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Effects of Habitat Fragmentation on the Distribution and Movement of Tropical Forest Birds

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UNIVERSITY OF MIAMI

EFFECTS OF HABITAT FRAGMENTATION ON THE DISTRIBUTION AND MOVEMENT OF TROPICAL FOREST BIRDS

By

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Habitat loss and fragmentation occur at unprecedented rates, especially in tropical countries where human activities have deforested or degraded around 80% of tropical rainforests. Tropical forest fragmentation is considered the main cause of extinction of tropical forest avifauna, yet the mechanisms by which fragmentation affects bird populations are poorly understood. The present study investigates the pattern of bird species distribution in a fragmented landscape in tropical southeastern Mexico and the relation of bird community and species distribution patterns to landscape and fragment characteristics. Area and isolation of forest fragments were the main determinant of species richness and abundance in fragments, especially for forest-dependent species. The significant effect of isolation on species persistence in forest fragments suggests that limitation of dispersal is one potential mechanism by which fragmentation affects species distribution in the landscape. To understand how fragmentation can affect bird dispersal in a fragmented landscape, the effect of open areas and corridors on movement patterns of forest birds was investigated. The evidence presented in this study supports the idea that bird movement is restricted by open areas, especially for forest-restricted birds.

Forested corridors had a positive effect on movement rates of forest birds, potentially acting to preserve movement and dispersal processes, and ultimately species persistence, in heavily fragmented landscapes.

To my family and Edgar, always there

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Chapter I

Introduction

The process of land clearing and environmental degradation is continuing rapidly all around the globe, but especially in areas of tropical rainforest. It has been estimated that by 1990, on average, 24% of the lowland tropical forest on Earth had been cleared and only 22% of the original forest cover remained in large, unbroken areas without substantial human influence (FAO 1993). In many countries of the tropics deforestation rates exceed the global average and rainforests occur only as isolated remnants. Between 1990 and 2000 natural forests were lost at a rate of 16.1 million ha per year and the countries with the highest net loss of forest were Argentina, Brazil, the Democratic Republic of Congo, Indonesia, Mexico, Nigeria, Sudan, Zambia and Zimbabwe (FAO 2006).

Removal of native vegetation results not only in the loss of significant areas of original habitat, but also in its fragmentation. Fragmentation results from the selective removal of areas of vegetation, leaving behind patches of native habitat that are not suitable for development (e.g. due to terrain steepness, poor soil quality or flood risk) or serve a specific function (e.g. nature reserves, protection for river banks or hunting areas). These remnants of native habitat exist as a collection of isolated fragments in a heterogeneous landscape dominated by anthropogenic habitat (e.g. urban developments, agroecosystems, secondary growth vegetation) and vary in size, shape, position and isolation (Saunders et al. 1991, Laurance et al. 2002). Although habitats may be naturally patchy due to discontinuities in environmental factors (e.g. soil types, elevation), anthropogenic fragmentation is a major concern for conservation due to its rate and extent.

Tropical forest loss and fragmentation have been advocated as the main causes of population declines and faunal extinction in the tropics (Turner 1996, Laurance et al. 2002), especially of large carnivores, large herbivores and birds (Turner and Corlett 1996, Corlett and Turner 1997). Studies of tropical bird communities in fragmented forests have reported that up to 30% of previously present species have been lost from forest fragments after isolation from continuous forest (Newmark 1991, Renjifo 1999, Robinson et al. 2000, Ribon et al. 2003).

Two main mechanisms have been proposed to explain the patterns of species distribution and extinction of birds in fragmented landscapes: decreased fitness in lower quality habitat and reduced colonization of isolated patches. A number of studies in temperate areas have focused on fitness measures such as nesting success (probability that a nest will fledge young) or fecundity (number of offspring per adult per year) in relation to patch size, isolation and edge effects (Brittingham and Temple 1983, Donovan et al. 1995, Robinson et al. 1995, Porneluzi and Faaborg 1999, Chalfoun et al. 2002). In a recent review of 82 studies of demographic responses of birds to forest fragmentation, Lampila et al. (2005) found that overall, associations among fragmentation and nest success, nest predation, nest parasitism, and pairing success were significantly negative for forest birds. All of the studies included in this review were from temperate areas. Direct studies of the demographic response of birds to forest fragmentation in the tropics are much more limited (Lampila et al. 2005). Although controversial, indirect evidence provided by experiments using artificial nests suggests that predation rates in fragments of tropical forest are higher compared to continuous tracts of forest (Fahrig and Merriam 1994, Estrada et al. 2002, Stratford and Robinson 2005).

The second mechanism that has been hypothesized to influence the probability of persistence of species in fragmented landscapes is colonization and dispersal. The theory of island biogeography (MacArthur and Wilson 1967) and metapopulation theory (Hanski and Gilpin 1997, Hanski and Ovaskainen 2003) have provided a framework for studies of fragmentation. Both approach fragmentation as a spatial problem, emphasizing the central role of dispersal among fragments in determining whether or not populations will persist. Despite the theoretical role of movement and dispersal on the persistence of species in fragmented landscapes, studies of the effect of habitat configuration on bird movements have only recently focused on how fragmented landscapes affect the movement of individuals.

While early studies on fragmentation used area and isolation of habitat fragments as the main explanatory variables for species distribution in fragmented landscapes, it has been recently recognized that landscape attributes (composition and spatial arrangement) and behavioral attributes of the species (mobility, dispersal ability) may interact to determine the species response to fragmentation (Hamer and Hill 2000, Major et al. 2001, Steffan-Dewenter 2003). To evaluate the role of factors interacting at the landscape level, studies of fragmentation need to include quantitative descriptions of landscape structure. These studies should be linked to studies of how species respond to and use landscape elements such as corridors to move and disperse in a fragmented landscape. Although colonization and dispersal among fragments are major features of most theories of fragmentation (island biogeography and metapopulation models), empirical evidence usually focuses on demographic mechanisms. Lampila et el. (2005) suggest that the fact that pairing success seems to be the demographic variable most associated with fragmentation (Brooker and Brooker 2001, Brooker and Brooker 2002) could indicate a significant role of dispersal in fragmented landscapes. Research efforts to evaluate the effects of fragmentation and the role of behavioral responses in fragmented landscapes have accumulated in the last ten years for temperate areas. In the tropics, however, studies of this type have only recently started and information is thus far available only from a handful of them.

For my dissertation, I combined a series of approaches to investigate the effects of fragmentation on tropical forest birds at different levels, from the individual to the community level. In the second chapter, I used a community approach and investigated whether patterns of species richness in forest fragments are related to patch- and landscape-level attributes such as area, isolation and vegetation characteristics. In the third chapter, I applied a species-specific approach and investigated what patch- and landscape-level characteristics affect bird occurrence and abundance in forest fragments and whether these effects are consistent across species with different degrees of forest dependence. In the fourth and fifth chapters I took the approach of individual behavior and investigated the effect that fragmented landscapes have on bird movement. In the fourth chapter I studied the effects that open areas have on the movement of tropical forest birds and in the fifth chapter I investigated how forested corridors affect movement rates in fragmented landscapes.

Chapter II

Effects of tropical forest fragmentation on bird communities: the influence of fragment- and landscape-level factors

Background

Throughout human history the vegetation cover of the Earth's surface has been extensively modified as a result of the development of agricultural systems, logging activities and the expansion of urban areas. Habitat loss due to anthropogenic activities is recognized as the most pervasive and conspicuous threat to biodiversity in the tropics (Laurence et al. 2002).

Over the last few decades, forest fragmentation, or the breaking apart and isolation of formerly continuous forest (Saunders et al. 1991), has been found to have a number of negative ecological effects (Turner 1996, Laurance et al. 2002). Traditionally, the effects of fragmentation have been considered in terms of the impact of the size of the remaining forest patches (Laurance et al. 2002) but increasing evidence shows that such effects may also stem from the spatial distribution (e.g., degree of isolation, location along altitudinal gradients) and shape (e.g. edge:area ratio) of the remaining forest patches resulting from current land use patterns (Laurance et al. 2002).

The immediate effects of habitat fragmentation are the reduction of total area and the isolation of remaining patches. As a result of habitat reduction some species will be lost from the landscape simply because their original ranges did not include any of the remnant patches (Saunders et al. 1991). Due to this sampling effect, endemic species that are rare and have narrow distributions have a higher probability of extinction than common species with wide distributions (Gentry 1992). In addition, as area is reduced, fragments are less likely to provide resources for species that require large areas or rare resources. Habitat fragments usually contain modified and impoverished communities of plants and animals (Collinge 2000, Hamer and Hill 2000, Goosem 2002, Brown and Sullivan 2005) and small areas of forest may only support small populations of most of the species.

Early interest in habitat fragmentation was closely linked to the theory of island biogeography (MacArthur and Wilson 1967). As a result, fragmentation studies initially focused on local patterns of species distribution and abundance in relation to patch area and isolation (Haila 2002). Most of the studies in temperate areas seem to support the theoretical prediction that species distribution and abundance may be affected by changes in both, the reduction of total amount of native habitat and the isolation of the remnants (e.g. Robinson 1989, Faaborg and Arendt 1995, Donovan and Flather 2002). In contrast, some studies have demonstrated that species abundances increase with fragmentation, especially for forest-edge species (McGarigal and McComb 1995, Trzcinski et al. 1999, Villard et al. 1999).

Studies of tropical bird communities in fragmented forests have reported that up to 30% of previously present species have been lost from forest fragments after isolation from continuous forest (Newmark 1991, Renjifo 1999, Robinson et al. 2000, Ribon et al. 2003). In accordance with the theory of island biogeography, area of remaining patches and their distance from continuous forest are often the best predictors of rates of local extinction, particularly for forest specialists such as understory insectivores and ant-follower birds (Christiansen and Pitter 1991, Renjifo 1999, Stratford and Stouffer 1999, Robinson et al. 2000). The combination of large territory sizes, strong preference for old-growth forest, sedentary lifestyles and reduced ability to disperse from source habitat to patches have been suggested as traits that make forest specialists particularly prone to extinction in highly fragmented landscapes (Kemp 1999, Davies et al. 2000, Lens et al. 2002, Sekercioglu et al. 2002). Fragment area is not always a factor, even in similar tropical systems. Estrada et al. (1997) studied the bird assemblages in forest fragments surrounding a main tract of forest in Los Tuxtlas, Mexico and found that species richness was not related to area of forest fragments. They detected a significant negative relationship between species richness and bird abundance with isolation distance of forest fragments.

Fragment-level characteristics known to influence birds in fragments include shape, plant species composition and vegetation structure (Karr and Roth 1971, Whelan 2001, Tews et al. 2004). Fragment shape is related to the proportion of the fragment area subject to edge effects that affect reproductive success, bird behavior and distribution (Rodriguez et al. 2001, Estrada et al. 2002, Haynes and Cronin 2006). Plant species richness is usually positively related to bird species richness and abundance (Estrada et al. 1997) because of the greater availability of food resources provided by a more diverse plant community. Vegetation structure (density and size distribution of trees and vertical density of vegetation layers) determines the structural heterogeneity of the habitat and influences habitat use by birds (Karr and Roth 1971, Brokaw and Grear 1991, Barlow et al. 2002). Arriaga et al. (2008) investigated the influence of habitat characteristics, representing a range of vertical structure, tree density and habitat complexity, on resident bird feeding guilds in forest fragments of different sizes in southeastern Mexico. They found that the main habitat variables that explained the presence of most feeding guilds were tree height, tree density, degree of human disturbance and fragment area.

The main objective of this study was to describe patterns of bird species richness and abundance in forest fragments and determine the relative influence of fragment- and landscape-level characteristics that explain the variation of species richness and abundance. I hypothesized that area and isolation of fragments would be the two factors that most strongly affect bird species richness and abundance in forest fragments. Vegetation structure would only have a secondary effect when area and isolation variables are taken into account.

Methods

Field Site

Palenque National Park (PNP) is located in the north central area of the state of Chiapas (Fig. 2.1) in southeastern Mexico (17°27’51”-17°30’05” N; 92°01’30”-92°04’42” W). The average annual precipitation is 2,000 mm, with a drier season between January and April (average monthly rainfall = 62 ± 18 mm) and a wetter season between May and December (average monthly rainfall = 240 ± 106 mm). The mean annual temperature is 26 ºC (range 22-29 ºC). The forest in the Palenque area is classified as tropical wet forest (Holdridge et al. 1971) with a canopy height of 25-30 m (Diaz-Gallegos 1996).

Palenque National Park offers favorable ecological conditions to investigate the effects of habitat fragmentation on forest bird communities. Ecologically, PNP represents one of the few forest reserves officially protected in southeastern Mexico. Due to federal protection, a large tract of forest has been preserved in a region where forests have been heavily fragmented. PNP covers an area of 1,780 ha, about 630 ha of which consist of primary rainforest.

The land surrounding PNP (in a 10 km radius) is dominated by pasturelands, but clusters of forest fragments remain dispersed in the area amid cattle pastures, alongside streams and rivers, and on the slopes of nearby mountains (Fig. 2.1). Mendoza-Ramos (2002) reported 326 fragments of tropical rain forest in the area. The mean size of fragments was 4.4 ha (0.61- 583 ha) and 29% of the fragments had an area of 2-4 ha. Fragments < 8 ha represented 70% of the total area and only 4% of fragments were larger than 65 ha.

Focal Fragments

Using a combination of field surveys, aerial photographs and published information (Mendoza-Ramos 2002), I selected 17 fragments of remnant forest vegetation with areas that range from 2.72 to 46.35 ha (mean=14.28 ha; S.D.=14.55) (Fig. 2.2). Although the exact ages of the fragments are unknown, all the focal fragments existed as isolated fragments by 1984 (Mendoza-Ramos 2002). Distance of focal fragments to PNP ranged from 50 m to 18 km (mean=6.3 km; S.D.= 6.48) (Fig. 2.3).

Fragment-level characteristics investigated in this study included measures of area, shape and vegetation structure. Landscape-level attributes included three measures of isolation for each fragment.

Fragment-level attributes. Area is defined as the area, in ha, covered by forest vegetation in each fragment and represents the amount of habitat available for forest organisms. Shape is defined as the ratio of a fragment perimeter to its area (edge:area) and represents the amount of the fragment area potentially affected by edge effects.

These fragment attributes were estimated using a digitized and orthocorrected aerial photograph (scale 1:20,000) of the Palenque municipality area (INEGI 2001). All focal fragments and the arboreal vegetation surrounding them were digitized from the photograph using ArcGIS 9.0 (ESRI 2008) and area and edge:area ratio were estimated using the Spatial Analyst tool from ArcMap 9.3 (ESRI 2008).

Vegetation structure was defined using a set of attributes reported to influence habitat use by birds (Karr and Roth 1971) and consisted of two sets of variables: horizontal structure and vertical structure. Horizontal structure variables included ground covered by vegetation, litter, logs or rocks (Veg, Lit, Log and Rock) and canopy cover, all represented as percentages. Horizontal structure variables also included density of small (<10 cm DBH), medium (10-25 cm DBH), big (25-40 cm DBH) and grand (>40 cm DBH) trees and logs. All these variables were expressed as trees per square meter. With the exception of canopy cover (see below), all measures of horizontal structure (ground coverage and tree density) were estimated using 12 m x 12 m quadrats (up to 9 quadrats per fragment, depending on fragment size). Ground coverage was determined by estimating coverage percentage in each class (vegetation, litter, logs or rocks) in four

1-m^2 subplots within the 12 m x 12 m quadrats. Tree and log density were estimated by directly counting the presence of trees in each one of the size classes inside the quadrat. Canopy cover was estimated using 2 m x 25 m transects (up to 9 transects depending on fragment size) with sampling points every 2.5 m along a transect. At each sampling point, canopy cover was estimated using a convex densiometer and taking four measurements, one in each cardinal direction.

Vertical vegetation structure was defined by canopy height and the presence of vegetation in the understory for each of five height strata: 0- 0.5 m, 0.5-1.0 m, 1.0-1.5 m, 1.5-2.0 m and 2.0-3.0 m. Both variables were measured using the same 2 x 25 m transects mentioned above. Canopy height was estimated by measuring the highest point in the canopy at each sampling point using a clinometer. Vegetation per strata was estimated at each sampling point using a 3-m sighting pole and recording the presence of vegetation within 5 cm of the pole in each stratum. For each fragment, the vertical vegetation variable is defined as the proportion of sampled points with vegetation present in each stratum.

Quadrats and transects within each site were placed perpendicular to, and on alternating sides of, the trail used during bird surveys. A minimum of three to nine transects and quadrats were surveyed in each fragment, depending on fragment size. All variables were standardized by area or number of sampling points to correct for differences in sampling effort.

In order to detect co-linearity and reduce the number of vegetation variables, I used principal component analysis (PCA) to obtain composite descriptors of vegetation structure. PCA of vegetation variables showed that the variation in the 16 vegetation variables could be expressed by four main PCA axes (Table 2.1). Veg_PCAI explained 34.7% of the variation and represented sites with high levels of ground cover by live vegetation and dense vegetation in the understory from 0.5 to 1.5 m in height. Veg_PCAII explained 17.8% of the variation and was dominated by sites with dense vegetation from 1.5-2.0 m in height. Veg_PCAIII explained 15.1% of the variation and was related to sites with high density of logs. Finally, Veg_PCAIV explained 11.1% of the variation and was related to sites with high percentage of canopy cover. For subsequent analysis, only these four PCA components were retained.

Landscape-level attributes. At the landscape level I measured three estimates of isolation for each forest fragment: 1) distance to PNP (linear distance in m from the center of each forest fragment to the closest edge of the main tract of forest in PNP, 2) Cover_100 or proportion of arboreal vegetation within a 100 m band surrounding the fragment, and 3) C_500 or proportion of arboreal vegetation within a 100-500 m band surrounding the fragment. These variables were estimated using the same procedures used to estimate the area and shape variables mentioned above.

Bird Surveys

I conducted bird surveys in the forest fragments from May-Aug during 2006-2008. Each one of the focal fragments was visited at least three times in this period. During bird surveys, I recorded presence-absence and number of individuals of each bird species by intensive surveys (Ralph et al. 1996) using fixed-radius point counts. Point counts had a fixed radius of 25 m and were separated from each other by at least 150 m to reduce the probability of counting the same individual twice. The number of point counts in each fragment depended on fragment area and there were no less than three and up to 12 points in the largest fragments. During each survey I visited all the points in a fragment. At each point, I conducted a standard 10-min count, recording all the individuals seen or heard inside the fixed radius. A species was registered as present at a sampling point if it was visually or vocally detected at any time during the 10-min point count. All surveys started at dawn (0600-0630 hours) and no surveys were conducted during rain or strong wind conditions. Only birds detected within the forest fragment were recorded. Individuals flying over the canopy were not considered. Only resident species were considered for the subsequent analysis.

