



AN ABSTRACT OF THE DISSERTATION OF

Randall Moore, for the degree of Doctor of Philosophy in Wildlife Science presented on December 1, 2005.

Title: Biogeographic and Experimental Evidence for Local Scale Dispersal Limitation in Central Panamanian Forest Birds.

Abstract Approved:

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William D. Robinson

I examined the avian biogeography of the islands of Lago Gatun, Panama, in an effort to better understand the effects of forest fragmentation in this biodiverse region, and specifically to understand the importance of fragment isolation and the mechanism behind its effects on tropical bird distribution. I combined exhaustive surveys of 29 islands with an experimental release program. Analyses of these data were conducted in a hierarchical fashion to evaluate evidence for avian dispersal limitation at multiple scales. First, I assessed the potential roles of area and isolation in determining avian species richness across this series of fragments, and how these relationships may differ for edge and forest dependent birds. Next, I analyzed community structure and species distributions to determine the relative contributions of island area and isolation in creating patterns of species-specific insular occurrence. Lastly, I assessed the results of

the experimental investigation to evaluate the hypothesis that dispersal limitation explains the insular distribution patterns of several tropical forest birds. Isolation is a significant predictor of avian species richness, but only after accounting for the stronger effect of area. Species-isolation relationships are different in this archipelago for birds that rely on forest and edge habitats, respectively. Species-specific distributions are significantly nested when islands are ordered by area, and by isolation once the effect of area is considered. Occurrence of most forest species is sensitive to area and isolation of the archipelago. Examination of guild structure suggests that multiple mechanisms are responsible for these occurrence patterns. There are distinct species-specific differences in ability to cross small gaps, and species which are better able to cross these gaps are more widely distributed across the archipelago than those species that negotiate the same barriers poorly. Species that performed uniformly well in release experiments were much less likely to have suffered insular extinction in the preceding 25 years than those species that showed moderate to poor experimental performance. There is strong evidence of a morphological basis for the patterns. The cumulative evidence from these analyses is the most comprehensive evidence to date of local-scale dispersal limitation in volant birds.

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Biogeographic and Experimental Evidence for Local Scale Dispersal Limitation in Central  
Panamanian Forest Birds

by  
Randall Moore

A DISSERTATION

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Doctor of Philosophy dissertation of Randall Moore presented on December 1, 2005.

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I understand that my dissertation will become part of the permanent collection of Oregon State University libraries. My signature below authorizes release of my dissertation to any reader upon request.

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Randall Moore, Author

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## **Chapter 1: Dissertation Introduction**

### **Introduction**

Species richness increases as habitat area increases. This pattern is as close to a general rule of ecology as exists (Schoener 1976), and it is an expected result of any biogeographic study. It has long been recognized that the species-area relationship has important conservation implications (MacArthur and Wilson 1967) for the maintenance of biodiversity in fragmented landscapes. Where all else is equal, bigger is almost always better from a conservation standpoint.

But given that a preserved patch of habitat is almost never the largest possible block, it is important to understand how the distributions of component species vary across fragments of different size. If assemblages were simply a random assortment of the regional pool with fewer species in smaller parcels, conservation planning for the region's biodiversity would be problematic. Fortunately, at least as far as most higher order plants and animals are concerned, this is almost never the case. Insular biotas almost always display some sort of nested structure whereby the set of species in the less speciose fragments are a proper subset of successively richer ones (Patterson and Atmar 1986). Since area and richness are almost always correlated, fragments very often exhibit significantly nested structure when ordered by area. It is thus possible to gain insight into

the requisite area of an effective reserve through biogeographic study of a series of existing fragments.

Area seems to function as an umbrella surrogate variable for many other variables that influence patterns of species occurrence more directly (Whittaker 1998). But do these patterns vary with factors outside the influence of area? They do, but not nearly so often or as clearly as with area (Lomolino 1984). The degree to which fragments are isolated from larger blocks of contiguous habitat (species source pools) can be another variable important to patterns of insular occurrence; metapopulation theory indicates that persistence of some populations will be dependent on consistent interchange of individuals between separated populations (Hanski 1998b). If this interchange is disrupted, it can lead to population declines and local extinctions in patches that may be entirely suitable in a different landscape context. This has been empirically demonstrated for a variety of taxa (e.g., Ehrlich 1961) and it has been argued that it is a common arrangement for patchily distributed birds (Ehrlich 1961, Westemeier et al. 1998, Walters et al. 1999, Martin et al. 2000).

Broadly stated, the main purpose of this dissertation is to investigate the role of dispersal in the persistence of forest birds in a set of neotropical forest fragments.

Traditionally, birds have been viewed as superior dispersers. Several studies of avian biogeography across a variety of spatial scales have shown that there is little effect of patch isolation on the distribution of some temperate zone birds (Brown 1978, Estades and Temple 1999, Fernandez-Juricic 2000, Watson et al. 2004), although exceptions do

occur (Wiggins et al. 1998, Walters et al. 1999). There is evidence that isolation has affected distribution of birds across tropical oceanic islands, but these fragments are isolated by hundreds to thousands of kilometers and occurrence of isolation effects are not surprising at distances so great; even good volant dispersers have limits to how far they can fly (Diamond 1981, Mayr and Diamond 2001). Recently, however, biologists have begun to suspect that the distribution of tropical forest birds is not only affected by habitat isolation, but that this limitation may take place on the modest scale at which deforestation often occurs in the tropics, so that remnants separated by a few hundred meters may be effectively inaccessible to some birds. The evidence, however, is indirect and sometimes contradictory (e.g., Renjifo 2001, Koh et al. 2002).

A system of known-age forest fragments in Lago Gatun, Panama, offers a great opportunity for investigating biogeographical processes that influence bird distributions (Diamond 2001, Leigh et al. 2002). The largest of these fragments, Barro Colorado Island (BCI), is probably the best studied tropical forest fragment in the world. Since it was isolated during the construction of the Panama Canal, this 1500+ ha tropical forest fragment has lost dozens of forest dependent bird species in what is often cited as a classic case of post-isolation faunal relaxation. The most popular historical explanations for these extinctions have focused on island-specific ecological processes (e.g., mesopredator release); alternative explanations of how current avian community structure has developed on the island have been limited and empirically unsupported. A broader view of the geographic context in which BCI exists offers insight into the role of small

scale dispersal limitation in structuring avian communities in this set of lowland tropical forest isolates.

The goals of this study were: 1) to establish the extent to which area and isolation affect the distribution of bird species richness across the set of tropical fragments in Lago Gatun, Panama; 2) to ascertain the degree to which these species-neutral biogeographic patterns reflect species-specific patterns in distribution with respect to the same explanatory variables (area and isolation); and 3) to investigate, as robustly as possible, the mechanisms that drive distributional sensitivity to isolation for a subset of understory tropical forest birds.

The first two goals are addressed in chapters one and two, respectively, and are based on biogeographic analysis of species inventory data from a subset of 29 of the forested islands of Lago Gatun, Panama. The third is accomplished through a translocation experiment designed to generate estimates of species-specific ability to fly across water, and the analysis of morphological and ecological correlates of that experimental measure of flight ability.

## **Chapter 2: Biogeography of forest and second-growth dependent birds on the islands of Lago Gatun, Panama.**

### **Abstract**

We studied the species-area and species-isolation relationships of forest and edge birds using exhaustive surveys of the forested islands of Lago Gatun, Panama. Using a variety of regression techniques, we assessed the potential roles of area and isolation in determining avian species richness across this series of fragments, and how these relationships may differ for the two groups of birds. Area is a strong predictor of richness across the archipelago, and slopes of the species-area relationships differ significantly for forest and edge birds. Isolation is not a significant predictor of richness until the effects of area are taken into account; the species-isolation relationship is then important in explaining variation in species richness. The slopes of both species-area and species-isolation relationships are different for forest and edge birds. This difference disappears for the species-area slopes when an index of suitable habitat area for both groups is used to calculate the relationship. These results are suggestive of dispersal limitation that differs for the forest and edge species present across this series of fragments, but more detailed distributional analysis is needed to clarify the mechanisms behind these relationships.

## **Introduction**

The species-area relationship, the tendency for species richness to increase as the area of a habitat patch increases, is considered by some to be the nearest thing to a general law of ecology (Schoener 1976). The other stalwart of MacArthur and Wilson's (MacArthur and Wilson 1967) theory of island biogeography, the species-isolation relationship, is not as universal as the species-area relationship, and is not invoked nearly as often by researchers to plan reserves and/or to make predictions of species loss from fragmented landscapes. This relationship is largely dependent on the distribution of immigration abilities of the focal taxa and, perhaps to a lesser extent, on the magnitude of the fragmented system's isolation. Quantifying these variables, however, can be unexpectedly difficult. For example, there is a strong species-isolation relationship for non-volant mammals on nearshore (generally < 3km from source pool) islands in Lake Huron (Lomolino 1994). For vertebrates, these islands are not well isolated by conventional biogeographic standards, but the effect of isolation is predictable in hindsight because these mostly small ectothermic organisms have to swim through cold water or cross over exposed winter ice in order to colonize historically unoccupied islands or to replace extinct populations.

The basic species-area and species-isolation relationships for nearshore lacustrine archipelagos have received little attention from island biogeographers, and almost none at all for birds. This may be partly due to the conventional view that superior dispersal abilities in birds likely negates the effect of isolation in systems that do

not have a very wide range of isolation values among fragments. Such a range of isolation values in insular biogeographic studies is uncommon (Brown and Lomolino 1996). It is also especially true in the temperate zone, where a large proportion of bird species are migratory and undertake seasonal migrations of 100's of kilometers over water, that many species do in fact possess dispersal abilities far in excess of what might be required to immigrate to any nearshore island.

Some researchers have demonstrated isolation effects for near shore temperate archipelagos (e.g., Wiggins and Moller 1997), but there are few studies of islands separated from mainland source pools on the scale of 0 - 3km, and none with birds as the focal taxon. The tropics are even more poorly represented in this regard; to our knowledge, species-area and species-isolation relationships have never been detailed for a tropical lacustrine archipelago. There is a suggestion, however, that even taxa that are traditionally regarded as good dispersers may be negatively affected by mild isolation of tropical patches (Stouffer and Bierregaard 1993, 1995b, Sekercioglu et al. 2002, Laurance 2004, Laurance et al. 2004, Laurance and Gomez 2005). Barro Colorado Island (BCI), a 90 year-old landbridge island in Panama's Lago Gatun, is one of the best studied tropical fragments in the world and offers some of the most intriguing evidence. BCI's avifauna is heralded as a classic example of post-isolation faunal relaxation. Dozens of formerly resident bird species have become extinct and remained undetected for decades despite thorough census efforts (Robinson 1999). Although many of these extinctions can be explained by habitat change caused by forest succession on BCI (Willis 1974),

explanations remain elusive for the loss of ~30 species for which apparently suitable habitat is still present on the island, and whose abundances in nearby mainland forest remain high (Willis 1974, Karr 1982, Robinson 1999, Robinson et al. 2000). BCI is separated from large tracts of mainland forest by only a few hundred meters.

Herein we present an investigation into factors affecting species richness in a tropical archipelago by describing the species-area and species-isolation relationships for the fragmented system of which BCI is the largest member, the forested islands of Lago Gatun, Panama.

Our goals were to delineate species-area and species-isolation relationships for two habitat specific groups of tropical birds in a fragmented nearshore island system, to interpret with these relationships the contribution of selective extinctions and colonizations to present day species richness on these islands, and to record community composition for comparison with future census efforts. We also use the opportunity to evaluate a longstanding hypothesis that birds of second growth and edge habitats are less sensitive to the effects of fragmentation than are forest obligate species. We then discuss the general implications for the avifaunas of fragmented tropical systems.

### History of the Islands

In 1911-1914, Gatun Lake was created during construction of the Panama Canal. The Chagres River, which ran through a tract of well forested land on the Caribbean Slope of the canal zone, was dammed to facilitate the movement of ships across the Isthmus of Panama. As a result, a great swath of lowland forest was drowned and dozens of hilltops in the formerly forested landscape became islands in the lake. These new land-bridge islands varied in size from many unnamed sites of less than a hectare to the 1560-ha Barro Colorado Island. The islands also varied in distance from the surrounding mainland forest by several orders of magnitude, with some islands as close as 5 m and the most isolated islands over 3000 m distant (see Fig. 1, Chapter 4).

Thorough bird community inventories exist for several islands. The longest running series of inventories are from Barro Colorado Island, which was first studied in the late 1920s and 1930s by Chapman (1928, 1938) and has been inventoried regularly since then (Willis and Eisenman 1979). Six other islands were inventoried from 1976-1981 (Wright 1985).

## **Methods**

We inventoried 29 of the largest islands, which varied from 1.6 ha to 1560 ha in area and from 17 to 2600 m (distance from the nearest large landmass) in isolation. From 2001-2003, we surveyed each island between mid-February and mid-April, the period corresponding to peak vocal activity of local forest birds (Robinson et al. 2000). We conducted each survey until the observer had been within 200m of every point on the island and a species

accumulation curve indicated that 20% of the cumulative effort produced no new species detections. This is the same technique Wright (1985) used in his survey of a subset of six of these islands from 1977-1981.

While we are certain that these surveys were successful in detecting all birds that vocalize regularly (the vast majority in the region), there are a few cryptic species that are extremely difficult to detect even when regularly present. Our experience conducting bird surveys in the region allowed us to make *a priori* decisions concerning which species from the regional pool to exclude from analysis. For example, we excluded blue cotinga (*Cotinga nattererii*) because it is a canopy species that very rarely vocalizes, and is thus rarely recorded even when present. Also excluded were nocturnal species and those that use the islands for roosting only (e.g., vultures and most parrots). We also excluded aquatic and aerial feeding species (e.g., such as swifts, swallows, herons, and rails) that use the islands' terrestrial habitats only secondarily if at all. In effect, these rules resulted in the inclusion of only those species that at least potentially reside on the islands, and that vocalize regularly during the hours of our survey periods. We provide a list of included species in Appendix 1.

To generate standard species-isolation relationships, one must generate meaningful measures of isolation for an insular system (Brown and Lomolino 1996). The goal for almost all biogeographic studies is to use a measure of isolation that identifies the distance to the source of all potential immigrants to each island, a task that may not be possible when the taxa under consideration vary widely in dispersal ability. It is often necessary to examine several potential

measures of distance to find out which explains most of the isolation-induced variation in species richness. We identified 5 isolation measures of potential ecological significance (Appendix 2). In order to identify the best measure of isolation for the islands of this archipelago, we compared output from the regression of area (A) and each of the 5 measures of island isolation (I) on species richness (S). We performed this analysis on two configurations of the inventoried islands (hereafter referred to as unlumped and lumped data); one with all 29 islands considered separately (unlumped,  $n = 29$ ), and one with two isolated island clusters, the Islas las Brujas ( $n = 5$ ) and the Islas los Gatos ( $n = 3$ ), lumped into two composite islands called “Brujas” and “Gatos” respectively (lumped,  $n = 23$ ). Each composite island has the combined area of its component islands and the isolation value for the least isolated of the component islands. The islands in a particular cluster are much closer to each other (30-70m) than to any other islands or the mainland ( $>2000\text{m}$ ), and it is therefore likely that islands within a cluster act more as a single biogeographic unit than as independent islands. Also, because all statistical analyses assume independence of island units, the lumped arrangement allows a more conservative analytical approach for this system in which inter-island colonization likely occurs for a few island clusters, resulting in a degree of non-independence of some data points.

After logarithmic transformation of area and isolation parameters, we used simple linear regression models (semi-log) to generate standard species-area and species-isolation curves for 3 groups of species richness data: all species, interior forest species, and edge species (Appendix 1). All species is the composite of forest species and edge species. The decision as to which group (forest or edge) a given species belonged was straightforward for all but a handful of species.

Almost all designations were determined following the extensive published history of bird study in the region (Karr 1971, 1991, Robinson 1999, Robinson et al. 2000a, 2000b). For all 3 groups, semi-log models explained more of the variation in species-area and species-isolation relationships than their log-log counterparts. If there was a significant relationship between species richness ( $S$ ) and the predictor variable (either area or isolation) for both forest and edge birds, we tested for differences in the slopes of the linear associations by plotting the difference in species richness (edge bird  $S$  - forest bird  $S$ ) against area or isolation and using a t-test to assess whether the resulting regression line was significantly different from zero.

We used multiple linear regression to assess the relative contributions of area and isolation in the determination of species richness across the archipelago for all three species groups. Semi-log models ( $\ln$  area and  $\ln$  isolation regressed on species richness) explained more variation in species richness than log-log counterparts, as in the simple linear regressions above. To graphically represent the manner in which species richness changes with increasing area or isolation, we created partial residual plots for the species-area/species-isolation regressions described above. This method details the relationship between species richness and one variable while holding the other constant (Brown and Lomolino 1996). We tested for differences in the slopes of the partial residual plots for forest and edge birds (e.g.,  $S \sim \ln$  area residuals vs.  $\ln$  isolation for forest birds compared to the same for edge birds) by plotting the difference in residuals against area or isolation and using a t-test to assess whether the resulting regression line was significantly different from zero.

We calculated the same multiple regression for edge species, but using an index of each island's marginal area for area values. These marginal area index values were calculated as the area of a circular ring with long radius that of a circle with the same area as that of the island in question, and short radius 20m shorter than the long radius. This gives a rough index of the area of a 20m wide margin of each island, an arbitrary measure of the available edge habitat on a given island. We then calculated the forest species regression again using core area in place of total island area. We defined core area as that which remained after subtracting the marginal area from the island's total area. This adjustment allows us a loose test of the prediction that the slopes of the species-area relationships for edge and forest birds will more closely resemble each other when a more realistic estimate of utilizable habitat area (as opposed to a single island area variable) is used to generate the respective curves. We tested for differences in slopes of these new regression lines using t-tests as described in Zar (1996).

Regression analyses were performed with S+ version 6.2 statistical software (Lucent\_Technologies 2003)

## **Results**

### Biogeographic patterns

We included for analysis 144 species for the entire archipelago, 81 of which were forest obligate species and 63 of which were edge species. Both area and isolation contributed significantly to the patterns of distribution. Area and isolation are not correlated in this archipelago (Pearson's  $r = 0.32$ ,  $p = 0.369$ ). Log-log slopes of the inclusive species-area relationship is 0.267, very close to the canonical value of 0.27 calculated by Preston (1962).

We regressed species richness ( $S$ ) on island area ( $\ln A$ ) and each of 5 isolation variables ( $\ln I_{1-5}$ ) in 5 separate multiple regressions. Distance from “mini archipelago” to the nearest land mass  $>500\text{ha}$  ( $I_{\text{arch}}$ ) using lumped data explained the most variation in the  $S \sim \ln area + \ln isolation$  regression ( $r^2 = 0.916$  lumped, 0.887 unlumped). The islands of a mini archipelago are defined as those for which the distance from the least isolated island in the group to the nearest large landmass ( $>500$  ha) is at least three times the distance between islands. All islands in a mini archipelago are assigned the same measure of isolation. All subsequent analyses were conducted with lumped data and with  $I_{\text{arch}}$  (hereafter simply referred to as isolation) as the measure of island isolation.

Area was a strong positive predictor of species richness for all species in simple linear regression ( $S \sim \ln area$ ; slope = 13.17,  $p < 0.001$ ). The same was true for forest species (slope = 8.52,  $p < 0.001$ ) and edge species (slope = 4.66,  $p < 0.001$ ). The magnitude of the increase in richness with a doubling of island area was significantly different for forest and edge species (t-test,  $p = 0.006$ ).

Isolation alone was never a significant predictor of species richness in simple linear regression for any of the three groups ( $S \sim \ln \text{isolation}$ ; all species  $p = 0.22$ , forest  $p = 0.18$ , edge  $p = 0.41$ ).

Although the magnitude of change in richness varies for forest and edge species, both area and isolation were significant predictors of richness in multiple linear regressions for both groups. Forest birds both gained and lost species more quickly than did edge species with changes in area and isolation, respectively (Table 1). Plots of species-area residuals vs. isolation, and vice versa, graphically show differences in slope for forest and edge species (Fig. 1). Change in residuals with changes in area (t-test,  $p < 0.001$ ) and isolation (t-test,  $p = 0.016$ ) were significantly different for edge and forest species.

When species richness is regressed on area ( $S \sim \ln \text{area}$ ) for forest and edge species using core and marginal area values for forest and edge species, respectively, the difference between slopes of the resulting regression lines is not significantly different (t-test,  $p = 0.130$ ). Differences in slope of the species-area relationship for forest and edge species decrease by more than half when core and marginal areas are used in the respective multiple regressions ( $S \sim \ln \text{area} + \ln \text{isolation}$ , Table 1).

## **Discussion**

### General species-area and species-isolation relationships

These results can give us general insight into the role of the most basic drivers of biogeographic pattern, extinction and colonization, in determining species richness in this fragmented system. Insular communities on landbridge islands are expected to be structured mostly by extinctions of relict fauna (Lawlor 1986), leading to a strong species-area relationship. From long term work conducted on BCI, there is little doubt that such relaxation is at least partially responsible for the strong relationship between species richness and area in the Gatun archipelago. With very few exceptions, the species that have disappeared from this largest fragment in the archipelago are also absent from every other island in the lake.

Our results support a growing body of work suggesting that even small-scale isolation of tropical fragments can disrupt movement among vertebrates traditionally considered highly vagile. The role of immigration in producing insular biogeographic pattern has often been discussed in the context of defaunated or new islands that span a range of isolation values that overlaps the varied maximum dispersal range of the taxa under study. Such islands can be quite near (Simberloff and Wilson 1969), but in most cases for birds, they are isolated oceanic islands (Diamond et al. 1976). If one assumes that there is a range of dispersal abilities among birds in this area, the association of

species richness and isolation for all groups in the Gatun archipelago (after accounting for area effects) is suggestive of dispersal limitation among volant vertebrates on a very local scale. The same pattern could, however, be the result of immigration probabilities that decline with distance when all taxa have equivalent dispersal abilities.

