

LETTER

Dispersal of Amazonian birds in continuous and fragmented forest

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Abstract

Many ecologists believe birds disappear from tropical forest fragments because they are poor dispersers. We test this idea using a spatially explicit capture data base from the Biological Dynamics of Forest Fragments Project near Manaus, Brazil. We measure bird movements directly, over relatively large scales of space and time, both before and after landscape fragmentation. We found that species which disappear from fragments move extensively between plots before isolation, but not after, and often disperse to longer distances in continuous forest than in fragmented forest. Such species also preferentially emigrate from smaller to larger fragments, showing no preference in continuous forest. In contrast, species that persist in fragments are generally less mobile, do not cross gaps as often, yet disperse further after fragmentation than before. ‘Heavy tailed’ probability models usually explain dispersal kernels better than exponential or Gaussian models, suggesting tropical forest birds may be better dispersers than assumed with some individuals moving very long distances.

Keywords

Dispersal kernels, forest fragmentation, gamma, gap crossing, log-hyperbolic secant, long-distance dispersal, population extinctions, Rayleigh, understory forest birds.

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INTRODUCTION

What happens to populations in fragmented habitats compared with naturally continuous ones? The question (Lovejoy *et al.* 1986) is a pressing practical one, as well as one of intrinsic interest. Species are going extinct at a rate one-hundred times faster than expected, with future rates likely to rise to 1000 times faster (Pimm *et al.* 1995, 2006). Habitat loss, particularly in tropical moist forests, is the principal driver of these high rates. Human actions do not simply destroy such habitats, for what remains is fragmented and isolated. Our first analyses emerge from the existing literature that supports the idea that tropical understory forest birds are sedentary and avoid gaps. If true, forest clearing should imprison all species in fragments, where the small remnant populations are unsustainable and die out (Pimm *et al.* 1993). In this study, we directly estimate how far species move using the unique experimental design of

the Biological Dynamics of Forest Fragments Project (BDFFP) near Manaus, Brazil. To do so requires a probability model that describes both short distance movement and long-distance dispersal. We find that species differ considerably in how far they move before and after fragmentation. Some move unexpectedly long distances and some readily cross gaps between plots. Our second set of analyses stem from knowing most species disappear from fragments rapidly, while some remain (Lovejoy *et al.* 1986; Ferraz *et al.* 2003; Van Houtan *et al.* 2006). We show that dispersal and risk of extinction are linked.

The reluctance to emigrate

In their classic theory of island biogeography, MacArthur & Wilson (1967) start with its application to habitat ‘islands’, or fragments. Like oceanic islands, fragments gain species through immigration and lose them through extinction.

'Extinction' in this context refers not only to species lost through individuals dying out locally, but also equally to those lost from a lack of immigrants (Brown & Kodric-Brown 1977) or from individuals actually choosing to leave a fragment (Hanski 1999). For birds on small British islands – a system long considered canonical in island biogeography (e.g. Lack 1969) – smaller islands have higher extinction rates than larger ones, and remote islands gain fewer immigrants than ones near the mainland (Russell *et al.* 2006). Significantly, by far the largest effect is that species remain on remote islands longer than on near ones, as they are likely reluctant to cross large water barriers.

In tropical forest fragments, are birds reluctant to emigrate through a hazardous matrix? The literature suggests so. The corresponding arguments rely on evolutionary constraints: the birds do not range widely, do not disperse far from their natal territory, and avoid unsuitable habitat due to physical or behavioural limits (e.g. Ehrlich & Raven 1969; Willis 1974; Terborgh *et al.* 1990; Sodhi *et al.* 2004). Corroborating these claims, several studies find cattle pasture and agricultural fields a near absolute barrier for tropical forest birds (e.g. Stouffer & Bierregaard 1995; Sieving *et al.* 1996), while others report these birds avoid roads and forest edges (e.g. Stouffer & Bierregaard 1995; Devey & Stouffer 2001; Laurance *et al.* 2004). Still other analyses find that the same species which are absent in older fragments are seldom detected in the deforested matrix between them (Gascon *et al.* 1999; Şekercioglu *et al.* 2002).

However, these arguments suffer from a number of problems. To begin with, studies from temperate and boreal forests do not confirm the idea that forest birds are sedentary and gap-shy. While many agree (e.g. Desrochers & Hannon 1997; Sisk *et al.* 1997; Haddad *et al.* 2003; Levey *et al.* 2005) a significant number do not (Howe 1984; Moore & Dolbeer 1989; Norris & Stutchbury 2001; Fraser & Stutchbury 2004). Evidence from the tropics also varies. Some studies find tropical forest birds cross large gaps often (e.g. Harper 1987, 1989) and even colonize islands isolated by open water (e.g. Wright 1985). Second, results from tropical forest studies should not be extrapolated too far beyond the scope of their experimental designs. For example, many studies either infer gap-crossing ability from indirect evidence (e.g. Stouffer & Bierregaard 1995; Gascon *et al.* 1999; Şekercioglu *et al.* 2002), affect behaviour by using audio devices (e.g. Sieving *et al.* 1996; Devey & Stouffer 2001), overlook the different selective pressures for crossing gaps in continuous and fragmented forests (e.g. Devey & Stouffer 2001; Laurance *et al.* 2004), or are confined to small spatial or temporal scales (e.g. Sieving *et al.* 1996; Devey & Stouffer 2001; Laurance *et al.* 2004).