Data gathered during the 10-min point counts were used to calculate species richness, total number of individuals, and a punctual abundance index (PAI, from now on described as bird abundance) for all species present in each fragment. To control for sampling effort, I used the program EstimateS (Colwell 2006) to generate estimates of species richness (Chao II estimator, S_{est}) using observed values of species richness in each fragment (S_{obs}) (Chao et al. 2005). This method allows standardizing species richness values as a function of survey effort and is recommended when survey effort is not exhaustive and varies among sites. PAI is calculated as the number of contacts, visual and/or auditory divided by the number of sampled points (Uezu et al. 2005).

Analysis of Data

Effects of fragment- and landscape-level characteristics on species richness and bird abundance were investigated using backward stepwise multiple regression for all pooled species in each fragment.

Results

General Results

I recorded 3343 individuals representing 124 species in the forest fragments. Mean number of individuals per fragment was 197 (range = 70-348; S.D. = 99), while mean number of species per fragment was 37 (range = 25-53; S.D. = 8). Estimated number of species per fragment (Chao II estimator) ranged from 24.74 to 65.75, with an average of 39.67 species per fragment.

Completeness of samples per fragments estimated using Chao II species richness estimator ranged from 80%-98%. This indicates that bird samples, although not complete, are a good representation of bird communities, especially for those fragments where point counts accounted for at least 90% of estimated bird species richness.

Effects of Fragment- and Landscape-level Variables on Species Richness

The three best predictive multiple regression models (Table 2.2) indicated that Area, Distance to PNP, Cover_100, Cover_500 and Vegetation_ PCA III were the best predictors of Estimated Species Richness in the landscape. The only difference between the models was the subsequent removal of the isolation measures based on percentage of forest cover surrounding the fragments (Cover_100 and Cover_500).

Relatively large correlation coefficients (R=0.720-0.785) for these three models indicate a strong relationship between the observed and model-predicted values of species richness. The three models explained from 52-62% of the variation in species richness values. Model 1 explained the highest proportion of the variation in the number of species in each fragment (61.6 %) as indicated by the coefficient of determination (R^2).

The effects of the significant predictors on Estimated Species Richness are summarized in Table 2.3. In all models Estimated Species Richness is positively correlated with Area, Cover_100, Cover_500 and Veg_PCAIII and negatively correlated with Distance to PNP. However, only Area and Distance to PNP remain significant in all three models.

These results indicate that Estimated Species Richness in the landscape is affected by a combination of both fragment (area and vegetation structure represented by amount of logs on the ground and medium trees) and landscape attributes (Distance to PNP and the amount of forest cover in the vicinity of the fragments). Distance to PNP has a stronger effect on Species Richness than area, especially for large fragments far from PNP (Fig. 2.4). The strength of the relationship between species richness and area is mainly driven by fragments close to PNP. In contrast, the largest fragments far away from PNP have a significantly smaller number of species than predicted by their area.

Effects of Fragment- and Landscape-level Variables on Bird Abundance

Multiple regression models (Table 2.4) indicated that Distance to PNP, Veg_PCAI, Veg_PCAII and Veg_PCAIV were the best predictors of bird abundance in these fragments. The most significant model retained these four variables, regardless of the measures of area and shape (Table 2.4).

Relatively large correlation coefficients (R) for all models indicated a strong relationship between the observed and model-predicted values of the dependent variable, bird abundance. The large coefficient of determination (R^2) for the significant model (Table 2.4) showed that this model explained 87% of the variation in bird abundance.

The effects of the significant predictors on bird abundance are summarized in Table 2.5 and indicate that bird abundance is positively correlated with vegetation structure variables Veg_PCAI, Veg_PCAIII, Veg_PCAIV and negatively correlated with Distance to PNP.

These results indicate that bird abundance was mostly related to patch attributes that are related to vegetation structure (ground cover by vegetation and logs and canopy cover) and isolation distance (Distance to PNP). Area was not a significant factor, although it was retained in some models.

Discussion

The 124 species recorded in forest fragments in this study represent 63% of the 197 bird species recorded in the forest habitat of PNP (Ibarra pers. obs.), the largest forest tract remaining in this area. This indicates that, although decreased, a large proportion of the avifauna associated with forest is represented in this highly modified landscape. However, the highest estimated number of species in a single fragment was 65.75 species (53 observed species), which indicates that it is the additive effect of multiple fragments that allows this large proportion of forest species to persist in the landscape.

Studies in similar fragmented landscapes in the tropics have found a similar proportion of bird species being supported in forest fragments. Estrada et al. (1997) studied bird communities in a fragmented forest in Los Tuxtlas, Mexico (around 360 km NE of PNP) and found that forest fragments retained 60-70% of the species historically reported in the area. Arriaga et al. (2008) reported that forest fragments retained around 62% of the bird species reported in a continuous forest in a nearby protected area (around

60 km east of PNP). This suggests that both sites have not only similar biogeographic histories, but also have experienced the same deforestation and landscape change dynamics. Conclusions from this study could therefore be considered representative of fragmentation in the Mexican tropical areas and comparative studies between these areas should be conducted in order to strengthen our knowledge of fragmented communities in this region.

Effects of Area

A pattern of increased species richness with patch area has been widely reported in studies of the effects of anthropogenic habitat fragmentation (Christiansen and Pitter 1991, Renjifo 1999, Stratford and Stouffer 1999, Robinson et al. 2000). In this study only species richness was related to fragment area, while abundance was not.

The immediate effects of habitat fragmentation are the reduction of total area and isolation of remaining patches. As a result of area loss some species will be lost from the landscape simply because their original ranges did not include any of the remnant patches (Saunders et al. 1991). Due to this sampling effect, endemic species that are rare and have narrow distributions have a higher probability of extinction than common species with wider distributions (Gentry 1992). In addition, as area is reduced, fragments are less likely to provide resources for species that require large areas or rare resources. Habitat fragments usually contain modified and impoverished communities of plants and animals (Collinge 2000, Hamer and Hill 2000, Goosem 2002, Brown and Sullivan 2005) and small areas of forest may only support small populations of most of the species.

The lack of a relation between bird abundance and fragment area may be due to the effect of very low population densities because of the extreme deforestation in the region (Graham and Blake 2001) with fragments containing only a small number of individuals despite their carrying capacity. Stouffer et al. (2006) also suggest that bird abundances in forest fragments may not be due simply to fragment size or dynamics within the fragments. Landscape dynamics and time since isolation may influence abundance beyond the sole effect of area. For example, recently fragmented areas may show a crowding effect of fragments after fragmentation due to the influx of individuals displaced from cut forest. As time progresses, the overcrowding effect may disappear and bird abundances reach an equilibrium based on fragment area. The fragmented landscape in this study, although mostly fragmented 50 years ago, is very dynamic with new areas currently being deforested for cattle pastures and forest fragments being cleared for human colonization in the present.

Effects of Isolation

In the present study bird species and abundance were related to isolation which coincides with findings of other bird studies in tropical forests in the neotropics (Estrada et al. 1997, Stouffer et al. 2006, Ferraz et al. 2007). The effects of isolation on bird communities in fragmented landscapes have been explained in terms of the equilibrium theory of island biogeography (ETIB; MacArthur and Wilson 1967). ETIB proposes that species richness on islands is driven by opposing rates of immigration and extinction, with immigration rates negatively correlated with isolation. As the distance of habitat islands from the species source increases, fewer individuals are able to reach them and therefore species richness and abundance decrease.

The decrease in species richness as fragment isolation increases suggests that physical isolation of fragments may impact the movement of those species that perceive the modified matrix as a barrier, thereby decreasing recolonization events. As a result, habitat fragments that may provide necessary resources are not occupied because some species are unable to reach them. Although the cost of reaching isolated forest fragments (e.g. higher predation rates in the open matrix, higher energy expenditure) might be high, bird species able to abandon the forest patch in which they live and traverse modified landscape to reach more isolated forest patches may benefit from resources provided by these patches and meet survival requirements.

Results from these studies contrast with similar studies from the tropics as to what measure of isolation influences species composition in fragments. While I found that distance to nearest continuous forest influenced species richness and abundance, other studies (Graham and Blake 2001, Stouffer et al. 2006) have found that measures of isolation related to amount of forest habitat surrounding the fragments are better at explaining species richness. The lack of concordance among these results could be due to the fact that these other studies were conducted in landscapes with more heterogeneous matrices, where the distinction between forest and non-forest habitat is less marked. In these circumstances, birds moving through the landscape, a potential source for recolonization, encounter a series of landscape elements (plantations, secondary growth, etc.) that modify their dispersal patterns beyond the simple effect of distance.

Effects of Vegetation Characteristics

The relationship between bird species richness and vegetation structure variables indicate that forest fragments, although slightly disturbed by human activities, provide resources that attract a considerable number of birds and bird species. The density of the ground vegetation and logs as well as the presence of a well developed canopy cover with fruiting trees offer protective cover and food resources for birds of several guilds, especially insectivorous birds of the understory.

In this study, species richness was related to Veg_ PCAIII or percentage of ground covered by logs, while bird abundance was related to density of foliage in the understory. These sites represent forest fragments with low levels of human disturbance where some insectivores of the understory may take advantage of the opportunities created by increased levels of structural complexity and the resources associated with them (foraging, refuge, etc.).

In this landscape, although fragmentation and history of land use have significantly altered vegetation structure, forest fragments may be providing resources that allow forest species to persist in an otherwise inhospitable habitat. Different guilds may benefit from vegetation characteristics retained in fragments. Wide ranging arboreal frugivores (parrots and toucans) present in this study may be taking advantage of large fruiting trees present in these fragments.

The rapid extinction of forest bird species at a regional scale has been linked to the extent of reduction of the original habitat and isolation (Renjifo 2001). Disruption of the habitat by human activities may reduce the space occupied by forest dwelling species and affect the type and amount of resources available (Turner 1996). As a result, fewer species can occupy the habitat and only extensive tracts of forest can contain a full assemblage of resident species. Guarantees of protection from human alteration for such tracts should be a first priority for bird conservation. With increasing development pressure on Mexican tropical forests, as well as in other tropical regions, urgent conservation actions are vital for the preservation of their biodiversity.

Chapter III

Forest bird responses to habitat fragmentation: how consistent are they across species?

Background

Extensive loss and fragmentation of forest cover in the tropics have prompted studies on what the impacts of such changes are on animal abundance, species richness, and community dynamics. Understanding the relationship between habitat fragmentation and community dynamics is not only crucial for ecological theory (Rosenzweig 1995, Hanski and Gilpin 1997) but also for the management and conservation of biodiversity.

Species-area models are commonly applied to this issue and the ecological literature contains numerous hypotheses about the effects of habitat fragmentation on species composition (Brown and Sullivan 2005). The hypothesis that species richness on islands is a direct function of island size and degree of isolation has been prevalent given the relative success of the equilibrium theory of island biogeography (ETIB; MacArthur and Wilson 1967) in explaining species richness patterns in fragmented landscapes. Current theories are not capable of similar predictions related to community composition, even among well studied forest systems. Haila et al. (1993) predicted that “species accrual in assemblages of single fragments over years follows the pattern of random sampling.” This prediction contrasts with studies in North American systems that suggest that forest fragmentation leads to non-random reduction in species richness caused by losses of area-sensitive species (Blake and Karr 1987, Boulinier et al. 2001). Species within the local community would be lost from a given fragment if the fragment does not meet the ecological needs of these species. Isolation may also limit avian population persistence in heavily fragmented landscapes given the possible effects of fragmentation on bird movement (Andren 1994). Thus, fragmentation is predicted to differentially influence bird species dependent upon the life histories and/or ecological requirements of forest birds.

The intensity and type of response of forest birds to fragmentation largely depend on the natural history and ecology of the species considered. Less abundant and range-restricted species seem to be particularly affected by habitat changes (Raman 2006). Bird species restricted to very specific and specialized habitats such as the floor of old-growth forests, should be more sensitive to habitat fragmentation than birds inhabiting modified forest habitats such as forested plantations or secondary growth. Species distribution data are consistent with this prediction, revealing that gap tolerant and edge species, such as many types of hummingbirds, are tolerant to fragmentation (Stouffer and Bierregaard Jr 1995a).

Mechanisms suggested to influence bird community composition in fragmented landscapes (e. g. reduced habitat area, poor habitat quality, nest predation and parasitism) are not sufficient to predict what species exist in a given forest fragment, or how habitat fragmentation affects the abundance of individual species. Some forest species may benefit from fragmentation and increase their relative abundances (Austen et al. 2001), while other species may be absent from forest fragments with apparently suitable habitat and area to meet their ecological requirements (Martin 1981).

Community-level analyses may not fully represent the complexity of bird species' responses to fragmentation (Sieving and Karr 1997). Studies that describe the effects of fragmentation based solely on basic community descriptors, such as species counts, may limit our understanding of the mechanisms that determine population changes of individual species (Turner 1996). As a consequence, a thorough study of the responses of bird communities to habitat fragmentation must recognize the role that species-specific life histories plays in the mechanisms accounting for the persistence or disappearance of bird species in fragmented landscapes, and ultimately bird communities in these systems.

Some studies of species extinctions related to habitat fragmentation have grouped species by their respective responses (highly, moderately or not sensitive to fragmentation) and have found that certain life history traits such as large body size (Willis 1979), restricted mobility (Diamond 1981), specialized patterns of resource use (Willis and Oniki 1978, Stouffer et al. 2006) and terrestrial foraging and nesting (Stouffer and Bierregaard Jr 1995b) help identify species highly sensitive to fragmentation.

Using life history traits as proxies to determine species' responses to habitat fragmentation, although informative in some cases, may be misleading due to notable exceptions. Some terrestrial insectivorous birds, despite being considered as highly sensitive to fragmentation, persist in relatively small forest fragments and some small-bodied species disappear as readily as large ones (Sieving and Karr 1997, Robinson 1999). In addition, responses of particular groups of species may vary geographically. Species defined as sensitive in one area, may not be considered sensitive in a different location (Watson et al. 2005, Cowlishaw et al. 2009).

In my previous work, I determined that area and isolation were the main determinants of overall bird species richness in a landscape of forest fragments in Chiapas, Mexico. However, because generalizations derived from a whole-community perspective can be misleading, the present study explores the response of avian communities to fragmentation by grouping species based on their degree of forest dependence and it also explores the response of individual species to forest fragmentation.

My objective was to determine whether species richness of different bird species groups show the same responses to fragment area and isolation. In addition, I tested the hypothesis that species in different groups have different patterns of frequency of occurrence in forest fragments. Finally, I investigated the effects of area and isolation on the occurrence and abundance of individual species.

I predicted that species richness of forest restricted bird species would be more strongly affected by area and isolation than species richness of the group of partially restricted or unrestricted species. If forest restricted species are more strongly affected by area and isolation, then forest restricted species would be recorded in fewer fragments than partially restricted or unrestricted species. Species in the forest restricted species group are considered to have very specialized foraging habits (e.g. army-ant swarm followers) and low mobility. As a result, larger and less isolated fragments that provide more habitat resembling mature forest (less fragment area affected by edge effects) would favor the persistence of forest restricted species. In contrast, partially restricted and unrestricted species are considered less specialized and more mobile than forest restricted birds, and therefore should be able to use more vegetation elements in the landscape (secondary growth, forested plantations, riparian corridors) even if large distances separate these landscape elements. When considering the response of individual species, I predicted that the occurrence and abundance of the forest restricted species would be influenced by area and isolation, while the occurrence and abundance of partially restricted and unrestricted species would not show a strong effect of area or isolation of fragments.

Methods

Field Site

Palenque National Park (PNP) is located in the north central area of the state of Chiapas (Fig.2.1) in southeastern Mexico (17°27’51”-17°30’05” N; 92°01’30”-92°04’42” W). The average annual precipitation is 2,000 mm, with a drier season between January and April (average monthly rainfall = 62 ± 18 mm) and a wetter season between May and December (average monthly rainfall = 240 ± 106 mm). The mean annual temperature is 26 ºC (range 22-29 ºC). The forest in the Palenque area is classified as tropical wet forest (Holdridge et al. 1971) with a canopy height of 25-30 m (Diaz-Gallegos 1996).

Palenque National Park (PNP) offers optimal ecological conditions in which to investigate the effects of habitat fragmentation on forest bird communities. Ecologically, PNP represents one of the few forest reserves officially protected in southeastern Mexico. Due to federal protection, a large tract of forest has been preserved in a region where forests otherwise have been heavily fragmented. PNP covers an area of 1,780 ha, about 630 ha of which consist of primary rainforest.

The land surrounding PNP (in a 10 km radius) is dominated by pasturelands, but clusters of forest fragments remain dispersed in the area amid cattle pastures, alongside streams and rivers, and on the slopes of nearby mountains (Fig. 2.1). Mendoza-Ramos

(2002) reported 326 fragments of tropical rain forest in the area. The mean size of fragments was 4.4 ha (0.61- 583 ha) and 29% of the fragments had an area of 2-4 ha. Fragments < 8 ha represented 70% of the total area and only 4% were fragments larger than 65 ha.

Focal Fragments

Using a combination of field surveys, aerial photographs and published information (Mendoza-Ramos 2002), I selected 17 fragments of remnant forest vegetation with areas that range from 2.72 to 46.35 ha (mean=14.28; S.D.=14.55) (Fig. 2.2). Although the exact ages of the fragments are unknown, all the focal fragments existed as isolated fragments by 1984 (Mendoza-Ramos 2002).

For each fragment I determined area and isolation. Area was defined as the area, in ha, covered by forest vegetation within each fragment and represents the amount of habitat available for forest organisms. I defined isolation as the distance of each focal fragment to PNP (linear distance in m from the center of each forest fragment to the closest edge of the main tract of forest in PNP).

Fragment attributes were estimated using a digitized and orthocorrected aerial photograph (scale 1:20,000) of the Palenque municipality area (INEGI 2001). All focal fragments were digitized from the photograph using ArcGIS 9.0 (ESRI 2008) and area and isolation were estimated using the Spatial Analyst tool from ArcMap 9.3 (ESRI 2008).

Bird Surveys

I conducted bird surveys in all forest fragments from May-August during 2006-2008. I visited each focal fragment at least three times during this period. During bird surveys, I recorded presence-absence and number of individuals of bird species by intensive surveys (Ralph et al. 1996) using fixed-radius point counts. Point counts had a fixed radius of 25 m and were separated from each other by at least 150 m to reduce the probability of counting the same individual twice. The number of point counts in each fragment depended on fragment area and there were no less than three and up to 12 points in the largest fragments. During each survey I visited all the points in a fragment. At each point, I conducted a standard 10-min count, recording all the individuals seen or heard inside the fixed radius. A species was registered as present at a sampling point if it was visually or vocally detected at anytime during the 10-min count. All surveys started at dawn (0600-0630 hours) and no surveys were conducted during rain or strong wind conditions. I only recorded birds detected within the forest fragment and did not consider individuals flying over the canopy. Only resident species were included in the subsequent analysis.

I used data gathered during the 10-min point counts to calculate species richness for each species group (see description below), and abundances for the species present in each fragment. To control for sampling effort, I used the program EstimateS (Colwell 2006) to generate estimates of species richness (Chao II estimator, S_{est}) using observed values of species richness in each fragment (S_{obs}) (Chao et al. 2005). This method allows standardizing species richness values as a function of survey effort and it is recommended when survey effort is not exhaustive and varies among sites. I calculated bird abundance as a punctual abundance index (PAI). The PAI for each species is calculated by dividing the total number of observed individuals of each species by the number of points used during the census (Uezu et al. 2005) and is expressed as mean abundance per point.

