LETTER

Experimental evidence for extreme dispersal limitation in tropical forest birds

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Abstract

Movements of organisms between habitat remnants can affect metapopulation structure, community assembly dynamics, gene flow and conservation strategy. In the tropical landscapes that support the majority of global biodiversity and where forest fragmentation is accelerating, there is particular urgency to understand how dispersal across habitats mediates the demography, distribution and differentiation of organisms. By employing unique dispersal challenge experiments coupled with exhaustive inventories of birds in a Panamanian lacustrine archipelago, we show that the ability to fly even short distances (< 100 m) between habitat fragments varies dramatically and consistently among species of forest birds, and that this variation correlates strongly with species' extinction histories and current distributions across the archipelago. This extreme variation in flight capability indicates that species' persistence in isolated forest remnants will be differentially mediated by their respective dispersal abilities, and that corridors connecting such fragments will be essential for the maintenance of avian diversity in fragmented tropical landscapes.

Keywords

Archipelago, dispersal, dispersal limitation, extinction, forest fragmentation, island biogeography, population persistence, tropical forest birds.

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INTRODUCTION

Mobility is fundamental to the structuring and geographical distribution of populations. Empirical and theoretical approaches have emphasized the role of mobility in mediating differentiation and speciation (Wallace 1889; Mayr 1942; Slatkin 1987; Barton 2001), migration, connectivity and gene flow (Hanski & Gilpin 1997; Hanski 1999) and dynamics of recolonization and persistence in fragmented landscapes (Burkey 1989; Robinson *et al.* 1992; Robinson 1999; Kisdi 2002; Sekercioglu *et al.* 2002). Yet direct knowledge of a species' mobility or dispersal ability is rare and difficult to obtain (Paradis *et al.* 1998). This lack of information limits our ability to understand population-level processes that influence species' responses to habitat fragmentation and, therefore, the design of effective conservation strategies for mobile organisms. In tropical landscapes that support the majority of global biodiversity (Whitmore & Sayer 1992) and where forest fragmentation is accelerating (Achard *et al.* 2002), there is particular urgency to understand how dispersal between habitat patches

mediates the demography, distribution, and differentiation of organisms.

Although dispersal abilities of tropical organisms are generally expected to be poor relative to those of temperate organisms (Janzen 1967; Dynesius & Jansson 2000), we know little about the dispersal abilities of particular species, even in well-known taxa such as birds. Knowledge has been limited by the difficulties inherent in tracking individual organisms and by the low likelihood of observing rare but potentially important movements across barriers. As a result, most birds are assumed to be relatively vagile, especially over short distances. Conversely birds of tropical rainforest have long been suspected to have low mobility (Willis 1974). The majority of tropical birds do not migrate seasonally, and most are extremely sedentary (Karr 1971). Tropical ornithologists hypothesized decades ago that certain bird species avoided, or were extremely reluctant to cross, water or pastures separating forest patches. Mayr (1941), for example, suggested that short water barriers (> 1.7 km, a span crossed in < 4 min by a bird flying a modest 30 km h^{-1}) between islands in the Central

Solomons of southeast Asia severely restrict dispersal by understory birds. Likewise, Diamond (1981) argued that many species of island birds are 'psychologically flightless' in that they refuse to disperse across water even though they frequently fly across land. This reluctance to cross water has been the prevailing explanation for the complete absence from oceanic islands of representative species from many widespread Neotropical families. Recently, experimental evidence from Amazonia suggests that many of these same species rarely move across narrow gaps created by roads (Develey & Stouffer 2001; Laurance *et al.* 2004), but move readily through continuous forest and, less commonly, across small forest gaps (Van Houtan *et al.* 2007). These patterns suggest that movement abilities are species specific and that we should be able to predict the distribution of species across groups of isolated habitat patches based on knowledge of relative dispersal abilities.