In this study, we examine avian movement from direct empirical evidence, both before and after the isolation of forest plots, and at spatial and temporal scales that are

comparatively extensive. For the first time, we analysed dispersal kernels for tropical forest birds by using a large spatially explicit capture data base from the BDFFP. We use these data to estimate the parameters for a variety of probability distribution models, which correspond to different types of bird movement decidedly. We expect the model that best fits the data will also offer the best conceptual description of how tropical forest birds move in continuous and fragmented forest.

Dispersal kernels

For a given model of bird behaviour, there is a probability density function for dispersal distances x and y from the starting point. This probability function is called the dispersal kernel. As we compute movement from spatial coordinates, we derive a univariate quantity from two-dimensional data. The distance from the origin to a point x , y in the plane, $r = (x^2 + y^2)^{1/2}$, is called the amplitude. The corresponding amplitude kernel has a distribution of its own which is related to, but distinct from, the distributions of x and y . Based on different hypotheses of bird behaviour, we select several distributions for x and y , and fit their corresponding amplitude kernels to the empirical distributions of r . All our models are radially symmetric; birds are assumed to move in all directions equally. A discussion of dispersal kernels can be found in Hastings *et al.* (2005) (see also Clark *et al.* 1999).

The normal, or Gaussian, distribution describes an individual whose movement is shaped by multiple external stochastic forces – a random walk (Appendix A). Such individuals diffuse through space, and as a result, their populations spread rather slowly. For this model the corresponding amplitude kernel is the Rayleigh distribution:

$$g(r) = \left(\frac{r}{\alpha^2}\right) \exp\left(-\frac{r^2}{2\alpha^2}\right), \quad r \geq 0, \quad \alpha > 0, \quad (1)$$

where α is the scale parameter ($\alpha > 0$), a measure of the average dispersal distance.

Another candidate model, the negative exponential distribution describes individuals that move in one direction with a constant probability of not making it any further than they are. It also arises as a result of random diffusions aggregated over a long time (Appendix A). If x and y follow an exponential distribution, then r is a special case of the gamma distribution, which has the general probability density function:

$$g(r) = \frac{1}{\alpha\Gamma(\beta)} \left(\frac{r}{\alpha}\right)^{\beta-1} \exp\left(-\frac{r}{\alpha}\right), \quad r \geq 0, \quad \alpha > 0, \quad (2)$$

where α is again the scale parameter, β is the shape parameter of the kernel, and Γ represents the gamma function. When the gamma distribution represents the

amplitude of an exponential model, $\beta = 2$. Note the similarity of form to eqn 1 but the tail of the amplitude kernel has a slower decay than the Rayleigh.

Unlike the Rayleigh or gamma models, 'heavy-tailed' or 'fat-tailed' probability functions allow movement to greater distances, other factors being equal. Heavy-tailed models assume that some individuals tend towards long-distance movement and the corresponding distributions are typically characterized by power-law tails. Various heavy-tailed models have been used previously in ecological studies, the: Cauchy (e.g. Paradis *et al.* 2002), log-hyperbolic secant (henceforth 'log-sech', e.g. Halley & Inchausti 2002), Lévy-stable (e.g. Brockman *et al.* 2006), the two-dimensional Student's *t* (e.g. Clark *et al.* 1999), as well as various mixed models with power law tails (e.g. Bullock & Clarke 2000; Montoya *et al.* 2006). Heavy-tailed dispersal kernels are not expected under conditions of classical short-range diffusion (Appendix A) but are expected under 'Lévy-flight' diffusions (Viswanathan *et al.* 1996; Atkinson *et al.* 2002) and have been increasingly used to describe both passive dispersal (Clark *et al.* 1999) and active dispersal (Atkinson *et al.* 2002). Here we follow Halley & Inchausti (2002), assuming a dispersal kernel such that r has a log-sech distribution:

$$g(r) = \frac{2/(\pi br)}{(r/\alpha)^{1/b} + (r/\alpha)^{-1/b}}, \quad r \geq 0, \quad \alpha, \beta > 0, \quad (3)$$

where α is the scale parameter as before, and b is a shape parameter. We define β as the tail index, with $\beta = 1 + 1/b$, because the probability density function 3 has the form $g(r) \approx (2/\pi br)(\alpha/r)^\beta$ for large values of r . The tail index is not fixed but can lie anywhere in the range $(1, \infty)$, allowing the rate of decay to vary. When $\beta = 2$ the distribution reduces to the Cauchy form.

Dispersal and extinction risk

One might expect that species that disperse widely in continuous forest might be those most able to do so after habitat fragmentation. If so, wide dispersers would be those that persist in the fragments, even only as transient and occasional visitors. We presented the opposite hypothesis elsewhere (Van Houtan *et al.* 2006). Other things being equal, widely dispersing carnivores are more prone to local extinction than those that readily occupy smaller areas (Woodroffe & Ginsberg 1998). In other words, wide dispersers run into the hazards associated with meeting or crossing unsuitable habitats. We found a similar effect with the birds in this study site: species that joined flocks or followed army ant swarms quickly disappeared from small fragments. Species joining flocks only facultatively persisted (Van Houtan *et al.* 2006). In that study, we did not have spatial coordinates for captures and only inferred dispersal behaviour. Here we rectify that omission.