Species Groups

To examine the response to area and isolation by species group and individual species, I categorized bird species as forest restricted, partially restricted or unrestricted according to Estrada et al. (1997) and Graham and Blake (2001). These authors worked in a similar fragmented landscape in southeastern Mexico and their data set is the closest (geographically) reference available. Estrada et al. (1997) reported abundances for bird species found in forest patches, arboreal crops (cacao, coffee, mixed crops, citrus, allspice) and non-arboreal crops (corn, jalapeno, chili pepper, bananas, pasture). Species were classified according to the following criteria:

- *Forest restricted*: Species whose abundance in forest patches was at least two times greater than their abundances in other sites, and were absent from non-arboreal crops.
- *Partially restricted*: Species that had similar abundances in forest patches and in two or more arboreal crops.
- *Unrestricted*: Species that were more abundant in non-forest habitats and were present in at least two of the non-arboreal crops.

Analysis of Data

Area and isolation were log n transformed to meet the assumptions of linear and logistic regression. I tested for the effects of area and isolation on species richness in each of the three groups by using stepwise multiple regressions. I also used stepwise multiple regressions to test for the effects of area and isolation on individual species abundances in each fragment. To determine if individual species occurrence had a significant relationship with area and isolation, occurrence data were modeled using binomial logistic regression. For these last two analyses, I included only species that were present in five or more fragments and that had normal distributions of abundance values (in some cases a ln transformation was applied to conform to normality).

Results

Species Group Responses

I recorded a total of 124 species in the present study. The majority of species belonged to the partially forest restricted group (n=54, 43.6%), while the forest restricted and forest unrestricted groups each had 35 species (28.2%) (Table 3.1). Multiple regression models that included area and isolation explained species richness only for the group of forest restricted species (Table 3.1). Forest restricted species richness was positively influenced by fragment area and negatively affected by isolation (Fig. 3.1). The effect of isolation was greater than the effect of area as indicated by the coefficient of the isolation factor in the regression model (Table 3.1). Species richness for the partially restricted and unrestricted species groups was not significantly affected by either area or isolation in this study (Table 3.1).

The frequency of occurrence of species was not independent from species group (G=14.031, df=6, p=0.029). In general, the majority of species in the three groups were present in less than nine fragments. This pattern was highly significant for forest restricted species (X^2=38.686, df=2, p<0.001), with the majority of forest restricted species (80%) occurring only in one to four fragments and only 6% occurring in more than nine fragments (Fig. 3.2). In contrast, only 40% of forest unrestricted species were recorded in fewer than five sites and 34% of species were recorded in five to eight fragments. Up to 25% of forest unrestricted species were recorded in more than nine fragments (X^2=8.543, df=3, p=0.036) (Fig. 3.2). Partially restricted species showed an intermediate pattern of occurrence (X^2=24.074, df=3, p=<0.001). As with forest restricted species, the majority of partially restricted species (52%) was present in only one to four fragments, but the proportion of species present in more than nine sites (22%) was more similar to that of forest unrestricted species.

Individual Species Responses

The individual responses to area and isolation were analyzed for 54 species' occurrence and abundance (Table 3.2).

Forest restricted species. Of the seven forest restricted species analyzed, only three species showed effects of area or isolation. The occurrences of *Piaya cayana* and *Ramphastus sulphuratus* were positively associated with area. Of these two, only the abundance of the latter had a strong negative relationship with isolation. A third species, *Elaenia flavogaster*, showed a strong positive effect of isolation on abundance (Table 3.2).

Partially restricted species. Of the 26 species analyzed in this group, only eight showed effects of area or isolation. Area had a positive effect on two species (*Dryocopus lineatus* and *Trogon melanocephalus*), while isolation had a positive effect on six species (*Arremon aurantiirostris*, *Lepidocolaptes souleyetti*, *Myiarchus tuberculifer*, *Aratinga nana*, *Trogon melanocephalus* and *Thryothorus maculipectus*). Isolation had a strong negative effect for only one species (abundance of *Saltator atriceps* was negatively affected by isolation) (Table 3.2).

Unrestricted species. Of the 21 species analyzed in this group, only five showed effects of area or isolation. One species showed effects of area and four species showed effects of isolation. Area had a strong negative effect on the abundance of *Amazilia tzacatl.* The occurrence of *Campylorhynchus zonatus* and *Pitangus sulphuratus,* and the abundance of *Zenaida asiatica,* were positively influenced by isolation, whereas the abundance of *Herpetotheres cachinnans* was strongly and negatively affected by isolation (Table 3.2).

Discussion

Species Group Responses

The positive relationship observed between species richness and habitat area has been called "one of community ecology's few genuine laws" or "universal regularities" (Schoener and Schoener 1983b, a). Although less prominent, isolation is also considered a relevant factor in determining species richness in habitat islands, second only to habitat area. As a general rule, isolation has a negative effect on bird species richness on islands (Wiens 1989).

Although the general species-area and isolation pattern has been well-documented for birds in temperate forests (Blake and Karr 1987, Freemark and Collins 1989), much less is known about tropical forest bird communities in fragmented landscapes and the existence of a positive relationship between habitat area and species richness is less constant. While several tropical studies have reported increased species richness and abundance with area (Guindon 1996, Warburton 1997, Arriaga-Weiss et al. 2008), others have not found the expected positive relationship between area and species richness or the negative relationship between species richness and isolation (Estrada et al. 1997, Graham and Blake 2001).

In the present study, only species richness of forest restricted species showed the expected relationship to area and isolation, while species richness for the partially restricted and unrestricted species groups showed no effects. The lack of consistency of species richness response to area and isolation could be related to differences in species composition and species-specific responses to habitat fragmentation.

Wiens (1989) suggests that groups of ecologically different species may follow distinct patterns of species-area relationships and the same argument can be extended to species-isolation patterns. According to Wiens (1989), bird species differ ecologically and these differences can affect species-area patterns. Terborgh (1973) studied species-area relationships for different bird families in the West Indies and found that different families showed family-specific species-area relationships. He interpreted these differences as evidence of different colonization potentials and dispersal abilities. According to Terborgh (Terborgh 1973), weaker species-area relationships indicate good dispersal ability and a tendency for all species in a group to reach all islands. Other studies support the idea that groups of ecologically different species may follow different species-area patterns. Schoener and Schoener (1983a, b) found that occurrences of resident species on Bahamian islands were more closely related to area than were those of migrants, whose distribution was more closely related to distance from a larger island.

A strong species richness-isolation relationship is to be expected when focal species differ in the probability of successful immigration, usually mediated by differences in dispersal ability (Diamond and Terborgh 1967, Lomolino 1996). However, the studies in which this has been investigated typically focus on taxa with relatively poor dispersal abilities (Rundle et al. 2002) or on archipelago systems that are well isolated (Diamond et al. 1976). Considering the relatively modest spatial scale at which the present analysis was conducted, it is not obvious or empirically well supported that tropical birds differ in dispersal ability to a degree that would generate the species-isolation pattern reported here. There is nevertheless indirect evidence that many tropical birds do differ in their abilities to cross even small habitat gaps (Develey and Stouffer 2001, Laurance et al. 2004, Laurance and Gomez 2005). As a consequence it is possible that the species-isolation relationship in this system stems from species-specific differences in dispersal abilities, which in turn result in distance-limited distributions across this landscape.

Individual Species Responses

For forest restricted species, effects of area and isolation were equally present when explaining species occurrences or abundances. The generality of this conclusion is limited by the small number of species analyzed in this group.

The proportion of species in the partially restricted and unrestricted groups that responded to area or isolation in this study was relatively low, indicating that most species do not respond to either attribute. For those species that showed a response, the more prevalent factor when explaining individual species occurrences or abundance was isolation (landscape variable), which was according to expectations. Both the partially restricted and unrestricted groups contain species that are present in mature forest as well as in modified habitats such as secondary growth and man-made shade plantations of coffee and cacao. Their presence in these, sometimes highly modified, habitats indicates more generalized requirements and the ability to exploit resources outside mature forest. As a result, these species are considered to be less sensitive to fragment attributes such as area or habitat quality than species that require mature forest. However, the effects of isolation on these species indicate some restriction on movement or dispersal ability similar to the one displayed by species in the restricted group.

A final consideration should be made as to the validity of the categories used to group species in this study. Species that are considered restricted in one geographic area may not be so in another area, obscuring the response and patterns found in individual studies. In addition, similar studies have been conducted where categories are based on feeding guilds (Arriaga-Weiss et al. 2008), nesting guilds (Matlock and Edwards 2006) and home range size or body mass (Brown and Sullivan 2005). In the majority of these cases species responses corresponded to expectations. It seems that beyond the categories used, responses may be species-specific and vary depending on geographic location, limiting the use of arbitrary categories in trying to generalize conclusions. These studies indicate that taxonomically or ecologically distinct groups differ from one another in their response to patch and landscape variables. Diverse combinations of species from different areas are likely to yield special patterns, and inferring general processes from these patterns should be done with caution, especially when trying to extrapolate results to different geographic areas.

A greater understanding of the role of area and isolation on species richness is of practical as well as theoretical interest. A decrease in habitat area often results in an increase in the distance separating neighboring fragments (Andren 1994), a pattern seen in very diverse tropical forests (DeFries et al. 2005). As protected areas become more isolated, it may be expected that the effect of isolation as a driver of patch richness will increase. This calls for an increase in the magnitude of conservation actions designed to mitigate the negative effect of isolation on patch biota.

Chapter IV

Effects of open areas on the movement of tropical forest birds

Background

Animal movement affects biological processes at different taxonomic and ecological levels. At the individual level, movement influences mating strategies, home ranges, habitat selection and dispersal. At the population level, movement influences the distribution and abundance of individuals, which in turn determine population and community dynamics.

Functional connectivity or "the degree to which the landscape facilitates or impedes the movement among resource patches" (Tischendorf and Fahrig 2000, Belisle 2005) is a measure that integrates the combined effects of individual behavior and landscape attributes into animal movement. Species life history traits such as dispersal strategies, mobility and degree of specialization on certain habitat types are associated with the individual's probability to move but movement does not happen in a featureless environment. Individual behavior is influenced by the landscape. As a consequence, movement decisions are expected to be determined by the type and spatial arrangement of landscape structures such as habitat patches and ecotones.

Currently, only about 22% of the Earth´s tropical forests remain as unbroken, continuous areas (FAO 2005). Most forest areas now exist as collections of isolated fragments in landscapes dominated by anthropogenic habitat (e.g. agroecosystems) and vary in size, shape, and distance from one another. Given the magnitude of habitat fragmentation by human activities, understanding how these landscapes affect individual movement will help in determining the effects of habitat fragmentation on population and community dynamics and in improving conservation practices.

It is often assumed that because birds are highly mobile organisms, their movements are not restricted by open areas in forested landscapes. Studies on the response of temperate species to forest gaps (Desrochers and Hannon 1997, St. Clair et al. 1998, Bayne and Hobson 2001, Norris and Stutchbury 2001) support the assumption that open areas in fragmented landscapes may not constrain movement of migratory birds, even for species considered to be affected by fragmentation in northern latitudes. The migratory behavior of a species, its degree of habitat specialization and the characteristics of the landscape seem to interact to determine the effects of fragmentation on bird movement (Belisle et al. 2001, Norris and Stutchbury 2002, Fraser and Stutchbury 2004).

In the tropics, little is known about movement patterns of forest birds, and the effects of open areas on bird movement are practically unknown. Studies in the Amazon forest provide indirect evidence of the negative effects of road openings and gaps on the movement of tropical forest birds. Laurance et al. (2004) assessed local movement patterns of understory rainforest birds in Central Amazonia and found that movements across a cleared road (25 m wide) were greatly reduced, especially for army-ant follower birds and solitary understory species. Studies using playbacks have found that even small gaps (< 30 m wide) may restrict forest bird movement (Develey and Stouffer 2001, Awade and Metzger 2008). As suggested by these studies, open areas seem to represent strong barriers to the movement of tropical resident birds, especially for terrestrial insectivores. Gaps less than 100 m wide either prevented these species from crossing, or represented a boundary for territories. A recent study by Moore et al. (2008) directly tested the gap-crossing abilities of ten tropical forest bird species with different ecological requirements and forest dependence in the island system of Lake Gatun in central Panama. Using a “dispersal challenge” in which birds were released in the middle of the lake and had to fly to reach the nearest island, Moore et al. (2008) found that most birds in forest-specialist families like antbirds would not cross even 100 m over water. In addition, Moore et al. (2008) found that the success ratio or the relative ability of species to cross water gaps is highly correlated with the distribution of these species in the island system of Gatun Lake.

The success of the experimental release approach of Moore et al. (2008) to explain one of the possible mechanisms that drive species distribution in a system of lake islands raises the question of whether species responses under these conditions (extreme contrast between habitat and non-habitat matrix such as water gaps) could be extrapolated to more traditional fragmented systems. Forest fragmentation occurs more often in the context of removal of areas of native vegetation and the creation of a heterogeneous matrix surrounding habitat islands. In this case, the contrast between habitat islands (or fragments) and the matrix varies depending on the patterns of land use specific to the region and the response of the species to cross habitat gaps is expected to be different from the response shown during over-water release experiments.

The objective of this study was to investigate how open habitat or gaps affected movement patterns of forest birds. I assessed two main hypotheses using a release experiment. First I tested the hypothesis that movement patterns of birds of the tropical forest are affected by the size of the open area or gap-width. I predicted that as gap-width increases, birds would take longer to initiate flight into the open and general orientation towards the forest would decrease. Second, I tested whether movement patterns of forest birds in open areas are homogeneous across different species or whether different species respond in different ways to open habitat. I predicted that movement patterns would vary among species depending on their degree of forest dependence.

Methods

Field Site

This study was conducted in Palenque National Park (PNP) located in the north central area of the state of Chiapas (Fig.4.1) in southeastern Mexico (17°27’51”-17°30’05” N; 92°01’30”-92°04’42” W). The average annual precipitation is 2,000 mm, with a drier season between January and April (average monthly rainfall = 62 ± 18 mm) and a wetter season between May and December (average monthly rainfall = 240 ± 106 mm). The mean annual temperature is 26 ºC (range 22-29 ºC). The forest in the Palenque area is classified as tropical wet forest (Holdridge et al. 1971) with a canopy height of 25-30 m (Diaz-Gallegos 1996).

Palenque National Park offers the optimal ecological and logistical conditions to investigate the effects of habitat fragmentation on forest bird movement. Ecologically, PNP represents one of the few forest reserves officially protected in southeastern Mexico. Due to federal protection, a large tract of forest has been preserved in a region where forests have been heavily fragmented. PNP covers an area of 1,780 ha, about 630 ha of which consist of primary rainforest. The landscape surrounding PNP is dominated by cattle pastures, isolated forest fragments and riparian corridors. Logistically, this landscape provides easy access to landscape sections appropriate to study movement patterns in relation to elements such as forest gaps.

Focal Species

The release experiment focused on six species of forest birds. Three are categorized as forest restricted species (common inhabitants of mature forest and rarely found in degraded forests) and three are considered partially forest restricted species (present in mature and degraded forest, secondary growth and arboreal plantations) according to Estrada and Coates-Estrada (1997) and Robinson et al. (2000). The forest restricted species were represented by the White-breasted Woodwren (*Henicorhina leucosticta*), the Black-faced Ant-thrush (*Formicarius analis*) and the Wedge-billed Woodcreeper (*Glyphorhynchus spirurus*). Partially forest restricted species were represented by the Red-throated Ant-tanager (*Habia fuscicauda*), the Orange-billed Sparrow (*Arremon aurantiirostris*) and the Ochre-bellied Flycatcher (*Mionectes oleagineus*). All six species have similar distributions from southeastern Mexico to northern South America and are considered common to frequent residents of the Atlantic slope from Chiapas, Mexico to Honduras (Howell and Webb 1995). These species were selected because they were the six most-captured species during preliminary mist netting sessions in the main forest tract of PNP (Ibarra unpbl. data).

Bird Captures

To investigate the ability of the six focal bird species to cross narrow habitat gaps, I captured birds using mist nets during June-July 2006 and May-June 2007. All birds were captured in the main forest tract of PNP and the release site was located 1-1.5 km away from any of the capture sites.

At each capture site, a mist netting station consisting of a series of up to 10 mist nets (12 m x 2.5 m, 30 mm mesh size) separated by no more than 50 m was used to capture birds of the forest understory. A netting session consisted of a net station operated for up to four consecutive days. Nets were opened at dawn (0630 h) and remained open until noon (1200 h).

After retrieval from mist nets, birds of the focal species were weighed, visually sexed (when possible) and marked with a combination of colored plastic or aluminum bands or by clipping a small portion (< 2 mm) of a wing feather to allow for detection of recaptured birds. Once marked, birds were individually placed in a soft cloth bag and then inside a shaded box for transportation from capture site to the release landscape (see next section). Other than marking, birds were not manipulated in any way before release. Individuals with visible signs of stress or injury or that were molting more than one flight feather were immediately released at the capture site and were not included in the experiments.

To keep captive and handling times at a minimum, nets were checked to retrieve captured birds at intervals of no longer than 25 minutes. Time spent in captivity (mean=30.7 min, S.D.=12.3) for individuals used in release trials was the time elapsed between removal from the net and experimental release, which varied depending on number of birds captured in the nets at one time.

Release Experiment and Gap-crossing Decisions

I conducted experimental releases to investigate the probability that the six focal bird species would cross forest gaps (covered by cattle pasture) of different sizes. For the purposes of this study, gap-crossing is defined as any movement across non-forested open gaps that represent inhospitable habitat such as cattle pastures (Grubb and Doherty 1999). The landscape used for release experiments consisted of two adjacent rectangular forest patches (~ 3 ha) that shared one of their vertices. These patches were completely surrounded by cattle pastures with isolated trees (Fig. 4.2). In this landscape, I established four release stations in the cattle pasture at incremental distances from the forest edge (Control=0 m, 50m, 100m, 150m). The control group included birds that were subjected to the same manipulations as the rest of the groups, except that they were released at the edge of the forest, under the canopy of overhanging trees and therefore did not have to cross any open gap to enter the forest.

At each release station a release box was placed 1.50 m above ground level with its main door facing the forest fragments. This release box was a wooden box with a front door of translucent but frosted plastic. The box was designed so the front, the top and back doors could be opened, independently, from a distance. At the release station, each individual was retrieved from the cloth bag and placed in the release box. Immediately, observers (two) moved at least 20 m from the release point so the experimental subject was located between the observers and the forest fragments. Individuals were left in the box for 30 seconds for a calming period, period during which the bird stopped fluttering. At the end of the calming period, the front door was remotely opened, starting a decision period of 60 seconds, giving the subject the option of leaving the box and initiating flight or staying. If a bird did not abandon the box during the initial 60-second period, the top door was remotely opened allowing for a second 60-second period. If after this second period the individual still remained in the box, the back door was manually opened by an observer close to the box, forcing the bird to abandon the box. If the bird still failed to leave the box, the observer would retrieve the bird manually, place it in a cloth bag and return it to the capture site and release it.

