

Body size and the occurrence of avian species on land-bridge islands

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Abstract. In insular faunas, large-bodied species are thought to be extinction-prone due to small population sizes. We tested for biogeographic patterns of size-related avian occurrence on seven Neotropical land-bridge islands (Trinidad, Tobago, Margarita, Aruba, San Jose, Rey and Coiba). For each island, we classified breeding land-bird species into one of six non-overlapping size classes and compared size distributions to a source pool of adjacent mainland species.

Both within and between avian families, there was a slight excess of large-bodied species on islands, compared to mainland source pools. Thus, there was no evidence that large-bodied species are extinction-prone and no evidence of size-related, ecological truncation *at the family level*. Neotropical land-bridge islands are separated from the mainland by relatively narrow water gaps, and there have probably been numerous opportunities for recolonization during the past 10,000 years of 'isolation'.

Fifteen mainland species occurred on mesic land-bridge islands (Trinidad, Tobago, San Jose, Rey and Coiba) whenever appropriate habitat was present. These persistent

species were usually associated with second-growth, clearings, and residential areas. In contrast, thirty-two mainland species were never found on land-bridge islands in spite of the presence of appropriate habitat. These missing species were mostly associated with primary and second-growth forest. We believe that at least some of the species that never occur on land-bridge islands are extinction-prone. This list includes representatives from seventeen avian families and several diverse foraging guilds (e.g., insectivores, carnivores, and frugivores). The range of body masses spans almost three orders of magnitude (6–650 g). With respect to body size, we conclude that there are no simplified 'rules' for predicting the occurrence of most Neotropical bird species in insular communities. However, species that are often missing from land-bridge islands are primarily associated with primary or second-growth forest. These species may require additional autecological study to ensure their preservation in Neotropical parks.

Key words. Body size, Neotropics, avian extinction, ecological truncation, land-bridge islands.

INTRODUCTION

The extinction of species following insularization of a community remains a major focus of theoretical ecology and conservation biology. Theoretical treatments emphasize the effect of insular area, a surrogate variable for population size, on the probability of extinction (e.g. Preston, 1962; MacArthur & Wilson, 1967). Species–area data are used to model equilibrium species number, extinction rates, and time to equilibrium following insularization (Terborgh, 1974, 1975; Soule, Wilcox & Holtby, 1979; Wilson & Willis, 1975).

In contrast, applied conservation biologists focus less on area and species number and more on species identity (e.g. Lynch & Whigham, 1984; Zimmerman & Bierregaard, 1986). The important question is not 'what is the equilibrium species number?', but 'which species are likely to go extinct following insularization?' or 'are there any ecologi-

cal or taxonomic similarities among species lost to extinction?' Answers to these last two questions may help biologists devise plans to save targeted species.

The faunas of 'land-bridge' islands are a convenient model of the extinction process. The rise of ocean levels at the end of the Wisconsinan Glacial of the Pleistocene, about 10,000 years ago, has provided replicated 'natural experiments' (*sensu* Connell, 1975) on the effects of faunal insularization. Islands on the continental shelf presently separated from the mainland by ocean depths of less than 120 m were once connected to the mainland and presumably shared the mainland fauna. Today, these land-bridge islands support fewer species than mainland tracts of comparable area. Most biologists assume that land-bridge island faunas represent the subset of mainland species that have resisted extinction, a premise that has served as the basis of numerous analytical treatments (e.g. Diamond, 1972; Terborgh, 1974, 1975; Wilcox, 1978; Soule *et al.*, 1979).

Many analyses have led to the conclusion that extinction of insular avifaunas is non-random. Species in specialized families (Faaborg, 1979), frugivorous birds (Terborgh & Winter, 1978), ground-dwelling species (Karr, 1982a), ant-following species (Willis, 1974), and, especially, species of large body size (Willis, 1974, 1980; Terborgh & Winter, 1978) are thought to be extinction prone in insular communities. The loss of specialist species and of large-bodied members of ecological guilds has been referred to as 'ecological truncation' (Wilson & Willis, 1975).

In higher vertebrates, body size usually correlates with territory size and population density: large bird and mammal species tend to have larger territories and lower population densities than do small species (McNab, 1963; Schoener, 1968; Damuth, 1981, 1987; Robinson & Redford, 1986). Because extinction probability correlates negatively with population size (MacArthur & Wilson, 1967), larger species in any taxonomic group may be relatively extinction-prone (Brown, 1971; Willis, 1974; Brown & Maurer, 1987; but see Pimm *et al.*, 1988).

For very large bodied species, this generalization is probably correct. Common sense tells us that a 10,000 or even a 50,000 ha island or nature reserve will not maintain a viable population of the largest carnivore species (e.g. *Harpia harpyja* (Linnaeus) 1758; see also Figs. 2 and 3 in Brown & Maurer, 1987). Fortunately, most vertebrate species have small body sizes, and may require far smaller areas for population persistence. It becomes more of a challenge to predict what island population of antbird or cricetid rodent will go extinct and whether extinctions are generally related to body size for most species in an assemblage.

In this paper we compare the body size distributions of bird species on seven Neotropical land-bridge islands (Trinidad, Tobago, Margarita, Aruba, Coiba, San Jose and Rey) to the size distribution of species in mainland source pools. We ask two questions: (1) With respect to body size, are the species from land-bridge islands a random subset of mainland species? (2) If not, are certain size-classes of species, both within and between avian families, consistently over- or under-represented on islands?

MATERIALS AND METHODS

We compiled lists of breeding land bird species (Columbidae to Corvidae) for the islands of Trinidad, Tobago, Margarita, Aruba, San Jose, Rey and Coiba. We excluded bird families ecologically dependent on water (Alcedinidae) and those whose breeding status is difficult to establish (Falconiformes, Apodidae). We also excluded three taxa of large-bodied species (Tinamidae, Cracidae and Phasianidae) because they are especially susceptible to hunting and transportation by Amerindians. For each island, we compiled a list of breeding species on the adjacent South and Central American mainlands. To qualify as a potential land-bridge island species, a mainland species had to occur within 300 km of the island (Fig. 1). We constructed a separate source pool for each island that was tailored to the existing island resources and habitats (Table 1). Details of procedures for compiling island and mainland species lists can be found in Graves & Gotelli (1983).

TABLE 1. Number of breeding land bird species in the total pool and habitat pool of seven land-bridge islands. From Graves & Gotelli (1983).

	Total pool	Habitat pool	Island
Trinidad	470	445	190
Tobago	399	342	77
Margarita	456	231	63
Coiba	513	348	64
Aruba	434	121	25
San Jose	560	390	36
Rey	560	390	38

It is unclear whether Tobago (Snow, 1985) and Aruba were ever connected to the mainland. Both islands lie between the 100 m and 200 m isobaths, so they may have remained separated from the mainland during the Wisconsin Glacial, when sea level dropped approximately 120 m. However, for our analysis, we assumed both islands were connected to the mainland at some time in the past, or at least were close enough so that their avifaunas were very similar to those of adjacent mainland communities.