METHODS

Study area and sampling

The BDFFP (59°58'11" W, 2°22'25" S) near Manaus, Brazil, is an unrivalled empirical setting to study how populations respond to forest loss and fragmentation. From 1979 to 1983, 11 forest plots (five 1 ha, four 10 ha and two 100 ha) were established in primary, lowland moist forest at three sites: Dimona, Porto Alegre and Esteio. At varying times thereafter, the forests immediately surrounding the study plots were clear-cut for cattle pasture, leaving the plots isolated from nearby continuous forest. The resulting fragments were 70–800 m (average = 230 m) from continuous forest after isolation, and separated 250–2450 m (average = 1150 m) from other fragments at the same site. An additional 17 plots, ranging from 1 to 1000 ha, located in continuous forest were never isolated. Linear mist-net transects regularly sampled birds in plots from their establishment until 1993, before and after isolation at each site. Transects consisted of eight 2 × 12-m nets (*c.* 100 m) in 1-ha plots, 16 nets (*c.* 200 m) in 10 plots, and 48 nets in 100-ha plots. Transects were typically sampled monthly, and never on consecutive days. Captured birds were described, marked with uniquely numbered leg bands, and released, with the net location noted. These efforts provide 8799 recaptures – 3122 before isolation and 5677 after – from 106 species. Further experimental details appear elsewhere (Stouffer & Bierregaard 1995; Ferraz *et al.* 2003).

For this study, we consider only species with ≥ 100 recaptures (100–872, average = 255), and grouped according to extinction risk. We consider a species 'extinction-prone' if it was not detected in 1-ha fragments 1 year after their isolation, and not detected in 10-ha fragments 3 years after isolation (although some returned to fragments after extended absences; Stouffer & Bierregaard 1995). We consider a species 'persistent' if it was detected in 1-ha fragments after a year of isolation, and detected in 10-ha fragments after 3 years of isolation. In actuality, the majority of extinction-prone species disappeared from fragments in short order and the majority of persistent species remained in fragments for the entire census period. This method netted 13 extinction-prone species and eight persistent species.

Data analysis

To limit the effect of frequently captured individuals, we exclude same-day recaptures within 200 m, the length of the longest net transect. (If we excluded all same-day recaptures, however, we would miss the five occasions when individuals were netted in different plots, a few hours apart.) Because we document movements from recapture data, the exact date of the movement is often uncertain. For example, when

a bird is captured in two separate plots, a year apart, it cannot be determined when the bird actually made the flight. Knowing the precise dates when plots were isolated (Lovejoy *et al.* 1986), deducing the state of the matrix between plots in the time between successive captures was often straightforward. As a result, we distinguished movements through continuous forests from those through cattle pasture in most cases. We employ several analyses to understand how isolation affects movements between plots.

First, we quantified movements between plots, relative to the time since a plot's isolation. Time is an important factor as birds were thought to colonize fragments through forest regrowth that occurred after cattle grazing ceased (Stouffer & Bierregaard 1995; Van Houtan *et al.* 2006). Categorizing time, we consider movements as occurring on the median date between captures and group them in two-year bins relative to the date a plot was isolated. Two-year bins maximized time resolution and maintained sufficient sample sizes. As exceptions, we group all captures after 8 years post-isolation, and pool all pre-isolation captures. Given the data's uncertainty towards gap-crossing dates (see above), this method minimizes date estimation error, yet does not likely skew results (< 8% of the capture intervals exceed 2 years). We represent movements in proportion to a plot's total recaptures for that period, achieving a 'movement rate' to account for sampling differences between plots. This rate effectively records the proportion of recaptured birds either coming or leaving a particular plot over a given time period. We make no statistical conclusions from these time-explicit analyses, but use them to estimate how isolation time affects the flow of birds between fragments and how it interacts with other factors.

Next, we used an analysis of covariance to test the relative importance of fragmentation, species, and plot size as determinants of movement rates. For the response variable we used the number of inter-plot movements (as a proportion of recaptures) with plot size as a continuous variable, and plot treatment and species type (extinction-prone or persistent) as discrete variables. Although plots are categorized as 1, 10 and 100 ha, we include their slight variations in area here determined from aerial photographs (Ferraz *et al.* 2003). In this analysis, we exclude plots with < 20 recaptures before or after isolation, eliminating some plots that were censused minimally, and exclude one 10-ha plot (no. 3209) that was more isolated than the others. Using this analysis we can test whether the effect of isolation is indeed as great as has been argued and how much it depends on species type.

Following this, we used a contingency table analysis to detect whether emigrations after isolation indicate the selection of certain plots over others. As in the first model, we separated movements into the categories of before and after isolation (resolving time no further), then

characterized all emigrations as a movement to a plot that is smaller, larger or of equal size. For the null model observations, we tallied all such possible permutations at each site (between site movements were uncommon, see below) from the number and size of the plots at that site; a result of the experimental design. Permutations from all sites were totalled, providing the expected observations when movements between plots within each site are of equal probability. Null model observations are then compared against observed emigrations in continuous forest and those between fragments. We tested all statistical models with SAS 9.1 (SAS 2003).