Two observers recorded the time of departure after the door was opened as either departing during the first or the second 60-second period, or whether the bird was forced out of the box after opening the third door (bird latency to cross the open gap to reach for the forest fragment). After bird departure, two observers recorded flight orientation (direct or indirect toward fragment) and the destination of the first flight bout (fragment, shade tree or ground).

Since ambient light and wind conditions may affect navigation and orientation ability of tropical forest birds (Stratford and Robinson 2005), wind speed and direction and light intensity were recorded at the end of each set of trials (a set included all trials conducted during a sinlge trip to the release station). Light intensity (lux) was recorded as a 15-second exposure average using an Extech® EasyView Light Meter held at the front opening of the release box. Wind speed (m/s) and direction were measured using a Kestrel® 2000 Pocket Wind Meter Plus. Holding the wind meter at breast height, wind speed was recorded as the average of a 10-second exposure in the direction of the highest wind speed during the recording. All trials were conducted on days without rain and with minimum or no wind. No individual was used in more than one release trial.

Protocols for capturing, handling and bird banding follow the Guidelines to the Use of Wild Birds in Research by The Ornithological Council (Gaunt and Oring 1997) and were approved by University of Miami IACUC (protocol number 06-041).

I conducted a total of 299 release trials with the six focal species. Sample sizes ranged from six to 18 per species per distance (Table 4.1). *H. leucosticta* had the lowest sample size (n=6) at 150 m due to its consistent failure to sustain flight when released at that distance. All individuals of *H. leucosticta* released from this distance were able to abandon the box and initiate flight but landed on the ground, a few meters from the release station. Once on the ground, these individuals were unable to reinitiate flight in order to reach any shade or cover and had to be caught by hand by the observers in order to release them in their original capture sites. Given the difficulty of recovering them from the ground and the high probability of predation and excessive stress under the open field conditions (high temperatures, bright light), only six release trials were conducted at 150 m for this species.

The rest of the species had an average of 14 trials per release distance, with the exception of *F. analis*. This species had lower sample sizes for all release distances (seven to nine trials per distance). This was due to their lower abundance in the capture sites and because individuals of these species, even though they were present in the capture sites, tended to detect and avoid mist nets.

Analysis of Data

Potential stressors. The effects of time in captivity, light intensity and wind speed on gap-crossing decisions were tested by using logistic regression. For all distances and for all six species pooled, the probability of initiating flight after the first door was opened (shortest latency to cross gaps) was modeled using logistic regression with time in captivity, light intensity and wind speed as explanatory variables. Logistic regression was also applied to test the association between time in captivity and environmental stressors on flight orientation (direct or indirect) and destination (forest, shade, ground) for all distances.

Gap-crossing behavior. To test the effects of gap-width and species group on the main variables of gap-crossing behavior (latency, orientation and destination), I used three-way contingency tables and log-likelihood ratios. First, for each gap-crossing behavior variable, I conducted a test of overall independence with gap-width, species group and movement behavior variables as factors and frequency of individuals in each cell of the table as the dependent variable. In cases of significant interaction among the three factors, I conducted tests of partial independence for pairs of factors, with special emphasis on the interaction of distance and species group on the response variable. All tests were conducted using general log-linear models in SPSS 17.0 (SPSS 2008) at a significance level of 0.05.

Results

Effects of Handling and Environmental Stressors on Gap-crossing Behavior

Logistic regressions indicated that stress of handling, as measured by time in captivity, was never a significant predictor of movement decisions during release trials. The environmental variables, light intensity and wind strength, also were never predictors of release trial outcomes (Table 4.2).

Effects of Gap-width and Species Group on Gap-crossing Behavior

Latency. Gap-width, species group and level of latency were not independent (*G*=87.039, df=17, *P*<0.001) during release trials (Fig. 4.3). While gap-width had no significant effect on level of latency to abandon the box (*G*=26.581, df=15, *P*=0.115), the effect of species group on latency to cross the gap was highly significant (*G*=60.457, df=2, *P*<0.001). At all gap-widths, the majority of individuals of partially restricted species (85-100%) showed little or no latency to initiate flight to cross the open area once the first door was opened, and only a small proportion of individuals (up to 10% at 50 m) was forced to abandon the box at 50 m and 100 m (Fig.4.3B). In contrast, individuals of the restricted species showed greater levels of latency to abandon the box at all gap-widths. On average, 50% of individuals at each gap-width abandoned the box as soon as the first door was opened, showing little latency to initiate flight into the open, but a substantial proportion of individuals of the restricted species had to be forced to abandon the box even at the smallest gap (36% at 0 m) (Fig.4.3A).

Orientation. Gap-width, species group and orientation of initial flight were not independent (G=100.265, df=10, P<0.001) during release trials. While the effects of gap-width on orientation were independent of species group (G=2.634, df=7, P=0.917), orientation of flight after abandonment of the box was significantly dependent on gap-width (G=97.632, df=3, P<0.001) (Fig. 4.4). For both species groups, at small gap-widths (0 m and 50 m), most individuals (up to 97% and 76% respectively) initiated flight directly towards the forest fragment. At larger gaps (100 m) most individuals in both species groups (up to 76%) displayed an indirect flight path. At the largest gap-width, most individuals (67%) of the restricted species group displayed a direct flight towards the forest whereas at this gap-width, individuals from the partially restricted species group displayed direct and indirect flight in similar proportions (Fig. 4.4 A and B).

Destination. Gap-width, species group and destination of initial flight were not independent (G=266.375, df=17, P<0.001) during release trials. The interaction of distance and destination was independent of species group (G=0, df=11, P=1). For both groups, the proportion of individuals for each destination at each gap-width was similar. Destination of first flight was significantly dependent on gap-width (G=257.144, df=6, P<0.001) (Fig. 4.5). For both species groups, at small gap-widths (0 m and 50 m), most individuals (up to 98% and 79% respectively) reached the forest fragment in a single flight bout. At larger gaps (100 m and 150 m), the majority of individuals in both groups did not reach the forest fragment. Instead, birds of the restricted species flew to reach an isolated tree in the cattle pasture (shade) or landed on the ground near the release site (less than 50 m away) in similar proportions (48-52%) (Fig. 4.5A). Birds of the partially restricted species reached an isolated tree the majority of the time (68%) instead of landing on the ground (32%) (Fig. 4.5B).

Discussion

As expected, open areas affected the movement of tropical forest birds and movement decisions depended on species characteristics. When released in the middle of the cattle pasture, birds of the restricted species showed greater latency to abandon the box and cross the open area to reach the forest fragment, independent of gap-width. While at all distances the majority of individuals of the restricted species showed little latency to cross the open area, a significant proportion of individuals had to be forced to abandon the box and initiate flight at all distances. In contrast, the proportion of individuals of the partially restricted species that refused to abandon the box promptly or were forced to abandon it was minimal at all distances.

The reluctance of some bird groups to cross inhospitable habitat has long been recognized. Diamond (1981) proposed that bird families such as Furnariidae, Formicariidae and Dendrocolaptidae (tropical forest birds) that normally fly over land are behaviorally constrained not to fly over small water gaps. Moore and collaborators (2008) present evidence that supports this idea. In Barro Colorado Island in Gatun Lake, some birds of the tropical forest showed reluctance to cross water gaps as small as 100 m. This reluctance to cross water has been suggested as an explanation for the failure of understory birds to recolonize islands in Gatun Lake (created after the flooding of the area for the Panama Canal) even though the same species are common on the nearby mainland.

In the case of habitat islands, the contrast between the habitat islands (forest fragments) and the modified habitat (cattle pasture) surrounding them, although not as strong as a land-water contrast, may be sufficient to prevent birds adapted to forest conditions from venturing out into the open and crossing even small forest gaps. Studies conducted with Amazonian forest birds showed that gaps as small as 30 m wide prevented army-ant follower birds and mixed species flocks from crossing them (Develey and Stouffer 2001, Laurance et al. 2004). For these species, forest gaps may represent a barrier to their movement and these conclusions are supported by the results of the present study.

Two main mechanisms have been proposed to explain the latency of some tropical forest bird species to fly across open habitat. On the one hand, physiological constraints may be behind the latency or inability of some species to venture into and across open areas. For many species the matrix constitutes unsuitable and potentially hostile habitat (Robinson et al. 1995, Turcotte and Desrochers 2003). Abrupt forest ecotones near agricultural systems are subject to diverse edge effects that alter forest structure, light levels and thermal regimes (Murcia 1995, Laurance et al. 2002). Such environments may pose physiological stresses such as increased temperatures, dehydration and even increased starvation risk to bird species adapted to the dark, humid conditions of forest interiors. Some understory birds appear so specialized on dark forest conditions that they have been observed avoiding even tree-fall gaps and forest regrowth (Thiollay 1992, Borges and Stouffer 1999).

On the other hand, other authors (Greenberg 1989, Lima and Zollner 1996) have suggested that latency to cross open areas is a behavioral response to inhospitable habitats in which predation risks may be different and higher. In open habitats, the relative risks posed by predators such as diurnal hawks and falcons are different from the typical ones that forest interior species may encounter (aerial predators vs. terrestrial predators). In open areas, forest interior birds may lack efficient strategies to avoid such predators and the avoidance of open areas may be the response to reduce predation risks (Rodriguez et al. 2001).

While the effects of species characteristics (restricted vs. partially restricted) are significant during the initial response of birds to open gaps (latency), once birds have entered the open area, size of the gap significantly influences movement decisions for both groups. At small gaps, birds flew directly towards the forest and reached it in a single move. At larger gaps, bird flight became indirect and aimed toward isolated trees in the open with some birds landing on the ground.

A main assumption in this study was that birds would always prefer to move towards the forest fragment (their preferred habitat) and reach its cover as soon as possible. As expected, gap-width affected movement decisions. A possible explanation as to how gap-width may affect movement decisions has been proposed by Lima and Zollner (1996). According to these authors, an animal's 'perceptual range' is the range or distance at which an animal can perceive a landscape element. Lima and Zollner (1996) propose that this perceptual range determines the ease with which individuals can locate habitat patches, and hence the time they spend searching in a hostile matrix for resources or refuge to prevent predation (Gaines and McClenaghan 1980). Two hypotheses can explain how perceptual range could affect the lack of initial orientation during the release trials at wider gaps. First, species included in this study could have inherent short perceptual ranges and as gap-width increases birds are unable to efficiently locate the forest and fly directly towards it. Although birds in general are expected to have long-distance perception (Blough 1971, Zollner 2000), perceptual distance is expected to be highly dependent on the species (Lima and Zollner 1996). Species that have had a long-term evolutionary history in open or naturally fragmented landscapes should have increased perceptual abilities appropriate to the scale of their environment (Zollner and Lima 1999), whereas forest interior species could have shorter perceptual ranges adapted to conditions of denser vegetation and low light levels. Unfortunately, little is known about the perceptual ranges of forest interior birds and their relation to environmental conditions to support this assumption. Second, forest birds could have perceptual ranges similar to species adapted to conditions of open landscapes. However, the “harsh” environmental conditions in the open could affect the perceptual ranges of forest species. A bird used to dim light in the forest understory could be temporarily “blinded” by the bright conditions in the open matrix, and unless the individual is close enough to the forest fragment for it to dominate the field of view, the individual is unable to locate the forest fragment efficiently.

Perceptual range is certainly not the only factor affecting movement decisions. Landscape characteristics such as the presence of fence rows, isolated trees or the composition of the matrix may be significant for dispersing animals as suggested in this study. At larger gaps, both restricted and partially restricted species of birds tended to fly to isolated trees in the middle of the cattle pasture, probably using these isolated trees as stepping stones. This behavior reduced the maximum distance crossed in the open in a single flight and therefore the potential risks of physiological stress or predation. In doing so, the existence of corridors or even isolated trees may facilitate the movement of forest birds in fragmented landscapes.

Understanding movement patterns of animals in fragmented landscapes is a major goal for the integration of behavioral and landscape ecology. In order to provide models used to predict species persistence in fragmented landscapes with sound biological information, the understanding of how landscape characteristics impede or facilitate individuals' movement among patches is essential. By studying movement patterns in relation to landscape attributes, this study showed that habitat gaps of increasing width affect movement decisions of birds in open areas. This increases our understanding of the potential effects of habitat fragmentation on mechanisms that affect population processes, such as dispersal, and species persistence in fragmented tropical landscapes. This study also provides empirical data on bird movement that can be used to improve conservation practices such as the implementation of stepping stones in the open matrix that may facilitate bird movement in fragmented landscapes, mitigating the effects of tropical forest loss and fragmentation.

Chapter V

Effects of corridors on the movement of tropical forest birds

Background

Throughout human history the vegetation cover of the Earth's surface has been extensively modified as the result of the development of agricultural systems, logging activities and the expansion of urban areas. Removal of native vegetation results not only in the loss of significant areas of original habitat, but also in its fragmentation. Fragmentation results from the selective removal of areas of vegetation, leaving behind patches of native habitat that are not suitable for development due to terrain steepness, poor soil quality or flood risk, or serve a specific function such as nature reserves, protection for river banks and hunting areas. These remnants of native habitat exist as a collection of isolated fragments in a heterogeneous landscape dominated by anthropogenic habitat (e.g. urban developments, agroecosystems, secondary growth vegetation) and vary in size, shape, location and isolation (Saunders et al. 1991, Laurance et al. 2002).

Habitat corridors are a common strategy to reduce the negative impacts of habitat fragmentation. Corridors connect otherwise isolated patches of habitat, connecting isolated populations with sources of migrants and therefore reducing the negative effects of demographic and genetic stochasticity or inbreeding associated with habitat fragmentation (Clinchy 1997, Moilanen and Hanski 1998, Fleishman et al. 2002, Ovaskainen and Hanski 2004).

The use of corridors in conservation has been controversial since it is unclear which species benefit from corridors. While some studies show that movement rates, gene flow and population sizes of taxa such as birds (e.g. Haas 1995, Warkentin et al. 1995, Lees and Peres 2008), and mammals (e. g. Bakker and van Vuren 2004, Lada et al. 2008) effectively increase in the presence of corridors, other studies have shown no effects of corridors on animal movement rates or population sizes of the same groups (Arnold et al. 1991, Date et al. 1991, Lees and Peres 2008).

While studies on the effect of forest corridors on bird movements have been focused on temperate regions (Machtans et al. 1996, Belisle 2005) questions remain about whether open areas in tropical forests prevent bird movement and to what extent corridors mitigate these effects.

I previously demonstrated that forest gaps prevent bird movement and that when crossing large gaps, birds use isolated trees as stepping stones across forest gaps (Ibarra unpublished data). If the presence of trees in forest gaps facilitates bird movements, then forested corridors should also have a positive effect on bird movements.

The main objective of this study was to investigate whether forested corridors facilitate the movement of tropical forest birds in a deforested landscape. Using a translocation experiment in the presence and absence of corridors, I tested the hypothesis that forest corridors facilitate the movement of forest birds in a deforested landscape. I predicted that if corridors facilitate bird movement, birds would be more likely to move between patches connected by forest corridors than between patches that lack the connection provided by corridors. Therefore, return rates of individuals translocated between patches connected by corridors would be higher than the return rates of individuals translocated between patches that lack a physical connection.

The second objective of this study was to investigate whether species characteristics influence the use of forested corridors by tropical forest birds in a deforested landscape. I tested the hypothesis that the effect of corridors on bird movement would be different for different species groups. Using the degree of forest dependence as an indicator of the species' willingness to cross forest gaps, I predicted that, because forest restricted species are less likely to cross forest gaps, corridors would have a strong positive effect on the return rates of individuals of the forest restricted species. In contrast, individuals of the forest unrestricted species are more likely to cross forest gaps and as a result, return rates between connected or unconnected patches should not be significantly different.

Methods

Field Site

This study was conducted in Palenque National Park (PNP) located in the north central area of the state of Chiapas (Fig.5.1) in southeastern Mexico (17°27'51"-17°30'05" N; 92°01'30"-92°04'42" W). The average annual precipitation is 2,000 mm, with a drier season between January and April (average monthly rainfall = 62 ± 18 mm) and a wetter season between May and December (average monthly rainfall = 240 ± 106 mm). The mean annual temperature is 26 ºC (range 22-29 ºC). The forest in the Palenque area is classified as tropical wet forest (Holdridge et al. 1971) with a canopy height of 25-30 m (Diaz-Gallegos 1996).

Palenque National Park offers excellent ecological and logistical conditions to investigate the effects of habitat fragmentation on forest bird movement. Ecologically, PNP represents one of the few forest reserves officially protected in southeastern Mexico. Due to federal protection, a large tract of forest has been preserved in a region where forests have been heavily fragmented. PNP covers an area of 1,780 ha, about 630 ha of which consist of primary rainforest. The landscape surrounding PNP is dominated by cattle pastures, isolated forest fragments and riparian corridors where bird movement in relation to fragments, forest gaps and corridors can be studied.

Translocation and Effect of Corridors

The effect of forest corridors on bird movement was investigated by studying return rates of birds translocated under two treatments: 1) birds translocated between pairs of *unconnected* patches (patches separated about 518 m and completely surrounded by cattle pasture, and therefore not physically linked) and 2) birds translocated between pairs of *connected* patches (patches separated about 580 m and surrounded by cattle pasture but connected by forested corridors, and therefore physically linked).

Using a combination of field surveys and aerial photographs I selected 10 pairs of fragments (5 pairs for trials with connected patches and 5 pairs for trials with unconnected patches) and kept area of capture and release patches, as well as distance between pairs of patches, relatively similar between treatments (Fig. 5.1).

In order to determine the potential effects of area and distance between patches, I determined area of capture and release patches and distance between them for all trials. I estimated the area, in ha, covered by forest vegetation in each patch. Distance between patches was defined as the Euclidean distance between the closest points of the two patches in each pair. These patch attributes were estimated using a digitized and orthocorrected aerial photograph (scale 1:20,000) of the Palenque municipality area (INEGI 2001). All focal fragments were digitized from the photograph using ArcGIS 9.0 (ESRI 2008) and area and distances were estimated using the Spatial Analyst tool from ArcMap 9.3 (ESRI 2008) followed by corroboration in the field.

Bird Capture and Translocation

Birds were captured in each of the capture patches using mist nets. In each capture patch a series of up to ten mist nets (12 m x 2.5 m, 30 mm mesh size) separated by up to 100 m was operated daily from dawn (0630 h) until 1700 h. All birds captured were weighed, visually sexed (when possible) and marked with a combination of color plastic bands to allow individual identification. Only healthy adult birds were used for translocation. Birds with visible signs of injury, molting of flight feathers or low weight were not included in the study.

In both treatments, connected and unconnected, birds were captured in one patch (capture patch) and released in the other patch of the pair (release patch) in order to investigate the effect of corridors on return rates.

To detect birds that returned from the release patch to the capture patch, mist nets were operated at the capture patch for seven consecutive days (three days open, one day closed, three days open). On the fourth day nets remained closed to help reduce bird awareness of net position, thus increasing the probability of recaptures. From capture-recapture data I calculated the return rate for each trial as the proportion of translocated individuals that were recaptured in the capture patch after being translocated.