Habitat availability on land-bridge islands

Historical changes in habitat and habitat differences between islands and mainland are important sources of bias in estimating land-bridge island extinctions. The Neotropical climate was much drier during the Pleistocene (e.g. Haffer, 1974; Bradbury *et al.*, 1981), and some loss of arid-adapted bird species may have been caused by the disappearance of dry scrub habitat (see Pregill & Olson, 1981) from presently mesic land-bridge islands (e.g. Trinidad). Extinctions caused by habitat change or human activity should be distinguished from extinctions caused by insularization *per se* (Lynch & Johnson, 1974; Lack, 1976; Olson & James, 1982). Even in cases where habitats have not changed historically, some species may be absent from land-bridge islands because appropriate habitat has always been lacking. These species were presumably missing even when the islands were connected to the mainland, and should not be counted as extinctions.

Existing habitat differences between Neotropical land-bridge islands and adjacent mainland areas are often dramatic. For example, of the 434 species in the mainland source pool for Aruba, less than one third can be considered as potential island residents, based on the availability of habitats on Aruba (Table 1). We have incorporated habitat effects in our analyses by excluding mainland species from source pools when appropriate habitat was lacking on a particular island (Graves & Gotelli, 1983). This technique allows us to standardize island-mainland comparisons for islands that differ greatly in habitat diversity.

Crossing and non-crossing species

Many species of birds are unwilling to cross even small water gaps (Diamond, 1972). Consequently, extant land-bridge island avifaunas may be comprised of two distinct

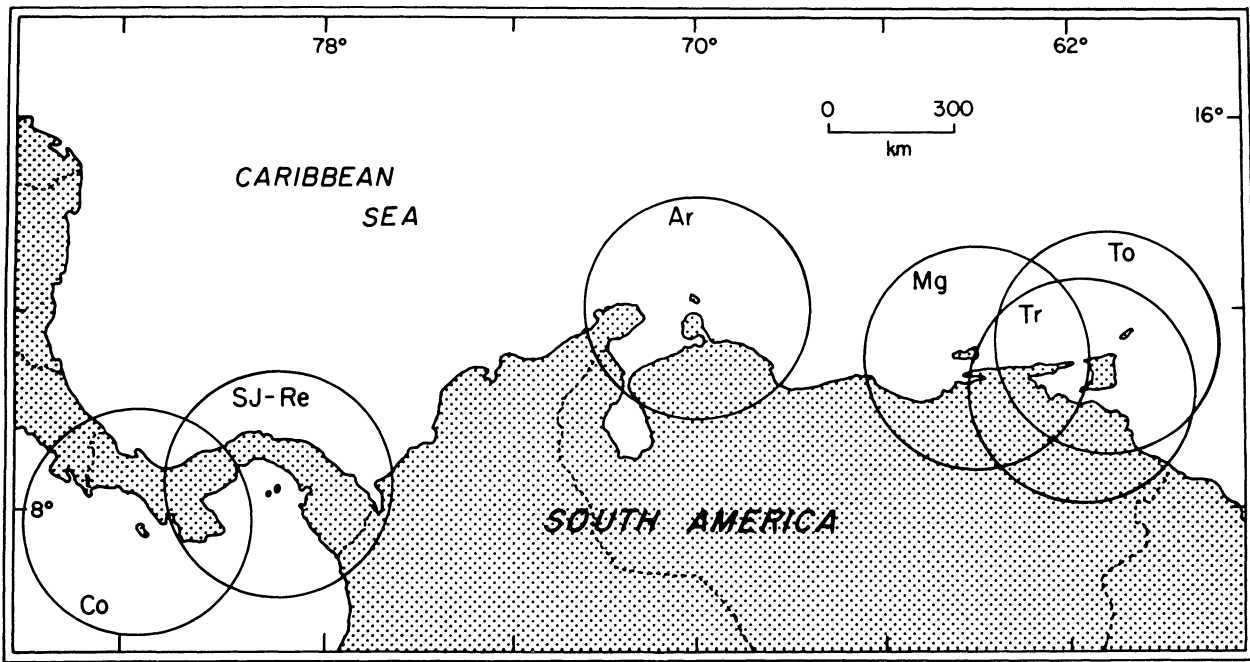


FIG. 1. Source pool circles for seven Neotropical land-bridge islands. Co=Coiba; SJ=San Jose; Re=Rey; Ar=Aruba; Mg=Margarita; Tr=Trinidad; To=Tobago. The circles have a radius of 300 km and are drafted from the closest mainland approach to the island. The same circle was used for San Jose and Rey. Species that occur in a circle and have appropriate habitat on the island are included in the source pool list for that island. Figure adapted from Graves & Gotelli (1983).

subsets: those that do not cross water and have presumably resisted extinction, and those that do cross water and may have recolonized following an earlier extinction (Diamond, 1984). Results of total avifauna analyses may be misleading if there are different body size patterns within each group.

Unfortunately, it is difficult to determine whether a particular species will cross stretches of open water. Several arbitrary criteria have been used to delineate crossing and non-crossing species. For example, Diamond (1972) defined non-crossing species of the New Guinea archipelago as those species that were never found on oceanic islands separated by water gaps from the mainland more than 5 miles wide. MacArthur, Diamond & Karr (1972) defined non-crossing species of the Pearl archipelago (including San Jose and Rey) as those species which did not occur on six oceanic islands. For birds of the Solomon archipelago, Diamond, Gilpin & Mayr (1976) delineated three dispersal groups: (1) non-water crossers (species confined to land-bridge islands); (2) superior short-distance colonizers (species that occurred relatively infrequently on remote versus central islands); (3) superior long-distance colonizers (species that occurred relatively frequently on remote versus central islands). Finally, Diamond & Gilpin (1983) accepted three kinds of evidence for water-crossing ability of Phillipine birds: (1) occurrence on an island beyond the 100 fathom line (presumably oceanic); (2) occurrence on very small land-bridge islands (where population persistence since the Pleistocene would be unlikely); (3) occurrence of a species as a migrant or straggler on an island where it does not breed.

We believe that last method is superior because it is not

entirely derived from the distribution of species on the islands under investigation. The other methods are somewhat circular because the definitions of 'crossing' and 'non-crossing' species are derived, in part, from the biogeographic distributions being analysed. However, biogeographic data are sometimes all that is available for determining crossing status. For our purposes, we categorized water-crossing species on a family basis. If at least one species of a family occurred on a Neotropical oceanic island, every species in that family was judged to have the latent ability to cross water ('crossing'). 'Non-crossing' species are found in families which were never represented on Neotropical oceanic islands.

This classification is tentative at best. With so few Neotropical land-bridge islands, it is difficult to reliably delineate crossing status (cf. Diamond & Gilpin, 1983). Furthermore, at least some of the individual species in the crossing families probably cannot cross water gaps. Nevertheless, this classification allows for a preliminary comparison of body sizes of crossing and non-crossing bird families.