We determined through experimentation the relative abilities of several tropical understory forest birds to cross small habitat gaps of increasing breadth. We then examined the results of this experiment in the context of present and historical distributions of those species across a series of known-age forested islands in central Panama. Our purpose was to directly assess interspecific variation in mobility of understory forest birds, and to determine the degree of correlation between our experimental index of dispersal ability and species-specific distributions and extinction frequencies across the archipelago.

MATERIALS AND METHODS

Measuring ability to cross habitat gaps

A novel 'dispersal challenge' approach allowed us to create an index of dispersal ability for 10 common understory forest-specialist birds (Table 1) at our study site in lowland central Panama (Fig. S1 in Supporting Information). 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 (< 2 mm) 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 were not used in experiments. Each individual was tested only once.

We immediately transported captured birds to a small boat propelled by a quiet electric trolling motor. Subjects (in bags) were placed in a shaded enclosure during transport to a release boat 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. The release 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 s, during which the subject typically stopped the movements initiated upon placement into the enclosure. The door was then opened remotely.

If a bird failed to cross successfully to forest after exiting the enclosure, 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.

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 (*c.* every 25 min), by quickly placing each subject in its own opaque cloth bag upon extraction, by using a quiet

Table 1 Understory forest bird species included in the dispersal challenge experiment

Family	Species	Foraging guild	Breeding system
Thamnophilidae	Checker-throated Antwren *Myrmotherula fulviventris*	Dead leaf insectivore	Monogamous territorial
Thamnophilidae	Chestnut-backed Antbird *Myrmeciza exsul*	Terrestrial insectivore	Monogamous territorial
Thamnophilidae	Spotted Antbird *Hylophylax naevioides*	Terrestrial insectivore	Monogamous territorial
Thamnophilidae	Western Slaty Antshrike *Thamnophilus atrinucha*	Understory insectivore	Monogamous territorial
Emberizidae	Red-throated Ant-tanager *Habia fuscicauda*	Understory omnivore	Monogamous territorial?
Dendrocolaptidae	Cocoa Woodcreeper *Xiphorynchus susurrans*	Trunk insectivore	Monogamous territorial
Pipridae	Golden-collared Manakin *Manacus vitellinus*	Understory frugivore	Lekking
Tyrannidae	Ochre-Bellied Fycatcher *Mionectes oleagineus*	Understory frugivore	Lekking
Pipridae	Red-capped Manakin *Pipra mentalis*	Understory frugivore	Lekking
Trochilidae	Long-billed Hermit *Phaethornis longirostris*	Understory nectarivore	Lekking

motor to transport subjects to release stations, and by shading subjects in an enclosure during transport. Researchers minimized noise during the entire process between capture and release. Birds rarely uttered alarm calls from the cloth bags during transport, so the possibility of vocal interactions influencing behaviour of subjects was minimal. 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 and exclusion from experimental trials. In four instances, birds refused to leave the enclosure, and in three other trials, birds left the box but never attempted to leave the boat – these trials were not included in the analyses.

Because ambient light conditions may affect navigation and orientation ability of tropical forest birds (Stratford & Robinson 2005), we measured light intensity at the mouth of the opened release box before all trials. Intensity (lux) was averaged over a 7-s exposure with a handheld Minolta® T-10 illuminance meter (Minolta, Tokyo, Japan). We took one measurement per set of releases (all of the one to seven trials conducted during a trip to a 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 resulting from arrangement of land in relation to the rising sun.

Trials were conducted adjacent to capture locations, and successful dispersers returned immediately to land on or near their home range; all unsuccessful subjects were retrieved immediately, dried and returned quickly to their site of capture. Birds were not harmed by landing in water and behaved normally when released at their site of capture. Each species was tested at successively greater distances. To further minimize handling stress, species that exhibited > 90% failure in ≥ 10 trials at a given distance were not challenged at greater distances. For example, *Myrmotherula fulviventris* (checker-throated antwren), having failed in all attempts from 100 m, was never tested from 200 m under the assumption that all such trials would also end in failure.