Recapture probabilities may vary due to species and habitat specific characteristics. To control for possible species and habitat effects that may confound the effects of corridors on return rates, I conducted capture-recapture studies in six of the ten capture fragments included in this study (three capture patches of the connected treatment and three capture patches of the unconnected treatment). In each of these, I used the same capture protocol described above except that all birds captured were released in the capture fragment (not translocated) and recapture probabilities were calculated as the proportion of captured birds that were recaptured during the sampling period.

Protocols for capturing, handling and bird banding follow the Guidelines to the Use of Wild Birds in Research by The Ornithological Council (Gaunt and Oring 1997) and were approved by University of Miami IACUC (protocol number 06-041).

Species Groups

To examine how species characteristics may influence the role of corridors on bird movement, species were categorized as forest restricted or forest unrestricted according to Estrada et al. (1997) and Graham and Blake (2001). These authors worked in a similar fragmented landscape in southeastern Mexico and their studies represent the closest geographically related data set to the one in the present study. Estrada et al. (1997) reported abundances for bird species found in forest patches, arboreal crops (cacao, coffee, mixed crops, citrus, allspice) and non-arboreal crops (corn, jalapeno, chili pepper, bananas, pasture). Species were classified according to the following criteria:

- *Forest restricted*: Species whose abundance in forest patches was at least two times greater than its abundance in the arboreal crops, and were absent from non-arboreal crops.
- *Unrestricted*: Species that were more abundant in arboreal crops than in forest patches and were present in at least two of the non-arboreal crops.

Analysis of Data

To control for the potential effects of landscape variables on return rates I used a t-test to evaluate differences in landscape variables (area of capture site, area of release site and distance between pairs of sites) between connected and unconnected treatments. I also tested for potential correlation between landscape variables and overall return rates (all species pooled together) in both treatments by performing a linear regression analysis with area of capture site, area of release site and distance between sites as independent variables and return rates per site as the dependent variable.

To investigate the possible effects of habitat on recapture probabilities, I compared recapture rates in the three capture fragments of the connected treatment versus the recapture rates in the three capture fragments of the unconnected treatment.

To investigate if corridors facilitate bird movement (first objective), I compared return rates using a Wilcoxon rank-sum test with treatment (*connected* vs. *unconnected*) as the explanatory variable and return rate for all species pooled together (proportion of translocated individuals that return to the capture patch) as the dependent variable to test the hypothesis that return rates are equal between connected or unconnected sites. If corridors facilitate bird movement, birds are more likely to return to their capture patch (higher return rates) under the connected treatment than under the unconnected treatment.

To test the hypothesis that species group and the presence of a corridor interact to influence bird movement in fragmented landscape (second objective), I grouped translocated birds into two groups: forest restricted species (species found only in mature forest or old secondary growth and thought to be more sensitive to habitat fragmentation) and unrestricted species (species found in old forest but also found in more open habitats and less sensitive to fragmentation) (Graham and Blake 2001). I calculated mean return rates for both groups across the five replicates to test the hypothesis that corridors affect return rates. If corridors facilitate movement, and this effect is stronger for restricted species, movement rates of restricted species would be higher between connected patches and lower between unconnected patches. If movement of unrestricted species is less affected by corridors, movement rates between connected and unconnected patches would be similar.

To investigate the effects of corridors and species group on return time for translocated individuals, I used a Cox regression to compare return times of returning individuals in both treatments or in both species groups. Cox regression builds a predictive model for time-to-event data. This model produces a survival function that predicts the probability that the event of interest (return) has occurred at a given time t for given values of the predictor variables (corridor treatment or species group).

Results

Effects of Landscape Variables on Return Rates

Area of capture site, area of release site and distance between capture and release site were not significantly different between the connected and unconnected treatments (Table 5.1).

None of the landscape variables entered models of linear regression of landscape variables on return rates (all species pooled or return rates for restricted and unrestricted species separately). This indicates that none of these landscape variables explain significant variation in return rates for either treatment or species group.

Effects of Corridors on Return Rates

A total of 235 individuals were translocated during this experiment (connected=90 individuals; unconnected=145 individuals). Of those, only 13% (31 individuals) were recaptured during this experiment (Table 5.2).

Corridors had a positive effect on return rates. Return rates (all species pooled together) between connected sites were significantly different from return rates between unconnected sites (Table 5.2). On average, return rates between connected sites were six times higher than those in unconnected sites (Table 5.2).

Effects of Species Group on Return Rates

For the forest restricted species group, although return rates seem higher in the connected treatment than in the unconnected treatment, this difference was not statistically significant (W=19.5; P=0.190). This indicates that the presence of corridors did not affect return rates for the restricted species group since in both cases (connected and unconnected) return rates were low (Table 5.2) with only up to 12% of individuals being recaptured after translocation (Fig. 5.2).

In contrast, return rates for the unrestricted species group were significantly different when comparing connected vs. unconnected patches (W= 15.0; P=0.008). For this species group, corridors did have a positive effect and the return rate between connected patches was around eight times greater than the return rate between unconnected patches (Table 5.2, Fig. 5.2).

Effects of Corridors on Return Times

The mean return time for translocated birds was 51.2 hr for the connected treatment and 45.9 hr for the unconnected treatment (Fig. 5.3). Return times, measured using Cox proportional hazards regressions, were not significantly different between treatments (Table 5.3) indicating that birds that returned took on average the same time regardless of the presence of a corridor.

Effects of Species Group on Return Times

The mean return time for returning birds was 54.3 hr for individuals of the unrestricted species and 34.7 hr for individuals of the restricted species (Fig. 5.4.). Return times, measured using Cox proportional hazards regressions, were significantly different between the two species groups (Table 5.3), with individuals of the unrestricted species taking longer to be recaptured at their original capture site.

Discussion

The efficacy of wildlife corridors in facilitating animal movements between habitat patches remains controversial (e. g. Rosenberg et al. 1997, Beier and Noss 1998). Many forest taxa appear to respond positively to corridors. Corridors can be used by forest wildlife as conduits through which animals can disperse between forest patches, providing habitat linkages (forest habitat that supports resident populations or links populations among patches) (Rosenberg et al. 1997, Lidicker 1999).

In translocation studies that explored effects of landscape on return rates (e.g. Boscolo et al. 2008, Gillies and St. Clair 2008), distance between fragments was found to predict return rates for forest birds and it should be acknowledged when interpreting results of translocation trials. The fact that landscape variables (area of patches and distance between them) did not affect return rates in the present study is expected given the effort made to keep variation of landscape variables between treatments to a minimum. The homogeneity of landscape variables among trials, for both connected and unconnected treatments, increases the confidence that the results found were mainly determined by the presence of corridors or the effects of species group.

As I predicted, when considering all species pooled together, corridors had a positive effect on return rates, indicating that they facilitate bird movement in deforested landscapes. These findings are comparable to other translocation studies that have found that forest cover facilitates movement of forest birds, which were more likely to return to their territories as forest cover increases (Belisle et al. 2001, Boscolo et al. 2008). Corridors may affect bird return rates by providing forest cover that facilitates bird movement in an otherwise completely open landscape. Studies with tropical forest birds have shown that forest birds show latency to cross open areas (Moore et al. 2008) and birds will use isolated trees as stopping points when crossing cattle pastures (Ibarra unpublished data). Higher predation risk and physiological stress associated with crossing open areas (Laurance and Gomez 2005, Zollner and Lima 2005, Moore et al. 2008) may be ameliorated by the use of forest or tree cover during movement. Studies have demonstrated that when given the choice of reaching a destination either by crossing an open area or by using a detour under forest cover, birds usually choose the detour option, although the latter can substantially increase the duration and distance that they must travel (e.g. St. Clair 2003, Gillies and St. Clair 2008, Ibarra unplublished data). Although limited in area, forested corridors provide this type of forest cover, increasing the chances that birds will move between patches when corridors are available.

The prediction that the effects of corridors would be stronger for forest restricted species than for forest unrestricted species was not supported by the present study. My results showed that corridors have a positive effect on return rates for both groups. However, this effect was not stronger for the forest restricted species whose return rates were not significantly different between treatments. In contrast, corridors had a strong effect on the return rates of unrestricted species for which corridors increased return rates significantly.

When comparing return rates between species groups, one has to take into account that different species may differ in their recapture probabilities, which will affect any comparisons. The lack of effect of corridors on the restricted species group may be due to very low recapture probability for restricted species, regardless of the presence of corridors. Low recapture rates, especially for individuals of the restricted group, make it difficult to draw strong inferences about the effects of forested corridors and species characteristics on bird movement and return rates. Without explicit information on recapture probabilities of the species included in this study, conclusions should be drawn with caution.

Contrary to expectations, when all species are pooled together, overall return times were not affected by the presence of corridors. On average, translocated individuals took a similar amount of time to return to the capture site, regardless of the presence of a corridor. This is unexpected because previous translocation studies (Belisle et al. 2001) have found that forest cover reduces the return time of homing birds. My unexpected results could be due to the predominance of individuals of unrestricted species in the overall sample and their movement patterns in fragmented landscapes. Individuals of unrestricted species show relatively high mobility and less reluctance to cross gaps in deforested landscapes (Diamond 1981, Laurance and Gomez 2005, Moore et al. 2008). As a result, individuals of the unrestricted species can use shorter routes and move faster even in the absence of forested habitat. Despite the lack of effects of corridors on return times, the strong effect of corridors on return rates supports the idea that open areas limit bird movement (Gillies and St. Clair 2008, Moore et al. 2008).

When return times are compared between species groups, data from this study suggest that restricted species took less time to return to the capture site after translocation. This result is unexpected given evidence from other studies that show that restricted species are less likely to cross open areas and therefore, less likely to return to their territories if they have to traverse forest gaps (Castellon and Sieving 2006, Shirley 2006). Gillies and St. Clair (2008), who had information on the traveling paths of translocated individuals, found that return times of a forest generalist were significantly shorter than those of a forest specialist. Without information on movement patterns of individuals of both species groups included in this study, interpretation of the unexpected results should be made with caution. One possible reason as to why individuals of the unrestricted species took longer to return, regardless of the presence of corridors, is that these species tend to be more mobile and less restricted by open areas (Haas 1995, Ibarra unpublished data), Belisle 2005, Stratford and Robinson 2005). This could allow individuals to explore the landscape, visiting various potential sites, before returning to their original capture site. In addition, species of the unrestricted group have been reported to use different types of vegetation in the landscape and are not restricted to mature forest, while forest restricted species are especially restricted to forest patches (Estrada et al. 1997, Graham and Blake 2001). In a heavily fragmented landscape, where forest patches are a limited resource but where shade plantations or secondary growth patches are readily available, the flexibility of unrestricted species to use alternative habitats may allow them to find refuge in surrounding vegetation patches, freeing them from the pressure to find their original patch, even if only temporarily.

In conclusion, when considering return rates alone, my results lend support to the idea that corridors affect the movement of forest birds in deforested landscapes. The evidence for the influence of species characteristics on return rates is inconclusive, especially due to small sample size for the forest restricted species group.

The biological benefits of corridors depend on landscape configuration. If corridors channel organisms to poor quality habitat or ecological traps, then corridors may actually increase the probability of adverse demographic and genetic effects on fragmented populations. To be beneficial, corridors must promote movement and provide a path directing organisms to high quality habitat. Only under these circumstances, would corridors actually help mitigate negative demographic and genetic effects of habitat fragmentation and isolation. Under these conditions, preservation of high quality habitat should be undertaken along with preservation of their physical connectivity.

Chapter VI

General conclusions

Area has an unquestionable effect on species richness in habitat islands. The pattern of species richness increasing with area has long been studied and recognized for oceanic islands and more recently for habitat islands in fragmented landscapes (MacArthur and Wilson 1967, Cook et al. 2002). As area is reduced, fragments are less likely to provide resources for species that require large areas or rare resources. Bird communities in forest fragments included in the present study follow the classic species-area relationship where larger fragments host richer bird assemblages.

Although less prominent in the literature, the potential relationship between habitat island isolation and species richness has recently emerged as a central theme in fragmentation studies (DeFries et al. 2005, Watling and Donnelly 2006, Ferraz et al. 2007). In the present study, fragment isolation, measured as distance of forest fragments from continuous habitat or as the proportion of forest cover surrounding focal fragments, was a significant predictor of species richness in fragments, especially for large fragments further away from the largest forest reserve in the landscape.

Analyses of the effects of area and isolation on species richness of groups with different degrees of forest dependence showed that only species richness of forest restricted species was affected by area and isolation, whereas species richness of the partially restricted or unrestricted species groups were not affected by these factors. The significant effects that area and isolation have on specific species groups suggest that habitat and species characteristics interact to limit species distribution through the effects of fragmented landscapes on bird movement.

As supported by the results of the release experiment, bird movement is affected by open areas and the effect depends on species characteristics to a great extent. Species group was a good predictor of the reluctance of birds to venture across a forest gap while gap-width influenced movement patterns in open areas indicating that open areas may restrict and negatively affect movement patterns in fragmented landscapes. The three species included in the forest restricted species group in the release experiment were present in less than five fragments, indicating a strong effect of area and isolation for this group. As an example, *H. leucosticta*, the species that showed the poorest performance during release trials (not a single individual was able to traverse 150-m gaps), was present only in the largest fragment that was the closest to PNP. For the unrestricted species, multiple regression analyses did not detect an effect of isolation.

For the set of species included in the present translocation study, corridors had a positive effect on bird movement facilitating the return of translocated birds to their territories. When combined with observations gathered during gap-crossing movements, where birds released at wider gaps used isolated trees as stepping stones while traversing a hostile matrix, the results of the translocation experiment reinforce the idea that in a heavily fragmented landscape, corridors may provide some of the functional connectivity required to maintain fragmented populations connected.

Although theoretical models such as island biogeography theory (MacArthur and Wilson 1967) and metapopulation models (Moilanen and Hanski 1998, Hanski and

Ovaskainen 2003) have proven to be a powerful tool in the study of species and population dynamics in fragmented landscapes, further progress in investigating the impact of habitat loss and fragmentation cannot be made without providing models with more biological realism, making more of the model assumptions explicit. Whether fragmentation impedes movement and disrupts dispersal seems to depend not only on landscape characteristics, but also on species attributes. Unfortunately, very little information exists on movement patterns and dispersal of tropical species. The aim of this study was to generate empirical data on movement patterns and response of individuals in fragmented landscapes that allow the improvement of conservation practices and theoretical tools used to predict metapopulation dynamics and species persistence.

Given the high competition for resources (money and land devoted to nature reserves) for conservation practices, especially in tropical countries that face strong socioeconomic pressures, information that allows efficient conservation practices is greatly needed. Knowing how fragmented landscapes modify individual behaviors that affect population dynamics and species persistence will improve conservation practices. If the modified landscape in which fragments are embedded prevents the movement of individuals and therefore disrupts metapopulation dynamics, special emphasis should be placed on maintaining habitat connectivity.

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Figures

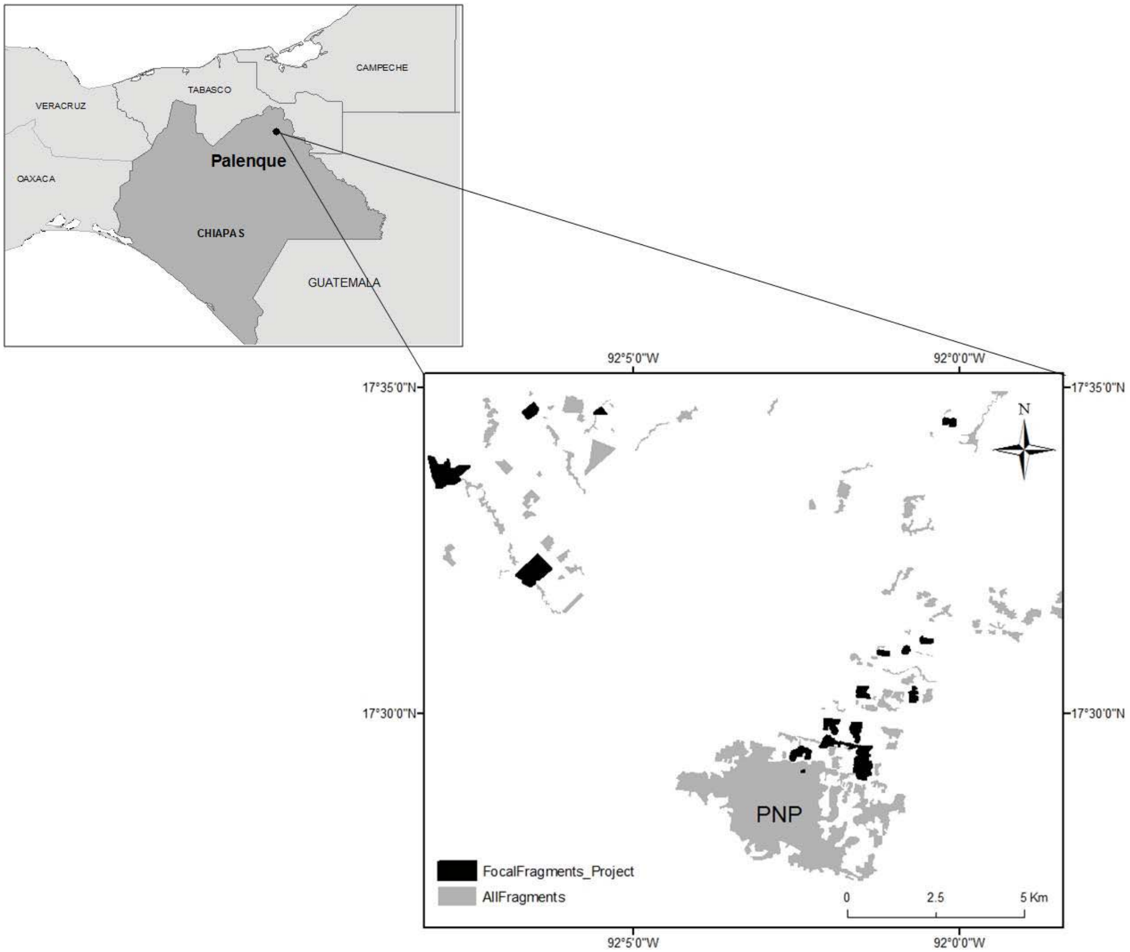


Figure 2.1. Map showing the geographic location of the field site, Palenque National Park (PNP), in the state of Chiapas, Mexico. Gray polygons represents forest habitat in PNP and isolated fragments. Black polygons represent the seventeen fragments included in the present study.