Estimation of body mass

The most useful measurement of overall body size is body mass (Calder, 1974). Measurements of trophic appendages, such as bill length, may correlate well with body mass within closely related assemblages of birds but correlate poorly across avian families. In many community studies, individual body masses are averaged to give population means that are used in Monte Carlo simulations and statistical tests of body size patterns (e.g. Strong, Szyska &

Simberloff, 1979). However, this procedure incorporates at least two potential sources of bias: (1) inadequate sample size; and (2) intra- and inter-population variation in mass.

For many bird species in our study, adequate population samples from the source pools of the islands were unavailable. Even when samples were adequate, mean values were affected by age, sexual, and seasonal variation in mass. Among the families included in this study, for example, males of some species were 50–100% heavier than females (e.g. *oropendolas*, *Icteridae*). Extreme sexual dimorphism made it difficult to interpret ‘average’ values of body mass, because such averages often represented a phenotype that did not occur in nature (cf. Schoener, 1984). Variation in mass as a function of age may also affect mean values of body mass. Immature birds, which may disperse and colonize distant habitats, often weigh substantially less than adults. Finally, dispersal and colonization of many source pool species is believed to be seasonal. However, reasonable estimates of variation in body mass due to age, sexual dimorphism, and seasonality were not available for most species. For these reasons we avoided the use of mean masses in our analyses.

From the primary literature and museum specimen tags, we compiled body-mass data for the 937 breeding land-bird species that occur on the islands and in the source pools. With few exceptions, we followed the taxonomy of Morony, Bock & Farrand (1975). Masses of at least a few individuals (≥ 5) were available for most species. However, insufficient data were available to calculate means accurately for all age and sex classes, or population means for all islands and source pools. Because of these limitations, we conservatively categorized each species into one of six non-overlapping size classes. Each successive size class is approximately 1.5 times larger than the previous one, forming an approximate geometric scale (see Van Valen, 1973): (1) 0–10 g; (2) 10–25 g; (3) 25–47 g; (4) 47–81 g; (5) 81–130 g; (6) >130 g.

When the range of masses for all age and sex classes of a species overlapped two size classes, we placed the species in the higher size class. As more mass data becomes available, we suspect that some species could be shifted into a higher size class. Thus, our present data set may be biased towards lower size classes, leading to an under-representation of ‘large-bodied’ species. However, this bias is probably constant across islands and source pools, so it should not greatly affect our analyses. We gave special attention to species that showed marked geographic variation in body mass along the northern coast of South America (e.g. *Leptotila verreauxi* Bonaparte 1855, *Xiphorhynchus guttatus* (Lichtenstein) 1820). No species varied so much geographically as to be classified in different size classes in different source pools. This was not true, however, when we used eight instead of six size categories. We avoided classification problems and the excessive dilution of cell totals by limiting the number of size classes to six.

Statistical tests

With a one-sample Kolmogorov-Smirnov (K-S) test, we tested the null hypothesis that the distributions of body

sizes among species on islands were not different from those on the mainland. The two sample K-S test was not appropriate because it tests the hypothesis that both species lists were drawn from the same parent distribution. Because the source pools were compiled independently, there was no need to resort to Monte Carlo simulations to analyse body size patterns.

For speciose families (Table 3), we pooled data across islands and mainland source pools and compared them with aggregate distributions of body size. This analysis included families with species that occurred on islands at least 10 times and in at least four size classes. Pooled data were not entirely independent because the same species may be counted more than once if it occurs on more than one island. However, the species would also be counted more than once in the mainland source pools, so the cumulative curves were directly comparable. Even for speciose families, sample sizes were too small to warrant an analysis of individual islands.

We examined the relationship between body mass and island occurrence for a subset of species that occurred in the source pools of Coiba, San Jose, Rey, Tobago and Trinidad and could potentially colonize all five islands. Aruba and Margarita were excluded because they are covered mostly by xerophytic scrub, and the list of species that could potentially colonize all seven islands was too small for analysis. For the five islands we examined the relationship between the number of island occurrences (0–5) and body size class (1–6). Data were analysed using Fisher’s exact *G* test. Adjacent cells were pooled (cell number reduced from thirty-six to twenty) to raise the cell expectations above 5.0, but the results were identical to the full analysis we present here. We analysed the residuals according to the methods of Whittam & Siegel-Causey (1981).

We did not consider the effects of island area in our analyses; island area was uncorrelated with body mass of island or source pool species.

RESULTS

Most neotropical species are small (86.5% of the source pool species were in size classes 1–5), and the median of all island and mainland source-pool distributions fell in size class 3 (25–47 g). Body size distributions of island and mainland assemblages did not differ significantly ($P > 0.20$, K-S test; Fig. 2). Pairwise differences between source pools and between islands were also non-significant (K-S tests, $P > 0.05$). However, deviations from the mainland distribution were not random: on all islands, there were fewer species in the third size class (25–47 g) and more species in the largest size class (>130 g), relative to source pool species (Fig. 2, Table 2).

How likely is this pattern if the deviations in each size class were random and followed a binomial distribution with $P = 0.50$? Although the deviations in each row of Table 1 are not entirely independent, the probability of getting seven minuses (size class 3, 25–47 g) and seven pluses (size class 6, >130 g) is $[(1/2)^7]^2 = 0.00006$. Because there are six different size classes, there are $\binom{6}{2} = 15$ unique size class pairs, and four different combinations of pluses and