#### Comparisons of edge and forest species: area

The slope of the species-area relationship is always significantly steeper for forest species than for edge species in this archipelago. It has been suggested that differences in vagility can account for such variability in species-area relationships because more vagile species can more easily maintain populations on large and small islands (Mayr and Diamond 2001). This can occur through decreased extinction rates (rescue effect, Brown and Kodric-Brown 1977), and perhaps through post-extinction recolonization rates that are so rapid that extinctions go undetected in temporally spaced sampling regimes. It is widely postulated that tropical edge/young second growth specialist birds should be more vagile in comparison with forest obligate species because of the necessity, at least historically, of finding suitable replacements for patchy and ephemeral successional habitat. Our data are consistent with this explanation, but other empirical evidence for it is almost non-existent (but see Brawn et al. 1996).

An alternative and perhaps more parsimonious explanation presents itself if the groups in question are segregated by habitat types whose availability changes

differentially with changes in island area. The forested islands we studied offered two gross categories of habitat type, forest and lakeshore edge. The intervening matrix of second growth forest often found around terrestrial fragments is absent from this system. As our fragments increase in area, the available core forest habitat increases more quickly than edge habitats which are confined to the margins of the islands and a few treefall gaps. Roughly speaking, the habitat for forest species increases with the square of island radius, while edge habitats increase in direct proportion to it. The useable area of an island likely increases more quickly for forest birds as island area increases, in effect, creating separate species-area relationships for the two groups. When we recalculated the regressions using different measures of area that reflected an index of suitable area for forest and edge species respectively, the manner in which species richness changed with island area for forest and edge species converged. The difference in slopes of the species-area relationships can thus be explained without invoking differential dispersal ability between the two groups.

These analyses and results offer support of the habitat unit model of island biogeography (Buckley 1982), which posits that a more meaningful species-area relationship is established when size of distinct habitat patches are employed as the biogeographic units of area. Our results should be interpreted more conservatively than previous work in this arena, as we, by necessity, approximated habitat area, and assigned species-habitat associations not by observed coincident occurrence but by an a priori classification scheme.

### Comparisons of edge and forest species: isolation

We found a pattern in species-isolation relationships that is very similar (though inverse) to that which we found for species-area relationships; as isolation increases, edge species richness declines at a significantly lower rate than that for forest species, producing a significantly flatter slope in the species-isolation relationship of the former. Unlike the species-area relationships, the respective species-isolation relationships for edge and forest birds do not change when core and marginal areas are used in place of actual island area in the  $S \sim \ln area + \ln isolation$  regression. A strong species-isolation relationship is to be expected when focal species differ in the probability of successful immigration, usually mediated by differences in dispersal ability (Diamond et al. 1976, Brown and Lomolino 1996). The studies in which this has been investigated, however, typically focus on taxa with relatively poor dispersal ability (e.g., Rundle et al. 2002) or on archipelagos that are well isolated (e.g., Diamond et al. 1976). Considering the relatively modest spatial scale at which this analysis was conducted, it is neither intuitively obvious nor empirically well supported that tropical birds differ in dispersal ability to a degree that would generate the species-isolation pattern reported here. In the absence of reliable information on relative dispersal abilities, the most parsimonious explanation for the Gatun pattern is that immigration ability at this spatial scale is uniform among all taxa and probability of successful immigration declines with distance. This is unlikely to be true for two reasons. First, it would require that dispersal abilities

be uniformly *poor* amongst the focal taxa, which is intuitively opposite from what one might expect of volant organisms at this spatial scale. Secondly, there is growing indirect and anecdotal evidence that many tropical birds do differ in their abilities to cross even small habitat gaps (Develey and Stouffer 2001, Laurance 2004, Laurance et al. 2004, Laurance and Gomez 2005). We think it more likely, therefore, that the species-isolation relationship in this system stems from species-specific differences in dispersal ability which in turn results in distance-limited distributions across these fragments.

As in the species-area analysis, there is an alternative explanation somewhat unique to this system of fragments. Differences in the species-isolation relationships for these two groups could be explained by something other than dispersal ability if some ecological correlate of island isolation were to affect the probability of *successful* immigration of forest species more strongly than edge species. Such a variable may exist in this system in the form of microclimatic differences among islands. Lago Gatun straddles Panama at its narrowest point, and strong oceanic dry season winds sweep across the isthmus annually from January through about mid-April. Since the most isolated islands in the lake are also the most exposed to these winds (most of the nearer islands are in the lee of larger landmasses, see Fig. 1 of Chapter 4), it is possible that they are drier than many of the nearer islands, and that they suffer a shortage of understory arthropod diversity and/or abundance as a result. Dessication mediated food limitation is often mentioned as a potential cause of population decline in insectivorous forest birds in fragmented tropical woodland (Karr and Freemark 1983, Canaday 1996, Ahumada 2001).

Such microclimatic effects have been demonstrated in a number of fragmentation studies (Laurance et al. 2002), but are apparently absent in others.

This is not an unreasonable explanation for the differences in species-area relationships of forest and edge birds in the Gatun system. Given the habitat affinities of the two groups, edge birds are likely better adapted to drier, hotter, and more exposed conditions than interior forest birds, and thus perhaps better adapted to fragment life in general. Many of the edge species recorded on these islands have lakeshore and riverbank affinities which suggests adaptation to exposed conditions as well.

At present, however, desiccation-mediated food limitation must remain speculative for the islands of Lago Gatun. In the only (indirect) investigation of this phenomenon in the tropics, Sekercioglu et al. (2002) found no evidence of consistent differences in invertebrate diversity or biomass in diet and sweep samples between continuous forest and fragments of various size. This study occurred in nearby Costa Rica, although at a mid-elevation site.

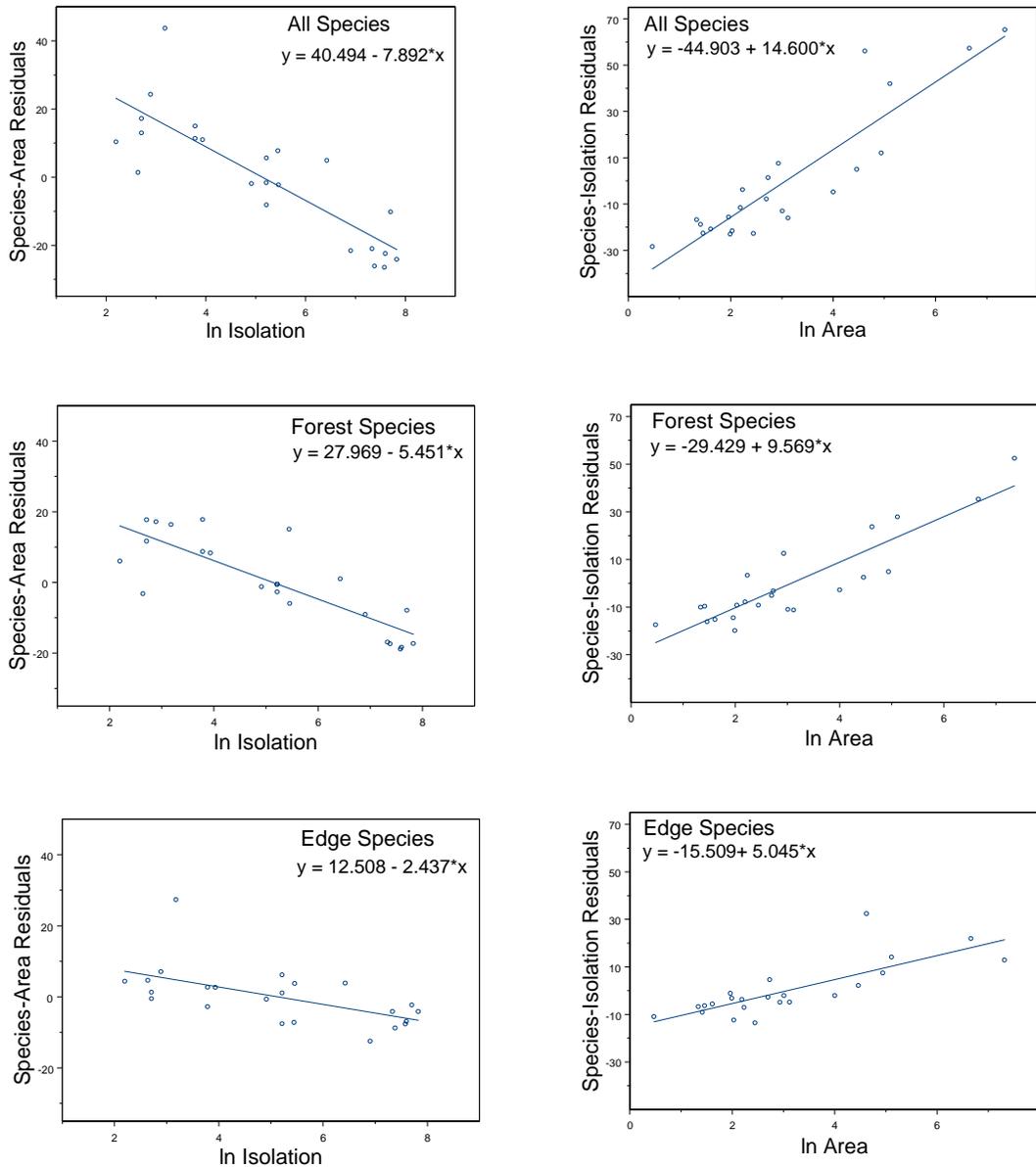
### Conclusions

These results offer support to the growing body of evidence that even volant vertebrates are subject to dispersal limitation on a very local scale in the tropics. While it is difficult to avoid the general impression, from graphics like Figure 2, that forest

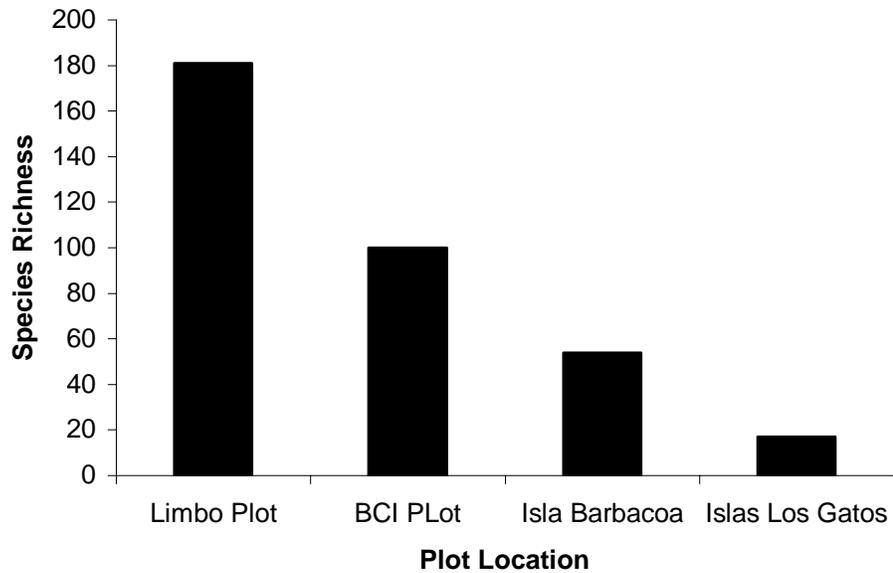
fragmentation is a conservation concern of the first order, it is equally difficult to translate these results into concrete conservation implications. While important in advancing our understanding of the basic relationship between landscape configurations and species richness for tropical birds, the species neutral analysis presented here is, in itself, adequate for the development of regional conservation plans only where the goal of such plans is to preserve the largest number of species. It suggests that in an “all else being equal” scenario, bigger and more connected reserves are better than smaller and more dispersed, but even these mundane (and oft-repeated) conclusions are difficult to defend when it is almost a certainty that all else is not equal in a tropical landscape that houses many species, those both regionally rare and common, with inexplicably patchy distributions. When combined with information on the identity of these most vulnerable organisms, however, the mechanisms outlined here can become important tools for biodiversity conservation. This information is presented in a separate analysis.

Our results are also consistent with the intuitive idea that edge specialist birds are less susceptible to the isolation-mediated effects of fragmentation than are forest obligate species. These conclusions, however, suffer from some of the same limitations as those presented above. Firstly, they hold only for the species present in our sample. If there are regional suites of both groups that are entirely absent from the set of fragments included in this study, then more regionally inclusive conclusions will be dependent on the reasons behind these absences. If forest birds are absent because they are regionally rare (but capable dispersers) and edge species are absent because they are severely

dispersal limited, then the picture may change dramatically. Species identification is important both in interpreting the results fully, and in understanding their conservation implications.



**Figure 1-** Partial residual plots that detail species-area and species-isolation relationships for forest ( $n = 81$ ), edge ( $n = 63$ ), and all (the previous two combined,  $n = 144$ ) species. Equations of the best fit (least squares) lines are reported. Notice the steeper slopes of both isolation and area lines of forest birds in comparison with those of edge birds.



**Figure 2-** Forest bird species richness values for plots of roughly the same size that vary in their degree of isolation from immigrant source pools. Limbo Plot is a 100 ha plot of mature forest embedded in the 19,341 ha Parque Nacional Soberanía, BCI Plot is the 100 ha mature forest plot embedded in 1562 ha Barro Colorado Island, Isla Barbacoa is a nearshore island of 166 ha, and Islas Los Gatos are 140 ha of maximally isolated mature forest in Lago Gatun.

**Table 1-** Results of multiple linear regressions of area and isolation on species richness. All coefficients represent the change in mean species richness associated with a doubling of one predictor variable while holding the other constant. Note that S changes much less rapidly for edge species than for forest species when the same area values are used in both regressions, but are nearly the same when area values modified to reflect available habitat for each group are used.

Group	Area Measure <sup>a</sup>	Regression Coefficient, mean change in species richness with one unit change in:		Adjusted r <sup>2</sup>	Number of Species
		In Area	In Isolation		
All Spp.	Actual	16.28***	-8.80***	0.912	144
Forest Spp.	Actual	10.67***	-6.08***	0.892	81
Edge Spp.	Actual	5.63***	-2.72*	0.679	63
Forest Spp.	Core	9.89***	-6.16***	0.882	81
Edge Spp.	Margin	12.16***	-2.84*	0.694	63

\*\*\* p < 0.0001

\* p < 0.003

<sup>a</sup> Area measurement used in regression. Actual is actual island area, see methods for descriptions of core and margin areas.

### **Chapter 3: Sensitivity of forest birds to area and isolation in central Panamanian forest fragments**

#### **Abstract**

We studied island communities of tropical forest birds across a series of poorly isolated fragments in Lago Gatun, Panama. Community structure and individual distributions were analyzed with Monte Carlo simulations and regression techniques, respectively, to determine the relative contributions of island area and isolation in creating patterns of species-specific insular occurrence, and to assess the concordance of these results with previous species-neutral biogeographic analysis. Communities were significantly nested with respect to island area, but not with isolation until the effects of area were considered. The distributions of individual birds showed a variety of responses to the area and isolation structure of the archipelago, but most forest species show sensitivity to both variables. These results are concordant with analysis of patterns in forest bird species richness in this system. The combination of these analyses provides evidence that differential extinction of isolated populations is the dominant driver of biogeographic pattern in the system, but that differential immigration mediated by several possible factors is also at play, and operates at a surprisingly local scale.

## **Introduction**

Inference from patterns of species occurrence in fragmented landscapes has advanced understanding of factors that affect creation and dissolution of biotic communities (MacArthur and Wilson 1967, Hanski 1998b). Application of these advances to conservation theory have been extensive (Pimm and Raven 2000). The explosion of biogeographic studies that followed the publication of MacArthur and Wilson's (1967) theory of island biogeography has resulted in refinement of general, species-neutral biogeographic analyses in which identities of species are ignored. Such species-neutral approaches are valuable for drawing inference about the forces that are ultimately responsible for structuring community diversity in fragmented landscapes; extinction, immigration, and speciation (Lomolino 1984, 1994, 1996).

For conservation purposes, however, species-neutral analyses are limiting. Although they give insights into the respective roles of habitat area and isolation in determining species richness patterns in a given insular system, the species richness patterns do not allow assessment of which particular species or guilds are dispersal- or resource-limited. There are cases in which significant effects of fragmentation would have been missed if analysis had stopped with the investigation of patterns in richness (Robinson et al. 1992). Nested subset analysis and related methods for analyzing individual species distributions have been developed as species-specific derivatives of the broader brush approaches described above (Schoener and Schoener 1983, Patterson and Atmar 1986, Wright et al. 1998). The

information these derivatives generate is specifically targeted at delineating distributional patterns of individual species across a fragmented landscape. In their applied form, these studies are often used to identify covariates associated with these distributional patterns, and by extension, to infer forces responsible for creating those distributions (Lomolino 1996, Butaye et al. 2001, Ganzhorn and Eisenbeiss 2001, Mac Nally et al. 2002, Bruun and Moen 2003).

Many temperate fragmented landscapes have been well studied. Yet tropical areas, which house the majority of the world's biodiversity and experience high rates of deforestation, are relatively poorly studied and we know little about the way different taxa respond to changes in biogeographic variables as fundamental as area and isolation of forest patches (Koh et al. 2002).

Species-neutral biogeographic analyses of islands in Gatun Lake, Panama revealed sensitivity to area and isolation on a surprisingly small scale (Chapter 2). Therefore, we performed species-specific biogeographic analyses of the insular forest bird communities of these islands in an effort to better understand the degree to which area and isolation affect the insular distributions of particular forest bird species, and how persistence of these organisms may be affected in this increasingly fragmented regional landscape (Condit et al. 2001). The Gatun islands offer a unique opportunity to study known-age forest fragments embedded in a temporally constant matrix (water) that is uniformly hostile to forest-dwelling birds, and which are surrounded by very large tracts of relatively undisturbed forest that protect the

watershed of the Panama Canal. By removing the complicating factor of species-specific matrix use patterns (which can affect insular distribution patterns, Stouffer and Bierregaard 1993, Sekercioglu et al. 2002), the effects of area and isolation should be more easily defined (Diamond 2001, Leigh et al. 2002).

## **Methods**

When Lago Gatun was created in 1911-1914 as part of the Panama Canal, dozens of hilltops in the formerly forested landscape became islands in the lake. These new land-bridge islands varied in size from many unnamed sites of less than 1 ha to the 1560 ha Barro Colorado Island. The islands also varied in distance from the surrounding mainland forest by several orders of magnitude, with some islands as close as 5 m and the most isolated islands over 3000 m distant. We studied 29 of the largest forested islands, ranging in size from 1.6 ha to 1560 ha, and in isolation from 18 to 2600 m (see Fig. 1, chapter 4).

We inventoried birds from January through April of 2002 and 2003 on the 29 islands. Species lists for each island were considered complete when 20% of the survey effort produced no new species detections and the observer had been within 200m of every point of each island. Details of our census methods are reported in (Chapter 2). Species were designated as forest-dependent or edge-dependent based on the extensive published history of bird study in the region, and our own experience in the region (Karr 1971, 1991, Robinson 1999, Robinson et al. 2000a, 2000b).

To assess the degree to which forest bird community composition is affected by area and isolation, we employed a nested subsets analysis that makes use of species-specific distribution data following Lomolino (1996). We addressed the null hypothesis that a specific explanatory variable, area or isolation, had no relationship to the distribution of forest birds in this system of fragments. We counted departures from perfect nestedness (an absence followed by a presence) for all forest species when islands were ordered by each of these variables. Each matrix was then reordered randomly 1000 times, and departures from perfect nestedness retabulated for each random matrix. The probability value for accepting or rejecting the null hypothesis was the proportion of the reordered matrices that showed cumulative departures from perfect nestedness that were greater than the total departures of the area- or isolation-ordered matrices. A binomial test was then used to evaluate the null hypothesis that no more than half of the deviations from perfect nestedness could be attributed to increases or decreases in the non-ordering variable. In effect, this analysis is the equivalent of a multivariate test of the effect on island incidence of one variable after taking into account the effect of the other (see Lomolino 1996 for a detailed explanation).

To assess the roles of area and isolation in affecting the distribution of individual species, we employed logistic regression analysis. Because statistical inference in logistic regression is based on asymptotic approximation of chi-square distribution, it is potentially sensitive to the small sample sizes found in most biogeographic studies. Since our aim was simply to determine which species are potentially sensitive to changes in fragment area

and/or isolation, the approximate nature of the regression coefficients and associated p-values of likelihood ratio tests do not hinder inference for the species' distributions we analyzed.

Because nestedness (see results) and species-neutral biogeographic analyses (Chapter 2) of our data show contributions of both area and isolation in structuring community composition, we fit a full logistic model with both of these explanatory variables (log transformed) against a binary (presence=1, absence=0) response variable for each species that was recorded from at least 5 fragments. Each of the variables was then individually dropped from the full model and a likelihood ratio test (LRT) performed to assess the contribution of the dropped variable in predicting the observed pattern of distribution while holding the effect of the other variable constant. Variables without significant LRT results ( $p > 0.05$ ) were dropped from the model.

In several cases, area and isolation predicted the odds of occupancy perfectly (or nearly so), resulting in complete or quasi-complete separation of the occurrence data. For these species we conducted simple logistic regressions for both variables. We then fit the best line of separation between occupied and unoccupied islands (see Lomolino et al. 1995) using multiple linear regression as a visual check for any obvious inadequacies.

All statistical analyses were performed with S+ version 6.2 (Lucent Technologies 2003) statistical software.

All analyses were performed on occurrence data for which we condensed two clusters of isolated islands into two composite islands. The islands in each of these respective clusters are much closer to each other (30-70m) than to any other islands or to the mainland (>2000m), and it is therefore likely that islands within a cluster act more as a single biogeographic unit than as independent islands; previous species-neutral analysis (Chapter 2) also supports this interpretation. Each composite “island” has the combined area of its component islands and the isolation value for the least isolated of the component islands. Because this lumping decreases the number of either occupied or unoccupied distant islands for a given species (and sample size changes from  $n = 29$  to  $n = 23$ ), there was potential to affect the results of these analyses. We therefore performed the analyses on both lumped and unlumped data. Because differences in results were very slight, and because we believe the results for the lumped data to be more reflective of the biogeographic reality of the system, we report only the results of the analyses of lumped data.

## **Results**

We detected 81 forest-dwelling bird species on the 23 islands. Island occupancy ranged from occurrences as low as one island ( $n=13$  species) to as high as 18 islands ( $n = 2$  species).

### Nestedness

Island forest bird communities are significantly nested when fragments are ordered by area ( $p = 0.002$ ). The isolation ordered matrix showed a non-nested incidence pattern nearly exactly what one would expect if this cohort of forest birds were randomly distributed across this archipelago with respect to island isolation ( $p = 0.482$ ). Binomial tests for both area- and isolation-ordered matrices showed that significantly more than half of the departures from perfect nestedness were associated with changes in the non-ordering variable (156 of 177,  $p < 0.0001$ , and 241 of 258,  $p < 0.0001$ , respectively). Therefore, the combined effects of area and isolation were likely important drivers of most species distributions.