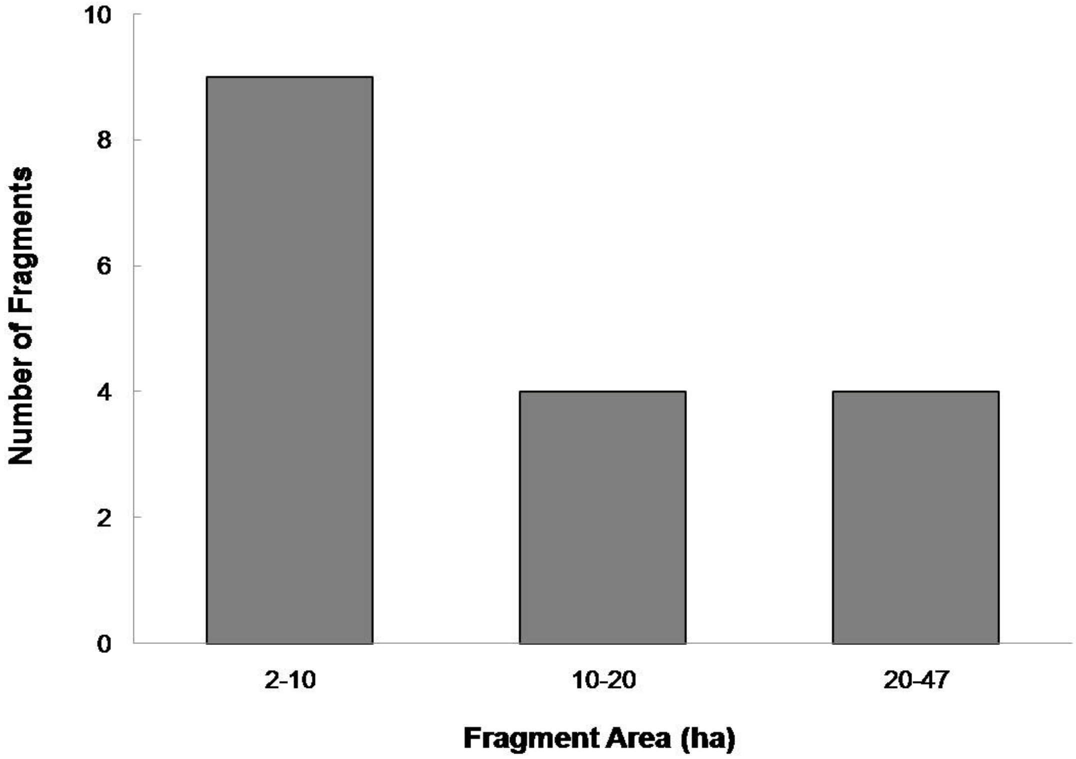


Figure 2.2. Number of focal fragments in each of three size classes.

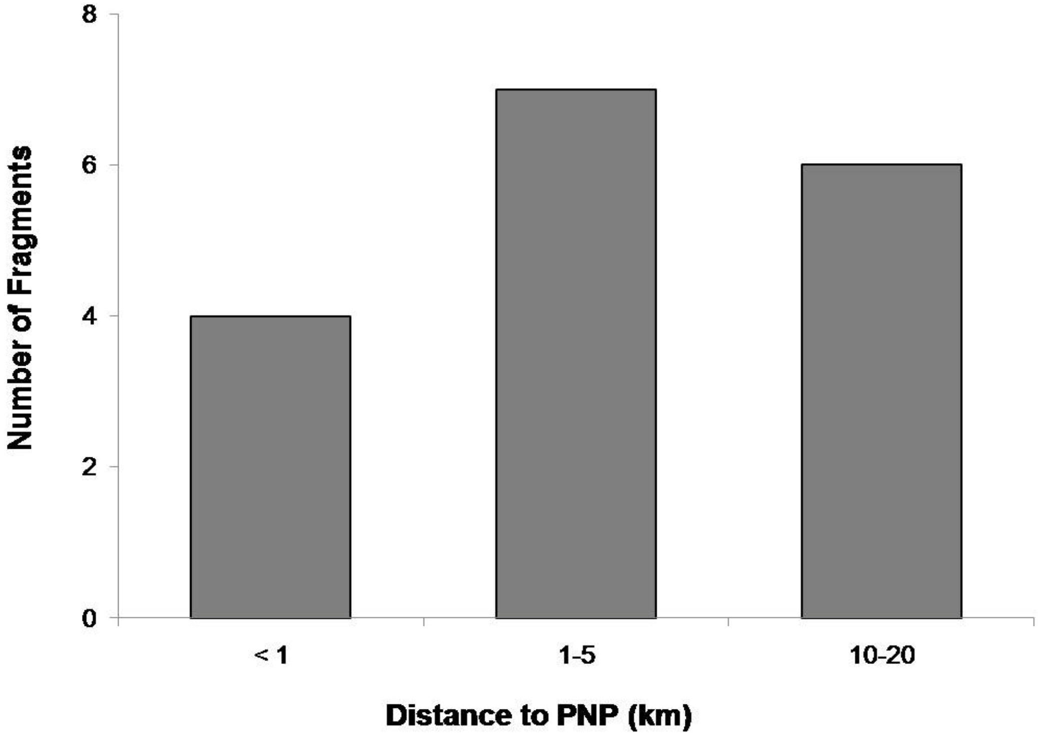


Figure 2.3. Number of focal fragments in each of three classes based on their distances from Palenque National Park (PNP).

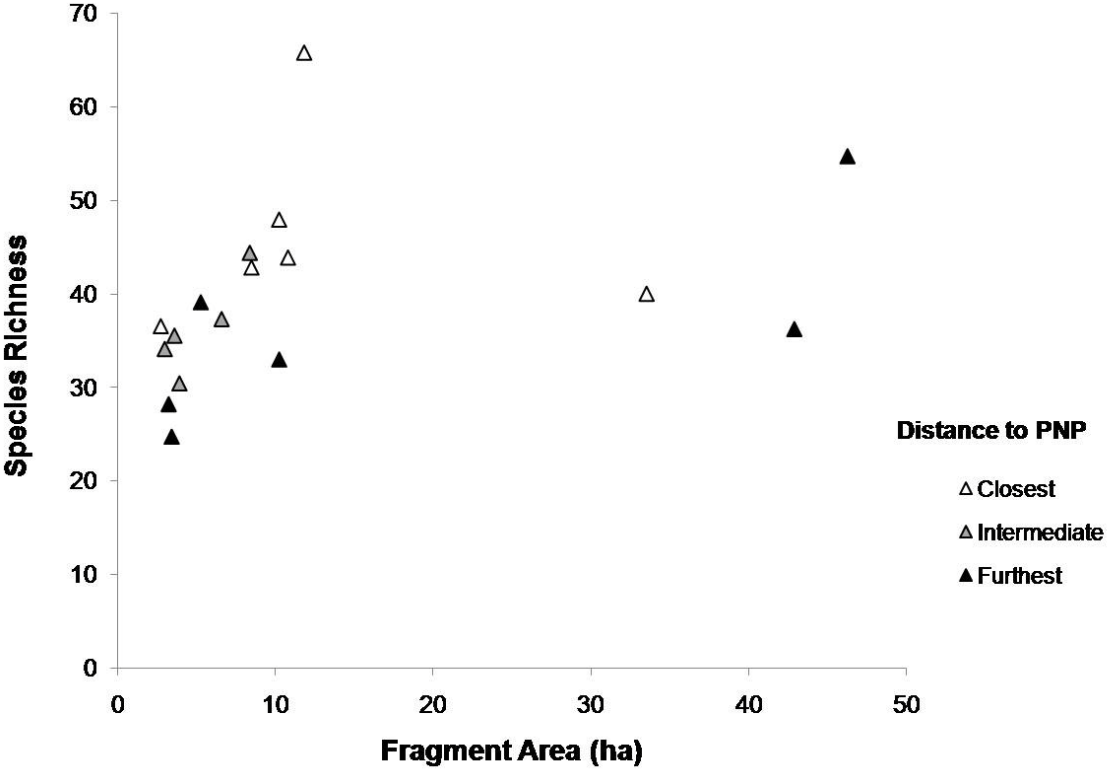
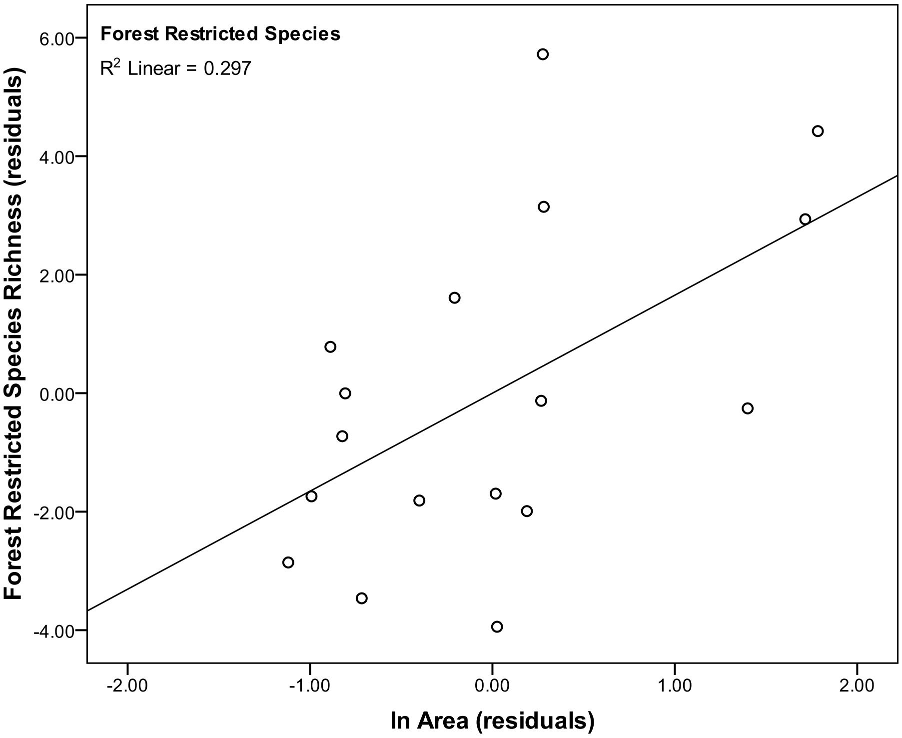


Figure 2.4. Relation between fragment area and species richness. Each point represents a focal fragment and its color represents its distance from Palenque National Park (PNP) in three categories: black (fragments closest to PNP), gray (fragments at intermediate distance from PNP) and white (fragments furthest away from PNP).



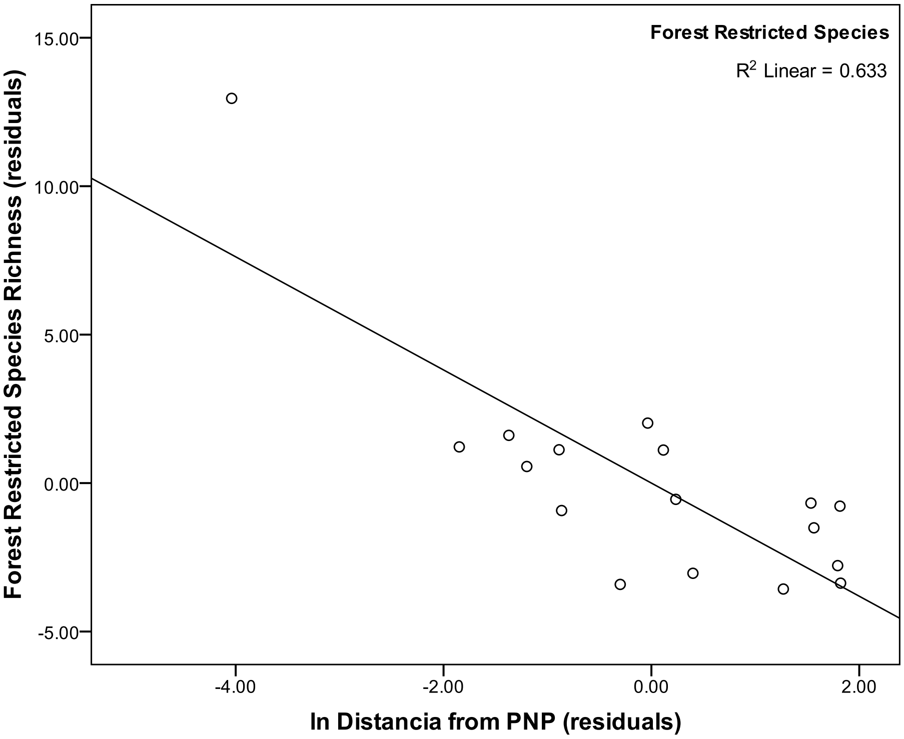


Figure 3.1. Partial residual plots showing the species-area and species-isolation, (Distance from Palenque National Park, PNP) relationship for forest restricted species.

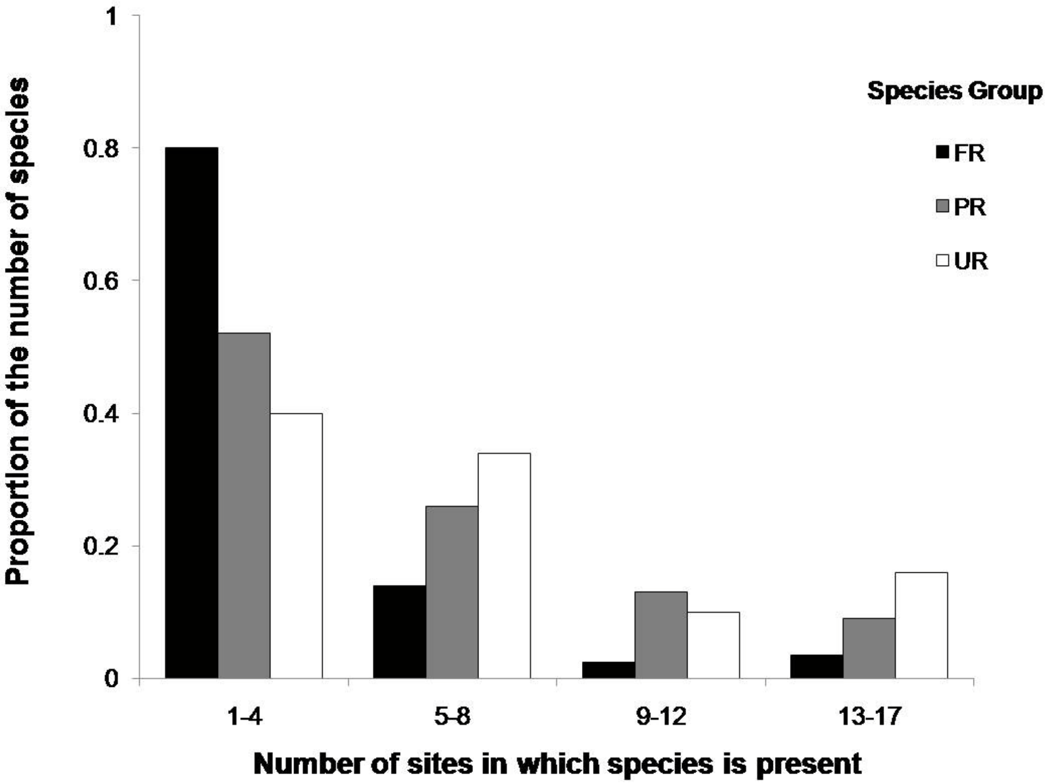


Figure 3.2. Frequency of occurrence of species per group in forest fragments (FR = Forest Restricted; PR = Partially Restricted; UR = Unrestricted).

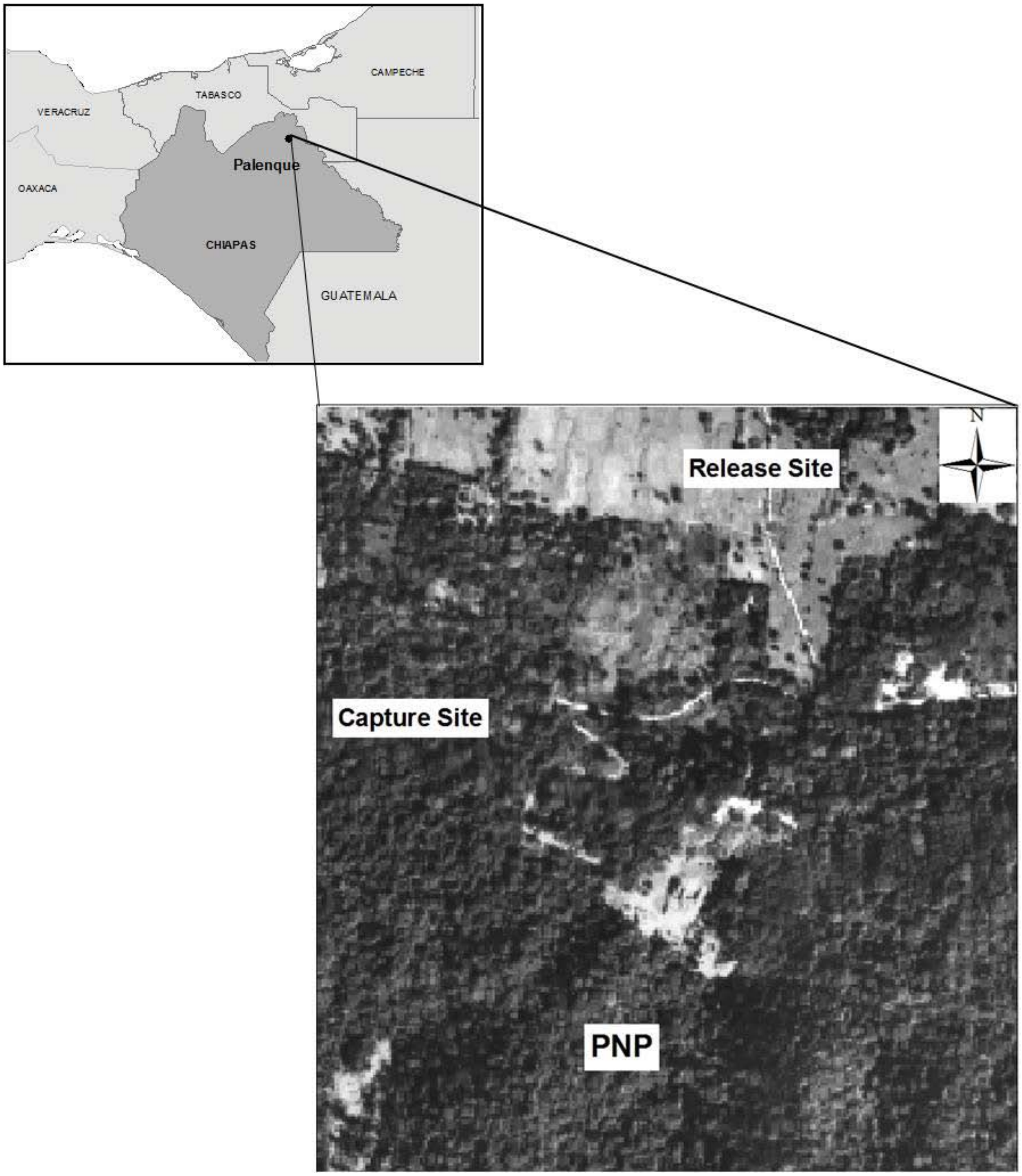


Figure 4.1. Map showing the geographic location of the field site, Palenque National Park (PNP) and the landscape in which the release experiment was conducted.