We refer to the proportion of individuals of a focal species that successfully flew over water back to land as the success ratio, calculated at each of the three release distances.

Study Species

We focused our analysis on the 10 most commonly captured forest species. These included species from six families, multiple foraging guilds and a range (3–45 g) of body masses (Table 1). We assigned habitat associations (forest dependent/not) following Robinson *et al.* (2000). 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. Choosing 10 focal species that are all in the top 10% of mainland forest bird abundance (Robinson *et al.* 2000; Robinson *et al.* 2004) increased the number of experimental releases we could conduct and reduced the potentially confounding effects of abundance and micro-habitat preferences on insular distributions. 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 & Wilson 1985). Conversely, uncommon or rare species may be absent simply because of their regional rarity (i.e. a low number of potential immigrants), regardless of dispersal abilities. Habitat preference can also mask the relationship between dispersal ability and distribution by causing absence from fragments that contain insufficient resources for species with specialized requirements. Our focal species, however, appear to be generally insensitive to differences in forest age and moisture conditions in central Panama; they are all common in both young and older forests and in both seasonally dry and wet sites across the entire Isthmus of Panama (Robinson *et al.* 2004).

Measures of distribution

Species inventories

Features of the landscape at our study site make it possible to assess whether the experimental results are predictive of these species' natural movements among isolated forest fragments. To measure concordance between our experimental index of dispersal ability (mean success ratio) and the current distribution of our 10 focal species across a series of forest remnants, we comprehensively surveyed the bird communities on forested islands created by the early 20th century flooding of Lago Gatun (where the experimental challenges were also conducted). All islands were isolated when this man-made lake was filled (1911–1914) during construction of the Panama Canal. We inventoried 29 islands that span nearly three orders of magnitude in area (1.6–1560 ha) and isolation (9 m to > 2500 m, distance from the nearest large landmass). Although two contained areas of young second growth, all islands included in the surveys were predominantly covered in closed canopy forest.

From 2001 to 2005 we surveyed islands between mid-February and mid-April, the period corresponding to peak vocal activity of local forest birds (Robinson 2001). We conducted each survey so that an observer had been within 200 m 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). We also used program EstimateS (Colwell 2005) to generate estimates of species richness (Chao II estimator, S_{est}) using observed values of island species richness (S_{obs}). Surveys were considered complete when S_{obs}/S_{est} was > 0.95, a goal reached for all islands. The survey of Barro Colorado Island (BCI) used different protocols. For this largest island, we used census data collected by the first two authors in the course of repeated, comprehensive surveys conducted over the preceding 10 years (Robinson 1999, unpub. data).

To generate data on historical extinctions of the focal species, we re-surveyed six islands from which one or more previous species inventories were available. These islands, originally surveyed by Wright (Wright 1985), were resurveyed in 2002 and 2003 using identical methodology.

Metrics of island isolation

We identified five isolation measures of potential ecological significance (Appendix 1). In order to identify the best measure of isolation for the islands of this archipelago, we regressed island area and isolation on island-specific forest bird species richness five times, once with each measure of island isolation (species richness and island area remained constant). We then compared the results to determine which measure of isolation best explained the variation in species richness across the archipelago. 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 composites (lumped, $n = 23$). Each composite has the combined area of its component islands and the isolation value for the least isolated of the component islands. Because all statistical analyses assume independence of island units, the lumped arrangement allows a more conservative analytical approach, as colonizations of the individual islands within each cluster are likely not independent events. Isolation measure 4 (mini archipelago) from Appendix 1 best explained variation in species richness for both lumped and unlumped configurations of islands, and we used this isolation measure in all subsequent analyses.

Statistical analyses

Unless otherwise stated, we employed an alpha value of 0.05 in assessing statistical significance. We used s+ STATISTICAL software (Lucent Technologies version 6.2 2003, Lucent Technologies, Chicago, IL, USA) for all regression analyses.