#### Species-level distributions

We performed logistic regression analysis on 17 forest species that occurred on 7 or more fragments. These analyses showed that distributions of 11 were significantly associated with changes in both area and isolation, and that 6 of these species were more strongly affected by isolation than by area. Four species showed distributions that were significantly associated with changes in only one of these variables, and 2 were not associated with either (Table 1). In total, 13 species showed distributional sensitivity to area, and 13 to isolation.

Distributions of 24 species (each recorded on 5-14 islands) showing complete or quasi- complete separation in the distribution of the response variables were analyzed using linear regression techniques. Visual examination of the lines of separation between occupied

and unoccupied islands calculated with the resultant regression equations (the equivalent of two-group discriminant analysis, Pimentel 1979) indicated that this method does an adequate job of describing the relationship between area, isolation, and insular occurrence (Fig. 1).

Nearly half ( $n=40$ ) of all forest species occurred on 4 or fewer fragments (Fig. 2). Nearly all occurrences for these species are on the largest and/or least isolated fragments in the system. The exceptional pattern of these 40 species is that of black-chested jay, anomalously found almost exclusively on the most isolated fragments of the lake.

Some members of all foraging guilds show sensitivity to both variables (Tables 1 and 2). With the exception of keel-billed toucan, all large-bodied frugivores (mass > 100g,  $n = 6$ ) showed sensitivity to both area and isolation. Small-bodied frugivores (mass < 25g,  $n=2$ ) were insensitive to isolation, and of these 2 species, only red-capped manakin showed sensitivity to area. With the exception of forest elaenia, all non-creeping insectivores had isolation-sensitive distributions, and with the exception of southern bentbill, all were sensitive to changes in area as well. Creeping insectivores (woodcreepers, woodpeckers, etc.) showed a mixed response.

## **Discussion**

Both area and isolation of Lago Gatun islands play an important role in determining avian community composition. While area contributes significantly to nestedness,

nestedness by isolation appears to be masked by the effects of area, but is potentially significant once area effects have been accounted for statistically. These community-wide results are mirrored by individual species' distribution patterns; area has a stronger effect than isolation for 78% of species whose distribution is significantly affected by both variables, and only 1 species shows a negative effect of isolation alone. Only two forest species' distributions were unrelated to either area or isolation.

Results showed concordance with those obtained from standard species neutral biogeographic analysis for this system, in which area and isolation are significant predictors of species richness (Chapter 2). Nestedness analysis demonstrates that community composition in this series of fragments has been strongly affected by selective extinctions, mediated by some correlate of island area. As in species-neutral biogeographic analysis of these data, only when one accounts for the strong effects of area in nestedness analysis is there evidence that fragment isolation does limit the distributions of forest species in a predictable manner.

The strong influence of area on avian distribution across the archipelago is further support of a pattern established in dozens of studies conducted on as many different types of insular systems. Although avian examples to the contrary exist (Loman 1991, Estades and Temple 1999), it is expected that probability of occurrence increases with increasing habitat area. Ordering habitat patches by area often reveals significant insular nestedness, perhaps because of the tight correlation between area and species richness (Wright et al. 1998).

Traditional interpretation of this pattern in a landbridge system is that species have become extinct predictably in accordance with variation in resource requirements resulting in post-isolation faunal relaxation (Wright and Reeves 1992). Relaxation is known to have occurred on BCI, an island famous in the ecological literature for its well documented loss of forest bird species in the 90 years since its isolation (Willis 1974, Robinson 1999). Disappearance of species in some foraging guilds has occurred in order from largest to smallest body size, which is a strong correlate of resource requirements (Wilson and Willis 1975).

The most important result from our study is the role of isolation in determining species' distributions, even though Gatun islands are all relatively close (<2500 m) to mainland source pools compared with most avian biogeographic studies. Whatever factor is responsible for sensitivity to isolation in this system often operates at an even smaller scale than this modest maximum isolation value of the archipelago. When the 2 largest islands, BCI and IJG, represent the most isolated islands a species occupies (see Tables 1 and 2 for a list of such species), they can mask isolation sensitivity because that species may never have had to immigrate to or recolonize these moderately distant islands; populations of many species have persisted since isolation. An example is the distribution of lesser greenlet, a small lower-canopy vireo abundant on BCI (230m) and IJG (617m), but otherwise present only on islands up to 51m away from source pools (Fig. 1).

We see three possible explanations for the levels of isolation sensitivity in forest birds of the Gatun system: 1) differential dispersal abilities limit how far each species is able or

willing to fly across water, 2) some ecological correlate (e.g., resource availability) of isolation exists that limits persistence of certain species, or 3) a strong interaction of area and proximity exists, where large islands are occupied regardless of isolation, and small islands are occupied only if they are close enough to the source pool that they are not treated as fragments but as part of a birds' home range. Explanation 3 suggests that isolation sensitivity in this analysis is an artifact, 2 suggests that it is an indirect effect of another consequence of fragmentation, and explanation 1 suggests that it is a direct function of individual species biology.

Although there is growing indirect evidence that differential dispersal ability limits distribution in several groups of tropical birds (Stouffer and Bierregaard 1993, Stratford and Stouffer 1999, Bates 2002, Sekercioglu et al. 2002, Bates et al. 2004, Laurance 2004, Laurance et al. 2004, Laurance and Gomez 2005), that explanation is difficult to assess robustly without direct observations of flight ability (Mayr and Diamond 2001) and/or behavioral responses to habitat gaps and edges. This study, however, offers a mixed bag of other supporting evidence through examination of these isolation-driven patterns as they relate to guild structure of the focal species. Although small-bodied frugivores (red-capped and golden-collared manakins) appear to be insensitive to isolation, large-bodied members of this guild are almost uniformly affected by both area and isolation. This is in general agreement with the few studies that have addressed the issue in the tropics (Renjifo 1999, Laurance et al. 2004). Although dispersal limitation (explanation 1) mediated by a perceptual problem or a psychological aversion to gaps cannot be ruled out, morphologically

based dispersal limitation is unlikely to explain the pattern in large frugivores because all of the species involved are strong fliers, and many have been seen flying long straight-line distances over or through continuous forest (RPM and WDR pers. obs.). And while many of the large frugivores show a distribution pattern similar to that described in explanation 3 above, that argument is weakened by the fact that the three large (>50ha) fragments from which this guild is uniformly absent are also the most isolated (all >1600m distant). However, for some species of large-bodied frugivores (Table 2), isolation sensitivity may be attributable to some form of resource limitation (explanation 2 above). These birds may be dependent upon fruiting plant species whose distributions are affected by area and/or isolation in this system; there is evidence that tree community composition and demography are different on these fragments in comparison with mainland forests (Arnold and Asquith 2002).

All but one of the non-creeping insectivores have isolation-sensitive distributions. All of these species inhabit the entire width of the moisture gradient that exists across the isthmus of Panama, and most are common residents of variably-aged adjacent forests. The tolerance of moisture levels and prey species availability that must accompany such ecological plasticity in regional distribution suggests that changes in resource availability may not be responsible for sensitivity to isolation. As with large-bodied frugivores, those insectivores that show strong area sensitivity are generally not distributed on large, isolated fragments. Thus unwillingness or inability to cross even modest water gaps is left as the most likely mechanism for the generation of this pattern for insectivores.

Isolation sensitivity of distinct guilds in this study is somewhat different than that reported previously. There are certain guilds of understory forest species that are routinely identified as those most susceptible to fragmentation effects; large frugivores, raptors, and terrestrial insectivores (Willis 1974, Kattan et al. 1994, Christiansen and Pitter 1997, Renjifo 1999, Stratford and Stouffer 1999, Ribon et al. 2003). Although this study has done nothing to dispel that conventional wisdom, it has shown that nearly all tropical guilds can be sensitive to the effects of fragmentation if a suitably broad range of area and isolation values are studied. It remains the subject of further research to determine the role of the immigration filter in creating this apparent increase in sensitivity, as ours was the only of these studies to be conducted on true islands.

### Conservation implications

These analyses demonstrate that differential extinction of isolated populations is likely the dominant driver of biogeographic pattern in the Gatun system, but that differential immigration mediated by several possible factors is also at play, and operates at a surprisingly local scale. One of the most important findings is that a 23 fragment system with 750-1500+ha islands is not large enough to maintain the avian biodiversity of lowland central Panama. Central Panama has 177 forest-dependent species (Robinson et al. 2004) but fewer than 100 (see Appendix 1 for a list of forest species excluded from these analyses) were found in the Gatun archipelago. This undoubtedly has its roots in several factors, not

the least of which is the habitat specificity of many of the rare and sparsely distributed forest species in the region (Robinson et al. 2000a); even topographically diverse and sizeable BCI does not contain habitats for all of these (Robinson 2001). If these results are applicable to terrestrial as well as insular fragments, this study further underscores the need for very large reserves in the tropics where many organisms are rare and very patchily distributed, increasing the chances of stochastic extinction even in large blocks of forest (Willis 1974).

Because we have no information to address the possibility that resources upon which a particular species depends vary in some predictable way with isolation, and because most of our isolated islands are also the most exposed to certain abiotic factors that have been implicated in increased edge effects (Laurance et al. 2002), the support for strong dispersal limitation in these tropical forest birds is still somewhat equivocal in the absence of direct evidence of differential dispersal abilities. Indirect and anecdotal evidence of small-scale dispersal limitation in tropical birds points to the need for a direct assessment of relative dispersal abilities, perhaps through experimental evaluations of flight performance.

**Table 1-** Results of logistic regression of fragment area and isolation on individual species' distribution. If a coefficient is listed, that variable was significant ( $p < 0.05$ ) in explaining variation in insular occurrence for that species. Occurrence data for species listed below the dashed line were completely or quasi-completely separated on a bivariate plot of isolation vs. area; the coefficients listed for these species are those from simple logistic regression of occurrence on either variable. Guild abbreviations are as follows and are modified from Robinson (2001): FL- Large frugivore, FS- small frugivore, IC- creeping insectivore, IG- gleaning insectivore, IS-sallying insectivore, IT- terrestrial insectivore, N- nectivore, OS- sallying omnivore, OG- gleaning omnivore. See Appendix 1 for scientific names.

species	guild	isolation coefficient	area coefficient <sup>2,3</sup>	occurs on islands beyond BCI and IJG? <sup>4</sup>
keel-billed toucan	FL	ns	ns	Y
golden-collared manakin	FS	ns	ns	Y
red-capped manakin	FS	ns	1.213	Y
cocoa woodcreeper	IC	-2.263	1.882	Y
plain xenops	IG	-1.248	1.467	N
white-flanked antwren	IG	-1.721	2.674	N
checker-throated antwren	IG	-1.721	2.674	N
chestnut-backed antbird <sup>1</sup>	IG/IT	-0.82	0.628	Y
slaty antshrike	IG	-1.616	1.436	Y
southern bentbill	IS	-0.493	ns	Y
tropical gnatcatcher	IS	-0.820	0.707	N
little hermit	N	ns	2.367	Y
violet-bellied hummingbird	N	-1.149	1.574	Y
black-throated trogon	OS	-1.049	0.962	N
slaty-tailed trogon	OS	-0.843	1.482	Y
red-throated ant-tanager	OG	-2.009	1.811	N
blue dacnis	OG	0.888	ns	Y

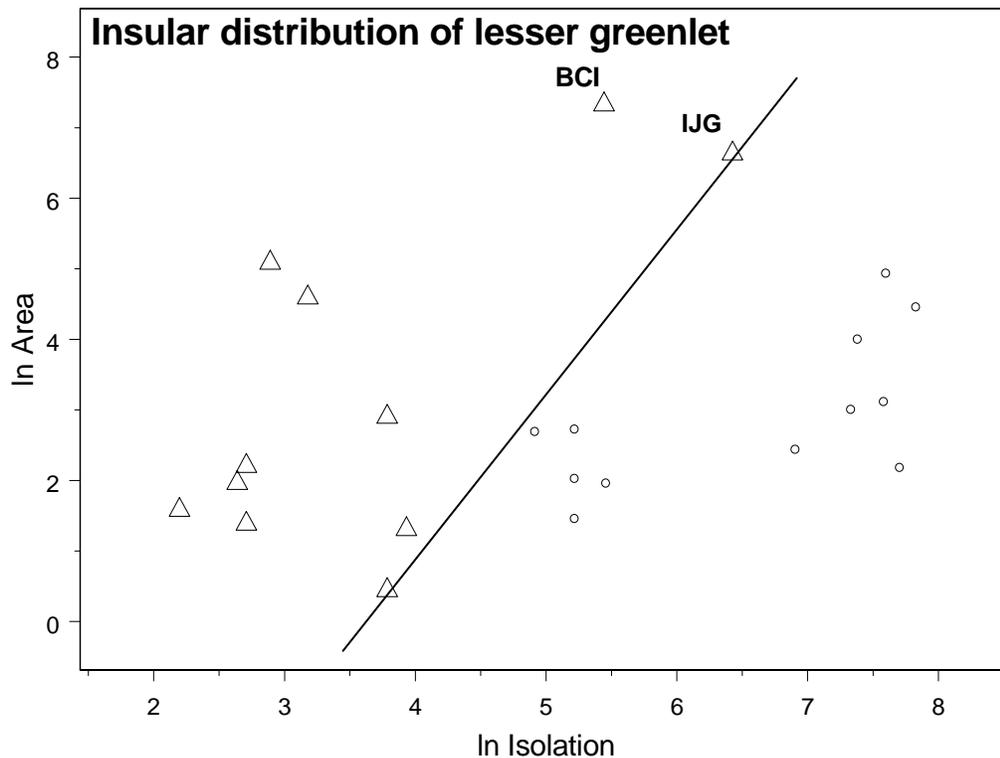
great tinamou	FL	0.977	**	N
short-billed pigeon	FL	0.648	**	N
scaled pigeon	FL	1.108	**	N
gray-chested dove	FL	1.075	**	N
chestnut-mandibled toucan	FL	0.977	**	N
collared aracari	FL	0.749	**	N
squirrel cuckoo	IG	1.317	**	N
black-cheeked woodpecker	IC	2.456	*	Y
crimson-crested woodpecker	IC	1.518	*	Y
plain-brown woodcreeper	IC	0.916	*	N
forest elaenia	IS	1.327	*	Y
ruddy-tailed flycatcher	IS	1.169	**	N
long-billed gnatwren	IG	**	**	N
lesser greenlet	IG	**	-1.579	N
long-tailed hermit	N	1.674	*	Y
blue-chested hummingbird	N	1.095	**	Y
violaceous trogon	OS	0.977	**	N
white-shouldered tanager	OG/OS	*	-1.131	Y
green honeycreeper	OG	1.128	*	Y
fulvous-vented euphonia	OG	1.317	**	N

<sup>1</sup> Molecular evidence indicates the small population of this species on the Islas Los Gatos (ca. 2km distant) has been isolated without immigration since the lake was formed (Sieving and Karr 1997).

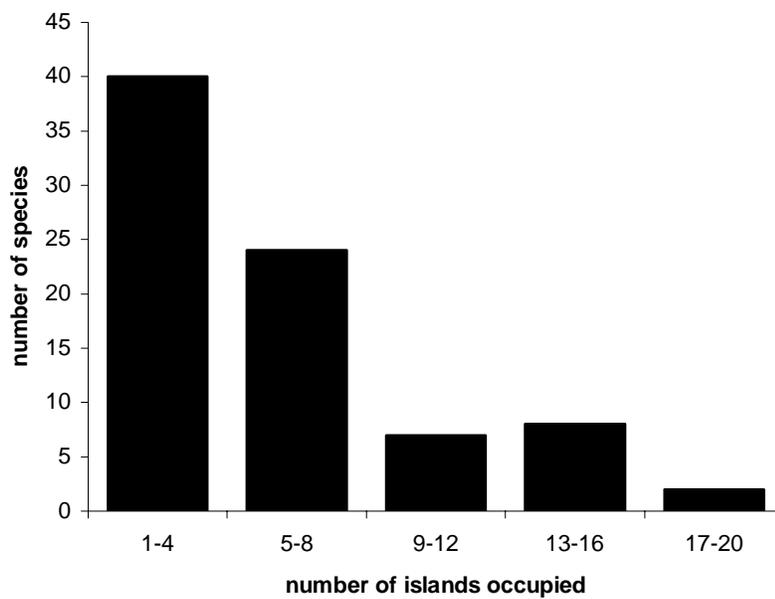
<sup>2</sup> An asterisk signifies that the variable was not a significant predictor of occurrence in simple logistic regression, nor was a term in the discriminant function that described the best fit line of separation between occupied and unoccupied islands.

<sup>3</sup> A double asterisk signifies that the variable was not a significant predictor of occurrence in simple logistic regression, but was included as a term in the discriminant function that described the best fit line of separation between occupied and unoccupied islands.

<sup>4</sup> BCI = Barro Colorado Island, IJG = Isla Juan Gallegos.



**Figure 1-** Distribution of lesser greenlet with respect to island area and isolation. Triangles represent islands on which the species was present, and circles are islands from which it was absent. The solid line represents the approximate line of separation between occupied and unoccupied islands, showing the completely separated nature of the distribution. BCI and IJG are Barro Colorado Island and Isla Juan Gallegos, respectively, the two largest islands. When BCI and IJG are discounted, this species shows a distribution very strongly influenced by isolation. It occupies islands with a wide range of areas, but only if they are closer than ~50m to source pools.



**Figure 2-** Frequency distribution of the number of forest bird species that occupied the indicated number of islands. It is common to be rare in this system, and uncommon to be common.

**Chapter 4: You can't get there from here: Over-water flight performance predicts  
bird distributions in Neotropical forest remnants**

**Abstract**

That ability to cross habitat gaps might influence bird distribution is a longstanding but untested hypothesis; here we report the results of an experimental investigation designed to evaluate the hypothesis that dispersal limitation explains the distribution patterns of several common and widespread tropical forest bird species on forested islands. We conducted exhaustive island bird inventories and an experimental over-water release program on Lago Gatun, Panama. We found that there are species-specific differences in ability to cross small gaps, and that species which are better able to cross water gaps are more widely distributed on islands than those species that negotiate the same barriers poorly. Species that performed well in release experiments were much less likely to have suffered insular extinction in the preceding 25 years than those species that showed moderate to poor performance. Proportion of wing area in the wingtip and size of heart and pectoral musculature all show strong positive association with the species-specific differences in experimental flight ability, suggesting a morphological basis for the patterns. We conclude that avian diversity in fragmented tropical forest is degraded when population declines are supplemented by disrupted dispersal movements.

## Introduction

Communities have traditionally been viewed as sets of co-occurring species whose interactions, be they competitive, predator-prey, or mutualistic, determine membership and abundances of community members (MacArthur 1965, 1969). Yet particular communities do not contain all species that are capable of maintaining a population within the bounds of those interactions. At one end of the spatial and temporal scale, history and geography limit which species have access to certain communities (Ricklefs 1987). On the other end, access to a particular community may be related to flexibility of species-specific behavioral or ecological traits (Holway and Suarez 1999). Scaling up from the behavior of individuals can help us understand the distribution of organisms within particular communities and across entire landscapes (Reed and Dobson 1993, Lima and Zollner 1996, Lens et al. 2002).

This approach can be instructive in the study of communities in spatially isolated habitat patches, which are usually depauperate when compared with similarly sized plots within larger expanses of habitat (Rosenzweig 1995). In bird communities of north temperate forests, lower richness in smaller tracts is caused by several factors, including reduced nest success and, presumably, recruitment (Brawn and Robinson 1996). Despite lower richness, however, most species recur intermittently even in very isolated fragments, so that the *permanent* local extinction of bird species from many temperate habitat patches is rare (Stratford and Robinson 2005).

Tropical fragments also lose biodiversity over time (Leigh et al. 1993, Leach and Givnish 1996, Turner 1996, Terborgh et al. 2001), but several studies have shown that certain subsets of common tropical forest birds are differentially prone to long-term local extinction (Willis 1974, Kattan et al. 1994, Robinson 1999, Ribon et al. 2003, Stratford and Robinson 2005). Explanations of the post-isolation forces responsible for the absence of such common forest birds have focused on changes in ecological interactions (e.g., Sieving 1992).

An explanatory mechanism that has not received much attention is variation in dispersal ability. Dispersal dynamics are important factors influencing community structure (Whittaker et al. 1989, Hanski 1998a, Kerr et al. 2002). They are fundamental mediators of intrapopulation demographics and metapopulation-level connectivity, and they influence the distribution of organisms in time and space (e.g., Rundle et al. 2002). The idea that ability to cross habitat gaps might influence tropical bird distribution and differentiation is a longstanding but untested hypothesis; the first published records of the idea reach back to the early 1850's when A. R. Wallace began his musings on the origins and maintenance of tropical biodiversity (Wallace 1852, 1876). Since then, indirect observational and genetic evidence has accumulated that supports the hypothesis of dispersal limitation, particularly among bird species of the forest interior (Willis 1974, Diamond et al. 1976, Capparella 1987, Mayr and Diamond 2001, Bates 2002, Bates et al. 2004). Furthermore, recent studies show that even very small gaps, such as roadcuts, can inhibit movements of forest birds (Develey and Stouffer 2001, Laurance et al. 2002, Laurance et al. 2004).

Experimental evidence evaluating interspecific variation in flight ability and the extent to which that variation can explain distributions across landscapes is, however, still lacking.

Here we report the results of an experimental investigation designed to evaluate the hypothesis that dispersal limitation explains the absence of several common and widespread tropical forest bird species on islands in a large tropical lake. We tested the predictions that there are species-specific differences in ability to cross narrow gaps, and that species that are better able to cross these gaps are more widely distributed on islands than those species that negotiate the same barriers poorly. More specifically, we predicted that species that fly effectively over water should be found on more isolated islands and should have wider insular distribution than poorly dispersing species, which should be restricted to islands closer to source pool forests. To evaluate these predictions we transported birds captured in mainland forest short distances over water and quantified their abilities to fly back to forest. We then examined the associations between flight abilities and distributions of species on differentially isolated islands. We also examined several potential morphological correlates of flight behavior/ability such as pectoral mass, heart size, and wing shape and size. Lastly, to better understand the external validity of our field experiment, we assessed the relationships between potential stressors and success or failure during our flight experiments.