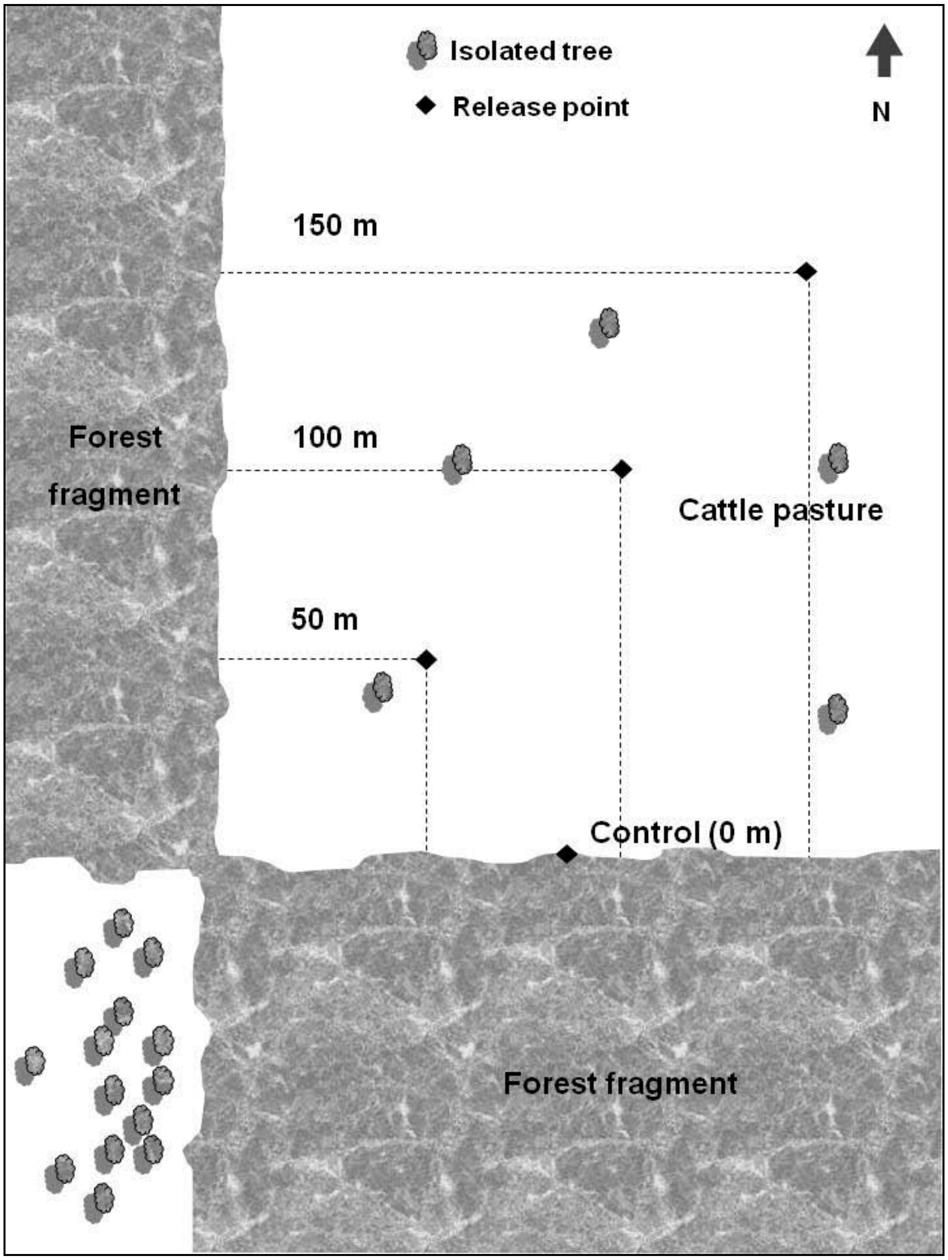


Figure 4.2. Configuration of the landscape section were release trials were conducted.

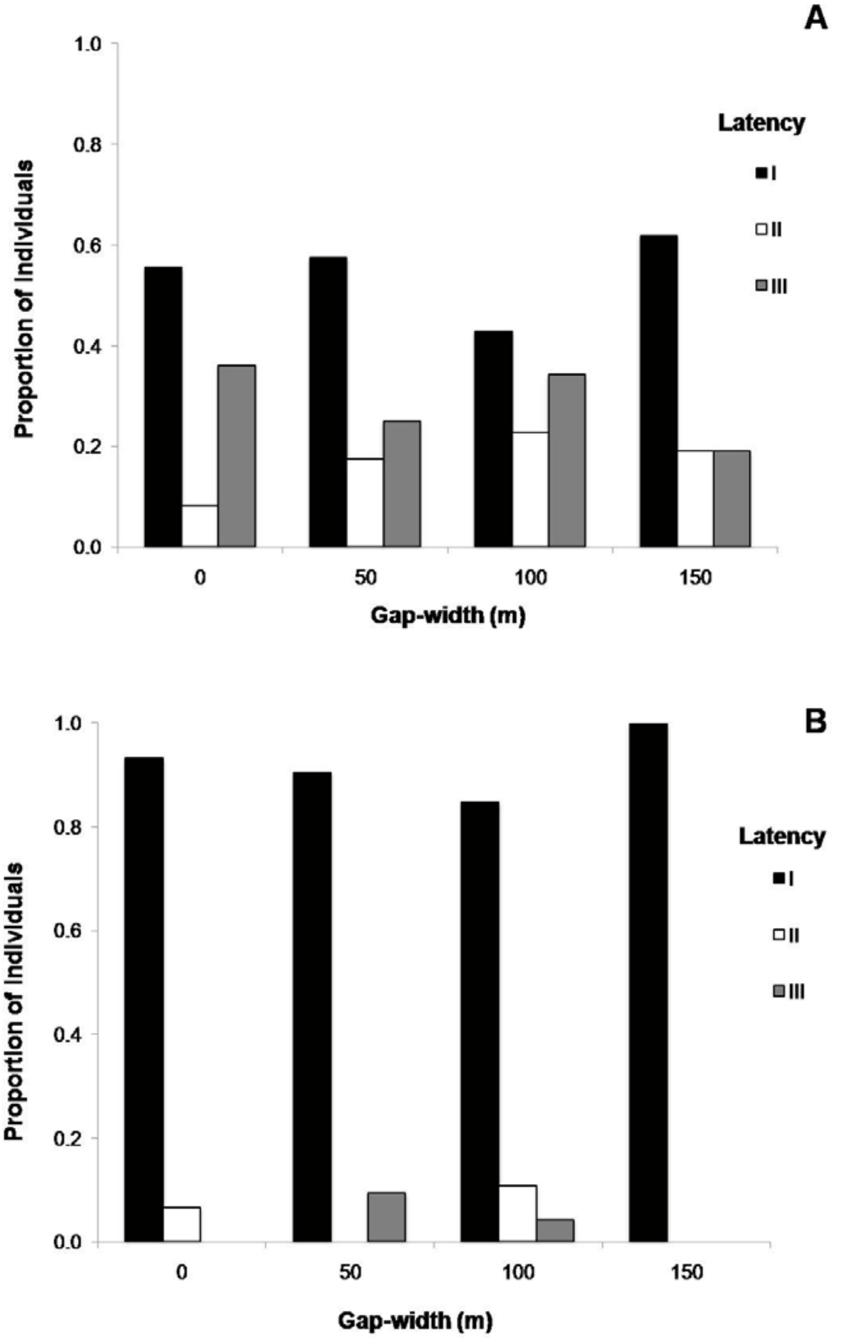


Figure 4.3. Latency (time taken) of birds to abandon the release box and to cross gaps of different widths during release trials. Latency: I) bird abandoned the box after first door was opened (black bars); II) bird abandoned the box after second door was opened (60 seconds after first door was opened) (white bars); III) bird was forced to abandon the box by an observer (60 seconds after second door was opened) (gray bars). A) Restricted species, B) Partially restricted species.

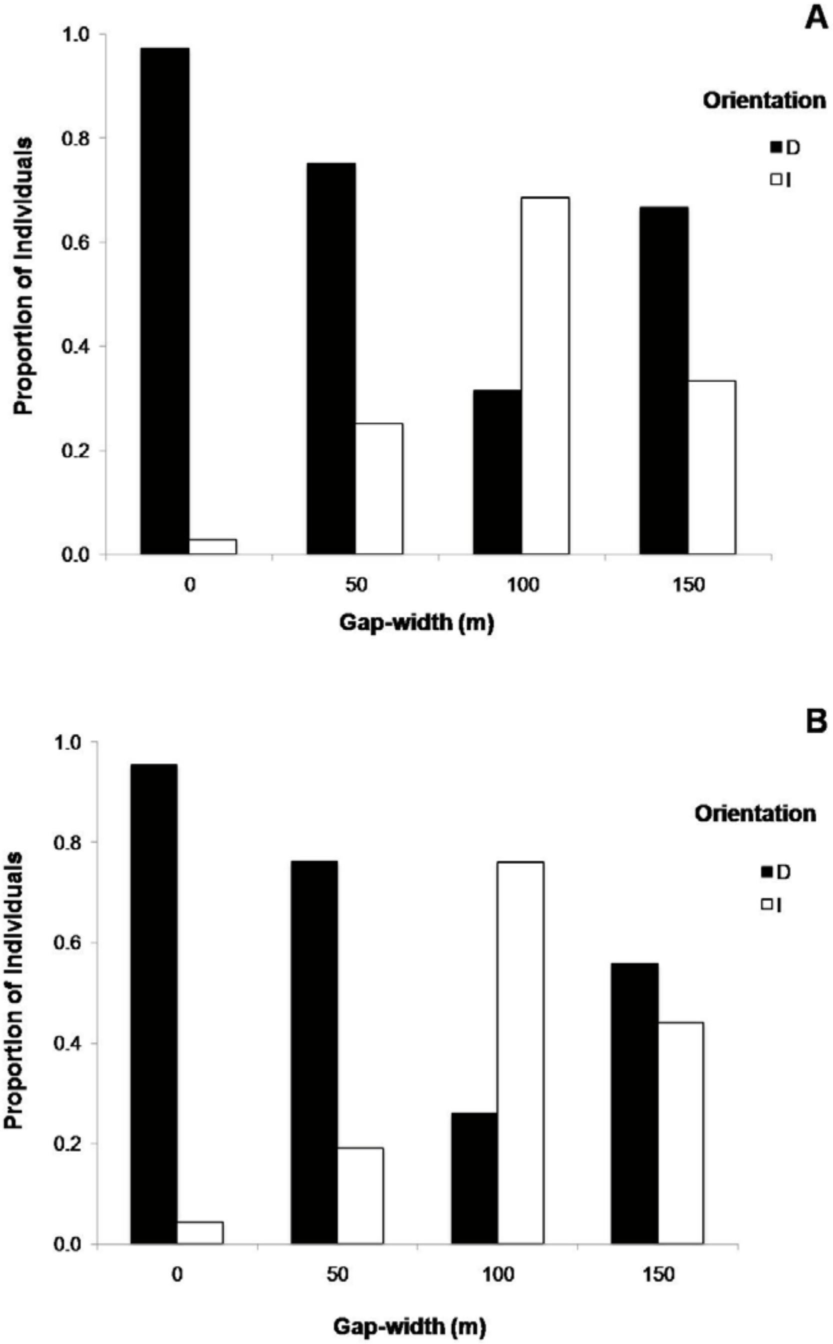


Figure 4.4. Orientation of first flight after abandonment of box during release trials at different gap-widths. Orientation: D) after abandonment of box, bird flight path was directed towards forest fragment (black bars); I) after abandonment of box, bird flight path was indirect or not directed towards forest fragment (white bars). A) Restricted species, B) Partially restricted species.

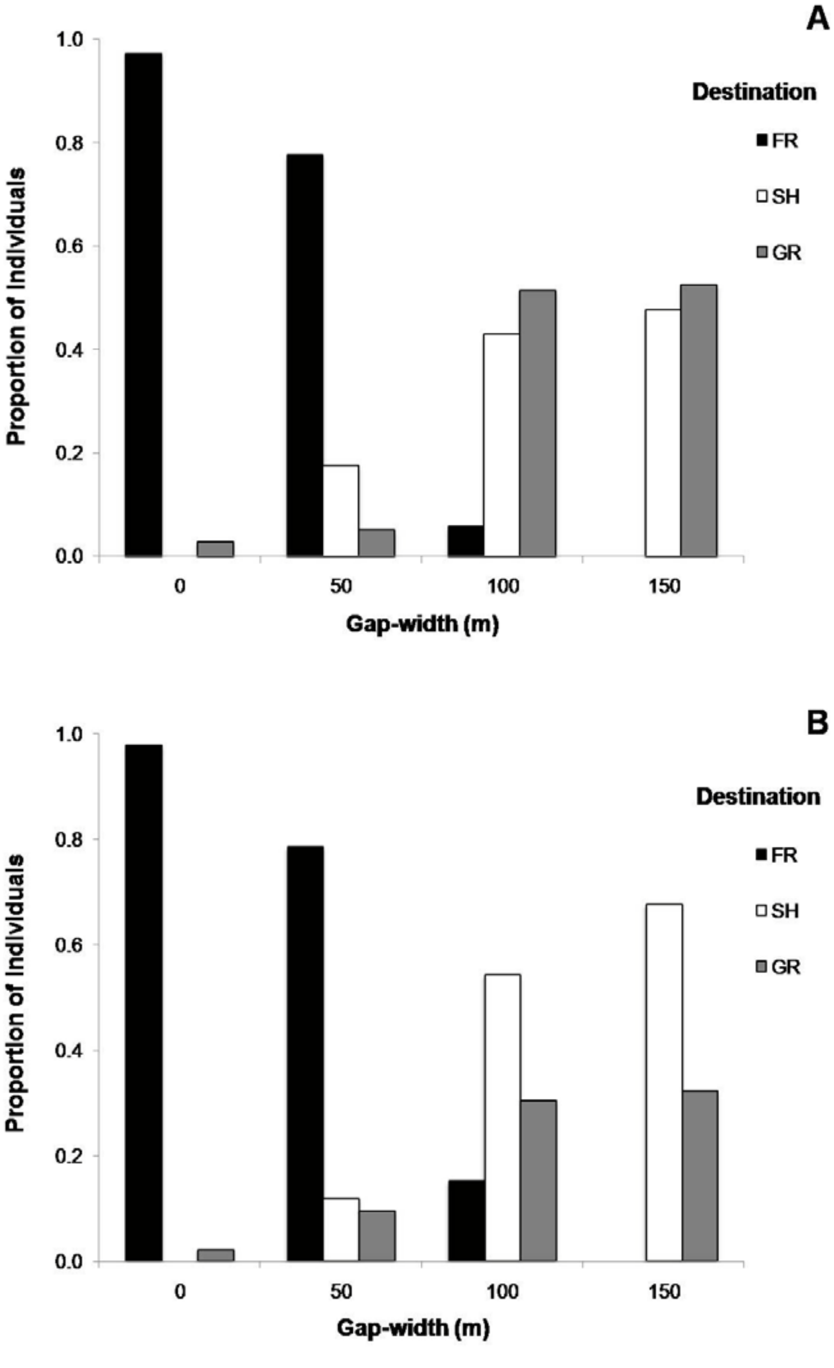


Figure 4.5. Destination of first flight after abandonment of box during release trials at different gap-widths. Destination: FR) forest fragment (black bars); SH) shade (isolated tree in the middle of the cattle pasture) (white bars); GR) ground (landed in grass on the cattle pasture) (gray bars). A) Restricted species, B) Partially restricted species.

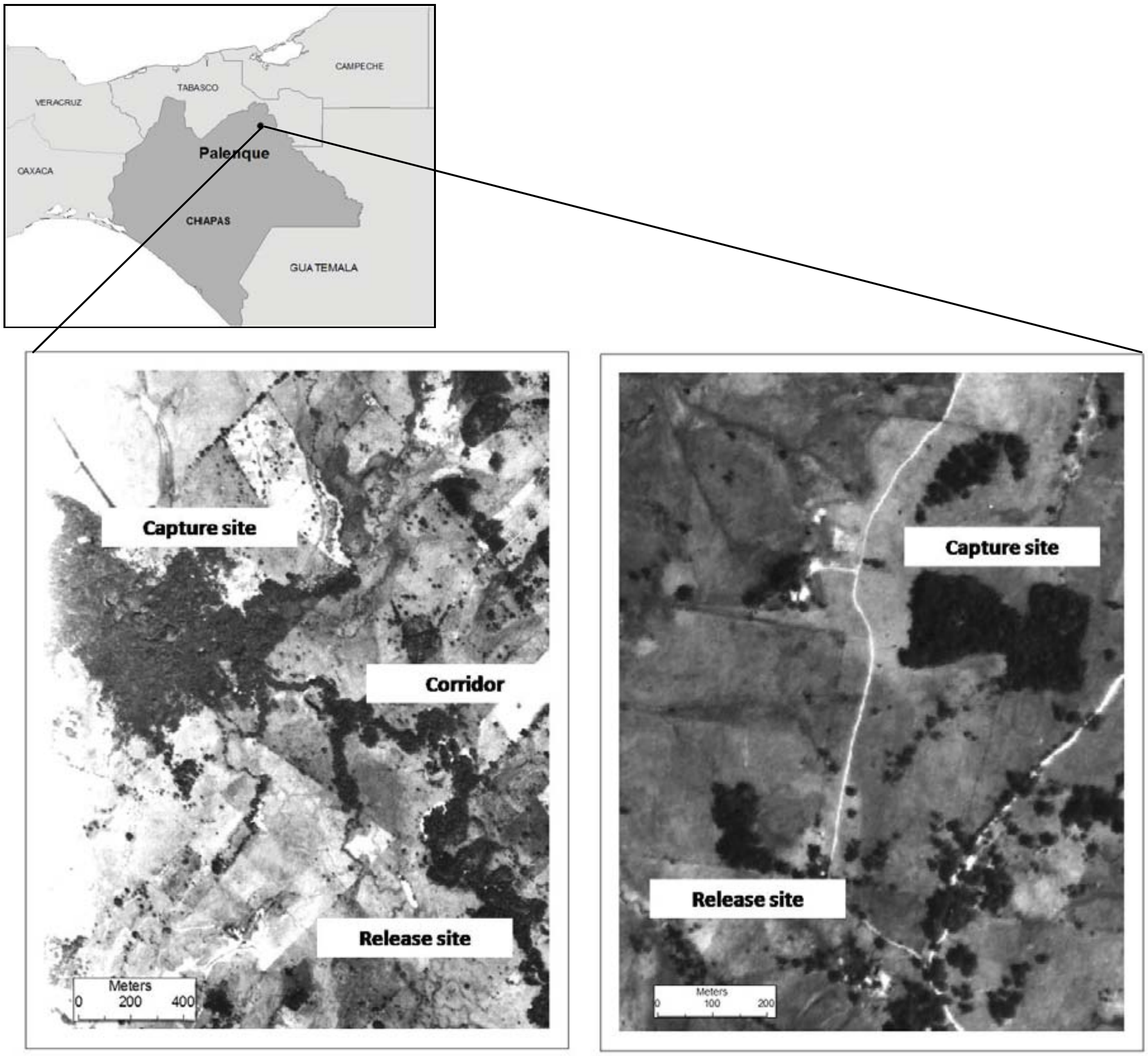


Figure 5.1. Aerial photograph of examples of the landscape sections used during translocation experiments. On the left, one of the landscape sections used in the connected treatment, with a riparian corridor present. On the right, a landscape section used in the unconnected treatment where the capture and release sites are not connected by the presence of a forested corridor.