Correlations

Because of uncertainty concerning the distributions from which the variables were drawn (Sokal & Rohlf 1995), and because of potential problems with using ratios in parametric correlation analysis (Edgington 1987; Jackson & Somers 1991), we used a sampling randomization procedure as a non-parametric analog to standard correlation analysis. With this method, we assessed the association between insular distribution (distance to most isolated island occupied for each focal species as determined by the chosen metric for island isolation) and our composite measure of release performance (mean success ratio, see above). All correlation coefficients were calculated with raw, species-specific values of mean success ratio. Tests were conducted with ECOSIM[©]: NULL MODELS SOFTWARE for ecology, Version 7.0 (Gotelli & Entsminger 2001).

Differences in proportional distribution across islands

We calculated the difference in species-specific occupancy rate for islands isolated from source pools by < 300 m (near islands, $n = 15$) versus those by > 300 m (isolated islands, $n = 8$). The method separates islands that fall within the range of distances employed in our experimental releases (near) from those that fall outside that range (far). To determine if the four focal species with high values of mean success ratio were distributed more equitably across the archipelago than the six species with low values, we performed a non-parametric resampling test (analogous to a two-sample t-test) in which we calculated the t-statistic for 10,000 randomized permutations of the 10 data points (holding the group sizes constant), and recorded as the test's P-value the number of times that value exceeded the t-statistic for the observed data.

Extinction analysis

To determine if patterns in our index of dispersal ability are reflected in rates of insular extinction on a subset of islands for which there is historical occurrence data, we employed a comparison of extinction frequencies for two groups of our focal species: those that exhibited poor flight ability in challenge experiments (< 65% success in all trials) and those that demonstrated good ability (> 90% success in all trials). The former group contains species that were almost uniformly unable to negotiate a 200 m or 300 m water barrier and the latter contains species that performed well at all release stations, including the most distant at 300 m. We know the six poor performers have difficulty beyond 100–200 m but have no reason to believe the four good performers cannot negotiate distances greater than 300 m. For each species, we calculated frequencies of insular extinction from a subset of six islands that were surveyed annually during the periods 1977–1981 (Wright 1985) and 2002–2003 (this study). For a given species, extinction was

defined as presence on an island in one annual survey period followed by a subsequent absence.

To evaluate the prediction that the 6 poor performers are more likely to have suffered insular extinction than the 4 good performers, we performed the same resampling test described above in the proportional distribution analysis.

Stressors

To assess potential effects of stressors on flight performance, we used logistic regression to evaluate 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 2).

RESULTS

Ability to cross habitat gaps: the experimental dispersal index

We found high and consistent variation in mobility among our 10 focal species (Fig. 1). One species (*Phaethornis longirostris*, the only hummingbird tested) did not fail at any distance, and one species (*M. fulviventris*) failed in all trials at the shortest distance of 100 m. Five other species exhibited sharply declining success rates at increasing distances, with success rates approaching zero at either 200 or 300 m (Fig. 1). The three remaining species succeeded in > 90% of trials at the greatest distance of 300 m.

Logistic regression indicated that stress of handling, as measured by time in captivity [mean 25.1 (SD 12.5) min for all species], was never a significant predictor of success or failure. Release distance was generally a significant predictor of trial outcome, while ambient light level was a never a significant predictor of failure (Table 2).

Distribution

The distribution of the 10 focal species was not continuous with respect to island isolation; no species occupied all of the islands it was physically capable of reaching by flight. This is likely attributable to the effect of island area, which has a strong influence on species distributions in this system (Wright 1985; Moore 2005). The regionally abundant but area-sensitive *Mionectes oleagineus* (ochre-bellied flycatcher), for example, occurred only on three of the largest islands, which span nearly the entire range of isolation distances.