### Lago Gatun as a Model Landscape

When Lago Gatun was created in 1911-1914 as part of the Panama Canal, dozens of hilltops in the formerly forested landscape became islands in the lake. These new land-bridge islands varied in size from less than 1 ha to the 1560 ha Barro Colorado Island. The islands also varied in distance from the surrounding mainland forest by several orders of magnitude, ranging from 5m to over 3000 m distant. We studied 29 of the largest islands, ranging in size from 1.6 ha to 1560 ha, and in isolation from 9 to >2500 m.

In addition to the substantial variation in island size and isolation within the archipelago, Lago Gatun is a model fragmented landscape for testing predictions of the dispersal limitation hypothesis for other reasons. First, characteristics of the regional bird community, including vocalizations and mainland community structure, are well-known, facilitating rapid and thorough inventories of island bird communities (Wright 1985, Karr 1991, Condit et al. 2001, Robinson et al. 2004). Second, water surrounding the islands has been constant across the entire landscape since the system was created, removing the confounding problem of habitat changes over time in the inter-fragment matrix that can strongly influence movement rates among fragments (Stouffer and Bierregaard 1993, Leigh et al. 2002, Huggins and Haddad 2003). Third, historical island inventories and historical records of habitat composition on several islands allow unique opportunities to evaluate by observation and inference two additional predictions of the dispersal limitation hypothesis.

Bird community inventories exist for several islands. The longest running series of inventories are from Barro Colorado Island, which was first studied in the late 1920s and 1930s by Chapman (1929, 1938) and has been inventoried regularly since then (Willis and Eisenmann 1980), (Robinson 1999). Six other islands were inventoried from 1976-1981 (Wright 1985). Those data provide long-term information on changes in species richness and on identity of species that recolonized or failed to recur after local extinction (Robinson 1999). Therefore, our recent inventories of the islands allow us to evaluate the prediction that poor performers in our over-water flight experiments should: 1) be less likely to be present on the islands if they were missing during earlier surveys; and 2) be more likely to have disappeared in the time interval between surveys than species that perform well in these experiments.

Another unique opportunity presented by this historically accessible archipelago is that some islands are known to have been continuously covered in forest whereas others were all but entirely cleared of forest during Canal construction. Although all islands we studied are now forested, aerial photos taken periodically during the 20<sup>th</sup> century provide information on historical island vegetation. This historical variation in forest structure allows us to evaluate another prediction of the dispersal limitation hypothesis. Species that perform well in over-water experiments should occur more often on all islands, regardless of history of forest availability, because they are more likely to recolonize historically deforested islands. In contrast, species that perform poorly in our experiments may occur on larger islands that have always had forest cover,

but should not have colonized historically deforested islands and should therefore be absent from those islands today.

## **Methods**

### Species distributions across fragments

We inventoried 29 islands that span more than two orders of magnitude in area (1.6 ha to 1560 ha) and isolation (9m to >2500 m, distance from the nearest large landmass). Although two contained areas of young second growth, all islands included in the surveys were predominately covered in closed canopy forest.

From 2001-2005 we surveyed islands between mid-February and mid-April, the period corresponding to peak vocal activity of local forest birds (Robinson et al. 2000). We conducted each survey so that an observer had been within 200m of every point on each island. We focused our inventories on resident (non-migratory) species, which are identified in Robinson et al. (2000). We constructed species accumulation curves and continued inventories until the curves indicated that 20% of the cumulative effort produced no new detections of forest-dependent species. Previous surveys of Gatun islands used the same technique (Wright 1985, Robinson 1999). BCI was the one exception to these rules; for that island we used census data collected by the first two

authors in the the course of surveys conducted in the preceding 10 years (unpublished data, Robinson 1999).

All analyses were performed on occurrence data for which we condensed two clusters of isolated islands into two composite islands. The islands in each of these respective clusters are much closer to each other (30-70m) than to any other islands or to the mainland (>2000m), and it is therefore likely that islands within a cluster act more as a single biogeographic unit than as independent islands; previous species-neutral analysis (Chapter 2) has also indicated that this is a realistic interpretation. Each composite “island” has the combined area of its component islands and the isolation value for the least isolated of the component islands.

### Study Species

Our experiment required capture of birds, so we focused our analysis on the ten most commonly caught forest species. These included species from 6 families, multiple foraging guilds, and a range (3-45 g) of body masses (Table 1). We assigned habitat associations (forest dependent/not) following Robinson (2000a). Because our goal was to evaluate the relationship between over-water flight ability and insular distribution, it was important to minimize the effects of other variables that might affect distribution. The choice of our ten focal species was instrumental to this end because all are in the top 10% of mainland forest bird abundance (Robinson et al. 2000a, Robinson et al. 2004), which

increased the number of experimental releases we could conduct and reduced the potentially confounding effects of abundance and microhabitat preferences on insular distribution. So called mass effects can result in the wide distribution of a common poor disperser simply by virtue of a high number of potential immigrants in source pools (Shmida and Wilson 1985). Conversely, uncommon or rare species may be absent simply because of their regional rarity, regardless of dispersal abilities. Similarly, habitat preferences or requirements can mask the relationship between dispersal ability and distribution by promoting absences from fragments that contain insufficient resources for focal species. Our focal species, however, appear to be generally insensitive to differences in age and moisture conditions in central Panama's forests; they are all found in both young and older forests and in seasonally dry and wet sites across the entire Isthmus of Panama (Robinson et al. 2000a).

#### Measuring ability to cross habitat gaps

During June-August 2003 and August-September 2004, we conducted experimental releases of forest birds at incremental distances from lakeshore forest. Upon capture in forest mist nets, birds were aged and sexed (if possible) visually, and placed individually in soft cloth bags. Other than removal from the nets and clipping the tip of a single outer rectrix (<2mm) to aid in identification of recaptured subjects, birds were not manipulated in any way before release. Subjects that showed any visible signs

of stress or injury at any point in the capture/release process, or that were molting (or had lost adventitiously) more than one flight feather, they were not used in experiments.

We immediately transported captured birds to a small johnboat propelled by a quiet, electric trolling motor. Subjects (in bags) were placed in a shaded enclosure during transport to another boat, which we hereafter call a release station, anchored at 100, 200, or 300 m from mainland forest. Before each release trial, an observer recorded wind speed/direction and light intensity at the mouth of an opened release enclosure into which subjects were subsequently placed individually. The enclosure was a wooden box with a front door of translucent but frosted plastic, and was designed so that only forest and water were visible to each subject during a given trial. Each bird was left for a calming period of 30 seconds, during which the subjects typically stopped the fluttering initiated upon placement into the enclosure. A decision period of 60 seconds began when the door was opened remotely, giving the subject the option of leaving or staying. If a subject failed to leave after 60 seconds, an encouragement sequence began in which the observer first shook the box gently, then inserted a hand through a rear portal, and eventually touched the subject if it had not already departed. Time to departure, and necessity and degree of encouragement were recorded for each trial.

As the subject exited the enclosure, an observer described its bearing (direct or indirect toward forest) and behavior (flight path, flight strength, flight height). A direct flight path was defined as departure from the release enclosure directly towards a point of

adjacent land. An indirect path was defined as departure in a direction other than towards a point of adjacent land. If a bird failed to cross successfully to forest, an observer measured the distance flown with a hand-held GPS unit while other personnel retrieved, dried, and returned the subject to its site of original capture. All trials were conducted on calm days without rain between dawn and noon when forest bird activity levels are highest.

Hereafter, we refer to the proportion of individuals of a focal species that successfully flew over water back to land as the success ratio. With the exception of those species showing near uniform failure from nearer release stations, and therefore not released from more distant stations (see below), each species has a separate success ratio for each of the three non-zero release distances. For some analyses we combined success ratios from all 3 distances and calculated the species-specific mean success ratio; we report those values as mean success ratio.

To minimize unnecessary stress, species that failed all attempts from one release distance were not tested from successively greater distances. For example, checker-throated antwren, having never succeeded in crossing from 100m, was never tested from 200m under the assumption that all such trials would end in failure. Even though no trials were conducted, these “missing” data points were considered zeros for calculations of species-specific mean success ratio.

### Potential Stressors

Because variables other than morphological or physiological flight ability may affect a subject's performance, we took steps to minimize potential stressors. We minimized capture-related stress by checking mistnets frequently (ca. every 25 min), by quickly placing the subjects in cloth bags upon extraction, by using a quiet motor with which to transport subjects to release stations, and by shading subjects in an enclosure during transport. Researchers took great care to minimize noise during the entire process between capture and release. Time between capture and release varied depending on the number of birds caught in mist nets at one time, but care was taken to minimize this interval. Any signs of capture stress (e.g., panting, grogginess) resulted in the subject's immediate release.

Because ambient light conditions may affect navigation and orientation ability of tropical forest birds (Stratford and Robinson 2005), we measured light intensity at the mouth of the opened release box before all trials. Intensity (lux) was averaged over a 7-second exposure with a handheld Minolta® T-10 illuminance meter. We took one measurement per set of releases (all of the 1 to 7 trials conducted during a trip to the release station) unless light characteristics changed noticeably during the course of the set, in which case a new reading was acquired. We selected overcast days for trials, avoiding sunny days and sites with bright conditions as a consequence of land arrangements relative to the rising sun.

Since wind can affect flight performance in birds, we conducted all trials on mornings with insignificant or no winds. These conditions are not uncommon at our selected release stations during the months of August through October. Trials were never conducted with wind blowing from shore towards the release station (head wind), and were never conducted when wind speeds exceeded 2 kph from any direction.

#### Potential correlates of flight performance

To help understand the degree to which we might extend the results from our ten focal species to other species, we obtained, by measurement in the field or from published data, values for variables that may explain variation among species in the experimental results. We examined several wing characteristics, body mass, and flight muscle and heart masses.

We measured wing shape and area by digitally photographing focal species (individuals either not used in the experiments or recaptured after they were used once in the experiments) with one wing extended so that the leading edge was straight and perpendicular with the long axis of the body. We then used program ImageJ (<http://rsb.info.nih.gov/ij/>) to measure wing area. For each species, we then calculated the ratio of mean body mass to total wing area (both wings and the surface between them, Pennycuick 2003) as a measure of wing loading, the ratio of total wing length to the

square of total wing area as a measure of aspect ratio, and the area of the polygon created by connecting the consecutive tips of extended primaries 1 through 9, numbered distally to proximally contrary to convention. We call this latter measurement wingtip ratio; it is a measurement similar to the “tip area ratio” used by Norberg and Rainer (1987). We also identified position of the longest primary as a rough measure of wing pointedness. Wings become more pointed as the position of the longest primary changes from proximal to distal. Mean body mass was calculated from captures in Canal Zone forests (Karr et al. 1990, Robinson et al. 2000). For 8 of our 10 focal species, we obtained values for flight muscle and heart mass from birds collected in central Panama by Hartman (1961).

### Statistical Analyses

Unless otherwise stated, we used p-values of 0.05 to establish statistical significance in the following analyses. We used S+ statistical software (Lucent Technologies version 6.2 2003) for all correlation and regression analyses.

To assess the association between insular distribution (distance to most isolated island occupied) and a composite measure of release performance (mean success ratio), we used randomization correlation analysis (Gotelli and Entsminger 2001). There are potential problems with using ratios in parametric correlation analysis, problems that are avoided with randomization techniques (Jackson and Somers 1991). All of the

correlation coefficients were calculated with raw, species-specific values of mean success ratio (MSR).

Because the study fragments are landbridge islands, however, the possibility exists that populations of certain focal species have persisted on some islands without immigration for the 90 years since isolation, clouding the contribution of dispersal to occurrence patterns. In other words, distance to the most isolated island presently occupied does not, in some cases, reflect the greatest distance that a focal species has had to negotiate to establish or maintain a population. There are several lines of evidence to suggest where and for which species this is true, so we evaluated the relationships between flight performance and distribution with several sets of incrementally adjusted isolation data. We generated two new sets of distance values, each set containing a “distance to most isolated island” value for each focal species. Each new set reflected the unadjusted distance data but with stepwise removal of the occurrence of chestnut-backed antbird and western slaty antshrike from a subset of islands (thus decreasing the distance to most isolated island occupied for those two species). With each stepwise removal, it is likely that the new set of distance values represents an increasingly accurate representation of the distances that all focal species have had to negotiate in order to maintain or reestablish a presence across this archipelago.

We repeated this process with distance data adjusted by grouping two isolated sets of islands. The Islas Las Brujas (5 islands) and Islas Los Gatos (3 islands) make up two island clusters near the center of Lago Gatun (Fig. 1). We surveyed eight of the larger

islands in both groups, and data from these eight islands were used to generate values of isolation distance for the correlation described above. Since the islands in a particular cluster are much closer to each other (30-70m) than to any other islands or the mainland, we hypothesized that islands within a cluster could act more as a single biogeographic unit than as independent islands. We repeated the correlation analyses described above with these two clusters lumped into two conglomerate “islands.” Each of the two conglomerates had the additive area of its constituent islands, and isolation distance value of the least isolated island in the group.

By examining the data presented in Figure 2 visually, it is clear that distance from which releases took place is a strong predictor of success and failure. We therefore used logistic regression to test the strength of the association between light intensity, time in captivity, and a binary value (success, failure) for experimental performance while controlling for distance of release. In the same vein of trying to determine the relationship between potential stressors and release performance, we used logistic regression to test for strength of association between a binary flight path variable (direct or indirect during release trials), light intensity, and release distance for each focal species.

Because of uncertainty concerning the distributions from which the variables were drawn (Sokal and Rohlf 1995), we used a sampling randomization procedure as a non-parametric analog to simple correlation analysis (Edgington 1987, Jackson and Somers

1991) to assess the relationship between measures of morphology and mean success ratio.

Tests were conducted with EcoSim<sup>®</sup>: null models software for ecology, Version 7.0 (Gotelli and Entsminger 2001).

To determine if MSR is related to probability of insular extinction on a subset of islands for which there is historical occurrence data, we employed a breakpoint comparison of frequency ratios for species ranked in order of increasing mean success ratio. We calculated species-specific frequencies of insular extinction for a subset of 6 islands that were surveyed annually during the periods 1977-1981 (Wright 1985) and 2002-2003 (this study). For a given focal species, extinction was defined as presence in one annual survey period followed by a subsequent absence. Because this novel analysis is easier to follow when methods and results are presented together, a more detailed explanation of this analysis follows in the results.

## **Results**

### Release experiment

The 10 focal species exhibited a wide range of responses in release trials. Most species showed graded flight performances in which success ratio declined as distance increased from 100 to 300 m (Fig. 2). Long-tailed hermit never failed from any distance, whereas checker-throated antwren never succeeded from 100m. For all other species,

success ratio diminished or remained static at successively more distant release stations,

although the magnitude of the diminution differed greatly among species (Fig. 2).

With the exception of long-tailed hermit, at least one individual of each species failed from at least one of the release stations. The 4 thamnophilid antbirds and red-throated ant-tanager are the only species that failed from the 100m release station (Fig. 2).

Mean and maximum distances flown during trials at each release station varied among species (Table 2). Maximum distances flown were positively correlated with mean success ratios (Ecosim<sup>®</sup> simulation correlation analysis,  $p = 0.01$ ). Focal species rank order by mean success ratio is generally preserved in the mean of distance flown from all release stations, showing that the inter-species pattern in trial success is mirrored by mean distance flown during those trials. The single exception was created by a single performance of an adult male red-throated ant-tanager (rtat) released from 200m. This 750m flight resulted in a mean distance flown value for the species placed slightly outside its rank order by success ratio at 200m (Table 2).

Some species, like golden-collared manakin, rarely flew indirectly (2 of 20 trials) while others, like red-throated ant-tanager, flew indirectly as often as they flew directly (11 of 22 trials). There is no consistent relationship (Pearson product-moment correlation,  $p = 0.48$ ) between the proportion of direct flights and flight performance as measured by mean success ratio.

For some species, there was a tendency for the trial to end in failure when the subjects flew indirectly. Western slaty antshrike flew indirectly in 2 of 14 trials that ended in success, but in 15 of 32 flights that ended in failure. The same figures for spotted antbird are 1 of 6 and 17 of 29. Of the four species that showed enough variation in flight performance for analysis, none showed a significant relationship between the binary variables of trial outcome (success or failure) and flight path (direct or indirect) in logistic regression analysis ( $p = 0.079$  to  $0.326$ ). Three of 10 species showed significant differences in flight path with increasing distance of release; ochre-bellied flycatcher, red-capped manakin, and long-tailed hermit (logistic regression, likelihood ratio test,  $p = 0.043, 0.017, 0.004$ , respectively). These species were the 3 best performers during release trials (Fig. 2). Spotted antbirds and chestnut-backed antbirds showed significant differences in flight path with increasing light intensity during trials (logistic regression, likelihood ratio test,  $p = 0.023$  and  $0.003$ , respectively).

#### Possible correlates of success

Light levels encountered during releases were generally higher than those encountered in forest understory. Ten measurements each at full shade, partial shade, and full sun locations at 0930 a.m. in the understory yielded mean (SD) light levels of 713 (148), 2567 (592), and 39153 (2220) lux, respectively. Measurements from release sites at 0930 a.m. yielded mean (SD) light level outside

the release box of 52965 (17212) lux. The difference between full sun forest and release site measurements is significantly different (t-test assuming unequal variance,  $p = 0.016$ ).

We evaluated relationships between trial outcome (success and failure) and handling time, ambient light levels, and release station distance for those four species that showed enough variation in trial performance (i.e., those that did not fail or succeed uniformly, or nearly so) for analysis (Table 3). The stress of handling, as measured by time in captivity, was never a significant predictor of success or failure. Release distance was generally significant, while ambient light level was a significant positive predictor for cocoa woodcreeper, and nearly a significant negative predictor for spotted antbird. There were, however, so few failures for cocoa woodcreeper and so few successes for spotted antbird that these results should be interpreted with caution.

We examined three aspects of wing morphology for associations with flight performance in all focal species except golden-collared manakin, for which we were unable to obtain morphological data. We were unable to use multiple linear regression because of significant multicollinearity of wingloading, aspect ratio, and wingtip ratio. The randomization procedure showed that mean success ratio was significantly correlated with higher values of wing loading ( $p = 0.042$ ,  $r = 0.589$ ) and aspect ratio ( $p = 0.015$ ,  $r = 0.574$ ). Wingtip ratio, however, was most strongly associated with mean success ratio. As proportion of wing area in the wingtip increased, mean success ratio decreased ( $p < 0.0001$ ,  $r = 0.958$ )

Heart and flight muscle mass showed a strong positive relationship with mean success ratio for the 8 focal species for which we were able to secure this data. Relative to body mass, those species that performed better in release trials have larger hearts (Pearson product-moment correlation,  $p = 0.003$ ,  $r = 0.876$ ) and heavier pectoral girdle musculature (relative mass of supracoracoideus and pectoralis combined,  $p = 0.002$ ,  $r = 0.879$ ).

#### Insular distribution

The number of islands a species occupied varied from a minimum of 4 (spotted antbird, ochre-bellied flycatcher) to a maximum of 18 (golden-collared manakin, Table 2).

Because it is not always obvious which geographic area serves as the source pool for a given set of islands, a difficult task in any biogeographic study is identifying the most biologically relevant measure of isolation for the various populations under study (Lomolino 1984). We followed Lomolino et al. (1989) in using the measure of isolation that explained the most variation, using multiple linear regression, in the standard biogeographic relationship between species richness, island area, and island isolation in our model system. We chose from among 5 measures of island isolation (see Chapter 2).

Adjusted  $r^2$  values were similar for most of these measures but were greatest for distance from mini-archipelago to the nearest landmass >500 ha, which we adopted as our measure of isolation for the archipelago (see Chapter 2 for details).

The distributions of all species were not continuous with respect to isolation; no species occupied all of the islands it was apparently capable of reaching. This may be partly attributable to the effect of island area, which has a very strong influence on species richness in this system (Chapter 2). Ochre-bellied flycatcher, for example, occurs only on the 3 largest islands (plus Orchid Island, a very close satellite of the largest island, BCI) which span nearly the entire range of isolation values for the archipelago.

Distance to the most isolated occupied island varied by an order of magnitude across species, from a low of 231m for spotted antbird to a high of 2504 m for 4 other species (using “lumped” data, see below). If BCI is removed from consideration (BCI supports relictual populations of all focal species), this maximum isolation value for spotted antbird drops to 44 m.

#### Insular distribution and flight performance

The correlation between distance to the most isolated occupied island and mean success ratio is significant when unadjusted present distribution of focal species is used to generate isolation distance values. Correlations using lumped isolated island clusters (see

methods) show a similar, but consistently stronger association between most distant occupied island and flight performance than do those using unlumped data (Table 4).

This mirrors the results of standard biogeographic analysis of this archipelago; more variation is explained in the relationship between species richness, island area, and island isolation when area and isolation values are adjusted by lumping these two island clusters (Chapter 2). We therefore used these lumped data in all other calculations that make use of insular distribution information.

We calculated the above correlation using focal species distribution data adjusted by removing probable relict populations of chestnut-backed antbird and western slaty antshrike. Chestnut-backed antbirds are found only on islands very close to mainland forest except for a single island cluster roughly 2 km from the mainland; the level of inbreeding indicated by Sieving and Karr's (1991) molecular work indicates that these chestnut-backed antbirds have very likely been present on the Islas Los Gatos since the lake was created, and that no immigration has occurred in the ensuing 90 years. There is anecdotal evidence (see discussion) that the most isolated populations of western slaty antshrike fall into this category as well. There is no evidence to suggest that any populations of the other focal species are relictual on the most distant islands that they occupy, and in most cases there is positive evidence, gathered during our resurveys of the islands surveyed by Wright in the late 1970's (1985), to show that immigration has taken place since isolation. As with the distance value adjustments, correlation coefficients that were significant with unadjusted data increase with each removal step (Table 4).

We conducted a simple analysis that assesses the relationship between a broader measure of insular distribution and MSR. We calculated the species-specific percent occupancy for islands isolated by <300m (n = 15) and >300m (n = 8), and then plotted the difference between these two values for each species in ascending order of MSR (Fig. 3). The resultant pattern shows moderate positive values for the 3 worst performers deriving from their limited distribution on near islands and nearly uniform absence on far islands, larger positive values for the next 3 species deriving from more extensive distribution on near islands and still very limited distribution on far islands, and an obvious low value cluster of the last 4 species deriving from approximately equal distributions (both limited and broad) on near and far islands.