Finally, for the dispersal kernel analyses, we first determined mist-net coordinates from archived maps of bird censuses, aided by our own GPS surveys. Obtaining spatial coordinates for each capture, we then computed the distance travelled between captures, r . The probability of observing a movement to any distance from where a bird was first caught, $\Pr(r_i | \epsilon)$, depends on the probability model, $\Pr(\epsilon | r_i)$, and the sampling effort at that distance, $\Pr(w_i)$. To obtain $\Pr(w_i)$, we use ARCGIS (ESRI 2006) to calculate the area censused in 100-m annuli radiating from each plot's centroid. We tally the area sampled in each annulus for all 11 plots that were eventually isolated, and divide this by the total area in that annulus, across all plots. This provides a single value, $\Pr(w_i)$, for each annulus of the amplitude data. This value is then used to weight the empirical amplitude data, to account for distances that were poorly censused. Lastly, we used maximum likelihood methods to find the parameter estimate(s) most likely given the data, for the Rayleigh, gamma and log-sech models, maximizing the likelihood function (Appendix B):

$$L = \prod_{i=1}^n \left[\frac{w(r_i)g(r_i)}{\int_0^{r_{\max}} w(r)g(r)dr} \right], \quad (4)$$

where $w(r)$ is the density of sampling at radius r .

We compare models 1–3 using the Akaike information criterion (AIC) test that compares models' likelihoods, but penalizes models with more parameters (Halley & Inchausti 2002). To compare models we first minimize the Akaike information associated with the likelihood in eqn 4. The parameters yielding the minimum are found using a Monte-Carlo search in parameter space. The model with the lowest Akaike information is the best-fitting model.

RESULTS

Rates of movement between plots

For the 21 species we consider, we observed 2405 individuals and identified 237 movements between plots from 2437 recaptures before isolation and 189 from 3996 recaptures after isolation. We excluded 66 plot-to-plot

movements from the analyses as we do not know whether they occurred before or after isolation.

Figure 1 shows the proportion of plot-to-plot movements divided by the total number of recaptures (both between and within plots). For extinction-prone species, such movements decline after isolation. They later rebound as *Cecropia sciadophylla* and *Vismia* spp., colonized the clearings between plots (Fig. 1a). This pattern is most pronounced in the 1-ha fragments, but is also observed to some extent in 10- and 100-ha plots. In contrast, persistent species do not move between fragments as often as extinction-prone species, and their movement rates do not change after isolation (Fig. 1b).

Figure 2 plots the same variable against plot size for the four combinations of continuous vs. fragmented forest and

extinction-prone vs. persistent species. Simple geometry expects that, other things being equal, the proportion of birds detected in > 1 plot will decline as plot area increases. (One leaves one's home daily, one's city occasionally, and one's continent seldomly.) On a log-log scale, the fraction of plot-to-plot movements decreases with increasing plot size ($F_{1,22} = 129.3, P < 0.0001$) at rates statistically similar in the four subsets of the data. For persistent species, (Fig. 2b) the fraction does not depend on whether the forest is continuous or fragmented – the species move as if it does not matter. For extinction-prone species, however, plot isolation significantly reduces plot-to-plot movements by 67%. For these species, isolation has an imprisoning effect. In continuous forest, however, extinction-prone species make more between-plot movements than do species that

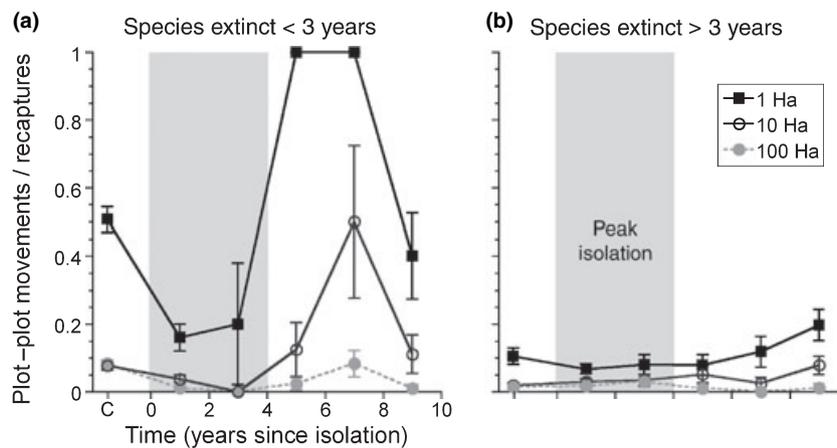


Figure 1 Extinction-prone species cross deforested gaps between plots more frequently than species that persist in forest fragments, and are adversely affected by plot isolation. (a) In plots of all sizes, extinction-prone species shows decreases in plot-to-plot movements immediately after a plot's isolation. Movements rebound as margins surrounding plots regenerate forest. (b) Species persisting in forest fragments do not move between plots as frequently as extinction-prone species, and show only minor differences before and after isolation. Paired-year data plotted as median date ('1' represents 1–729 days after isolation). Grey area represents peak isolation before secondary regrowth between fragments. 'C' indicates plots in continuous forest.