Relating distribution to the experimental dispersal index

To derive a single metric of experimental performance for each species, we pooled trial results across distances to

Table 2 *P*-values associated with regression coefficients of the backward 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	In ambient light
Hylophylax naevioides	0.792	0.000	0.056
Thamnophilus atrinucha	0.387	0.004	0.350
Habia fuscicauda	0.147	0.054	0.468
Xiphorynchus susurrans	0.951	0.001	0.020*

*Denotes a significant positive relationship between variables.

generate mean success ratio, our index of dispersal ability. For cases in which a species was not tested at one distance because of near complete failure at the previous (see above), we calculated mean success ratio with zeros at the untested distances (Fig. 1). Mean success ratio was significantly correlated with the maximum distance flown by any individual of a given species (randomization correlation analysis, $r = 0.74$, $n = 10$, $P = 0.01$, Table 3) and the mean of mean flight distance calculated for each species at each release distance (randomization correlation analysis, $r = 0.94$, $n = 10$, $P < 0.00001$, Table 3). There was also a significant positive relationship between mean success ratio and the distance to the most isolated island occupied by a species (randomization correlation analysis, $n = 10$, $r = 0.72$, $P = 0.013$ for unlumped data; $r = 0.70$, $P = 0.017$ for lumped data).

The comparison of differences in proportional occupancy of near and far islands reveals moderately positive values for the three species that performed worst in the challenge experiment, as these taxa have limited occurrence on near islands and nearly uniform absence from isolated islands; larger positive values for the three species intermediate in experimental flight ability, as these taxa had more extensive distributions on near islands but still limited occurrence on isolated islands; and low values for the four best performers that were nearly equally distributed among near and isolated islands (Figs. 2 and 3). The mean values of the difference in proportional occupancy were significantly different for the six worst and four best experimental performers (two-sample randomization test on *t*-statistic 5.106, $P = 0.005$); the four species with high mean success ratios were more equitably distributed with respect to isolation than were the six species with low values of mean success ratio.

Extinction analysis

The six species that performed poorly in experimental trials suffered significantly higher extinction rates across isolated
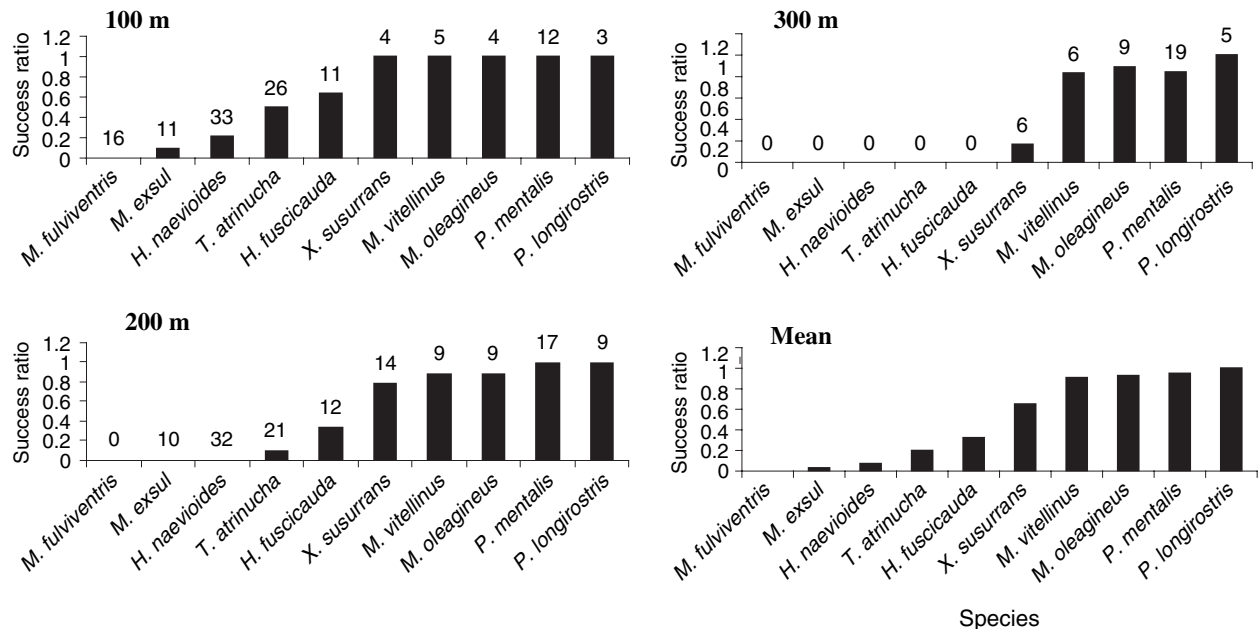
Figure 1 Flight performance across open-water gaps of increasing width (100, 200 & 300 m) for 10 species of tropical understory forest birds. Numbers atop columns indicate sample sizes of individuals tested at each distance. We did not conduct dispersal challenges at greater distances for species that had previously exhibited complete or nearly complete failure at a given distance. Lower right panel shows mean success rate pooled across all distances. Full binomial species names and common names are listed in Table 1.