There is a strong observational concordance between the results presented in Figures 2 and 3. The three poorest performers are those that rarely succeed from even 100m (Fig. 2, 100m); they occur on few islands even within the limited range of our experimental release distances, and on almost no islands outside that range (Fig. 3). The 3 middle performers succeeded reasonably well during 100 and 200m releases (Fig. 2, 100m and 200m) and are distributed widely amongst islands within that range, but very sparsely among those islands beyond 300 m (Fig. 3), a distance from which they rarely succeeded (Fig. 2, 300m). The best 4 performers succeeded consistently from all release distances (Fig. 2, 100m-300m) and are distributed quite uniformly with respect to distance (Fig. 3).

### Extinction probability and flight performance

Our inventories of 6 previously studied islands (Table 1) provide information on which species have disappeared between surveys. We predicted that species performing poorly in the release experiment would be more likely to have suffered extinction without recolonization than species performing well.

To evaluate that prediction, we ordered the focal species by increasing MSR and then split them into combinations of two groups (groups A and B) at each of the intervals between species, for a total of 9 paired groupings (e.g., for the first pair, group A<sub>1</sub> consisted of species 1 and group B<sub>1</sub> consisted of species 2-10, followed by group A<sub>2</sub> of species 1-2 and group B<sub>2</sub> of species 3-10, etc.). With one exception, we calculated a frequency ratio for each paired grouping using the cumulative (for all species in that half of the paired grouping) ratio of total number of extinctions incurred to the total number of possible extinctions. These ratios indicate, in relative terms, how much more likely members of group A are to have suffered extinctions in the past 25 years compared to group B. We were not able to calculate a ratio for the pair in which group B (long-tailed hermit) suffered no insular extinctions during the survey interval. The frequency ratio is near one if there is little difference in the likelihood of extinction between the two groups. The highest value identifies the two groups that are most divergent in their probabilities of extinction. When depicted graphically, the results show a breakpoint peak at which

members of group A are nearly 10 times more likely than group B to have suffered past extinctions (Fig. 4). We then created a resampling program which tested the null hypothesis that a peak in frequency ratio of this magnitude and with this arrangement of paired groupings is just as likely to have arisen in the absence of an association with experimental flight ability. The program made use of frequency ratios calculated with observed species-specific values of insular extinction, but randomized these values within paired groupings of four and six species. A frequency ratio was calculated for each of 1000 of these paired groupings, and the number of times this value exceeded or equaled the observed peak value was recorded as the p-value for the test.

These analyses demonstrate two patterns. The breakpoint peak divides the ranked focal birds at the point of separation between those species that almost never failed from any release distance and those that showed moderate to poor ability in the release trials (Fig. 4). The randomization test rejected the null hypothesis ( $p=0.009$ ); a peak of this magnitude is highly unlikely to occur between any groups of 4 and 6 species if they are not ordered by experimental flight ability. These 4 species are the same identified in Figure 3 as the most uniformly distributed species with respect to isolation.

## **Discussion**

This study implicates small-scale dispersal limitation as a factor influencing avian community composition in this fragmented system. The degree of correlation between

experimental flight performance, insular distribution, probability of insular extinction, and wing/internal morphology offers the strongest evidence to date of dispersal limitation at a surprisingly local scale in a taxon that is traditionally considered to be highly vagile.

Concerns about external validity of results from a naturally disruptive field experiment such as this necessitate caution when drawing inference. The strength of inference in this case, however, is increased greatly by the corroborative nature of the experimental and observational results. The most striking of these is the correlation between proportion of successful release flights (MSR) and insular distribution for these 10 species. The distance a species is able to negotiate in our release trials is significantly correlated with the distance to the most isolated island that species occupies. The strength of this correlation is dependent on how one interprets present day distribution of the focal species, but it is significant even when unadjusted, current distributions of the focal species are used. When occurrence data are adjusted to more closely reflect the species' purely dispersalist (as opposed to potentially relict) distributions, the correlation strengthens dramatically.

When a more inclusive measure of distribution is created within and beyond an isolation scale similar to that of our release experiments (300m), a similar and arguably more persuasive picture emerges. Generally speaking, the worst performers in our flight experiment are limited to the nearest islands, and the moderate performers are more widespread on the nearest islands but still very limited in their insular distribution beyond 300m. The best performers are the only group for which no putative limits to flight ability were suggested by experimental results, and they show very little difference in insular distribution with respect to distance (Fig. 3).

Because of the time and effort intensive nature of the release experiment, sample sizes of release trials for some focal species were necessarily small. This is potentially troubling because the strength of the inference drawn from the correlations of MSR and distribution declines with decreasing sample size for the calculation of MSR. The likelihood of making an error in interpretation in this case, however, is minimized by examination of other morphological and ecological covariates of experimental performance. Aspects of both internal (relative heart and flight muscle mass) and external (wingtip ratio) morphology are well correlated with MSR, as is an apparent ecological consequence of dispersal limitation, probability of insular extinction. In short, the analysis supported all investigated predictions that follow from the hypothesis that this cohort of understory forest birds varies predictably in species-specific ability to negotiate narrow water gaps. Forest bird communities in this fragmented landscape appear to be partially structured by permanent extinctions that are mediated by dispersal limitation. This result, at a spatial scale measured in tens of meters, is unprecedented for volant birds.

There are other lines of historical evidence that support the existence of relatively severe dispersal limitation in this system. Permanent disappearances of several forest bird species from BCI have already been mentioned. Two of the more isolated island clusters, the Islas Las Brujas and the Islas Los Gatos, offer similar evidence with an explanatory twist. These two clusters are similar in degree of isolation, and both harbor at least one relatively large island (Fig. 1). The Islas Los Gatos host a population of western slaty antshrike, an understory antbird with small territory requirements and relatively prodigious reproductive capability (Robinson, unpublished data). This

species is common in all isthmian forests and is an equally common resident of nearly all islands of sufficient size in Lago Gatun, regardless of isolation. Given the combination of its abundance, distribution, and life history traits, it is among the predictable insular survivors of the original isolation event among this guild of tropical birds. Western slaty antshrike is, however, absent from the Brujas; a seemingly anomalous fact until the history of this cluster is examined. Aerial photographs taken in the late 1920's during a visit by the newly famous Charles Lindbergh show that these islands were denuded by operation of a mine on the largest island in the group. It is the only large island cluster that does not retain a relict population of any of the poorly dispersing focal species, very likely due to the fact that these birds were extirpated in the 1920's and have never recolonized even though suitable habitat now exists.

More suggestive is the absence (or extreme rarity) of two of the worst dispersers from Isla Juan Gallegos, the second largest island in the lake at 750 ha. This island is capable of supporting large populations of chestnut-backed antbird and spotted antbird, two of the most common understory forest birds both in mainland forest and on 1560 ha BCI. The fact that both are currently missing from Juan Gallegos is likely due to the fact that, like the Islas Las Brujas, this island had been largely cleared of mature forest by the early 1920's. Any small populations that managed to persist in the small forest remnants apparently did not survive to the present day despite current availability of suitable forest habitat. There has apparently been little or no immigration, even though Juan Gallegos is separated from healthy mainland populations of these species by no more than a few hundred meters.

### Correlates of flight success

Limits to dispersal ability can be grossly broken down into two categories; those imposed by a physical incapacity to move from point A to point B, and those imposed by unwillingness to do so, regardless of physical capacity. There is evidence, both empirical and observational, to suggest that it is some combination of the two that is responsible for the patterns observed in the Gatun system.

Morphological limitation to flight performance would manifest itself in physical inability to cross habitat barriers. The most compelling indication of this type of limitation is the correlation between species-specific wing morphology variables and MSR. We examined two wing measurements that are often used to characterize flight performance in birds, wing loading and aspect ratio. Wing loading is important in determining flight speed characteristics but has no clearcut relationship to flight efficiency in vertebrates (Norberg and Rainer 1987); it was not significant in predicting probability of success in release trials. Neither was aspect ratio, although it did show a non-significant association with MSR. Aspect ratio is often associated with flight efficiency, but there can be important components of wing shape variation that are not captured by aspect ratio alone.

Of the three wing morphology variables investigated, percentage of wing area in the wingtip was most strongly associated with the probability of success during release trials. This characteristic, more so than other traditional measures of wing morphology, may largely determine efficiency of aerodynamic performance in flapping flight (Norberg and Rainer 1987, Lockwood et al. 1998, Combes and Daniel 2001, Swaddle et al. 2003b). Our measure of proportional wingtip area is reliably indexed by the position of the longest primary and length of the most distal primary; when values for these variables are increased and decreased, respectively, area in the wingtip increases, and vice versa. As a result, species with large values of proportional wingtip area generally have rounded wings, while those with smaller values generally have more pointed wings as the longest primary shifts towards the leading edge of the wing. Wing pointedness is a good predictor of migratory status (Lockwood et al. 1998) and presumably, therefore, of flight efficiency in birds. Performance among focal species in this study improved with decreasing values of this indicator of flight efficiency suggesting that differences in experimental flight performance are at least partly mediated by differences in flight morphology.

Relative mass of avian cardiac and flight musculature are good indicators of maximum sustained energetic output during flight (Bishop 1997). The strong associations of relative heart and flight muscle masses with MSR suggests that reduction in the relative size of these internal morphological characters translates to reduced sustained flight performance among focal species.

Differences in flight performance are strongly mediated by morphological limitations on flight efficiency. The 5 worst performers were all terrestrial or semi-terrestrial insectivores (with the exception of checker-throated antwren, an understory vine tangle specialist) with relatively rounded wings (area-rich wingtips) and relatively small hearts and flight muscles. Their flight morphologies are likely under stronger selection for efficient predator avoidance and pounce style foraging, both of which are favored by the increased power generation of rounded wings in a terrestrial setting (Swaddle and Lockwood 1998, Swaddle et al. 2003a), than for efficiency in distance flying. But regardless of the selective factors involved, there are very few instances in which these species are required to fly more than a few meters at a time in the structurally complex environment of the low forest understory. The four best performers are mainly frugivorous or nectivorous, with relatively pointed wings and large heart and flight musculature. Their lifestyle implies the need to move relatively long distances between patchy fruit resources of the tropical forest understory. Indeed, the best performer, long-tailed hermit, is a trap-line specialist hummingbird that routinely flies hundreds of meters between nectar sources.

Several of our focal species are probably capable of flying farther than they often did in our release trials. Actual and potential mobility, however, are not equivalent (Ehrlich 1961), even in birds (Diamond 1981). Distributions of birds on Northern Melanesian islands, for example, are strongly influenced by differences among species in dispersal ability (Mayr and Diamond 2001).

Although many of those species will fly readily across terrestrial habitats and could transit a 2 km gap between islands in 3 minutes or less, many will not make such flights (Diamond et al. 1976). Similar evidence has been gathered for the Seychelles warbler (Komdeur et al. 2004).

Although the local warbler population was super-saturated on the last island where this species occurred, and despite potentially large gains in fitness associated with colonizing nearby islands, inter-island immigration (of 1.6 or 9km) was never recorded in 9 years of study. After reintroduction efforts established large populations on two neighboring islands, only two instances of inter-island movement (both of 1.6km) were recorded in the following 11 years. We have shown by experiment that several neotropical forest birds fail to negotiate open spaces of even 100-200m, and so are even less likely to disperse to forest remnants isolated by water.

Our study offers evidence that problems in perception and/or orientation may contribute to the success with which some of these species negotiate habitat barriers. Distance at which birds were released was always the most significant predictor of trial success, but ambient light intensity during release trials was weakly implicated for spotted antbird. Cocoa woodcreeper actually succeeded more often under brighter conditions. The effects of light intensity may have been more pronounced had we not chosen overcast mornings for the majority of releases; even so, mid-morning light intensity at the release sites was still often higher than mid-morning light intensity of the forest interior. Some understory forest birds may be subject to light sensitivity mediated by adaptation for life in the dim conditions of the tropical forest understory (Stratford and

Robinson 2005). The data we have collected in the present study, however, cannot be considered more than a very preliminary test of that hypothesis.

More convincing evidence of perceptual problems is the behavior of many of the release subjects. During some trials, subjects did not orient towards land upon exiting the release enclosure, but instead performed an indirect, and often circular, low speed flight until failing or reorienting towards land. In a very few cases, subjects flew far enough to make landfall but failed in the trial because they did not orient to the closest point of land. We suspect that many of the birds that failed after very short flights (<20m) did not fly as far as they were able, but landed on the water as a result of stalling due to low flight speeds that accompanied disoriented behavior. This may be especially true of red-throated ant-tanager, a species that flew a maximum of 750m during one successful but indirect flight, but whose success ratio from 200m was just 0.286. This species also logged the highest proportion of indirect flights of all focal species. These long indirect flights were entirely confined to the 5 worst performers; the top 5 performers also flew indirectly at times (logging flights as long as 1000m for a 200m release) but never stalled or failed after flying short distances.

It is unclear how problems of perception manifest themselves in relation to dispersal limitation. Disorientation caused by lack of vertical habitat structure, light sensitivity, or neophobia would likely result in an unwillingness to attempt crossings of hostile terrain. Hesitancy or refusal to move into unsuitable gap habitats has been

demonstrated in tropical (Laurance et al. 2004) and temperate zone rainforests (Sieving et al. 1996). Regardless of the proximate causation, there is likely some interplay between physical and perceptual inability that results in poor gap-crossing performance in some of our focal species. For similar limits to perception in open spaces, species that are morphologically suited to flying relatively long distances are apparently not so constrained as are those species that are near the limit of their physical abilities in uninterrupted 100 or 200m flights.

The potential association of phylogeny and MSR does not imply bias in the context of our analysis. Because we investigated a consequence of behavioral/morphological differentiation and not its evolutionary origin, phylogenetic association strengthens our conclusions. If those birds with more area-rich wingtips, smaller hearts, smaller flight muscles, and stronger behavioral aversions to open space are poorer fliers, then it makes sense that related species, which are more behaviorally and morphologically similar to each other than to subjects in other taxa, would show clumping in a correlation analysis of experimental flight performance.

### Implications

The findings from this study will have important implications for many tropical disciplines in which dispersal ability figures prominently. Dispersal limitation at such a local scale lends some support to the notion that parapatric speciation in what would

appear to be poorly isolated populations may play an important role in the generation or maintenance of tropical biodiversity for some taxa. Metapopulation theory has suggested that such a scenario is plausible in circumstances where subdivided populations exchange immigrants only rarely (Levin 1995, Hanski 1998a).

Evolutionary implications are not limited by the degree to which these results are applicable to terrestrial fragments separated by terrestrial gaps, as rivers of even modest size may form nearly impenetrable barriers to gene flow for some species. In a natural experiment carried out at nearly the exact scale of our trials (100 to 300m), Bates et al. (2004) found evidence of genetic differentiation that varied among species whose populations were separated by the headwaters of a large Amazonian river. The most divergent forms were congeners of checker-throated antwren and spotted antbird, our first and third poorest performers. Neither of these species ever succeeded in crossing a 200m gap, and rarely succeeded from 100m.

Much of the application to conservation biology, however, is dependent on the degree to which the results are generalizable to forest understory birds in an increasingly fragmented tropical *terrestrial* landscape. The Lago Gatun system demonstrates that a narrow but uniformly hostile immigration filter can result in extinction that is likely to be permanent for a subset of understory forest birds. If a system is fragmented by habitat gaps for which nearly certain death is not the consequence of failure to cross in a single flight, the isolating potential of those gaps will be defined by the same combination of

species' characteristics that we have discussed above, but the relative contribution of each is likely to be skewed towards the sensory and psychological (perception) rather than the morphological (ability). The important question then becomes, is pasture/etc. as intimidating as water to forest birds?

### Movement

There is indirect evidence to suggest that certain terrestrial gaps are as intimidating as water. The general agreement of previously established patterns discussed below, and our direct test of crossing ability suggests that many understory forest species perceive completely deforested gaps similarly, regardless of matrix composition. Roads that create linear deforested barriers of <40m width in Amazonia created a suite of responses similar to those encountered in our study (Laurance 2004). Movements of frugivores were unaffected by the small gap with the important exception of two species, both of which are much more vulnerable to the effects of fragmentation than other species in the guild (Bierregaard and Stouffer 1997). Conversely, movements of mixed-flocking and terrestrial insectivorous species were significantly impeded by narrow road gaps that did not have regrowth of vegetation along road borders. The two exceptions to this pattern were species much less sensitive to fragmentation than others in these guilds. Those species in our study whose insular distribution was most limited by distance, and which ranked in the bottom 5 for flight performance, belong to these two guilds.

In another smaller translocation study, Laurance and Gomez (2005) showed that two species of terrestrial and mixed-flocking insectivores are inhibited from crossing large gaps of >250m, but not from crossing smaller gaps of 50-70m. These birds easily returned to their territories through 700m of continuous forest, a distance greater than birds were translocated across the large gaps. While problems with navigation are not entirely ruled out as the causal mechanism, the results strongly suggest that these species, two of which are congeners of two of our worst performers, would not or could not negotiate the 250m terrestrial gap.

#### Extinction and movement

Although no synthesized information exists on their relative sensitivity to extinction, terrestrial and semi-terrestrial insectivores are considered to be among the most extinction prone guilds following fragmentation of a continuously forested landscape. Several studies have demonstrated a disproportionate loss of Terrestrial insectivores from fragmented tropical woodland (Kattan et al. 1994, Renjifo 1999, Robinson 1999). To what degree might this phenomenon be related to lack of dispersal ability in a terrestrial system?

Using indirect evidence, Sekercioglu et al. (2002), suggested that extinction in Costa Rican forest fragments was tied to dispersal ability; those species that were best

able to use matrix habitat were the least susceptible to population declines in the fragments themselves. If true, this suggests that the factors responsible for making matrix habitat unsuitable for use also preclude sensitive species from traveling over or through it.

The study that most convincingly suggests the importance of isolation in maintaining local extinctions is the Biological Dynamics of Forest Fragments (BDFF) project near Manaus, Brazil. In the fragmented complex of mature forest plots of 1, 10, and 100ha created for that study, Terrestrial insectivores suffered many local extinctions and most had not returned 9 years after isolation despite healthy populations in nearby continuous forest and regeneration of young second growth woodland in the intervening matrix (Stouffer and Bierregaard 1995b, Stratford and Stouffer 1999).

Terrestrial insectivores in the Gatun archipelago are no exception to the pattern described above. Nearly all of the large bodied Terrestrial insectivores have disappeared from even the largest (BCI, 1560 ha) fragment in the lake (Robinson 1999). They are limited in distribution to the two largest and least isolated (<30 m from mainland forest) fragments in the system, both of which are at least an order of magnitude smaller than BCI.

Finally, the BDFF study also identified hummingbirds as one of the taxa least susceptible to the effects of severe fragmentation (Stouffer and Bierregaard 1995a). Our

data suggest that dispersal ability is one of the keys to this insensitivity; the Trochilidae was the only family (3 species,  $n=26$ , only one of these species was caught in sufficient numbers to be included in our focal species group) that succeeded uniformly from all distances in our release trials.

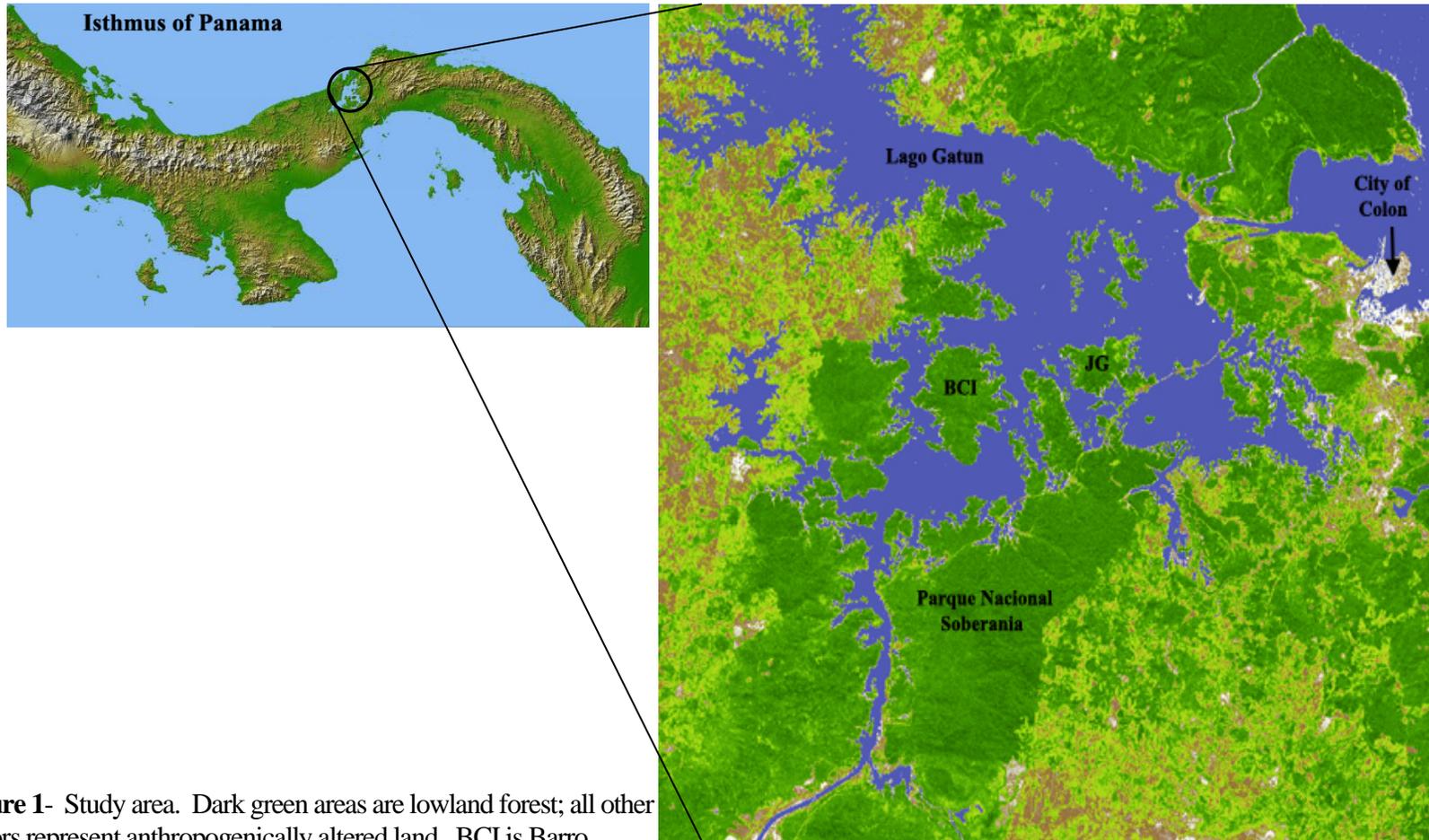
### Conclusions

It would be a very informative extension of this work to conduct similar experiments in pasture and second growth habitats. For circumstances in which the subjects could not be easily followed visually upon release, more complicated methods (e.g., telemetry) may be required. But the results of such studies will provide valuable information concerning how individual species are likely to respond to unsuitable gaps in terrestrial habitats; data sorely needed in the drive to understand the dynamics of persistence and extinction in an increasingly fragmented tropical landscape (Walters 2000).