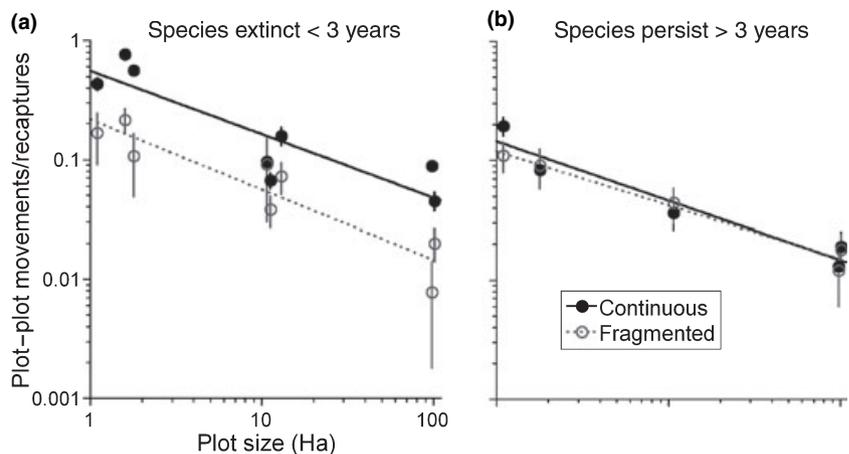


Figure 2 Movements between plots decrease with increasing plot size, consistent with a power law. (a) For extinction-prone species, movements decrease 67% after isolation. (b) Birds that persist in fragments, however, show no differences before and after isolation of plots. Bars are SE for the binomial proportion. For the full covariance model (see text for details), $R^2 = 0.89, F_{3,22} = 61.8, P < 0.0001$.

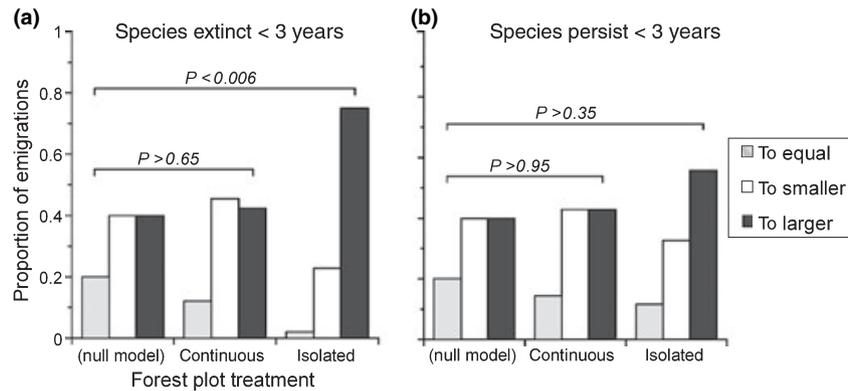


Figure 3 Extinction-prone birds more often emigrate from smaller to larger fragments, where persistent species show no preferences. (a) Emigrations of extinction-prone birds observed in continuous plots ($n = 99$) conform to null model expectation ($\chi^2 = 0.84$, $P > 0.65$), those observed after isolation ($n = 48$) differ ($\chi^2 = 10.3$, $P < 0.006$). (b) Persistent species show no preferences, either before or after isolation (see text). Null model proportions are the tally of all possible plot-plot movement permutations within the same site.

persist in isolated fragments. [Both species type ($F_{1,22} = 44.6$, $P < 0.0001$) and plot treatment ($F_{1,22} = 27.1$, $P < 0.0001$) are significant effects.]

Figure 3 plots the fraction of movements out of a plot divided by the total number of recaptures within the plot, comparing the results with contingency tables. Considering only movements within each site – because the distances between them are large – 40% of the possible plot-plot movements involve movements from a smaller to a larger plot. It follows that an equal fraction must be from a larger to a smaller plot. Only 20% of the possible plot-to-plot movements are between different plots of approximately equal size. For extinction-prone species (Fig. 3a), in continuous forest, the fraction of movements in these three classes is the same as this null model ($\chi^2 = 0.84$, $P > 0.65$). In contrast, extinction-prone birds in isolated fragments preferentially emigrate from smaller to larger plots, by more than a 3 : 1 ratio ($\chi^2 = 10.3$, $P < 0.006$). One might expect this result simply from sampling differences or from plot size alone. If this were the case, however, we would expect these patterns in continuous forest as well. We observe no such pattern (Fig. 3a). For persistent species, again there are no differences in emigration when comparing with the null model ($\chi^2 = 0.09$, $P > 0.95$). But nor does there appear a difference in the fragmented landscape. While there is a tendency for more movements from smaller to larger fragments, it is not statistically significant ($\chi^2 = 1.85$, $P > 0.35$). As we are interested in whether extinction-prone species select larger fragments more than persistent species, we compared emigrations between fragments for both species groups (i.e. the three columns on the right in Fig. 3a to those in Fig. 3b). There are no significant differences between species groups ($\chi^2 = 4.3$, $P = 0.12$), which likely indicates that the majority of species in our study do not fare well in 1-ha fragments.