forest fragments than did the four species that performed well (two-sample randomization test on t-statistic 2.44, $P = 0.011$).

DISCUSSION

To our knowledge, this is the first direct experimental demonstration of differential dispersal ability in tropical birds. Several of our 10 focal understory bird species were widely and consistently divergent in their abilities to cross habitat gaps of 100–300 m. Patterns in the experimentally derived index of dispersal ability for these species were concordant with patterns in historic extinction data and two measures of distribution across a series of differentially isolated forest fragments.

Although our standardized challenges reveal apparent differences in dispersal ability among the 10 focal species, our experimental approach challenged these taxa under non-natural conditions, a situation which can influence the external validity of any inference (Moore & Robinson 2004). It is the strong association with patterns in the biogeography of these birds that strongly suggests that these differences in experimental performance are reflective of actual divergence in dispersal ability. Interestingly, our measures of experimental dispersal ability are also consistent with aspects of the focal species' ecology; the four species that performed well in the dispersal trials are all lekking frugivores or nectarivores that often travel extensively within continuous

forest (Westcott & Graham 2000, Pers. obs.), whereas the six species with intermediate or low experimental dispersal ability are all more conventionally territorial and at least seasonally sedentary.

Stronger corroborative evidence of the external validity of the dispersal challenge results is evident in patterns of island occupancy. The distance to the most isolated occupied island for each focal species was closely correlated with the interspecific differences seen in the experimental challenge results. This association is particularly compelling because it occurs despite the fact that the most isolated island populations of some species are likely relictual, rather than derived from, or maintained by, dispersal. *Myrmeciza exsul*, for instance, is 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 (Sieving & Karr 1997) molecular work indicates that these birds have been very likely present on the Islas Los Gatos since the lake was created, and that no immigration has occurred in the ensuing 90 years. If this most isolated population of *M. exsul* is discounted and the second most isolated population on BCI (*c.* 230 m) is used in the correlation analysis, the relationship between experimental performance and distance to most isolated occupied island is strengthened considerably.

Although intuitively compelling, distance to the most isolated occupied island is a narrow measure of overall insular distribution. However, patterns in experimental flight

Table 3 Experimental performance of focal species listed in ascending order of mean success ratio