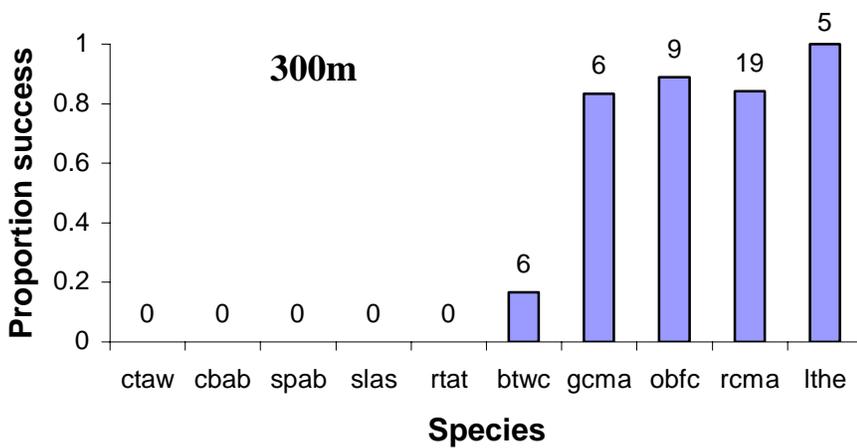
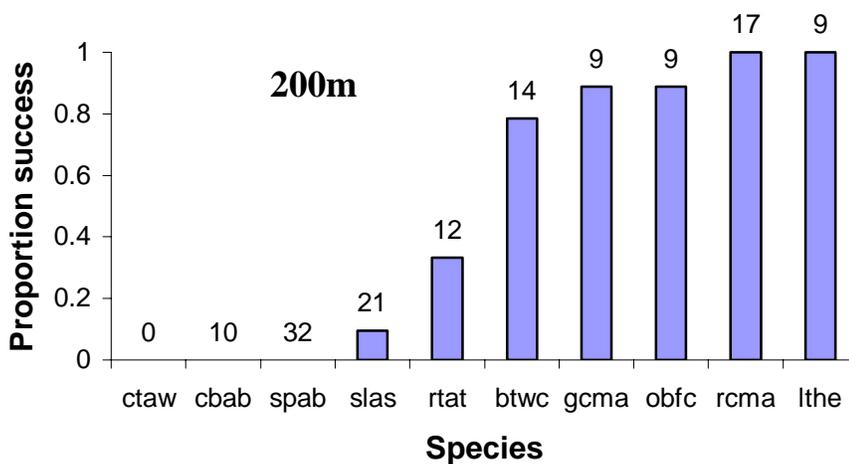
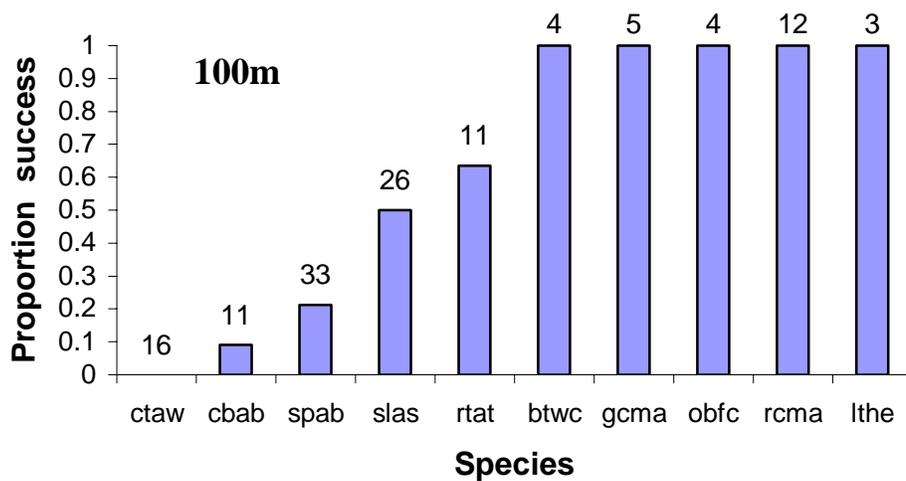
While the common species we studied do not require immense refugia to persist, it is sobering to realize that many of the regional species that live in much lower density (and occur on none of the smaller islands) have disappeared from the largest fragment in the study and have never returned despite healthy mainland populations almost literally a stone's throw away. Avian diversity in large tropical fragments is apparently degraded when population declines, mediated by any number of phenomena (e.g., altered

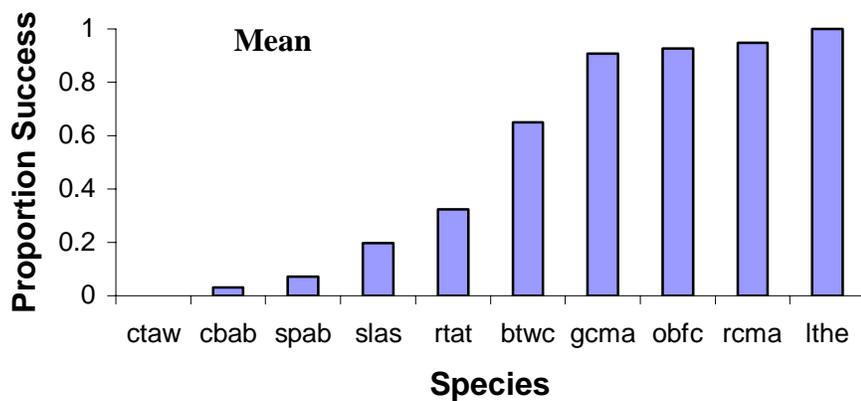
ecological conditions, normal source/sink population dynamics, etc.), act in concert with disrupted dispersal movements.

This inference has obvious implications for the design and maintenance of tropical reserves. Research on tropical fragments is still in its infancy, and it is unknown how study of landforms that are generally thought to increase fragment connectivity might alter the patterns observed in this study. For now, however, the absence of good information on the effectiveness with which increased connectivity abets persistence leaves no obvious alternatives to safeguarding very large forest reserves in which the maintenance of tropical avian biodiversity is among the management goals (Robinson 1999).

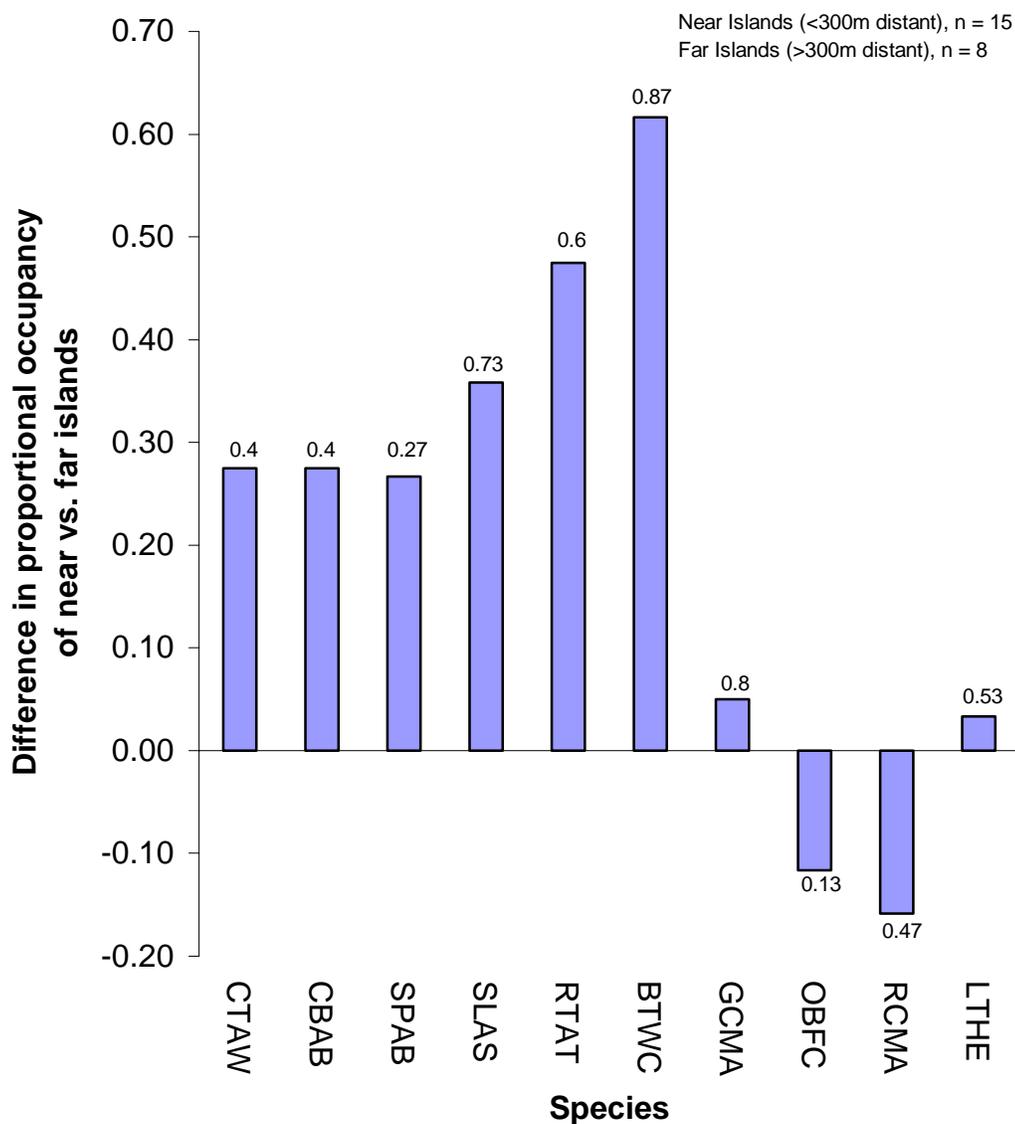


**Figure 1-** Study area. Dark green areas are lowland forest; all other colors represent anthropogenically altered land. BCI is Barro Colorado Island ( $9^{\circ} 10' N, 79^{\circ} 51' W$ ) and JG is Isla Juan Gallegos, the two largest islands in Lago Gatun. Many of the other fragments included in the study can be seen surrounding BCI, and directly north of JG.

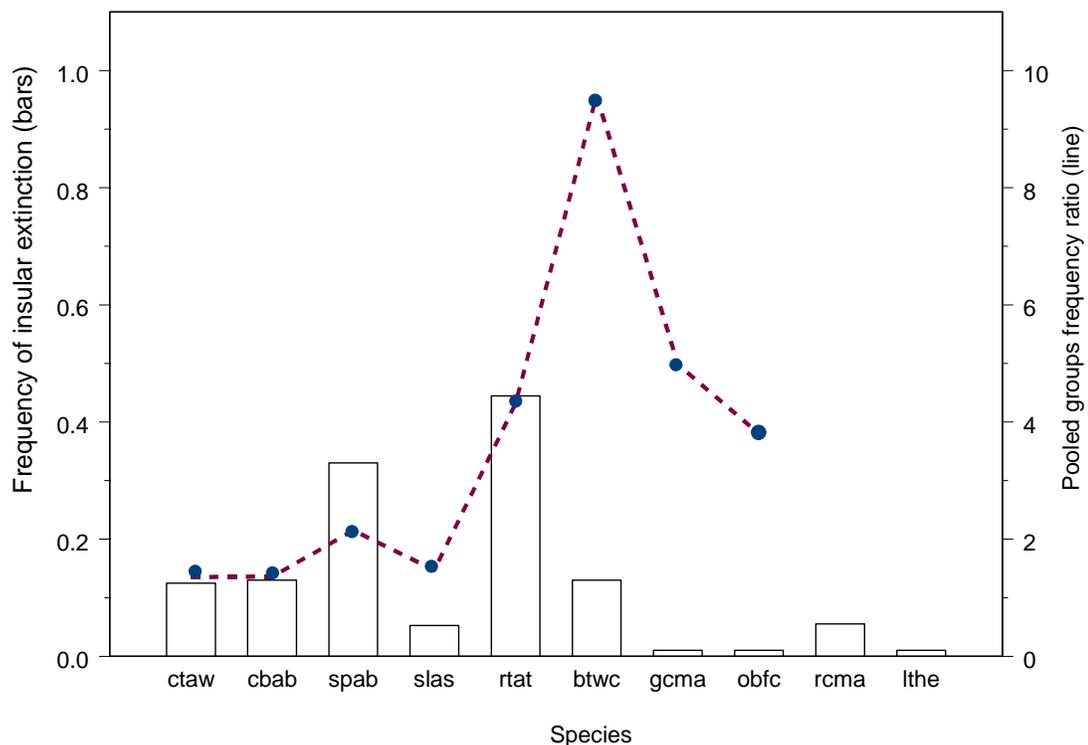




**Figure 2-** Proportion of individuals successfully completing flights from 3 distances across water, and the mean success rate for all three distances. Sample sizes are above bars. X-axis labels are species' abbreviations, defined in Table 1.



**Figure 3-** Difference in proportion of occupied near (<300m distant) and far islands (>300m distant) for the focal species listed in ascending order of mean success ratio. Bar labels are the proportion of occupied near islands; see Table 1 for clarification of species abbreviations. Note that the 4 best performers in release experiments show the most uniform insular distributions with respect to isolation. The figure also shows a similar pattern to that shown in Figures 2 and 4, with rough groupings of the first 3, second 3, and last 4 species.



**Figure 4-** Frequency breakpoint analysis of detected insular extinctions from 1977 to 2003 for a subset of the islands of Lago Gatun, Panama. X-axis labels are focal species abbreviations listed in order of ascending mean success ratio; see Table 1 for definitions. Bars (left axis) represent the total number of insular extinctions incurred to the total number of possible insular extinctions for the species. Line points represent the ratio (right axis) of pooled insular extinctions to the pooled possible insular extinctions for the two groups of species separated by the point. The point above *spab*, for example, represents the relative frequency of extinction for two groups, one consisting of *ctaw*, *cbab*, and *spab*, and the other of all remaining species to the right of *spab*. The peak in this chart represents those two groups that are most different in their probabilities of insular extinction; it separates those species that almost never failed from any release distance and those that gave moderate to poor performances during release trials. A randomization analysis of groups of 4 and 6 species showed this difference in frequency of extinction to be significant ( $p = 0.009$ ).

**Table 1-** Focal species included in the release experiment. The ten bird species studied represent 6 families, 10 genera, and 7 foraging guilds. Their occupancy of forested islands in Lago Gatun, Panama, during 2001-2003 surveys ranged from 4 to 18 of 23 forested islands. Maximum isolation of occupied islands varied across species by an order of magnitude.

Family	Species	Abbrev.	Foraging Guild	Number of Islands Occupied
Thamnophilidae	Checker-throated Antwren <i>Myrmotherula fulviventris</i>	ctaw	Dead Leaf Insectivore	7
Thamnophilidae	Chestnut-backed Antbird <i>Myrmeciza exsul</i>	cbab	Terrestrial Insectivore	7
Thamnophilidae	Spotted Antbird <i>Hylophylax naevioides</i>	spab	Terrestrial Insectivore	4
Thamnophilidae	Western Slaty Antshrike <i>Thamnophilus atrinucha</i>	slas	Understory Insectivore	14
Emberizidae	Red-throated Ant-tanager <i>Habia fuscicauda</i>	rtat	Understory omnivore	10
Dendrocolaptidae	Cocoa Woodcreeper <i>Xiphorynchus guttatus</i>	btwc	Trunk Insectivore	15
Pipridae	Golden-collared Manakin <i>Manacus vitellinus</i>	gcma	Understory Frugivore	18
Tyrannidae	Ochre-bellied flycatcher <i>Mionectes oleaginea</i>	obfc	Understory Frugivore	4
Pipridae	Red-capped manakin <i>Pipra mentalis</i>	rcma	Understory Frugivore	12
Trochilidae	Long-tailed Hermit <i>Phaethornis superciliosus</i>	lthe	Understory Nectarivore	12

**Table 2-** Mean distance flown (standard deviation in parentheses) at each release station, and maximum distance flown for any single release trial, by species. Species are listed in ascending rank order of mean success ratio (see Figure 2). See Table 1 for species abbreviations.

Species	Mean Distance Flown (m) from:			Max. Distance Flown (m)
	100m	200m	300m	
ctaw	24 (19.2)	-	-	70
cbab	48 (29)	34 (28)	-	100
spab	57 (40)	47 (37)	-	160
slas	86 (33)	118 (60)	-	240
rtat	104 (46)	216 (177)	-	750
cowc	128 <sup>1</sup> (25)	211 (24)	200 (52)	300
gcma	106 <sup>1</sup> (13)	211 (21)	273 (66)	330
obfc	100 <sup>1</sup> (0)	249 (153)	317 (91)	700
rcma	113 <sup>1</sup> (27)	224 <sup>1</sup> (43)	342 (154)	700
lthe	108 <sup>1</sup> (14)	211 <sup>1</sup> (24)	626 <sup>1</sup> (267)	1000

<sup>1</sup> Denotes species that never failed from this release station. Variation in mean distance flown at these stations reflects only differences in orientation to land, not potential differences in flight ability.

**Table 3-** P-values associated with regression coefficients of the backwards stepwise logistic regression of time in captivity, distance between release station and shoreline, and ambient light level on trial outcome (success, failure) for four focal species.

Species	Predictor Variable		
	Time in Captivity	Distance	ln Ambient Light
Spotted Antbird	0.792	0.000	0.056
Western Slaty Antshrike	0.387	0.004	0.350
Red-throated Ant-tanager	0.147	0.054	0.468
Cocoa Woodcreeper	0.951	0.001	0.020

**Table 4-** Correlation coefficients with associated randomization p-values for the association between focal species distribution and experimental flight performance. Values of mean success ratio were plotted against 1 unadjusted and 5 adjusted sets of data representing distance to most isolated island occupied for each focal species. The same coefficients calculated with arcsine square root transformations of mean success ratio are nearly identical in all cases.

Adjustment to:	r	
	No adjustment <sup>4</sup>	Gatos and Brujas lumped <sup>5</sup>
No adjustment <sup>1</sup>	0.72 (0.013)	0.70 (0.017)
cbab <sup>2</sup>	0.86 (0.005)	0.86 (0.003)
slas and cbab <sup>3</sup>	0.94 (< 0.001)	0.94 (0.001)

Distance data generated from:

<sup>1</sup> current insular distribution of focal species.

<sup>2</sup> as number 1, with Islas Los Gatos removed from the distribution of Chestnut-backed Antbird.

<sup>3</sup> as number 2, with Islas Los Gatos and Leon removed from the distribution of Western Slaty Antshrike.

<sup>4</sup> all islands considered separately.

<sup>5</sup> as number 4, with the 3 island cluster of Islas Los Gatos and the 5 island cluster of Islas Las Brujas lumped into two composite islands. See results for logic behind this.

## Chapter 5: Summary

As stated in the introduction to this dissertation, there are certain biogeographic processes that have been demonstrated so often that they have been elevated to near “law” status by ecologists; the general form of the species-area relationship foremost among them (Schoener 1976). Although much more uncommonly demonstrated, a species-isolation relationship may be nearly as predictable if less general, but it is so dependent on the focal taxa and the scale at which the study takes place that it is likely often drowned out by these sources of ecological “noise.” As seen in this study, the effects of area can be the noisiest of these sources, although it is relatively easy to deal with analytically.

These analyses have painted a hierarchical picture of sensitivity to isolation mediated in part by dispersal limitation in a cohort of tropical forest birds. Species-neutral and species-specific biogeographic analysis, respectively, show mutual and increasing support for this idea, and in combination with the experimental data, offer the strongest and most direct evidence to date that some of these birds are not able to negotiate habitat gaps that are measured in tens to a few hundreds of meters if the matrix that comprises those gaps is uniformly hostile.

Although the story likely would have been different earlier in the development of biogeographic thought, most ecologists today have at least an inkling that sensitivity to isolation can occur even with taxa that are considered capable dispersers. The scale at

which it has been demonstrated directly in these analyses, and indirectly in several other studies (Stratford and Stouffer 1999, Bates 2002, Bates et al. 2004, Laurance 2004, Laurance et al. 2004, Laurance and Gomez 2005), is suggestive of dispersal limitation in some tropical birds on a scale that is surprising and alarming at the same time. If the mechanism that drives this limitation is behavioral (e.g., avoidance of large open spaces or relatively bright light), then the implications for some understory bird populations in even very closely situated terrestrial fragments will be dire if those fragments are not individually large enough to provide shelter from various extinction processes. If the limitation is morphological, then the structure of the matrix (i.e., fragment connectivity) will play a critical role in how these populations are affected by isolation of the fragments in which they reside (Fahrig et al. 1985). In all likelihood, the mechanism is a mixture of these factors, and untangling their respective roles will require more study of tropical terrestrial fragments. Luckily, there appears to be a growing interest in assessing the role of tropical landscape structure in the persistence of forest dependent birds in fragmented systems (Sekercioglu et al. 2002).

In conclusion, this study does nothing to weaken the conventional wisdom that bigger reserve fragments are always better in the conservation of tropical forest birds . It also confirms, however, that big is a relative concept when the filter between fragments is impermeable enough (Lomolino 1984), and that for some understory species especially, impermeability may be surprisingly easy to achieve in the tropics.