Spatial displacement

We plot the aggregate percentage of area sampled in 100-m annuli radiating from each plot's centroid (Fig. 4a). Unsurprisingly, further distances are sampled less often than near distances. As described in the *Methods*, we use these data to correct for the incomplete sampling of the landscape. For example, plots cover < 10% of the landscape beyond 600 m from the point of capture (Fig. 4a). Because poor sampling surely inhibits the chance of observing dispersals to distances > 600 m, it is a critical factor for modelling dispersal.

To determine which model describes dispersal best, we use the AIC comparisons (Table 1). In all the cases examined, the heavy-tailed log-sech model has lower Akaike information than for either the Rayleigh or gamma distributions (associated with Gaussian and exponential dispersal kernels respectively; results for a larger range of models are presented in Appendix C). This indicates that it is a better description of the data. This can be seen visually in Fig. 4b. Here, we plot the probability density for the empirical data, and compare it with the maximum likelihood model for the Rayleigh, gamma and log-sech models (Fig. 4b). By visual inspection alone, the log-sech appears most similar to the empirical data particularly for far distances. In theory, the Rayleigh model expects most observations to fall close to the original capture, but to accommodate the long-distance dispersals present in the data, grossly underestimates the number of dispersals over short distances. Crucially, the Rayleigh model does not match the long distance movements of the empirical data. The one-parameter gamma model similarly describes the empirical observations poorly in the near regime and in the tail. Only the log-sech distribution achieves a close fit to the data both near the origin and at long distances (Fig. 4b).

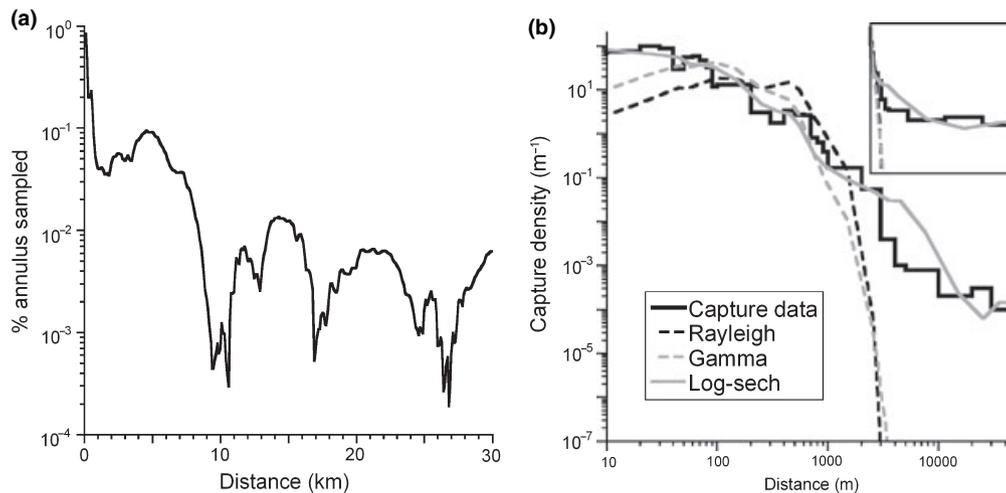


Figure 4 (a) Percentage of landscape sampled with mist nets decreases with increasing distance from original capture. We calculate 100-m annuli from the plot centroid, determining the area sampled and total area in each annulus. Data from all 11 isolated plots were added to achieve a single corrective value, $\Pr(p)$, for fitting distance kernels. (b) Histogram of recapture distances. The x -axis is the distance of the recapture from the previous capture. The bars represent the empirical data with the area of each bar equal to the number of recaptures for each distance interval. (Thus the height of each bar is the number caught in that interval divided by the interval size width of bar.) The total area is therefore 8799, the total number of recaptures. The axes of the histogram are logarithmic for visual clarity. The expected histograms for the three models are shown for comparison: the gamma distribution, the Rayleigh distribution and the log-sech distribution (fitted by maximum likelihood estimator). The intervals for the empirical histogram are 10-m wide up to 100, then 100-m wide up to 1000, then 1-km wide up to 5 km and 5–10 km. The last three bins are 10-km wide. Although this choice is arbitrary, it does not fundamentally alter the shape of the histogram (note also that the fitting procedure does not depend on the choice of intervals). Inset shows the same histogram with only the vertical axis logarithmic.

Table 1 The Akaike information criterion (AIC) for Rayleigh, gamma ($\beta = 2$) and log-sech kernels

Data category	AIC values			Log-sech parameters	
	Rayleigh	Gamma	Log-sech	α	β
All data	135 216	117 738	106 074	315	1.77
Demography					
Females	27 432	22 634	19 766	174	1.80
Males	36 698	31 286	28 025	186	1.80
Adults	74 242	66 979	61 064	309	1.76
Juveniles	2678	2563	2386	934	1.82
Isolation					
Before	46 605	41 444	37 602	310	1.77
After	88 450	76 284	68 476	317	1.77

The log-sech distribution consistently outperforms the exponentially bounded functions, achieving a good fit both near the origin and at long distances. We list the log-sech parameters, α and β , for each subset of the data. The AIC values highlighted in bold correspond to the best-fitting models for each grouping of data. Further results are given in Appendix C.

