an order of magnitude greater than those reported by Diamond for islands of similar size and species density. West Indian birds seem to have almost infinitely elastic niches. How then can Diamond's results be reconciled with ours? Unfortunately we cannot offer a satisfactory answer. The best clue is Diamond's comment that many of the species present at his netting stations, all of which were in interior forests, are good colonizers that inhabit coastal scrub on the source island of New Guinea. Earlier we noted that coastal scrub species have invaded the montane forests of the northern Lesser Antilles at appreciably reduced relative densities. Nevertheless the densities of just these species (recorded as the number captured per net-day) are still twice those reported by Diamond. It may be that the New Guinea scrub species suffer even more drastic reductions in abundance on entering forest vegetation. Whether this is the answer or not, more data from the southwest Pacific are needed to resolve the issue.

Determinants of colonizing success.—Although the two main parts of this paper have dealt with different sets of islands in different contexts, the results can be drawn together to produce a single conclusion. The wet and dry chains of islands in the northern Lesser Antilles considered in the first part, and the satellites considered in the second part, were colonized more or less independently from Guadeloupe. In view of this we are struck by the monotony with which a small subset of the Guadeloupe fauna appears on island after island. Colonizing success is very unevenly

TABLE 7
ISLAND COLONIZATION BY GUADELOUPE BIRDS

No. islands colonized	0	1	2	3	4	5	6	7	8	9	10	11	12	13
No. species	7	2	2	1	1	3	0	1	0	1	2	1	4	9

distributed as Table 7 plainly shows. Of the 24 species known from the satellites, all but one (*Dendroica plumbea*) have also established populations on one or more of the 10 northern islands. Some species have invaded every available island, while others apparently do not colonize small islands at all. Only a few display intermediate abilities. Is the bimodal distribution of colonizing success indicated in Table 7 due entirely to differential dispersal? Almost certainly not, as several clear ecological patterns are implicated in the results.

Birds that inhabit scrub habitats on the source islands achieve a much higher degree of colonizing success than those inhabiting forest, both because they seem to be better dispersers and because they show a distinctly greater versatility in accommodating to diverse vegetation conditions. The regular ordering of guilds on the Guadeloupe satellites suggests that dispersal ability alone is not a sufficient condition for establishment. The results imply that any potential colonist must fit into the structure of the community by being approximately twice as large and/or twice as small as its guild neighbors. Thus, some combinations of species are inherently incompatible and do not occur, while others occur repeatedly. Such community "assembly rules" have also been recognized in West Indian anoles (Williams 1969) and southwest Pacific birds (Diamond 1975).

The difficulties of coexistence are eased on larger islands where ecologically similar species can achieve spatial separation by sorting into distinct habitats or by segregating vertically in tall vegetation. Tighter species packing is also tolerated on large islands because the increased living space permits even uncommon species to attain sufficient population levels to resist extinction. This is the likely explanation for why species that fit into gaps in weight series and reduce the mean level of separation within guilds (such as *Saltator albicollis* and *Euphonia musica* in the Guadeloupe archipelago) are confined to larger islands (cf. Diamond's 1975 discussion of "incidence functions").

The consistency with which the same group of species appears on so many small Lesser Antillean islands is thus not solely a consequence of superior dispersal ability. Arriving potential colonists (propagules) are stringently screened by more subtle ecological criteria: versatility in habitat occupancy, trophic status, and size in relation to guild neighbors. While accidents of dispersal alone would be expected to produce a haphazard pattern of island occupancy, the superposition of these added ecological constraints imposes an orderliness that accounts for the striking homogeneity of small island avifaunas in the Lesser Antilles.

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