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APPENDICES

**Appendix 1, part 1-** Species, habitat affinities, islands, island characteristics, and survey results for islands 1-14 (when ordered by area). One signifies that the species was present, zero represents an absence. Islands marked with (\*) and (#) were lumped into two composite islands for analysis (see text). Area for islands > 15ha is rounded to the nearest hectare. Common names follow Ridgely and Gwynne (1989) except where subsequent changes have been made by the American Ornithologist's Union.

	Triangle	Range	Tres Almen dras Oeste	Abogado Oeste	Bajo	Sobre Pato Horqueta*	Mona Grita	L	Steep	Guanabano	Tres Almen dras Grande	Panteon*	Lirio	Pato Horqueta*	Cacao
<b>Area (ha)</b>	1.6	3.8	4.1	4.3	5	5.9	7.1	7.3	7.6	8.9	9.3	9.9	11.5	13.2	14.8
<b>Isolation (m)</b>	44	51	15	184	9	2504	234	14	184	2211	15	2504	995	2504	136

Species																Habitat	
Barred Antshrike	<i>Thamnophilus doliatus</i>	1	0	0	0	1	0	0	0	0	0	0	0	0	0	1	Edge
Bananaquit	<i>Coereba flaveola</i>	0	0	0	0	0	1	0	0	0	0	0	0	0	1	0	Edge
Black-bellied Wren	<i>Thryothorus fasciatoventris</i>	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	Edge
Black-striped Sparrow	<i>Arremonops conirostris</i>	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	Edge
Blue-black Grassquit	<i>Volatinia jacarina</i>	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	Edge
Blue-crowned Motmot	<i>Momotus momota</i>	0	0	0	0	0	0	1	0	0	0	0	0	0	0	0	Edge
Blue-gray Tanager	<i>Thraupis episcopus</i>	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	Edge
Boat-billed Flycatcher	<i>Megarhynchus pitangua</i>	0	1	0	0	0	0	0	1	0	0	0	0	0	0	1	Edge
Buff-breasted Wren	<i>Thryothorus leucotis</i>	1	0	0	0	0	0	0	0	0	0	0	0	0	0	0	Edge
Buff-throated Saltator	<i>Saltator maximus</i>	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	Edge
Chestnut-headed Oropendola	<i>Psarocolius wagleri</i>	0	0	0	0	0	0	1	0	0	0	1	0	0	0	0	Edge
Clay-colored Robin	<i>Turdus grayi</i>	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	Edge
Common Tody-Flycatcher	<i>Todirostrum cinereum</i>	0	0	0	1	0	0	1	1	0	0	0	0	0	0	0	Edge

		Island →														Edge	
		Triangle	Range	Tres Almendras Oeste	Abogado Oeste	Bajo	Sobre Pato Horqueta	Mona Grita	L	Steep	Guanabano	Tres Almendras Grande	Panteon	Lirio	Pato Horqueta		Cacao
Crimson-backed Tanager	<i>Ramphocelus dimidiatus</i>	0	0	0	0	0	0	0	0	0	1	0	0	0	0	0	Edge
Dusky Antbird	<i>Cercomacra tyrannina</i>	0	1	0	0	0	0	0	0	0	0	1	0	0	0	1	Edge
Fasciated Antshrike	<i>Cymbilaimus lineatus</i>	0	0	1	0	0	0	0	0	0	0	0	0	0	0	0	Edge
Golden-fronted Greenlet	<i>Hylophilus aurantiifrons</i>	1	0	0	0	1	0	0	1	0	0	0	0	0	0	0	Edge
Golden-hooded Tanager	<i>Tangara larvata</i>	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	Edge
Gray-capped Flycatcher	<i>Myiozetetes granadensis</i>	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	Edge
Gray-headed Chachalaca	<i>Ortalis cinereiceps</i>	0	0	0	0	0	0	0	0	0	0	1	1	0	0	0	Edge
Great Kiskadee	<i>Pitangus sulphuratus</i>	1	1	1	1	1	0	1	1	1	1	1	1	0	1	1	Edge
Greater Ani	<i>Crotophaga major</i>	0	1	1	0	1	1	1	1	0	0	1	1	1	1	1	Edge
Great-tailed Grackle	<i>Cassidix mexicanus</i>	0	1	0	0	0	0	0	0	0	0	0	0	0	0	0	Edge
Lesser Kiskadee	<i>Philohydor lictor</i>	0	0	1	0	1	0	0	0	0	0	0	0	0	0	0	Edge
Lesser Seed-Finch	<i>Oryzoborus angolensis</i>	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	Edge
Pale-vented Pigeon	<i>Columba cayennensis</i>	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	Edge
Palm Tanager	<i>Thraupis palmarum</i>	0	0	0	1	0	0	0	1	0	1	0	1	0	1	0	Edge
Panama Flycatcher	<i>Myiarchus panamensis</i>	0	0	0	1	1	0	1	0	0	1	1	1	0	1	1	Edge
Piratic Flycatcher	<i>Legatus leucophaeus</i>	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	Edge
Plain Wren	<i>Thryothorus modestus</i>	1	1	0	0	0	0	0	1	0	0	0	0	0	0	0	Edge
Plain-colored Tanager	<i>Tangara inornata</i>	0	0	1	1	1	0	0	0	0	0	1	0	0	0	1	Edge
Red-crowned Woodpecker	<i>Melanerpes rubricapillus</i>	0	1	0	0	0	0	0	0	0	0	0	0	0	0	0	Edge
Red-legged Honeycreeper	<i>Cyanerpes cyaneus</i>	1	1	1	1	1	1	1	1	1	1	1	1	0	1	1	Edge
Rosy Thrush-Tanager	<i>Rhodinocichla rosea</i>	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	Edge
Rufous-capped Warbler	<i>Basileuterus rufifrons</i>	0	0	0	1	0	0	0	0	0	0	0	0	0	0	0	Edge
Rufous-tailed Hummingbird	<i>Amazilia tzacatl</i>	0	0	0	0	0	0	0	0	0	1	0	0	0	0	1	Edge

		Island →															
		Triangle	Range	Tres Almendras Oeste	Abogado Oeste	Bajo	Sobre Pato Horqueta	Mona Grita	L	Steep	Guanabano	Tres Almendras Grande	Panteon	Lirio	Pato Horqueta	Cacao	
Rusty-margined Flycatcher	<i>Myiozetetes cayanensis</i>	0	0	1	0	1	0	1	1	0	0	1	0	0	0	1	Edge
Sapphire-throated Hummingbird	<i>Lepidopyga coeruleogularis</i>	0	0	0	0	0	1	0	0	1	1	0	0	1	1	0	Edge
Scrub Greenlet	<i>Hylophilus flavipes</i>	0	0	0	0	0	0	1	1	0	0	0	0	0	0	0	Edge
Smooth-billed Ani	<i>Crotophaga ani</i>	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	Edge
Social Flycatcher	<i>Myiozetetes similis</i>	1	1	1	1	1	1	1	1	0	1	1	1	0	1	1	Edge
Southern Beardless-Tyrannulet	<i>Camptostoma obsoletum</i>	1	0	1	1	1	1	1	1	0	1	1	1	0	1	1	Edge
Streaked Flycatcher	<i>Myiodynastes maculatus</i>	0	0	1	0	1	0	1	1	0	0	0	0	0	0	1	Edge
Streaked Saltator	<i>Saltator albicollis</i>	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	Edge
Thick-billed Euphonia	<i>Euphonia laniirostris</i>	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	Edge
Tityra sp.	<i>Tityra sp.</i>	0	1	0	0	0	0	0	1	0	0	1	1	0	0	0	Edge
Tropical Kingbird	<i>Tyrannus melancholicus</i>	1	1	0	1	1	1	1	1	1	1	1	1	0	1	1	Edge
White-bellied Antbird	<i>Myrmeciza longipes</i>	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	Edge
White-necked Jacobin	<i>Florisuga mellivora</i>	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	Edge
White-necked Puffbird	<i>Notharcus macrorhynchus</i>	0	0	0	0	1	0	0	0	0	0	0	0	0	0	0	Edge
White-tipped Dove	<i>Leptotila verreauxi</i>	0	1	0	0	1	0	1	1	1	0	0	0	1	1	0	Edge
White-winged Becard	<i>Pachyramphus polychopterus</i>	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	Edge
Yellow Tyrannulet	<i>Capsiempis flaveola</i>	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	Edge
Yellow-backed Oriole	<i>Icterus chrysater</i>	0	1	1	1	0	1	1	1	1	1	0	1	0	1	1	Edge
Yellow-bellied Elaenia	<i>Elaenia flavogaster</i>	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	Edge
Yellow-bellied Seedeater	<i>Sporophila nigricollis</i>	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	Edge
Yellow-billed Cacique	<i>Amblycercus holosericeus</i>	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	Edge
Yellow-crowned Euphonia	<i>Euphonia luteicapilla</i>	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	Edge
Yellow-crowned Tyrannulet	<i>Tyrannulus elatus</i>	0	0	1	1	1	1	1	1	0	1	1	1	0	1	1	Edge

		Island →															
		Triangle	Range	Tres Almendras Oeste	Abogado Oeste	Bajo	Sobre Pato Horqueta	Mona Grita	L	Steep	Guanabano	Tres Almendras Grande	Panteon	Lirio	Pato Horqueta	Cacao	
Yellow-green Vireo	<i>Vireo flavoviridis</i>	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	Edge
Yellow-olive Flycatcher	<i>Tolmomyias sulphurescens</i>	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	Edge
Yellow-rumped Cacique	<i>Cacicus cela</i>	0	0	0	0	0	0	1	0	0	0	0	0	0	0	0	Edge
Yellow-tailed Oriole	<i>Icterus mesomelas</i>	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	Edge
Bay Wren	<i>Thryothorus nigricapillus</i>	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	Forest
Bicolored Antbird	<i>Gymnopithys leucaspis</i>	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	Forest
Black-breasted Puffbird	<i>Notharcus pectoralis</i>	0	0	0	0	0	0	0	0	1	0	0	0	0	0	0	Forest
Black-capped Pygmy-Tyrant	<i>Myiornis atricapillus</i>	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	Forest
Black-cheeked Woodpecker	<i>Melanerpes pucherani</i>	0	0	0	0	0	0	0	0	0	0	0	0	0	1	0	Forest
Black-chested Jay	<i>Cyanocorax affinis</i>	0	0	0	0	0	0	0	0	0	1	0	1	0	1	0	Forest
Black-faced Ant-thrush	<i>Formicarius analis</i>	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	Forest
Black-striped Woodcreeper	<i>Xiphorhynchus lachrymosus</i>	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	Forest
Black-tailed Trogon	<i>Trogon melanurus</i>	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	Forest
Black-throated Trogon	<i>Trogon rufus</i>	0	1	1	0	0	0	0	0	1	0	1	0	0	0	0	Forest
Blue Dacnis	<i>Dacnis cayana</i>	0	0	1	0	0	1	0	0	1	1	0	1	1	0	1	Forest
Blue-black Grosbeak	<i>Cyanocompsa cyanooides</i>	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	Forest
Blue-chested Hummingbird	<i>Amazilia amabilis</i>	0	0	1	0	1	0	0	0	1	0	1	1	0	0	1	Forest
Bright-rumped Attila	<i>Attila spadiceus</i>	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	Forest
Broad-billed Motmot	<i>Electron platyrhynchum</i>	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	Forest
Brown-capped Tyrannulet	<i>Ornithion bruneicapillum</i>	0	0	0	0	0	0	0	0	0	0	1	0	0	0	0	Forest
Buff-throated Foliage-Gleaner	<i>Automolus ochrolaemus</i>	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	Forest
Checker-throated Antwren	<i>Myrmotherula fulviventris</i>	0	0	0	0	0	0	0	0	0	0	1	0	0	0	1	Forest
Chestnut-backed Antbird	<i>Myrmeciza exsul</i>	0	0	1	0	0	0	0	1	0	0	1	0	0	0	0	Forest

	Island →															
		Triangle	Range	Tres Almendras Oeste	Abogado Oeste	Bajo	Sobre Pato Horqueta	Mona Grita	L	Steep	Guanabano	Tres Almendras Grande	Panteon	Lirio	Pato Horqueta	
Chestnut-mandibled Toucan	<i>Ramphastos swainsonii</i>	0	0	0	0	0	0	0	0	0	1	0	0	0	0	Forest
Cinnamon Woodpecker	<i>Celeus loricatus</i>	0	0	0	0	0	0	0	0	0	0	0	0	0	0	Forest
Cocoa Woodcreeper	<i>Xiphorhynchus guttatus</i>	0	1	1	1	1	0	0	1	1	0	1	1	0	1	Forest
Collared Aracari	<i>Pteroglossus torquatus</i>	0	0	1	0	0	0	0	0	0	1	0	0	0	0	Forest
Crested Guan	<i>Penelope purpurascens</i>	0	0	0	0	0	0	0	0	0	0	0	0	0	0	Forest
Crimson-crested Woodpecker	<i>Campephilus melanoleucos</i>	0	0	0	0	0	0	0	0	0	0	1	0	0	0	Forest
Dot-winged Antwren	<i>Microrhoppias quixensis</i>	0	0	0	0	0	0	0	0	0	0	0	0	0	0	Forest
Dusky-capped Flycatcher	<i>Myiarchus tuberculifer</i>	0	0	0	0	0	0	0	0	0	1	0	0	0	0	Forest
Forest Elaenia	<i>Myiopagis gaimardii</i>	0	0	0	0	0	0	0	0	0	0	0	0	0	0	Forest
Fulvous-vented Euphonia	<i>Euphonia fulvicrissa</i>	0	0	0	0	0	0	0	0	0	0	0	0	0	0	Forest
Golden-collared Manakin	<i>Manacus vitellinus</i>	1	1	1	1	1	0	0	0	1	1	1	0	1	1	Forest
Golden-crowned Spadebill	<i>Platyrinchus coronatus</i>	0	0	0	0	0	0	0	0	0	0	0	0	0	0	Forest
Gray-chested Dove	<i>Leptotila cassinii</i>	0	0	0	0	0	0	0	0	0	0	0	0	0	0	Forest
Gray-headed Tanager	<i>Eucometis penicillata</i>	0	0	0	0	0	0	0	0	0	0	0	0	0	0	Forest
Great Jacamar	<i>Jacamerops aurea</i>	0	0	0	0	0	0	0	0	0	0	0	0	0	0	Forest
Great Tinamou	<i>Tinamus major</i>	0	0	0	0	0	0	0	0	0	1	0	0	0	0	Forest
Green Honeycreeper	<i>Chlorophanes spiza</i>	0	0	0	0	0	0	0	0	0	1	0	0	0	0	Forest
Green Shrike-Vireo	<i>Vireolanius pulchellus</i>	0	0	0	0	0	0	0	0	0	1	0	0	0	0	Forest
Keel-billed Toucan	<i>Ramphastos sulfuratus</i>	1	1	1	0	0	1	1	0	1	1	1	1	1	1	Forest
Lesser Greenlet	<i>Hylophilus decurtatus</i>	1	1	1	0	1	0	0	1	0	1	0	0	0	0	Forest
Little Hermit	<i>Phaethornis longuemareus</i>	0	0	0	0	0	1	0	0	0	0	1	1	1	1	Forest
Long-billed Gnatwren	<i>Ramphocaenus melanurus</i>	0	1	0	0	1	0	0	0	0	0	0	0	0	0	Forest
Long-tailed Hermit	<i>Phaethornis superciliosus</i>	0	0	0	0	1	0	0	0	0	1	1	0	0	1	Forest

		Island →															
		Triangle	Range	Tres Almendras Oeste	Abogado Oeste	Bajo	Sobre Pato Horqueta	Mona Grita	L	Steep	Guanabano	Tres Almendras Grande	Panteon	Lirio	Pato Horqueta		Cacao
Northern Barred-Woodcreeper	<i>Dendrocolaptes sanctithomae</i>	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	Forest
Ochre-bellied Flycatcher	<i>Mionectes oleaginea</i>	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	Forest
Olivaceous Flatbill	<i>Rhynchocyclus olivaceus</i>	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	Forest
Pheasant Cuckoo	<i>Dromococcyx phasianellus</i>	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	Forest
Pied Puffbird	<i>Notharcus tectus</i>	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	Forest
Plain Xenops	<i>Xenops minutus</i>	0	0	1	0	0	0	0	0	0	0	1	0	0	0	1	Forest
Plain-brown Woodcreeper	<i>Dendrocincla fuliginosa</i>	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	Forest
Purple-crowned Fairy	<i>Heliothryx barroti</i>	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	Forest
Purple-throated Fruitcrow	<i>Querula purpurata</i>	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	Forest
Red-capped Manakin	<i>Pipra mentalis</i>	0	0	1	0	1	0	0	0	0	0	0	1	0	1	1	Forest
Red-throated Ant-Tanager	<i>Habia fuscicauda</i>	0	1	0	0	1	0	0	1	0	0	1	0	0	0	1	Forest
Ruddy-tailed Flycatcher	<i>Terenotriccus erythrurus</i>	0	0	0	0	0	0	0	0	0	0	1	0	0	0	0	Forest
Rufous Motmot	<i>Baryphthengus martii</i>	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	Forest
Rufous Mourner	<i>Rhytipterna holerythra</i>	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	Forest
Scaled Pigeon	<i>Columba speciosa</i>	0	0	0	0	0	0	0	1	0	0	0	0	0	0	0	Forest
Scaly-throated Leaf-tosser	<i>Sclerurus guatemalensis</i>	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	Forest
Scarlet-rumped Cacique	<i>Cacicus uropygialis</i>	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	Forest
Shining Honeycreeper	<i>Cyanerpes lucidus</i>	0	0	0	0	0	0	0	0	0	0	1	0	0	0	0	Forest
Short-billed Pigeon	<i>Columba nigrirostris</i>	0	0	0	0	0	0	0	0	0	0	1	0	0	0	0	Forest
Slate-colored Grosbeak	<i>Saltator grossus</i>	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	Forest
Slaty-tailed Trogon	<i>Trogon massena</i>	0	1	1	0	1	1	1	0	1	0	1	1	0	1	0	Forest
Song Wren	<i>Cyphorhinus phaeocephalus</i>	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	Forest
Southern Bentbill	<i>Oncostoma olivaceum</i>	1	1	1	0	1	0	1	0	1	0	1	0	1	0	1	Forest

	Island →																
		Triangle	Range	Tres Almendras Oeste	Abogado Oeste	Bajo	Sobre Pato Horqueta	Mona Grita	L	Steep	Guanabano	Tres Almendras Grande	Panteon	Lirio	Pato Horqueta	Cacao	
Spot-crowned Antvireo	<i>Dysithamnus puncticeps</i>	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	Forest
Spotted Antbird	<i>Hylophylax naevioides</i>	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	Forest
Squirrel Cuckoo	<i>Piaya cayana</i>	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	Forest
Sulphur-rumped Tanager	<i>Heterospingus rubrifrons</i>	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	Forest
Sunbittern	<i>Eurypyga helias</i>	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	Forest
Thrush-like Schiffornis	<i>Schiffornis turdinus</i>	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	Forest
Tropical Gnatcatcher	<i>Polioptila plumbea</i>	0	1	1	0	0	0	1	0	1	0	1	0	0	0	0	Forest
Violaceous Quail-dove	<i>Geotrygon</i>	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	Forest
Violaceous Trogon	<i>Trogon violaceus</i>	0	0	0	0	0	0	0	0	0	0	1	0	0	0	0	Forest
Violet-bellied Hummingbird	<i>Damophila julie</i>	0	1	1	1	1	0	0	0	0	0	1	0	0	0	1	Forest
Violet-crowned Woodnymph	<i>Thalurania colombica</i>	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	Forest
Western Slaty Antshrike	<i>Thamnophilus atrinucha</i>	1	1	1	0	1	0	0	1	1	0	1	0	0	0	0	Forest
White-flanked Antwren	<i>Myrmotherula axillaris</i>	0	0	0	0	0	0	0	0	0	0	1	0	0	0	1	Forest
White-shouldered Tanager	<i>Tachyphonus luctuosus</i>	1	1	1	0	1	0	0	1	0	0	1	0	0	0	1	Forest
White-vented Plumeleteer	<i>Chalybura buffoni</i>	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	Forest
Yellow-margined Flycatcher	<i>Tolmomyias assimilis</i>	0	0	0	0	0	0	0	0	0	0	1	0	0	0	0	Forest
<b>Forest Bird Species Richness</b>		6	13	17	3	13	4	4	7	10	4	30	10	5	6	15	
<b>Edge Bird Species Richness</b>		10	14	13	13	17	10	18	19	7	13	15	13	4	14	17	
<b>All Species Richness</b>		16	27	30	16	30	14	22	26	17	17	45	23	9	20	32	

**Appendix 1, part 2-** Second half of island survey results; islands 15-29 (when ordered by area). See above for details.