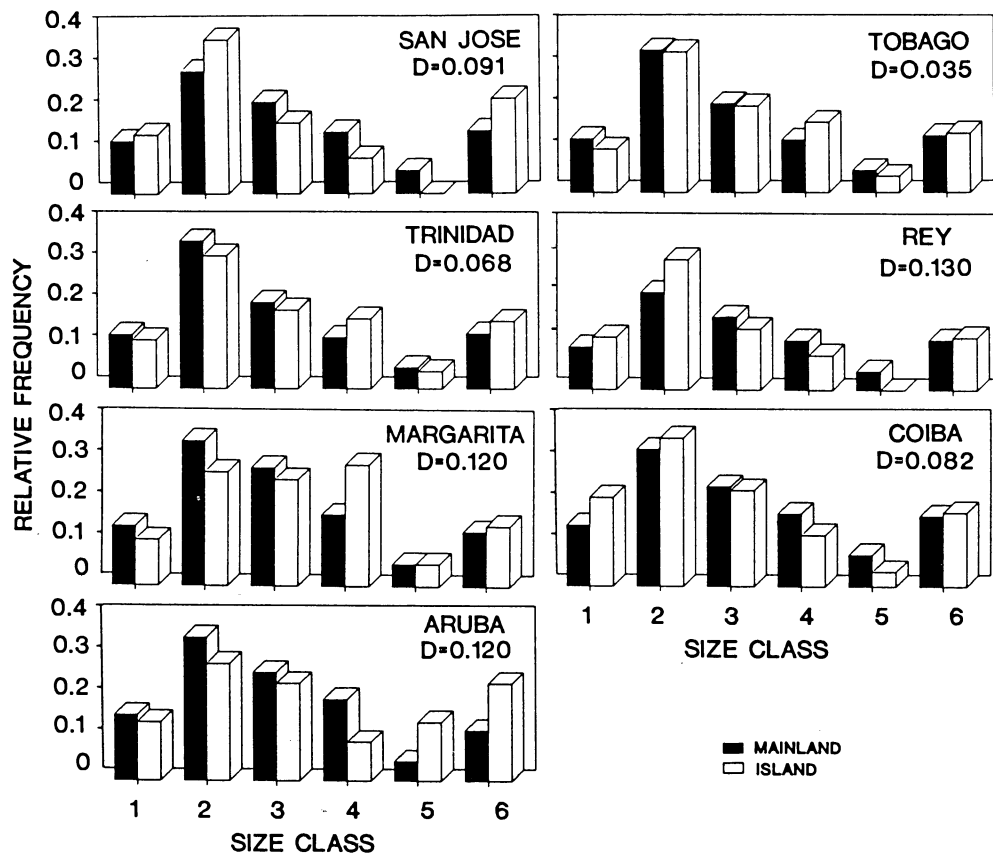


FIG. 2. The relative proportions of island and mainland species in six non-overlapping weight classes (see text for values). *D* is the Kolmogorov-Smirnov test statistic difference between the two distributions. *P* > 0.20 for all seven island-mainland comparisons.

minuses (++, +-, +- and --). Thus, the probability of observing two columns, each with all positive or all negative deviations, is $15 \times 4 \times 0.00006 = 0.0036$. If we consider only the deviations in the largest weight class (which are independent of one another), the probability is $(1/2)^2 = 0.0156$. In either case, the results suggest that the largest species of birds were slightly, but consistently, over-represented in island avifaunas.

The slight excess of large-bodied species on islands could be caused by non-random persistence of species in certain taxa. Therefore, it is important to distinguish body-size patterns that occur within and among avian families

TABLE 2. Island-mainland differences in the proportion of species in each weight class. Positive deviations mean the size frequency class was a greater proportion of the total for the island species than it was for the mainland. A zero means the size frequency class was the same size in island and mainland faunas.

	0-10 g	0-25 g	25-47 g	47-81 g	81-130 g	>130 g
Trinidad	-	-	-	+	-	+
Tobago	-	-	-	+	-	+
Margarita	-	-	-	+	0	+
Aruba	-	-	-	-	+	+
San Jose	+	+	-	-	-	+
Rey	+	+	-	-	-	+
Coiba	+	+	-	-	-	+

(Terborgh & Winter, 1978). At least among speciose families, island and mainland distributions do not differ strongly and cannot be distinguished statistically (Table 3). Thus, the excess of large-bodied birds on islands cannot be attributed to patterns within one or two families. Instead, the positive size deviations seem to be scattered among different bird families. Table 4 gives the deviations of median size classes within families for each island. Summing across all islands and families, and partitioning ties (island=mainland) equally, we find that seventy deviations

TABLE 3. Kolmogorov-Smirnov tests (*D*) for weight distributions of selected speciose families. Weight distributions were summed across islands and mainland habitat pools. *P* > 0.20 for all families.

Family	No. of mainland occurrences	No. of island occurrences	<i>D</i>
Columbidae	103	42	0.0728
Psittacidae	112	25	0.0632
Cuculidae	61	16	0.1752
Caprimulgidae	42	15	0.0381
Picidae	81	12	0.1605
Formicariidae	160	19	0.0421
Tyrannidae	363	92	0.1060
Emberiziidae	175	40	0.1850
Icteridae	100	21	0.0633

TABLE 4. Differences in the body sizes of island and mainland faunas. The left entry is the difference between the mainland and island median size classes; the right-hand entry is the difference in the relative proportion of mainland and island species in the terminal size class for that family. + = island > mainland. - = island < mainland. 0 = island = mainland. (0) = species occurring in only one weight class. NA = no species occurring on island.

Family	Trinidad	Tobago	Margarita	Aruba	San Jose	Rey	Coiba
Columbidae	-/-	+/+	0/-	+/+	0/+	0/-	-/-
Psittacidae	0/+	0/+	0/0	-/+	0/+	0/+	0/+
Cuculidae	0/+	+/+	0/+	0/-	+/+	+/+	+/+
Tytonidae	(0)	(0)	(0)	NA	(0)	NA	NA
Strigidae	0/0	0/+	0/-	0/+	NA	0/+	0/+
Steatornithidae	(0)	NA	NA	NA	NA	NA	NA
Nyctibiidae	(0)	(0)	NA	NA	NA	NA	NA
Caprimulgidae	0/+	0/+	-/-	-/-	0/-	0/-	+/+
Trochilidae	0/-	0/+	0/-	(0)	(0)	(0)	(0)
Trogonidae	-/-	0/-	NA	NA	NA	NA	NA
Momotidae	(0)	(0)	NA	NA	NA	NA	NA
Galbulidae	+/-	+/+	NA	NA	NA	NA	NA
Bucconidae	NA	NA	0/+	NA	NA	NA	NA
Capitonidae	NA	NA	NA	NA	NA	NA	NA
Ramphastidae	(0)	NA	NA	NA	NA	NA	NA
Picidae	+/+	0/-	0/-	NA	NA	0/-	-/-
Dendrocolaptidae	0/-	0/+	+/+	NA	NA	NA	NA
Furnariidae	0/-	+/+	0/-	NA	NA	NA	-/-
Formicariidae	+/+	0/-	-/-	NA	-/-	-/-	0/-
Cotingidae	+/+	-/-	NA	NA	NA	NA	0/-
Pipridae	0/-	0/+	(0)	NA	NA	NA	0/-
Tyrannidae	0/+	+/+	+/+	+/+	0/+	0/+	0/+
Hirundinidae	0/-	+/+	+/+	NA	+/+	+/+	+/+
Motacillidae	NA	NA	(0)	NA	NA	NA	NA
Troglodytidae	0/-	0/-	NA	NA	0/-	0/-	0/-
Mimidae	+/+	+/+	(0)	(0)	NA	NA	NA
Turdinae	0/0	(0)	0/+	NA	NA	NA	(0)
Poliophtilinae	+/+	NA	(0)	NA	NA	-/-	-/-
Vireonidae	0/+	0/-	0/-	(0)	0/-	0/-	0/+
Emberizidae	0/-	0/-	0/-	0/-	0/-	0/-	0/-
Thraupinae	+/+	0/-	+/+	NA	+/-	+/-	0/-
Tersininae	(0)	NA	NA	NA	NA	NA	NA
Parulidae	0/+	-/-	-/-	-/-	0/0	0/0	-/-
Icteridae	0/+	-/+	+/-	0/-	+/+	+/+	+/+
Corvidae	NA	NA	NA	NA	NA	NA	NA

are positive (median island body size exceeds median mainland body size), but only fifty-four are negative (mainland body size exceeds island body size). If positive and negative deviations were equally likely, the probability of obtaining this result by chance is 0.075 ($z=1.44$; binomial test large sample approximation).