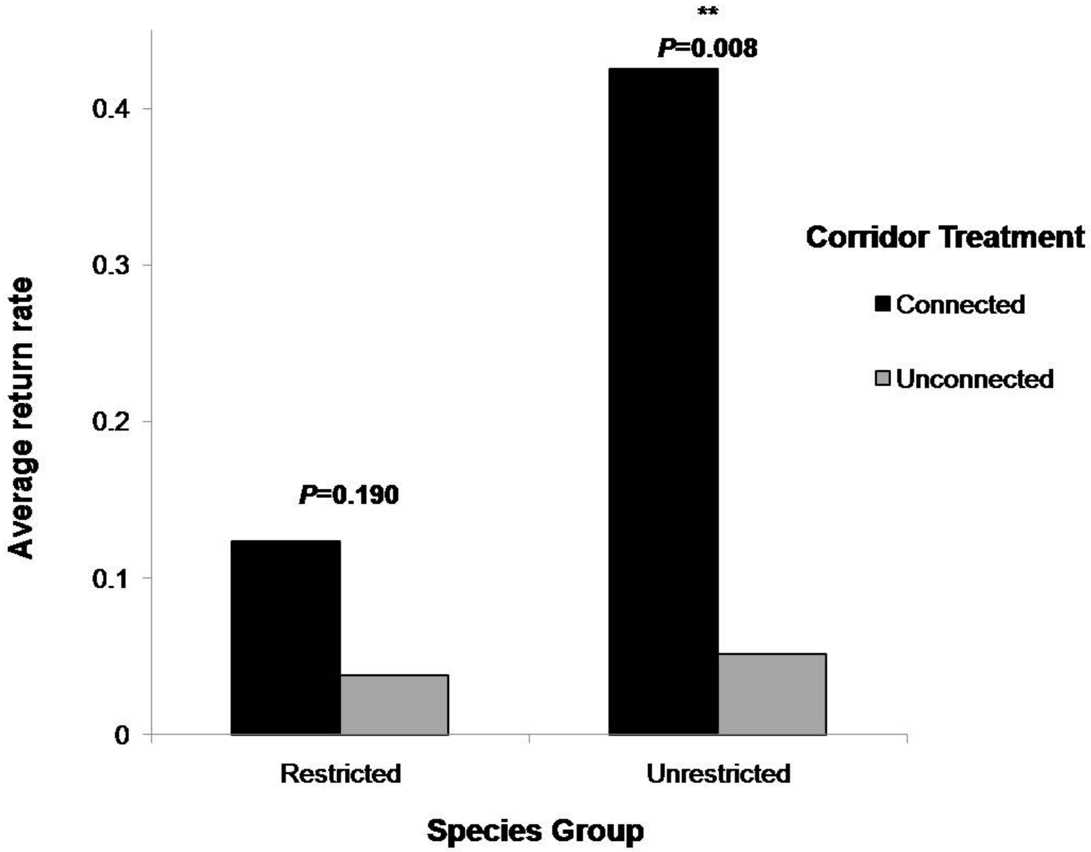


Figure 5.2. Effect of treatment (Connected=Corridor present; Unconnected=No corridor present) on average return rates (proportion of returning individuals) for both species groups.

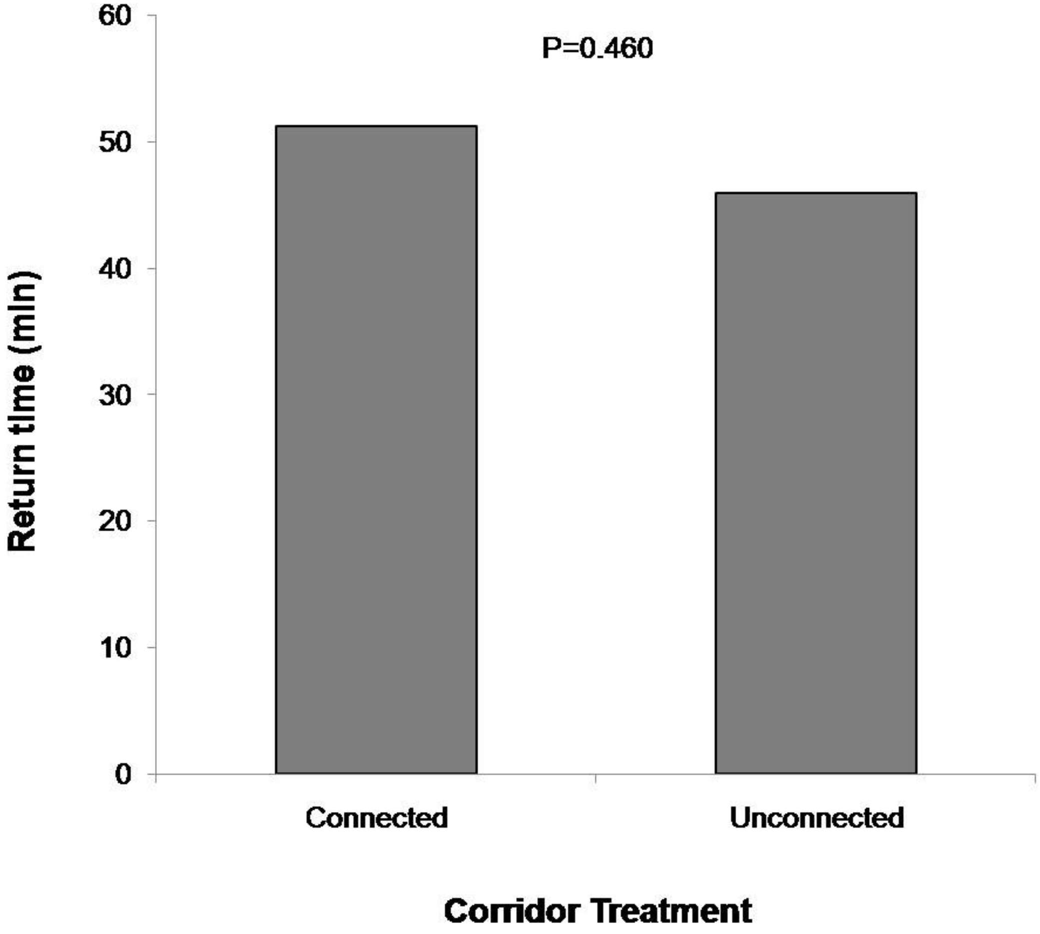


Figure 5.3. Effect of treatment (Connected=Corridor present; Unconnected=No corridor present) on time to return for individuals that returned to the capture site.

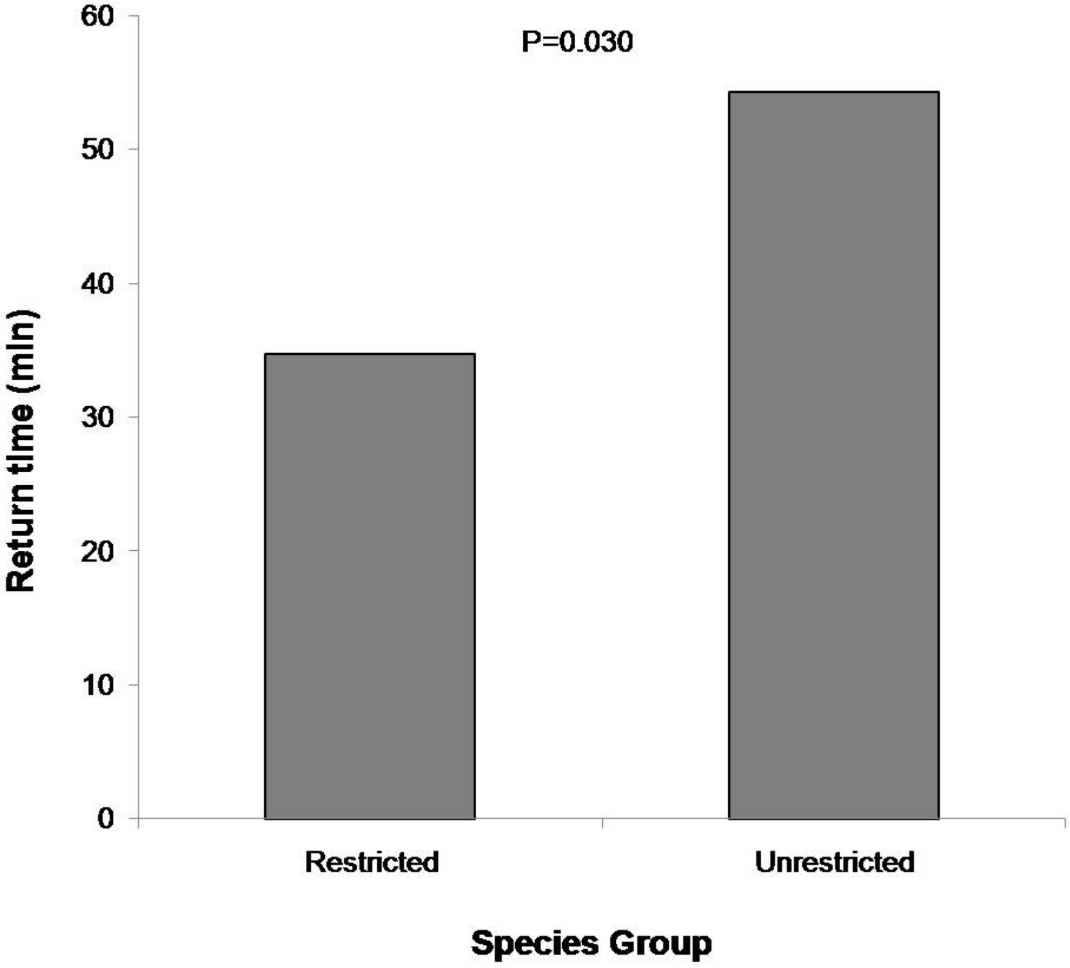


Figure 5.4. Effect of species group (Forest restricted and Unrestricted species) on time to return for individuals that returned to the capture site.

Table 2.1. Principal-component scores for horizontal and vertical vegetation variables based on analysis of all 17 forest fragments.

Vegetation Variable	Veg_PCAI	Veg_PCAII	Veg_PCAIII	Veg_PCAIV
Percentage of ground cover by:				
Vegetation	.875	.041	-.113	.131
Litter	.451	.240	.136	.562
Logs	-.095	.025	.895	-.059
Rocks	-.257	-.073	-.125	-.763
Tree density				
Small trees	.350	.830	-.061	.122
Medium trees	.161	-.075	.770	.437
Big trees	.015	-.489	-.294	.642
Grand trees	-.740	.261	.009	-.262
Logs	.232	.303	.847	.121
Vertical strata				
I (0-0.5 m)	.791	-.007	.271	-.035
II (0.5-1.0 m)	.852	.440	.091	.028
III (1.0-1.5 m)	.807	.338	.065	.117
IV (1.5-2.0 m)	.263	.867	.059	.114
V (2.0-3.0 m)	-.273	.863	.198	.055
Canopy cover	-.088	.235	.211	.869
Proportion of variance explained	0.347	0.178	0.151	0.111

Table 2.2. Best predictive models of multiple regression of fragment- and landscape-level variables on estimated species richness.

Model Predictors	R	Adjusted R^2	F	df	*P*
Model 1					
(Constant) + Area + Distance to PNP + Cover_100 + Cover_500 + Veg_PCAIII	0.785	0.616	3.526	16	0.038
Model 2					
(Constant) + Area + Distance to PNP + Cover_500 + Veg_PCAIII	0.766	0.587	4.263	16	0.022
Model 3					
(Constant) + Area + Distance to PNP + Veg_PCAIII	0.720	0.518	4.666	16	0.020

Table 2.3. Coefficients of determination and their associated probability for variables present in significant multiple regression models for the relation between fragment- and landscape-variables on estimated species richness.

Model Predictors	Coefficient	t	*P*
Model 1			
Area	0.510	2.616	0.024
Distance to PNP	-0.660	-2.269	0.044
Cover_100	0.206	0.909	0.383
Cover_500	0.273	1.095	0.297
Veg_PCAIII	0.552	2.142	0.055
Model 2			
Area	0.484	2.530	0.026
Distance to PNP	-0.664	-2.300	0.040
Cover_500	0.335	1.410	0.184
Veg_PCAIII	0.488	1.983	0.071
Model 3			
Area	0.487	2.455	0.029
Distance to PNP	-0.864	-3.312	0.006
Veg_PCAIII	-0.472	1.853	0.087

Table 2.4. Best predictive model of multiple regression of fragment- and landscape-level variables on bird abundance in forest fragments.

Model Predictors	R	Adjusted R^2	F	df	*P*
Model					
(Constant) + Veg_PCAIV + Veg_PCAI + Veg_PCAIII + Distance to PNP	0.931	0.867	19.569	16	<0.001

Table 2.5. Coefficients of determination and their associated probability for variables present in the significant multiple regression model for the relation between fragment- and landscape-variables on bird abundance.

Model Predictors	Coefficient	t	*P*
Model			
Distance to PNP	-0.574	-3.899	0.002
Veg_PCAI	0.348	3.304	0.006
Veg_PCAIII	0.824	5.793	<0.001
Veg_PCAIV	0.762	6.806	<0.001

Table 3.1. Effects of area and isolation on species richness by group, determined by multiple linear regression.

		β Coefficients		
Forest Dependence Group	Number of Species	ln Area	ln Isolation	Adjusted R^2
Restricted Species	35	0.363*	-0.731**	0.690
Partially Restricted Species	54	0.318	0.021	0.101
Unrestricted Species	35	0.167	0.197	0.064

*$p<0.05$

**$p<0.001$

Table 3.2. Results of stepwise multiple regressions of area and isolation on species occurrences (binomial logistic) and species abundances (linear regression) in 17 forest fragments.

	Species Occurrence				Species Abundance			
	Area		**Isolation**		**Area**		**Isolation**	
	$R^{2(a)}$	**p**	$R^{2(a)}$	**p**	$R^{2(b)}$	**P**	**β**	**P**
Restricted Species								
Elaenia flavogaster							0.914	0.03
Piaya cayana	0.377	0.022						
Euphonia hirundinacea	None							
Ramphastos sulfuratus	0.408	0.014					-0.936	0.019
Xyphorhynchus flavigaster	None							
Momotus momota	None							
Ortalis vetula	None							
Partially Restricted Species								
Arremon aurantiirostris			0.535	0.005				
Lepidocolaptes souleyetti			0.356	0.027				
Myiodynastes luteiventris	None							
Pteroglossus torquatus	None							
Arremon rufivirgatus	None							
Nyctidromus albicollis	None							
Trogon violaceus	None							
Patagioenas flavirostris	None							
Tolmomyias sulphurescens	None							
Tyrannus vociferans	None							
Dryocopus lineatus	0.297	0.04						
Amazilia beryllina	None							
Myiozetetes similis	None							
Psarocolius montezuma	None							
Saltator coerulescens	None							
Amazilia candida	None							
Saltator atriceps							-0.721	.019
Amazona autumnalis	None							
Amazona albifrons	None							
Amazilia yucatanensis	None							
Myiarchus tuberculifer			0.354	0.027				
Habia fuscicauda	None							
Leptotila verreauxi	None							
Aratinga nana			0.645	0.009				
Trogon melanocephalus			0.361	0.006	0.564	0.045		

Table 3.2. *continued…*

Thryothorus maculipectus						0.644	0.018
Unrestricted Species							
Campylorhynchus zonatus		0.347	0.026				
Columbina talpacoti	None						
Icterus gularis	None						
Tyrannus melancholicus	None						
Zenaida asiatica						0.997	0.048
Amazilia tzacatl				-0.972	0.028		
Cathartes aura	None						
Coragyps atratus	None						
Arremonops chloronotus	None						
Dendrocygna autumnalis	None						
Phaethornis longuemareus	None						
Herpetotheres cachinnans						-0.976	0.001
Tytira semifasciata	None						
Pitangus sulphuratus		0.392	0.016				
Buteo magnirostris	None						
Crotophaga sulcirostris	None						
Dives dives	None						
Quiscalus mexicanus	None						
Turdus grayi	None						
Cyanocorax morio	None						
Melanerper aurifrons	None						

(a) R^2=Nagelkerke R^2

"None" means that neither variable (area or isolation) entered the model.

Table 4.1. Sample sizes per species and distance for the release experiment.

	Release Distance			
Restricted Species	0 m	50 m	100 m	150 m
Formicarius analis	7	9	7	7
Glyphorhynchus spirurus	13	13	11	11
Henicorhina leucosticta	16	18	17	6
Partially Restricted Species				
Habia fuscicauda	16	12	17	12
Arremon aurantiirostris	15	16	13	12
Mionectes oleagineous	14	14	16	10

Table 4.2. Mean, standard deviation and *P*-values associated with regression coefficients of the backward stepwise logistic regression of time in captivity, ambient light and wind strength on movement decisions (Latency, Orientation and Destination) of birds during release trials.

	Predictor Variable		
	Captivity (min)	Light (lux)	Wind (m/s)
Mean	30.7	55,318.6	0.84
S.D.	12.3	32,072.4	0.57
Dependent Variables			
Latency	0.100	0.112	0.245
Orientation	0.310	0.572	0.293
Destination	0.148	0.201	0.457

Table 5.1. Landscape variables included in the analysis of the results of the translocation trials. Values given are mean and S. D.

Landscape Variables	**Connected Sites**	**Unconnected Sites**
Area of Capture Sites (ha)	14.64 (17.92)	8.59 (3.06)[a]
Area of Release Sites (ha)	3.94 (3.22)	5.41 (3.67)[b]
Distance between capture and release Sites (m)	579.86 (255.76)	517.9 (201.71)[c]

[a] t=0.744; df=8; *P*=0.478
[b] t=-0.673; df=8; *P*=0.520
[c] t=0.425; df=8; *P*=0.682

Table 5.2. Results of translocation trials per treatment and species group.

	Corridor Treatment	
	Connected n=5	Unconnected n=5
Number of individuals translocated (all species)	90	145
Restricted species	38	39
Unrestricted species	52	106
Recaptured (all species)	24	7
Restricted species	5	2
Unrestricted species	19	5
Average return rates (all species)	0.3219	0.0509
Restricted	0.1234	0.0381
Unrestricted	0.4252	0.0517
Mean return time (all species)	51.21 hrs	45.86 hrs
Min. return time	2 hrs	4 hrs.
Max. return time	119 hrs.	75 hrs

Table 5.3. Effect of treatment and species group on return time of translocated birds.

Factors	**Hazard ratio**	**df**	***P***
Treatment	0.546	1	0.460
Species group	1.057	1	0.030