It is obvious that the latter model is a better fit for the data both close to the origin and far from the origin.

That the log-sech distribution provides the best fit is especially significant as it holds no matter how we categorize

the data: according to age and sex (Table 1), by pre- and post-isolation categories (Table 1), or into species (Fig. 5). Juvenile birds disperse further than adults, which we expect as a consequence of observing natal dispersal (Table 1). Males and females show no differences (Table 1), which we anticipate as the majority of tropical forest birds are non-migratory and have similar sex roles. When all species are lumped, isolation does not appear to affect the dispersal kernels (Table 1), although we might expect gap avoidance when extinction-prone species are considered singly (Fig. 2a).

Finally, we further divide the data by species, organize them by the taxonomy of Sibley & Monroe (1990), and distinguish extinction-prone species from those that persist in fragments (Fig. 5). In continuous forests, extinction-prone species generally disperse to greater distances than persistent species. After plot isolation, such species – during the time they persist – tend to move shorter distances. The wing-banded antbird (*Myrmornis torquata*) is an extreme example of an extinction-prone species; with an extremely heavy tail before isolation ($\alpha = 256$, $\beta = 1.7$), but withdrawing after isolation ($\alpha = 67$, $\beta = 2.2$). We might expect an extreme reaction to landscape fragmentation in *M. torquata* as this terrestrial antbird may have difficulty traversing large areas without the cover of forest canopy. However, this species' terrestrial nature does not prevent long-distance

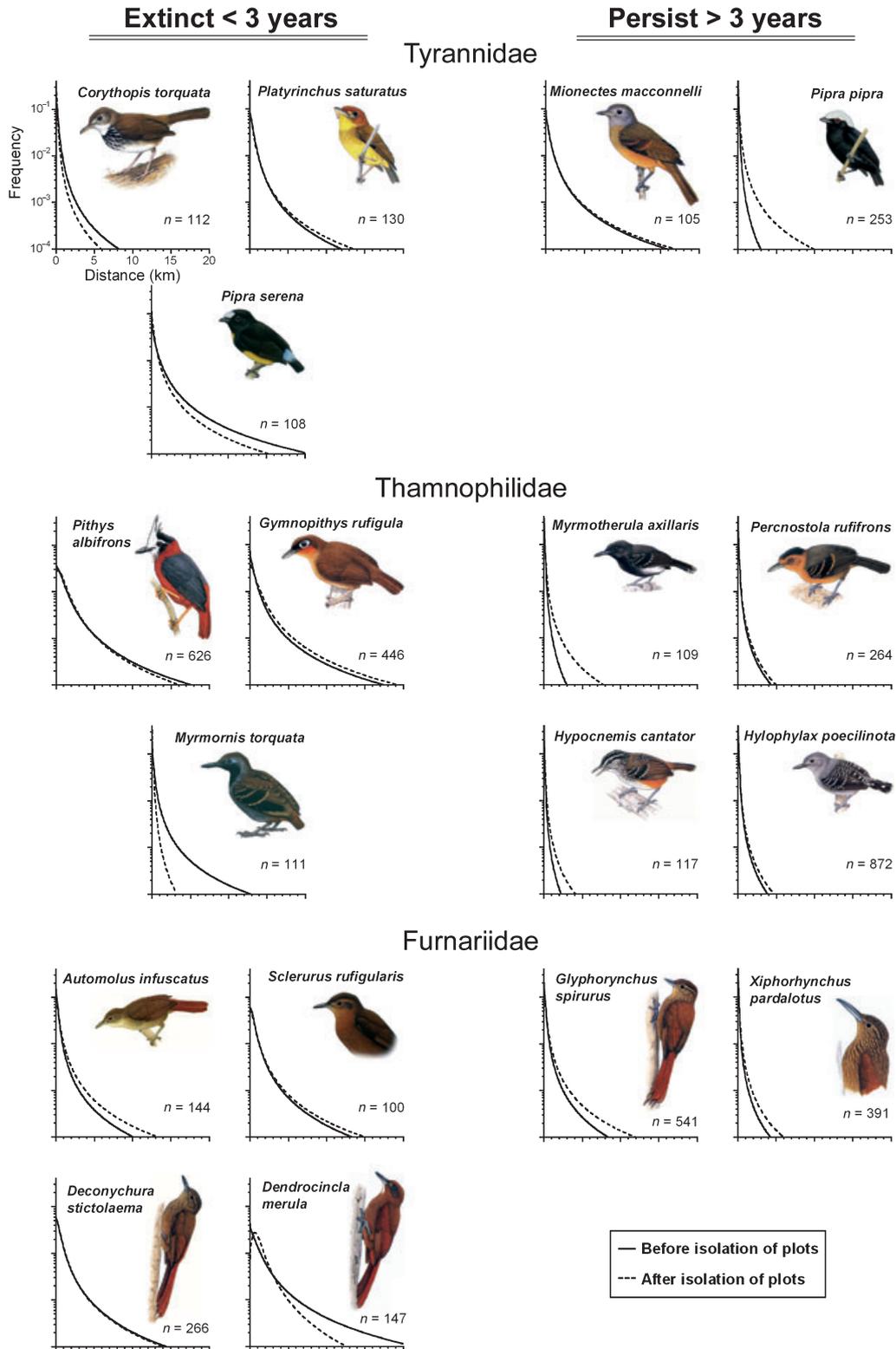


Figure 5 Forest fragmentation reshapes the dispersal kernels for many species. Extinction-prone birds move further than persistent birds in continuous forest, and show depression in long-distance movement after forest fragmentation. Persistent species, conversely, displace further after fragmentation. Displacement kernels are compared between closely related species, based on the taxonomy of Sibley & Monroe (1990). Bird plates courtesy of Ridgely & Tudor (1994), used with permission.