We tested for a pattern of 'ecological truncation' by examining the proportion of species in the terminal weight class of each family for each island and source pool. If truncation were prevalent, negative deviations in the terminal weight class of families on islands should predominate. There were sixty-one cases in which the relative proportion of island species in the terminal size class exceeded the mainland proportion and sixty-three cases in which the mainland proportion was larger (Table 4; $z=0.18$, $P=0.43$; binomial test large sample approximation). Thus, we found no evidence of ecological truncation in body size at the family level.

Although large-bodied species were slightly over-represented on islands, both within and among avian families, there seems to be no relationship between body size

and island occurrence of widespread species (Table 5; Fisher's $G=22.52$, $P>0.20$). These widespread species were found in the source pools of Coiba, San Jose, Tobago and Trinidad. For this subset of the data, there were no significant differences between body size distributions of species that occurred on most or all islands and species that occurred on few or no islands. Furthermore, there were no unusual patterns in the residuals from these data.

We tested for body-size differences between island and mainland birds of crossing and non-crossing species. For crossing species, body size patterns were similar to those of the total avifauna (Fig. 1): there were no significant differences between island and mainland birds (K-S tests; $P>0.20$), and positive deviations were common in the largest size class (Table 6). For non-crossing species, there were also no significant differences between island and mainland pools (K-S tests; $P>0.20$), although there were many more negative deviations compared to the distributions of crossing species (Table 7).

Negative deviations in the largest size class of non-crossing species could be taken as evidence for ecological

TABLE 5. Island occurrences as a function of size class. For species that were present in the mainland pools of all five islands, frequency of occurrence is shown in the six size classes (data from Margarita and Aruba are excluded). The observed number of species in each entry is followed by the expected value in parentheses and the standardized adjusted residual in brackets.

Size class	No. of island occurrences					
	0	1	2	3	4	5
0–10 g	3 (3.53) [-0.34]	5 (5.63) [-0.35]	5 (3.31) [1.11]	2 (1.10) [0.94]	1 (0.77) [0.24]	0 (1.66) [-1.44]
10–25 g	12 (10.70) [0.37]	17 (16.53) [0.17]	6 (9.72) [-1.63]	2 (3.24) [-0.87]	2 (2.27) [-0.22]	8 (4.86) [1.83]
25–47 g	7 (5.96) [0.54]	7 (9.50) [-1.12]	7 (5.59) [0.74]	1 (1.86) [-0.73]	2 (1.30) [0.69]	3 (2.79) [0.14]
47–81 g	1 (4.63) [-2.07]	11 (7.38) [1.79]	4 (4.34) [-0.20]	3 (1.45) [1.45]	0 (1.01) [-1.12]	2 (2.17) [-0.13]
81–130 g	6 (2.43) [2.70]	3 (3.87) [-0.57]	2 (2.28) [-0.21]	0 (0.76) [-0.94]	0 (0.53) [-0.78]	0 (1.14) [-1.17]
>130 g	3 (5.08) [-1.14]	8 (8.09) [-0.04]	6 (4.76) [0.70]	2 (1.59) [0.37]	2 (1.11) [0.94]	2 (2.38) [-0.28]

TABLE 6. Island–mainland differences in the proportion of ‘water-crossing’ species in each weight class. A positive deviation means that the size frequency class was a greater proportion of the total for the island species than it was for the mainland species. A zero means the size frequency class was the same size in island and mainland faunas. Negative deviations in parentheses mean there was no island species in a particular size class.

	0–10 g	0–25 g	25–47 g	47–81 g	81–130 g	>130 g
Trinidad	-	-	-	+	-	+
Tobago	-	-	-	+	-	+
Margarita	-	-	-	+	+	+
Aruba	-	-	-	-	+	+
San Jose	-	+	-	-	(-)	+
Rey	+	+	-	-	(-)	+
Coiba	+	+	+	-	-	-

TABLE 7. Island–mainland differences in the proportion of ‘non-crossing’ species in each weight class. Symbols as in Table 6.

	0–10 g	0–25 g	25–47 g	47–81 g	81–130 g	>130 g
Trinidad	-	-	+	-	+	+
Tobago	(-)	-	+	(-)	+	(-)
Margarita	(-)	+	-	+	-	-
Aruba*	()	()	()	()	()	()
San Jose	(-)	+	(-)	(-)	(-)	(-)
Rey	(-)	+	-	(-)	(-)	(-)
Coiba	(-)	+	-	(-)	(-)	(-)

* Aruba has no ‘non-crossing’ species

truncation, because they suggest large bodied species that do not cross water are under-represented on land-bridge islands. However, the comparisons are confounded by small sample size: nearly all the negative deviations are associated with zeroes in the data matrix. Only Trinidad has enough non-crossing species for a valid comparison, and in that case the deviations are similar to those found for crossing species.

DISCUSSION

The slight excess of large-bodied species on islands contrasts with the results of most previous studies, which suggested that large-bodied species, or the largest species in a particular guild, were extinction prone (Brown, 1971; Terborgh & Winter, 1978; Willis, 1974, 1980; but see Faaborg, 1982). The excess of large-bodied species could be due to differences in the occurrence of crossing and non-crossing species. A loss of large-bodied species in the latter group would provide strong evidence for ecological truncation. Our analysis of crossing and non-crossing species did not reveal any consistent differences between these two groups, although the classification scheme was crude. Whether or not the non-crossing species show evidence of ecological truncation, large-bodied species were over-represented in the total avifauna, and this pattern deserves explanation.

Previous studies emphasized demographic aspects of body size and extinction: large-bodied birds have low population densities and should therefore be susceptible to local extinction (Brown, 1971; Willis, 1974; Pimm *et al.*, 1988).

Large body size, however, is correlated with certain behavioural and physiological characters that may enhance a species' persistence on islands. Large-bodied birds may be able to exploit a wide range of resources, which could enhance survival in a variable environment (e.g. Boag & Grant, 1981). Because body size correlates with longevity, large-bodied species may be able to forego reproduction during times of resource limitation and survive extreme 'resource crunches' (*sensu* Wiens, 1977) or physiological stress (Bumpus, 1899). Finally, many of the large-bodied bird species on Neotropical islands (e.g. parrots and pigeons) are nomadic and regularly fly back and forth from the mainland to take advantage of seasonally distributed resources. Consequently, these correlates of large body size may counteract the effects of low population density on the probability of extinction. Similar mechanisms may account for the absence of small-bodied bird species on some depauperate West Indian islands (Faaborg, 1982). Pimm *et al.* (1988) discuss other factors that may complicate the relationship between body size and extinction probability.