Species	Mean distance flown in metres (SD) when released from				Maximum distance flown in metres when released from‡		
	100	200	300	Mean†	100	200	300
Myrmotherula fulviventris	24 (19.2)	–	–	24	70	–	–
Myrmeciza exsul	48 (29)	34 (28)	–	41	90	90	–
Hylophylax naevioides	57 (40)	47 (37)	–	52	160	150	–
Thamnophilus atrinucha	86 (33)	118 (60)	–	102	160	240	–
Habia fuscicauda	104 (46)	216 (177)	–	160	180	750	–
Xiphorynchus susurrans	128 (25)*	211 (24)	200 (52)	179	150	260	300
Manacus vitellinus	106 (13)*	211 (21)	273 (66)	196	130	240	330
Mionectes oleagineus	100 (0)*	249 (153)	317 (91)	222	100	700	475
Pipra mentalis	113 (27)*	224* (43)	342 (154)	226	190	350	700
Phaethornis longirostris	108 (14)*	211* (24)	626* (267)	315	125	270	1000

A dash indicates that experimental releases were not conducted for this species at this distance. Full species binomials and common names are shown in Table 1.

*Denotes a species that never failed from this release station. Variation in mean distance flown for these species at these stations reflects only differences in orientation to land, not potential differences in flight ability.

†Mean of results from all three distances. Significantly correlated with mean success ratio, randomization $r = 0.94$, $P < 0.00001$.

‡Maximum distance flown in all trials is significantly correlated with mean success ratio, randomization $r = 0.74$, $P = 0.01$.
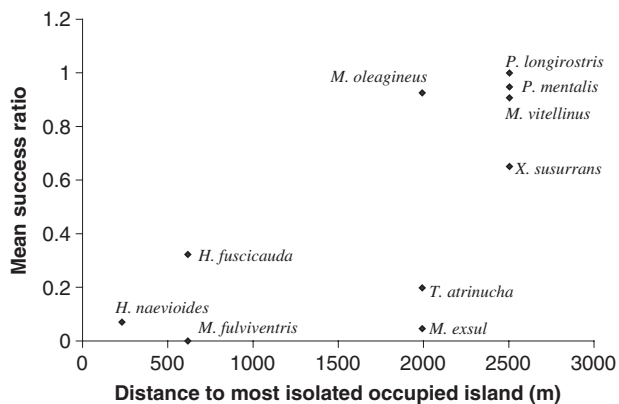

Figure 2 Plot of experimental dispersal ability (mean success ratio) against distance to the most isolated occupied island for 10 tropical understory forest birds.

ability were also mirrored by the broader measure of the difference in species-specific occupancy rates of nearshore and isolated islands. This analysis provides stronger evidence that it is very difficult for our poor/medium dispersers to emigrate beyond a few hundred metres over water, while our good dispersers show no such sensitivity.

Additional direct evidence of past insular extinctions not only supports the results of the dispersal challenge experiment, but suggests that some understory forest birds with poor dispersal ability do not readily colonize across short water gaps even over decades -long time periods. If dispersal has been important to the long-term population dynamics of our focal species, we predicted that individual island populations of the species performing poorly in the

dispersal challenge experiment would be more likely to suffer insular extinction between successive surveys than would populations of the more strongly dispersing species, for which immigration should buffer within-island demographic variation (Brown & Kodric-Brown 1977). Consistent with this prediction, the greater extinction rates of the six most weakly dispersing species implies a tight link between a species' dispersal ability and its persistence in habitat remnants in this insular system.

It has long been postulated that despite being capable of flight, some birds may be dispersal limited at both evolutionary and ecological scales (Diamond 1981). Indirect evidence has suggested that limited gene flow across rivers and other geographical barriers promotes the population differentiation of some poorly dispersing Amazonian bird species (Bates *et al.* 2004), and may ultimately contribute to the high species diversity of many tropical avian clades. In other settings, dispersal limitation is evident for island taxa like the intensively studied Seychelles warbler (*Acrocephalus seychellensis*), in which (1.6 or 9 km) inter-island movements originating from a saturated source island have never been recorded, despite the potentially large gains in fitness for pairs re-colonizing nearby unoccupied islands (Komdeur *et al.* 2004).