displacements before isolation. Conversely, persistent species tend to move further after isolation than before. The white-flanked antwren (*Myrmotherula axillaris*) is an example, with a much heavier tail after isolation ($\alpha = 174$, $\beta = 1.8$) than before ($\alpha = 63$, $\beta = 2.3$). This is perhaps expected as *M. axillaris* frequents primary forests, secondary forests, edges and gaps (Cohn-Haft *et al.* 1997); and even bred in small fragments at the BDFFP (Stouffer & Bierregaard 1995).

DISCUSSION

Isolation limits the propensity for some birds to move between forest fragments, by 67%, for the species that disappear from small fragments within 3 years after isolation. That said, 18% of the recaptures of these species in 1-ha fragments are outside those fragments, falling to 5% for 10 ha, and < 2% for 100-ha fragments (Fig. 2a). In the time these extinction-prone species remain in fragments, they preferentially disperse from smaller to larger plots, likely selecting forest patches with more area. Importantly, the distances moved for all birds are substantial, particularly for extinction-prone species. For most species shown in Fig. 5, we estimate that a small fraction disperse beyond 5 km. This statistic is certainly influenced by the few records at large distances, but these data are compelling precisely because those distances are sampled infrequently. If there were more nets spaced > 5 km apart, we would likely have detected more movements there. That the heavy-tailed model is the best fit for all the species we examine makes the result a general one, and confirms Grinnell's (1922) idea that long-distance movements by birds are not accidental, even for tropical forest birds. This also supports the Lévy-flight model of active dispersal that has been applied foraging patterns in other organisms (Viswanathan *et al.* 1996; Atkinson *et al.* 2002).

How do we reconcile our results with the existing literature? Stouffer & Bierregaard (1995) argue that forest fragments 'are analogous to true islands', and Develey & Stouffer (2001) claim that 'open pastures are nearly absolute barriers to movement' for many of the species we consider. The frequency and distance of movements came as some surprise both to ourselves and to some of our colleagues. That we found such long dispersals in the data from the BDFFP is in large part a testimony to the experiment and its data. It has large numbers of observations, taken over many years, and over a linear distance of 41 km. The BDFFP's unique experimental design made these analyses possible. We also documented long-distance dispersals as we anticipated their possibility. Laurance *et al.* (2004), in contrast, exclude all movements > 300 m from their analyses. Such movements constitute nearly 20% of the movements we document; excluding them misses data of huge significance.

The log-sech AIC value of 106 074 was the lowest value of any model and fits the data histogram reasonably well over four orders of magnitude for distance. The choice of the log-sech heavy-tailed model was made for convenience; other heavy-tailed families will not differ significantly in their performance. From our tests, for example, the Lévy-stable series (Nolan 1998) yielded similar AIC values. For one-parameter models, the best fitting was the Cauchy model (AIC = 106 694). Our choice of the Rayleigh and one-parameter gamma models is based on a theoretical model of classical diffusion, where the dispersal kernel tends to have either a two-dimensional Gaussian or exponential form, leading to a density of zero at $r = 0$. We can relax these assumptions and use either exponential or Gaussian models directly, the fitting of the model at $r = 0$ is better but still fits badly in the tail giving values of 107 192 and 111 864 respectively. A two-parameter gamma distribution reduces the AIC value to 106 158, but this fits the tail poorly. Thus, the main result of this analysis is that the amplitude kernel (distribution of distances between capture and recapture) tends to have an extremely heavy tail, supporting the biological conclusion that while most of any species do not move far, there is always a small number of individuals that move very long distances.

The results from extinction-prone and persistent species might also be unexpected. We found that species that range widely are those that disappear from the fragments more rapidly. Generally, the birds that go extinct in fragments are those that forage in groups – following army ant swarms or joining mixed-species flocks. Species only facultatively relying on either of these strategies, move to much shorter distances and cross gaps less often, but are more likely to persist within fragments. We documented this general pattern when using social tendencies as a proxy for ranging behaviour (Van Houtan *et al.* 2006). The present movement analyses confirm that social species range more widely than solitary ones, or those that only occasionally forage in groups.

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SUPPLEMENTARY MATERIAL

The following supplementary material is available for this article:

Appendix A Solving the classical diffusion problem under the conditions expected for the BDFFP data.

Appendix B Procedure used in the maximum-likelihood calculations.

Appendix C AIC comparisons over a larger selection of kernels than Table 1 provides.

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