With few exceptions, our results suggest that avian extinction on Neotropical land-bridge islands is not related to body size or phylogeny (Graves & Gotelli, 1983). Land-bridge islands in our study are presently separated from the mainland by water gaps of *c.* 15–120 km. Some species or genera appear to be physiologically or psychologically unable to cross even narrow water channels (MacArthur *et al.*, 1972). But we suspect that many Neotropical species, even those from families that have never been found on oceanic islands, occasionally reach land-bridge islands from the adjacent mainland (e.g. formicariids on Tobago). Snow (1985) suggested that the montane faunas of Trinidad and Tobago were derived primarily from mainland colonizations, and do not represent 'relict' communities that have resisted extinction.

Repeated colonization from the mainland (the 'rescue effect' of Brown & Kodric-Brown, 1971) may be tremendously important in maintaining island populations of some species. For example, Rosenberg (1985) has documented the annual recolonization of river islands in the Amazon, up to 4 km from shore, by species of the Formicariidae and Furnariidae, families thought to be poor dispersers. Although the distances separating the islands and mainland in our study were much greater, occasional colonization may have contributed to the persistence of some species on land-bridge islands (Snow, 1985).

Species with high and low persistence on land-bridge islands

Appendices 1 and 2 give the two extremes in island occurrence of widespread species: species that occurred on all five islands (excluding Aruba and Margarita) whenever appropriate habitat was present (Appendix 1) and species that never occurred on islands, even when appropriate habitat was present (Appendix 2). Although these groups do not differ significantly with respect to body size (Table 4), there are some differences in habitat associations. Species that occur on all five islands (Appendix 1) are primarily inhabitants of second growth, clearings and residential

areas. As the islands were presumably forested before human settlement, open habitat formations must have been patchily distributed in time and space. This suggests that many, if not all, of the species listed in Appendix 1 are vagile and have repeatedly colonized land-bridge islands. Two of the species on this list, *Myiodynastes maculatus* (Müller) 1776 (streaked flycatcher), and *Oryzoborus angolensis* (Linnaeus) 1766 (Lesser seed-finch), have been classified as land-bridge relict species (MacArthur *et al.*, 1973), but this designation seems doubtful because of their widespread occurrence on land-bridge islands.

In contrast, the majority of species absent from all five islands but present in mainland source pools (Appendix 2) inhabit old-growth and second-growth forest (Fig. 3). The few grassland species on this list (e.g. *Anthus lutescens* Pucheran 1855, yellowish pipit; *Sturnella magna* (Linnaeus) 1758, eastern meadowlark; *Sicalis luteola* (Sparrrman) 1789, grassland yellow-finch) have apparently been unable to colonize the extensive pastureland now present on the islands. Species restricted to forested habitats were probable island residents at the time of separation from the mainland. These species appear to survive poorly on land-bridge islands.

Graves & Gotelli (1983) found that species with restricted geographic ranges (total mainland geographic range <100–1°×1° blocks) were significantly under-represented on these islands. However, this pattern cannot account for most of the missing species in Appendix 2; only *Atalotriccus pilaris* (Cabanis) 1847 (pale-eyed pygmy-tyrant) and *Thryothorus rufalbus* Lafresnaye 1845 (rufous-and-white wren) have small geographic ranges, and even for these species, the total geographic range is not contained in a small contiguous area (Type II restricted; see Graves & Gotelli, 1983, for definitions of widespread and restricted species). Thus the species in Appendix 2 are missing from



FIG. 3. Male royal flycatcher (*Onychorhynchus coronatus* (Müller) 1776) displaying crest. This species is widespread in humid forest of continental Central and South America, but is not known to occur on oceanic or land-bridge islands. Photo by Gary R. Graves, Río Heath, Southeastern Peru, 1977.

land-bridge islands in spite of their large geographic ranges and the presence of appropriate habitat.

Karr (1982a), also found that lower-storey forest birds were extinction-prone on Barro Colorado Island (BCI). For example, *Dendrocolaptes certhia* (Boddaert) 1783 (barred woodcreeper), found on none of the islands in our study (Appendix 2), is a documented extinction on BCI (Table 1 of Wilson & Willis, 1975; Table 5a of Karr, 1982a). *Euphonia minuta* Cabanis 1849 (white-vented euphonia), also missing from land-bridge islands (Appendix 2), is a vagrant on BCI but is a permanent resident in the adjacent mainland forest (Table 5b of Karr, 1982a). Karr (1982b) has further established that extinction-prone bird species are more variable in population size than species that persist on BCI. A similar conclusion may well hold for the species listed in Appendix 2, but appropriate population data are lacking.

Bird species that do not persist on land-bridge islands (Appendix 2) share little in common besides a general affinity for old-growth and second-growth forest. The list includes insectivores (e.g. *Tyrannulus elatus* (Latham) 1790, yellow-crowned tyrannulet; *Thryothorus rufalbus* Lafresnaye 1845, rufous-and-white wren), carnivores (e.g. *Otus guatemalae* (Sharpe) 1875, vermiculated screech-owl; *Ciccaba nigrolineata* Sclater 1859, black-and-white owl), nectarivores (e.g. *Anthracothonax prevostii* (Lesson) 1832, green-breasted mango [also in scrub]) and frugivores (e.g. *Columba subvinacea* (Lawrence) 1868, ruddy pigeon; *Euphonia* spp., *Tityra inquisitor* (Lichtenstein) 1823, black-crowned tityra). Seventeen avian families are represented, and the range of body masses spans three orders of magnitude, from a minimum of 6 g (*Anthracothonax prevostii*, green-breasted mango) to a maximum of 650 g (*Ciccaba nigrolineata*, black-and-white owl).

Implications for conservation of Neotropical birds

Although we found that large-bodied birds were slightly over-represented on Neotropical land-bridge islands, we cannot conclude that these species are resistant to extinction, because of the potential for recolonization from the mainland during the past 10,000 years of isolation. With respect to body size, there do not appear to be any simplified 'rules' for predicting which species are likely to go extinct in isolated communities. However, species associated with old-growth and second-growth forest are often missing from land-bridge islands, even when appropriate habitat is present. Forest species might have lower population densities than non-forest species (e.g. Damuth, 1987, for mammals), which could increase the chances for local extinction.

The species that always occur on land-bridge islands (Appendix 1) conform, in some respects, to the 'nested subsets' hypothesis: species comprising a depauperate fauna constitute a proper subset of those in rich faunas (Patterson & Atmar, 1986). On large, diverse islands, these species constitute a small fraction of the total avifauna (8% of Trinidad's 190 species), but on small, depauperate islands, they may account for almost half the avifauna (42% of San

Jose's thirty-six species). For mammal species of several island archipelagoes, Patterson & Atmar (1986) suggested that selective extinction leads to numerical dominance of the nested subset in small communities, but this mechanism may not apply to Neotropical avifaunas. The same pattern might arise if the 'persistent' species in Appendix 1 are superior colonizers from the adjacent mainland.