In tropical lowlands, anthropogenic habitat gaps such as road clearings are thought to hinder understory bird movements (Laurance 2004), and terrestrial insectivores – the most dispersal-limited guild in our study – are disproportionately likely to become locally extinct in isolated forest patches (Robinson 1999; Stratford & Stouffer 1999; Sekercioglu *et al.* 2002). Occupancy modeling from the
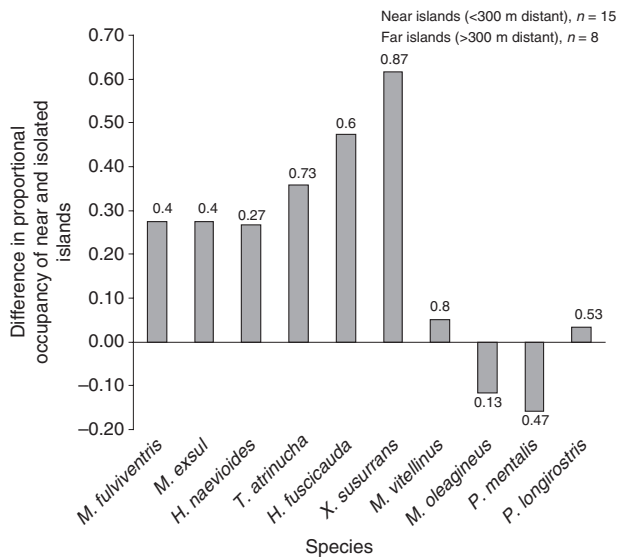
Figure 3 Difference in proportional occupancy of islands near (< 300 m, $n = 15$) and far (> 300 m, $n = 8$) from mainland forest for 10 tropical understory forest bird species. Positive deviations, as seen in the six species that performed moderately to poorly in the dispersal challenge trials (species are ranked left to right by ascending mean success ratio), indicate occupation of proportionately more islands that are nearer mainland source pools. Species with a difference near zero, seen in the four species that performed well in dispersal trials, occupy near and far islands nearly equally. Decimal values atop or beneath bars are proportion of near islands occupied.

BDFFP has suggested that some forest species are sensitive to fragment isolation on the modest scale of that system while others are not (Ferraz *et al.* 2007). Considered in concert, the known effects of fragmentation on tropical forest bird diversity and our experimental evidence of dispersal limitation in a subset of Panamanian forest birds suggest that some of these species will likely be permanently lost from some of the more isolated forest fragments in humid forest lowlands.

Interestingly, the link between occurrence, persistence and dispersal ability in our study is not mirrored in the only other experimental investigation of the topic. New data from the BDFFP (Van Houtan *et al.* 2007) show that isolation from continuous forest on the scale encountered in that experiment (150–900 m) is *not* an absolute barrier to inter-fragment movement of extinction-prone species. Although mensurally overlapping the scale of isolation in the present study, it is likely that the effective isolation of the BDFFP fragments is reduced by the presence of terrestrial matrix habitat. The fatal consequences of failure to cross between fragments in a single flight almost certainly increases the effective isolation of islands in the Gatun system in comparison with those of the BDFFP, potentially accounting for the apparent difference in dispersal dynamics between the sites. The BDFFP study also suggested that persistent species disperse much less frequently between forest fragments than do extinction-prone species, a finding that appears to be at odds with the implications of our study. The distinction is important; our study suggests that long-term persistence of the dispersal-limited taxa will require the maintenance of effective connectivity between existing and future forest remnants, and land-use strategies consistent with the protection of contiguous populations that are large enough to resist stochastic local extinction. If, however, persistence has more to do with demography than dispersal, then connectivity may play a less important role in the long-term prospects of these taxa in a fragmented landscape.

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SUPPORTING INFORMATION

Additional Supporting Information may be found in the online version of this article.

Figure S1 Study area.
Appendix S1 Descriptions of the five measures of island isolation tested in the regressions of island isolation and area on species richness.

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