Island →		Abogado	Bruja Chiquita*	Pantera #	Orchid	Guacha	Trinidad	Tigre #	Bruja Grande*	Leon	Puma #	Frijoles	Barbacoa	Juan Gallegos	Barro Colorado	
		Area (ha)	15	17	18	19	20	23	38	41	55	83	102	166	779	1560
		Isolation (m)	184	2504	1992	44	1523	1956	1992	2504	1604	1992	24	18	617	231
Species																Habitat
Barred Antshrike	<i>Thamnophilus doliatus</i>	1	0	0	0	0	0	0	0	0	0	1	1	1	0	Edge
Bananaquit	<i>Coereba flaveola</i>	0	1	1	0	0	0	0	1	1	0	0	0	1	0	Edge
Black-bellied Wren	<i>Thryothorus fasciatoventris</i>	0	0	0	0	0	0	0	0	0	0	1	0	0	0	Edge
Black-striped Sparrow	<i>Arremonops conirostris</i>	0	0	0	0	1	0	0	0	0	0	1	0	1	0	Edge
Blue-black Grassquit	<i>Volatinia jacarina</i>	0	0	0	0	0	0	0	0	0	0	0	0	1	0	Edge
Blue-crowned Motmot	<i>Momotus momota</i>	1	0	0	0	0	0	0	0	0	0	1	1	0	0	Edge
Blue-gray Tanager	<i>Thraupis episcopus</i>	0	0	1	0	0	0	0	0	0	1	1	0	1	1	Edge
Boat-billed Flycatcher	<i>Megarhynchus pitangua</i>	1	0	0	0	1	0	0	0	1	0	1	1	1	1	Edge
Buff-breasted Wren	<i>Thryothorus leucotis</i>	0	0	0	0	0	0	0	0	0	0	0	1	0	0	Edge
Buff-throated Saltator	<i>Saltator maximus</i>	0	0	0	0	0	0	0	0	0	0	1	0	0	0	Edge
Chestnut-headed Oropendola	<i>Psarocolius wagleri</i>	1	0	0	0	0	0	0	0	0	0	1	1	1	1	Edge
Clay-colored Robin	<i>Turdus grayi</i>	0	0	0	0	0	0	0	0	0	0	1	0	0	0	Edge
Common Tody-Flycatcher	<i>Todirostrum cinereum</i>	0	0	0	1	0	0	1	0	0	0	1	1	1	1	Edge
Crimson-backed Tanager	<i>Ramphocelus dimidiatus</i>	0	0	0	0	0	0	0	0	0	0	1	0	1	1	Edge
Dusky Antbird	<i>Cercomacra tyrannina</i>	1	0	0	1	0	0	1	0	0	0	1	1	1	1	Edge
Fasciated Antshrike	<i>Cymbilaimus lineatus</i>	0	0	0	0	0	0	0	0	0	0	1	1	0	0	Edge
Golden-fronted Greenlet	<i>Hylophilus aurantiifrons</i>	0	0	0	0	0	0	0	0	0	0	1	1	1	0	Edge
Golden-hooded Tanager	<i>Tangara larvata</i>	0	1	0	1	0	0	0	0	0	0	1	0	0	1	Edge
Gray-capped Flycatcher	<i>Myiozetetes granadensis</i>	0	0	0	1	0	0	0	0	0	0	0	0	0	0	Edge

		Island →														
		Abogado	Bruja Chiquita	Pantera	Orchid	Guacha	Trinidad	Tigre	Bruja Grande	Leon	Puma	Frijoles	Barbacoa	Juan Gallegos	Barro Colorado	
Gray-headed Chachalaca	<i>Ortalis cinereiceps</i>	1	0	1	0	0	0	1	1	0	1	1	1	1	0	Edge
Great Kiskadee	<i>Pitangus sulphuratus</i>	1	1	1	1	1	1	1	1	1	1	1	1	1	1	Edge
Greater Ani	<i>Crotophaga major</i>	1	1	1	0	1	1	1	1	1	1	1	1	1	1	Edge
Great-tailed Grackle	<i>Cassidix mexicanus</i>	0	0	0	0	0	0	0	0	0	0	0	0	0	1	Edge
Lesser Kiskadee	<i>Philohydor lictor</i>	0	0	0	1	0	0	0	0	0	1	1	1	1	1	Edge
Lesser Seed-Finch	<i>Oryzoborus angolensis</i>	0	0	0	0	0	0	0	0	0	0	0	0	1	0	Edge
Pale-vented Pigeon	<i>Columba cayennensis</i>	1	1	1	1	1	1	1	1	1	1	1	1	1	1	Edge
Palm Tanager	<i>Thraupis palmarum</i>	1	1	0	0	1	0	0	1	0	0	1	0	1	1	Edge
Panama Flycatcher	<i>Myiarchus panamensis</i>	1	1	0	1	1	1	1	1	1	0	1	1	1	1	Edge
Piratic Flycatcher	<i>Legatus leucophaeus</i>	1	0	0	0	0	0	0	0	0	0	1	1	0	0	Edge
Plain Wren	<i>Thryothorus modestus</i>	0	0	0	0	0	0	0	0	0	0	1	1	1	1	Edge
Plain-colored Tanager	<i>Tangara inornata</i>	1	0	0	1	0	0	1	1	0	0	1	1	1	1	Edge
Red-crowned Woodpecker	<i>Melanerpes rubricapillus</i>	0	0	1	0	0	0	0	0	0	0	1	0	0	0	Edge
Red-legged Honeycreeper	<i>Cyanerpes cyaneus</i>	1	1	1	1	1	1	1	1	1	1	1	1	1	1	Edge
Rosy Thrush-Tanager	<i>Rhodinocichla rosea</i>	0	0	0	0	0	0	0	0	0	0	1	1	0	0	Edge
Rufous-capped Warbler	<i>Basileuterus rufifrons</i>	0	0	0	0	0	1	0	0	0	0	0	0	0	0	Edge
Rufous-tailed Hummingbird	<i>Amazilia tzacatl</i>	0	0	1	0	0	0	0	0	0	1	1	0	1	0	Edge
Rusty-margined Flycatcher	<i>Myiozetetes cayanensis</i>	0	0	0	0	1	0	1	0	0	1	1	1	1	1	Edge
Sapphire-throated Hummingbird	<i>Lepidopygia coeruleogularis</i>	1	1	0	0	0	1	0	1	1	1	1	0	1	1	Edge
Scrub Greenlet	<i>Hylophilus flavipes</i>	0	0	0	0	0	0	0	0	0	0	1	0	0	1	Edge
Smooth-billed Ani	<i>Crotophaga ani</i>	0	0	0	0	0	0	0	0	0	0	1	0	1	0	Edge
Social Flycatcher	<i>Myiozetetes similis</i>	1	1	1	1	1	1	1	1	1	1	1	1	1	1	Edge
Southern Beardless-Tyrannulet	<i>Camptostoma obsoletum</i>	1	1	1	1	1	1	1	1	1	1	1	1	1	1	Edge
Streaked Flycatcher	<i>Myiodynastes maculatus</i>	1	0	0	1	1	0	0	1	0	1	1	1	1	1	Edge
Streaked Saltator	<i>Saltator albicollis</i>	0	0	0	0	0	0	0	0	0	0	1	0	0	0	Edge
Thick-billed Euphonia	<i>Euphonia laniirostris</i>	0	0	0	0	0	0	0	0	0	0	1	1	1	0	Edge

		Island →														
		Abogado	Bruja Chiquita	Pantera	Orchid	Guacha	Trinidad	Tigre	Bruja Grande	Leon	Puma	Frijoles	Barbacoa	Juan Gallegos	Barro Colorado	
Tityra sp.	<i>Tityra sp.</i>	1	1	1	0	0	0	0	1	1	0	1	1	1	1	Edge
Tropical Kingbird	<i>Tyrannus melancholicus</i>	1	1	1	1	1	1	1	1	1	1	1	1	1	1	Edge
White-bellied Antbird	<i>Myrmeciza longipes</i>	0	0	0	0	0	0	0	0	0	0	1	1	1	0	Edge
White-necked Jacobin	<i>Florisuga mellivora</i>	1	0	0	0	0	0	0	0	0	0	1	0	0	1	Edge
White-necked Puffbird	<i>Notharcus macrorhynchus</i>	0	0	0	0	0	0	0	0	0	0	1	1	0	0	Edge
White-tipped Dove	<i>Leptotila verreauxi</i>	1	1	1	1	1	0	1	1	1	1	1	1	1	1	Edge
White-winged Becard	<i>Pachyramphus polychopterus</i>	0	0	0	0	0	0	0	0	0	0	1	0	0	0	Edge
Yellow Tyrannulet	<i>Capsiempis flaveola</i>	0	0	0	0	0	0	0	0	0	0	0	0	1	0	Edge
Yellow-backed Oriole	<i>Icterus chrysater</i>	1	1	1	0	0	1	1	1	1	1	1	1	1	1	Edge
Yellow-bellied Elaenia	<i>Elaenia flavogaster</i>	0	0	0	0	0	0	0	0	0	0	1	0	1	0	Edge
Yellow-bellied Seedeater	<i>Sporophila nigricollis</i>	0	0	0	0	0	0	0	0	0	0	1	0	1	1	Edge
Yellow-billed Cacique	<i>Amblycercus holosericeus</i>	0	0	0	0	0	0	0	0	0	0	1	1	0	0	Edge
Yellow-crowned Euphonia	<i>Euphonia luteicapilla</i>	0	0	0	0	0	0	0	0	0	0	1	0	0	0	Edge
Yellow-crowned Tyrannulet	<i>Tyrannulus elatus</i>	1	1	1	1	1	1	1	1	1	1	1	1	1	1	Edge
Yellow-green Vireo	<i>Vireo flavoviridis</i>	0	0	0	0	0	0	0	0	0	0	1	1	0	1	Edge
Yellow-olive Flycatcher	<i>Tolmomyias sulphurescens</i>	0	0	0	0	0	0	0	0	0	0	1	0	0	0	Edge
Yellow-rumped Cacique	<i>Cacicus cela</i>	0	0	0	0	0	0	0	0	0	0	0	1	0	1	Edge
Yellow-tailed Oriole	<i>Icterus mesomelas</i>	0	0	0	0	0	0	0	0	0	0	1	1	1	0	Edge
Bay Wren	<i>Thryothorus nigricapillus</i>	0	0	0	0	0	0	0	0	0	0	0	1	1	0	Forest
Bicolored Antbird	<i>Gymnopithys leucaspis</i>	0	0	0	0	0	0	0	0	0	0	0	0	0	1	Forest
Black-breasted Puffbird	<i>Notharcus pectoralis</i>	0	0	0	0	0	0	0	0	0	0	0	0	0	1	Forest
Black-capped Pygmy-Tyrant	<i>Myiornis atricapillus</i>	0	0	0	0	0	0	0	0	0	0	0	0	0	1	Forest
Black-cheeked Woodpecker	<i>Melanerpes pucherani</i>	0	0	0	1	0	0	0	1	0	1	1	1	1	1	Forest
Black-chested Jay	<i>Cyanocorax affinis</i>	0	1	1	0	0	0	1	1	0	1	1	0	0	0	Forest
Black-faced Ant-thrush	<i>Formicarius analis</i>	0	0	0	0	0	0	0	0	0	0	1	1	0	0	Forest
Black-striped Woodcreeper	<i>Xiphorhynchus lachrymosus</i>	0	0	0	0	0	0	0	0	0	0	0	0	0	1	Forest

		Island →													
		Abogado	Bruja Chiquita	Pantera	Orchid	Guacha	Trinidad	Tigre	Bruja Grande	Leon	Puma	Frijoles	Barbacoa	Juan Gallegos	
Black-tailed Trogon	<i>Trogon melanurus</i>	0	0	0	0	0	0	0	0	0	1	1	0	1	Forest
Black-throated Trogon	<i>Trogon rufus</i>	0	0	0	1	0	0	0	0	0	1	1	1	1	Forest
Blue Dacnis	<i>Dacnis cayana</i>	1	1	1	1	1	1	1	1	1	1	0	1	1	Forest
Blue-black Grosbeak	<i>Cyanocompsa cyanoides</i>	0	0	0	0	0	0	0	0	0	1	0	1	1	Forest
Blue-chested Hummingbird	<i>Amazilia amabilis</i>	1	0	1	1	0	0	0	1	1	0	1	1	1	Forest
Bright-rumped Attila	<i>Attila spadiceus</i>	0	0	0	0	0	0	0	0	1	0	1	1	1	Forest
Broad-billed Motmot	<i>Electron platyrhynchum</i>	0	0	0	1	0	0	0	0	0	0	0	0	1	Forest
Brown-capped Tyrannulet	<i>Ornithion bruneicapillum</i>	0	0	0	1	0	0	0	0	0	0	1	1	1	Forest
Buff-throated Foliage-Gleaner	<i>Automolus ochrolaemus</i>	0	0	0	0	0	0	0	0	0	0	1	0	0	Forest
Checker-throated Antwren	<i>Myrmotherula fulviventris</i>	0	0	0	1	0	0	0	0	0	0	1	1	1	Forest
Chestnut-backed Antbird	<i>Myrmeciza exsul</i>	0	0	1	1	0	0	1	0	0	0	1	0	1	Forest
Chestnut-mandibled Toucan	<i>Ramphastos swainsonii</i>	0	0	0	1	0	0	0	0	0	1	1	1	1	Forest
Cinnamon Woodpecker	<i>Celeus loricatus</i>	0	0	0	0	0	0	0	0	0	0	0	0	1	Forest
Cocoa Woodcreeper	<i>Xiphorhynchus guttatus</i>	1	0	0	1	0	0	0	1	0	0	1	1	1	Forest
Collared Aracari	<i>Pteroglossus torquatus</i>	0	0	0	0	0	0	0	0	0	1	1	1	1	Forest
Crested Guan	<i>Penelope purpurascens</i>	0	0	0	1	0	0	0	0	0	0	0	0	1	Forest
Crimson-crested Woodpecker	<i>Campephilus melanoleucos</i>	1	0	0	0	0	0	0	0	0	1	1	1	1	Forest
Dot-winged Antwren	<i>Microrhoppias quixensis</i>	0	0	0	1	0	0	0	0	0	0	0	0	1	Forest
Dusky-capped Flycatcher	<i>Myiarchus tuberculifer</i>	0	0	0	1	0	0	0	0	0	1	1	1	1	Forest
Forest Elaenia	<i>Myiopagis gaimardii</i>	0	0	0	1	0	0	1	0	0	1	0	1	1	Forest
Fulvous-vented Euphonia	<i>Euphonia fulvicrissa</i>	1	0	0	0	0	0	0	0	0	1	1	1	1	Forest
Golden-collared Manakin	<i>Manacus vitellinus</i>	1	1	1	1	1	0	1	1	1	1	1	1	1	Forest
Golden-crowned Spadebill	<i>Platyrinchus coronatus</i>	0	0	0	0	0	0	0	0	0	0	1	0	1	Forest
Gray-chested Dove	<i>Leptotila cassinii</i>	1	0	0	1	0	0	0	0	0	1	1	1	1	Forest
Gray-headed Tanager	<i>Eucometis penicillata</i>	0	0	0	0	0	0	0	0	0	1	0	1	1	Forest
Great Jacamar	<i>Jacamerops aurea</i>	0	0	0	0	0	0	0	0	0	1	0	0	0	Forest

		Island →														
		Abogado	Bruja Chiquita	Pantera	Orchid	Guacha	Trinidad	Tigre	Bruja Grande	Leon	Puma	Frijoles	Barbacoa	Juan Gallegos		Barro Colorado
Great Tinamou	<i>Tinamus major</i>	0	0	0	1	0	0	0	0	0	0	1	1	1	1	Forest
Green Honeycreeper	<i>Chlorophanes spiza</i>	0	0	0	0	0	0	0	1	0	0	0	1	1	1	Forest
Green Shrike-Vireo	<i>Vireolanius pulchellus</i>	0	0	0	0	0	0	0	0	0	0	0	1	1	0	Forest
Keel-billed Toucan	<i>Ramphastos sulfuratus</i>	1	1	1	1	0	0	1	1	1	1	1	1	1	1	Forest
Lesser Greenlet	<i>Hylophilus decurtatus</i>	0	0	0	1	0	0	0	0	0	0	1	1	1	1	Forest
Little Hermit	<i>Phaethornis longuemareus</i>	1	1	1	0	0	0	1	1	1	1	1	1	1	1	Forest
Long-billed Gnatwren	<i>Ramphocaenus melanurus</i>	0	0	0	0	0	0	0	0	0	0	0	1	1	1	Forest
Long-tailed Hermit	<i>Phaethornis superciliosus</i>	1	0	1	1	0	0	1	1	1	1	1	1	1	1	Forest
Northern Barred-Woodcreeper	<i>Dendrocolaptes sanctithomae</i>	0	0	0	0	0	0	0	0	0	0	0	1	0	1	Forest
Ochre-bellied Flycatcher	<i>Mionectes oleaginea</i>	0	0	0	1	0	0	0	0	0	1	0	0	1	1	Forest
Olivaceous Flatbill	<i>Rhynchocyclus olivaceus</i>	0	0	0	0	0	0	0	0	0	0	0	1	1	1	Forest
Pheasant Cuckoo	<i>Dromococcyx phasianellus</i>	0	0	0	0	0	0	0	0	0	0	0	1	0	0	Forest
Pied Puffbird	<i>Notharcus tectus</i>	0	0	0	1	0	0	0	0	0	0	0	0	0	1	Forest
Plain Xenops	<i>Xenops minutus</i>	0	0	0	0	0	0	0	0	0	0	1	1	1	1	Forest
Plain-brown Woodcreeper	<i>Dendrocincla fuliginosa</i>	1	0	0	1	0	0	0	0	0	0	0	1	1	1	Forest
Purple-crowned Fairy	<i>Heliothryx barroti</i>	0	0	0	0	0	0	0	0	0	0	0	1	0	1	Forest
Purple-throated Fruitcrow	<i>Querula purpurata</i>	0	0	0	0	0	0	0	0	0	0	1	1	1	1	Forest
Red-capped Manakin	<i>Pipra mentalis</i>	0	0	1	1	0	0	1	1	1	1	1	1	1	1	Forest
Red-throated Ant-Tanager	<i>Habia fuscicauda</i>	0	0	0	1	0	0	0	0	0	0	1	1	1	1	Forest
Ruddy-tailed Flycatcher	<i>Terenotriccus erythrurus</i>	0	0	0	0	0	0	0	0	0	0	1	1	1	1	Forest
Rufous Motmot	<i>Baryphthengus martii</i>	0	0	0	1	0	0	0	0	0	0	0	1	0	1	Forest
Rufous Mourner	<i>Rhytipterna holerythra</i>	0	0	0	0	0	0	0	0	0	0	0	0	0	1	Forest
Scaled Pigeon	<i>Columba speciosa</i>	0	0	0	0	0	0	0	0	0	0	1	1	1	1	Forest
Scaly-throated Leaf-tosser	<i>Sclerurus guatemalensis</i>	0	0	0	0	0	0	0	0	0	0	0	1	0	1	Forest
Scarlet-rumped Cacique	<i>Cacicus uropygialis</i>	0	0	0	0	0	0	0	0	0	0	1	1	0	0	Forest
Shining Honeycreeper	<i>Cyanerpes lucidus</i>	0	0	0	0	0	0	0	0	0	0	1	0	1	1	Forest

		Island →														
		Abogado	Bruja Chiquita	Pantera	Orchid	Guacha	Trinidad	Tigre	Bruja Grande	Leon	Puma	Frijoles	Barbacoa	Juan Gallegos		Barro Colorado
Short-billed Pigeon	<i>Columba nigrirostris</i>	1	0	0	1	0	0	0	0	0	0	1	0	1	1	Forest
Slate-colored Grosbeak	<i>Saltator grossus</i>	0	0	0	0	0	0	0	0	0	0	0	0	1	1	Forest
Slaty-tailed Trogon	<i>Trogon massena</i>	0	1	0	1	0	0	0	1	1	1	1	1	1	1	Forest
Song Wren	<i>Cyphorhinus phaeocephalus</i>	0	0	0	0	0	0	0	0	0	0	1	0	0	0	Forest
Southern Bentbill	<i>Oncostoma olivaceum</i>	0	0	0	1	0	0	0	0	1	1	1	1	1	1	Forest
Spot-crowned Antvireo	<i>Dysithamnus puncticeps</i>	0	0	0	0	0	0	0	0	0	0	0	0	0	1	Forest
Spotted Antbird	<i>Hylophylax naevioides</i>	0	0	0	1	0	0	0	0	0	0	1	1	0	1	Forest
Squirrel Cuckoo	<i>Piaya cayana</i>	1	0	0	0	0	0	0	0	0	0	1	1	1	1	Forest
Sulphur-rumped Tanager	<i>Heterospingus rubrifrons</i>	0	0	0	0	0	0	0	0	0	0	0	0	0	1	Forest
Sunbittern	<i>Eurypyga helias</i>	0	0	0	0	0	0	0	0	0	0	0	0	1	1	Forest
Thrush-like Schiffornis	<i>Schiffornis turdinus</i>	0	0	0	0	0	0	0	0	0	0	1	0	0	0	Forest
Tropical Gnatcatcher	<i>Polioptila plumbea</i>	1	0	0	1	0	0	0	0	0	0	1	1	1	1	Forest
Violaceous Quail-dove	<i>Geotrygon</i>	0	0	0	0	0	0	0	0	0	0	0	0	0	1	Forest
Violaceous Trogon	<i>Trogon violaceus</i>	0	0	0	1	0	0	0	0	0	0	1	1	1	1	Forest
Violet-bellied Hummingbird	<i>Damophila julie</i>	1	1	0	1	0	0	1	0	0	1	1	1	1	1	Forest
Violet-crowned Woodnymph	<i>Thalurania colombica</i>	0	0	0	0	0	0	0	0	0	0	0	0	1	1	Forest
Western Slaty Antshrike	<i>Thamnophilus atrinucha</i>	0	0	0	1	0	0	1	0	1	1	1	1	1	1	Forest
White-flanked Antwren	<i>Myrmotherula axillaris</i>	0	0	0	1	0	0	0	0	0	1	1	1	1	1	Forest
White-shouldered Tanager	<i>Tachyphonus luctuosus</i>	1	0	1	1	0	0	0	0	0	1	1	1	1	1	Forest
White-vented Plumeleteer	<i>Chalybura buffoni</i>	0	0	0	0	0	0	0	0	0	1	0	0	1	1	Forest
Yellow-margined Flycatcher	<i>Tolmomyias assimilis</i>	0	0	0	0	0	0	0	0	0	1	1	1	1	1	Forest
<b>Forest Bird Species Richness</b>		16	7	10	36	2	1	11	12	11	14	49	54	51	71	
<b>Edge Bird Species Richness</b>		24	16	16	16	15	12	16	18	15	17	54	36	40	32	
<b>All Species Richness</b>		40	23	26	52	17	13	27	30	26	31	103	90	91	103	

**Appendix 2-** Descriptions of the 5 measures of island isolation tested in the regressions of island isolation and area on species richness.

*-Minor stepping stone*

The isolation value represents the least distance a bird would have to fly if it were to use any island, regardless of size, as a stepping stone to the focal island.

*-Major stepping stone*

The isolation value represents the least distance a bird would have to fly if it were to use an island larger than 5 ha as a stepping stone to the focal island. If there are no islands larger than 5 ha closer to mainland forest than the focal island, then the isolation value is the distance to the nearest patch of mainland forest.

*-500 ha*

The isolation value represents the distance to the nearest patch of forest larger than 500 ha.

*-Mini archipelago*

The islands of a mini archipelago (a well defined cluster) are defined as those for which the distance from the least isolated island in the group to the nearest landmass >500 ha is at least three times the greatest distance between islands. All islands in a mini archipelago are assigned the same measure of isolation. All non-archipelago islands are assigned isolation values that represent the distance to the nearest patch of forest larger than 500 ha.

*-Absolute*

The isolation value represents the distance to the nearest mainland.