Nevertheless, other factors being equal, bird species that are never found on land-bridge islands, in spite of the presence of appropriate habitat (Appendix 2), are probably more extinction prone than species that always occur on land-bridge islands (Appendix 1) in this particular area of the Neotropics. Autecological studies of demography, resource use, and minimal area requirements may help to preserve populations of these species in Neotropical parks.

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REFERENCES

- Boag, P.R. & Grant, P.R. (1981) Intense natural selection in a population of Darwin's finches (Geospizinae) in the Galapagos. *Science*, **214**, 82–85.
- Bradbury, J.P., Leyden, B., Salgado-Labouriau, M., Lewis, W.M., Jr, Schubert, C., Benford, M.W., Frey, D.G., Whitehead, D.R. & Weibezahn, F.H. (1981) Late Quaternary environmental history of Lake Valencia, Venezuela. *Science*, **214**, 1299–1305.
- Brown, J.H. (1971) Mammals on mountaintops: non-equilibrium insular biogeography. *Amer. Nat.* **105**, 467–478.
- Brown, J.H. & Kodric-Brown, A. (1971) Turnover rates in insular biogeography: effects of immigration on extinction. *Ecology*, **58**, 445–449.
- Brown, J.H. & Maurer, B.A. (1987) Evolution of species assemblages: effects of energetic constraints and species dynamics on the diversification of the North American avifauna. *Amer. Nat.* **130**, 1–17.
- Bumpus, H.C. (1899) The elimination of the unfit as illustrated by the introduced sparrow, *Passer domesticus*. *Biol. Lectures, Marine Biol. Lab., Woods Hole*, **1899**, 209–226.
- Calder, W.H., III (1974) Consequences of body size for avian energetics. *Avian energetics* (ed. by R. A. Paynter, Jr), pp. 86–151. Nuttall Ornithological Club, Cambridge, Mass.
- Connell, J.H. (1975) Some mechanisms producing structure in natural communities: a model and evidence from field experiments. *Ecology and evolution of communities* (ed. by M. L. Cody and J. M. Diamond), pp. 460–490. Harvard University Press, Cambridge, Mass.
- Damuth, J. (1981) Population density and body size in mammals. *Nature*, **290**, 699–700.
- Damuth, J. (1987) Interspecific allometry of population density in mammals and other animals: the independence of body mass and population energy-use. *Biol. J. Linn. Soc.* **31**, 193–246.
- Diamond, J.M. (1972) Biogeographic kinetics: estimation of relaxation times for avifaunas of southwest Pacific islands. *Proc. nat. Acad. Sci., U.S.A.* **69**, 3199–3203.
- Diamond, J.M. (1984) Distributions of New Zealand birds on real and virtual islands. *N.Z. J. Ecol.* **7**, 37–55.

- Diamond, J.M. & Gilpin, M.E. (1983) Biogeographic umbilici and the origin of the Phillipine avifauna. *Oikos*, **41**, 307–321.
- Diamond, J.M., Gilpin, M.E. & Mayr, E. (1976) Species–distance relation for birds of the Solomon Archipelago, and the paradox of the great speciators. *Proc. nat. Acad. Sci., U.S.A.* **73**, 2160–2164.
- Faaborg, J. (1979) Qualitative patterns of avian extinction on neotropical land-bridge islands. *J. appl. Ecol.* **16**, 99–107.
- Faaborg, J. (1982) Trophic and size structure of West Indian land bird communities. *Proc. nat. Acad. Sci., U.S.A.* **79**, 1563–1567.
- Graves, G.R. & Gotelli, N.J. (1983) Neotropical land-bridge avifaunas: new approaches to null hypotheses in biogeography. *Oikos*, **41**, 322–333.
- Haffer, J. (1974) *Avian speciation in Tropical South America, with a systematic survey of the Toucans (Ramphastidae) and Jacamars (Galbulidae)*. Nuttall Ornithological Club, Cambridge, Mass.
- Karr, J.R. (1982a) Avian extinction on Barro Colorado Island, Panama: a reassessment. *Amer. Nat.* **119**, 220–239.
- Karr, J.R. (1982b) Population variability and extinction in the avifauna of a tropical land bridge island. *Ecology*, **63**, 1975–1978.
- Lack, D.L. (1976) *Island biology, illustrated by the land birds of Jamaica*. University of California Press.
- Lynch, J.F. & Johnson, N.K. (1974) Turnover and equilibria in insular avifaunas, with special reference to the California Channel Islands. *Condor*, **76**, 370–384.
- Lynch, J.F. & Whigham, D.F. (1984) Effects of forest fragmentation on breeding bird communities in Maryland, U.S.A. *Biol. Conserv.* **28**, 287–324.
- MacArthur, R.H., Diamond, J.M. & Karr, J.R. (1972) Density compensation in island faunas. *Ecology*, **53**, 330–342.
- MacArthur, R.H. & Wilson, E.O. (1967) *The theory of island biogeography*. Princeton University Press.
- McNab, B.K. (1963) Bioenergetics and determination of home range size. *Amer. Nat.*, **97**, 133–140.
- Morony, J.J., Jr, Bock, W.J. & Farrand, J., Jr (1975) *Reference list of the birds of the world*. American Museum of Natural History, New York.
- Olson, S.F. & James, H.F. (1982) Fossil birds from the Hawaiian Islands: evidence for wholesale extinction by man before western contact. *Science*, **217**, 633–635.
- Patterson, B.D. & Atmar, W. (1986) Nested subsets in the structure of insular mammalian faunas and archipelagoes. *Biol. J. Linn. Soc.* **28**, 65–82.
- Pimm, S.L., Jones, H. Lee & Diamond, J. (1988) On the risk of extinction. *Amer. Nat.* **132**, 757–785.
- Pregill, G.K. & Olson, S.L. (1981) Zoogeography of West Indian vertebrates in relation to Pleistocene climatic cycles. *Ann. Rev. Ecol. Syst.* **12**, 79–98.
- Preston, F.W. (1962) The canonical distribution of commonness and rarity: Part I. *Ecology*, **43**, 185–215. Part II. **43**, 410–432.
- Robinson, J.G. & Redford, K.H. (1986) Body size, diet, and population density of Neotropical forest mammals. *Amer. Nat.* **128**, 665–680.
- Rosenberg, G.H. (1985) Habitat use and foraging behaviour of river-island birds of Amazonia. Unpublished master's thesis, Louisiana State University, Baton Rouge, Louisiana.
- Schoener, T.W. (1968) Sizes of feeding territories among birds. *Ecology*, **49**, 704–726.
- Schoener, T.W. (1984) Size differences among sympatric, bird-eating hawks: a world-wide survey. *Ecological communities: conceptual issues and the evidence* (ed. by D. R. Strong, Jr, D. Simberloff, L. G. Abele and A. B. Thistle), pp. 254–281. Princeton University Press.
- Snow, D.W. (1985) Affinities and recent history of the avifauna of Trinidad and Tobago. *Neotropical ornithology* (ed. by P. A. Buckley *et al.*), pp. 238–246. *Ornithological Monographs*, **36**.
- Soule, M.E., Wilcox, B.A. & Holtby, C. (1979) Benign neglect: a model of faunal collapse in the game reserves of East Africa. *Biol. Conserv.*, **15**, 259–272.
- Strong, D.R., Jr, Szyska, L.A. & Simberloff, D.S. (1979) Tests of community-wide character displacement against null hypotheses. *Evolution*, **33**, 897–913.
- Terborgh, J. (1974) Preservation of natural diversity: the problem of extinction prone species. *Bioscience*, **24**, 715–722.
- Terborgh, J. (1975) Faunal equilibria and the design of wildlife preserves. *Tropical ecological systems: trends in terrestrial and aquatic research* (ed. by F. B. Golly and E. Medina), pp. 369–380. Springer, New York.
- Terborgh, J. & Winter, B. (1978) Some causes of extinction. *Conservation biology: an evolutionary-ecological perspective*, (ed. by M. Soule and B. Wilcox), pp. 119–133. Sinauer, New York.
- Van Valen, L. (1973) Body size and numbers of plants and animals. *Evolution*, **27**, 27–35.
- Whittam, T.S. & Siegel-Causey, D. (1981) Species interactions and community structure in Alaskan seabird colonies. *Ecology*, **62**, 151–1524.
- Wiens, J.A. (1977) On competition and variable environments. *Amer. Sci.* **65**, 590–597.
- Wilcox, B.A. (1978) Supersaturated island faunas: a species–area relationship for lizards on post-Pleistocene land-bridge islands. *Science*, **199**, 996–998.
- Willis, E.O. (1974) Populations and local extinctions of birds on Barro Colorado Island, Panama. *Ecol. Monogr.* **44**, 153–169.
- Willis, E.O. (1980) Species reduction in remanent woodlots in southern Brazil. *Acta XVII Congressus Internationalis Ornithologici, Berlin, 1978*, **2**, 783–786.
- Wilson, E.O. & Willis, E.O. (1975) *Applied biogeography. Ecology and evolution of communities* (ed. by M. L. Cody and J. M. Diamond), pp. 522–534. Belknap Press, Harvard University, Cambridge, Mass.
- Zimmerman, B.L. & Bierregaard, R.O. (1986) Relevance of the equilibrium theory of island biogeography and species–area relations to conservation with a case from Amazonia. *J. Biogeogr.* **13**, 133–143.

APPENDIX 1. Mainland species in the source pools of Trinidad, Tobago, Coiba, San Jose, and Rey that occur on all five islands.

Columba cayennensis Bonnatere 1792 (pale-vented pigeon)
Columbina talpacoti (Temminck) 1811 (ruddy ground-dove)
Crotophaga ani Linnaeus 1758 (smooth-billed ani)
Tyrannus melancholicus Vieillot 1819 (tropical kingbird)
¹*Myiodynastes maculatus* (Müller) 1776 (streaked flycatcher)
Elaenia flavogaster (Thunberg) 1882 (yellow-bellied elaenia)
Mionectes oleagineus (Lichtenstein) 1823 (ochre-bellied flycatcher)
Progne chalybea (Gmelin) 1789 (gray-breasted martin)
Troglodytes aedon Vieillot 1808 (house wren)
²*Vireo olivaceus* (Linnaeus) 1766 (red-eyed vireo)
Coereba flaveola Linnaeus 1758 (bananaquit)
Cyanerpes cyaneus (Linnaeus) 1766 (red-legged honeycreeper)
Thraupis episcopus (Linnaeus) 1766 (blue-grey tanager)
Volatinia jacarina (Linnaeus) 1766 (blue-black grassquit)
¹*Oryzoborus angolensis* (Linnaeus) 1766 (lesser seed-finch)

¹Listed by MacArthur *et al.* (1972) as a land-bridge relict species.

²Includes *V. flavoviridis*.

APPENDIX 2. Mainland species in the source pools of Trinidad, Tobago, Coiba, San Jose, and Rey that occur on none of these islands.

Columba subvinacea (Lawrence) 1868 (ruddy pigeon)
Aratinga pertinax (Linnaeus) 1758 (brown-throated parakeet)
Dromococcyx phasianellus (Spix) 1824 (pheasant cuckoo)
Otus guatemalae (Sharpe) 1875 (vermiculated screech-owl)
Ciccaba nigrolineata Sclater (1859 (black-and-white owl)
Nyctibius grandis (Gmelin) 1789 (great potoo)
Anthracothorax prevostii (Lesson) 1832 (green-breasted mango)
Bucco macrorhynchus Gmelin 1788 (white-necked puffbird)
Glyphorhynchus spirurus (Vieillot) 1819 (wedge-billed woodcreeper)
¹*Dendrocolaptes certhia* (Boddaert) 1783 (barred woodcreeper)
Campylorhamphus trochilirostris (Lichtenstein) 1820 (red-billed scythebill)
Xenops minutus (Sparman) 1788 (plain xenops)
Thamnophilus punctatus (Shaw) 1809 (slaty antshrike)
Myrmotherula surinamensis (Gmelin) 1788 (streaked antwren)
Tityra inquisitor (Lichtenstein) 1823 (black-crowned tityra)
Myiozetetes cayanensis (Linnaeus) 1766 (rusty-margined flycatcher)
Myiozetetes similis (Spix) 1825 (social flycatcher)
Pitangus lictor (Lichtenstein) 1823 (lesser kiskadee)
²*Onychorhynchus coronatus* (Müller) 1776 (royal flycatcher)
Rhynchocyclus olivaceus (Temminck) 1820 (olivaceous flatbill)
Atalotriccus pilaris (Cabanis) 1847 (pale-eyed pygmy-tyrant)
Tyrannulus elatus (Latham) 1790 (yellow-crowned tyrannulet)
Thryothorus rufalbus (Lafresnaye) 1845 (rufous-and-white wren)
Anthus lutescens Pucheran 1855 (yellowish pipit)
³*Basileuterus rivularis* Wied 1821 (river warbler)
Sturnella magna (Linnaeus) 1758 (eastern meadowlark)
⁴*Euphonia minuta* Cabanis 1849 (white-vented euphonia)
Euphonia laniirostris d'Orbigny and Lafresnaye 1837 (thick-billed euphonia)
Saltator maximus (Müller) 1776 (buff-throated saltator)
Cyanocopsa cyanoides (Lafresnaye) 1847 (blue-black grosbeak)
Sicalis luteola (Sparman) 1789 (grassland yellow-finch)
Carduelis psaltria (Say) 1823 (lesser goldfinch)

¹Extirpated on Barro Colorado Island (Table 5a of Karr, 1982a, and Table 1 of Wilson & Willis, 1975).

²Includes *O. coronatus* and *O. mexicanus*.

³Includes *B. fulvicauda*.

⁴Vagrant on Barro Colorado Island, but a permanent resident on the adjacent mainland (Table 5b of Karr, 1982a).