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Effects of Forest Fragmentation on Central Amazonian Bird Demography

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EFFECTS OF FOREST FRAGMENTATION ON CENTRAL AMAZONIAN BIRD
DEMOGRAPHY

A Dissertation

Submitted to the Graduate Faculty of the
Louisiana State University and
Agricultural and Mechanical College
in partial fulfillment of the
requirements for the degree of
Doctor of Philosophy

in

The School of Renewable Natural Resources

by

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B.S., Humboldt State University 2005

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December 2014

Dedicated to the memory of my father, Larry Wolfe (1938-2009) –the world is a little less interesting place since he left.

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Phil Stouffer, my advisor, has been supportive and incredibly helpful during my dissertation.

Phil was particularly supportive of my seemingly strange ideas: gaining access and working in Balbina, starting Louisiana Bird Observatory, teaching annual banding courses in Brazil, and going on expedition to Equatorial Guinea. Phil was particularly critical in elevating the quality of my work, broadening its scope and teaching me about Brazilian and Louisiana Natural History - thank you Phil for the dedicated help, support, insight and friendship.

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ABSTRACT

Avian diversity in degraded fragmented Amazonian landscapes depends on the persistence of species in cleared and disturbed areas. Regenerating forest facilitates bird dispersal within degraded Amazonian landscapes and may tip the balance in favor of persistence in previously depauperate habitat patches. Despite the potential value of Amazonian second growth, we lack comparisons of demography among second growth, continuous forest, forest fragments in regenerating landscapes, and truly isolated fragments. Here, we used point-count and capture data to compare Amazonian bird communities among continuous forest plots, 100 ha forest fragments with adjacent second growth, 100 ha forested islands bounded by water, young and older second growth plots. We also compared differences in survival, population growth and age ratios between primary and mature secondary forest. Among foraging guilds, understory insectivores and obligate-flocking species were nearly absent in islands and young second growth. Fragments surrounded by a regenerating matrix were surprisingly species rich, suggesting that a developing matrix may mitigate extinction associated with fragmentation. Survival and population growth was lower in mature second growth relative to primary forest for all foraging guilds except frugivores, gap specialists and ant-following birds. Similarly, age ratios were skewed towards more adult insectivorous birds in older forest; these findings suggest that dominant individuals may preferentially use older forest. Our findings reinforce that true islands are extinction-driven systems with distinct, depauperate communities. Islands are not appropriate comparisons to forest fragments in some landscapes. In contrast, succession of bird communities in second growth facilitates recolonization of forest fragments, permitting fragments as small as 100 ha to support bird communities similar to continuous forest.

CHAPTER 1: GENERAL INTRODUCTION

AMAZON DIVERSITY, DEGRADATION AND SUCCESSION

The Amazon basin covers approximately 7,000,000 km² (1.5% of the earth's surface) and is host to nearly 10% of the planet's bird species (Clements and Clements 2007, Remsen et al. 2014; Figure 1.1). The Amazon's large and ancient landmass coupled with a warm climate probably buffered birds from the ice age extinctions that vanquished many temperate species, thereby increasing Neotropical diversification (Hawkins et al. 2007). In addition to biogeographic and climatic processes, the inability of many Amazonian bird species to disperse across rivers or clearings limited gene flow, thereby promoting allopatric speciation (Hayes and Sewlal 2004, Moore et al. 2008). The expansive and diverse nature of the Amazon is exemplified by the continuing discovery of previously undocumented bird species (Del Hoyo et al. 2013).

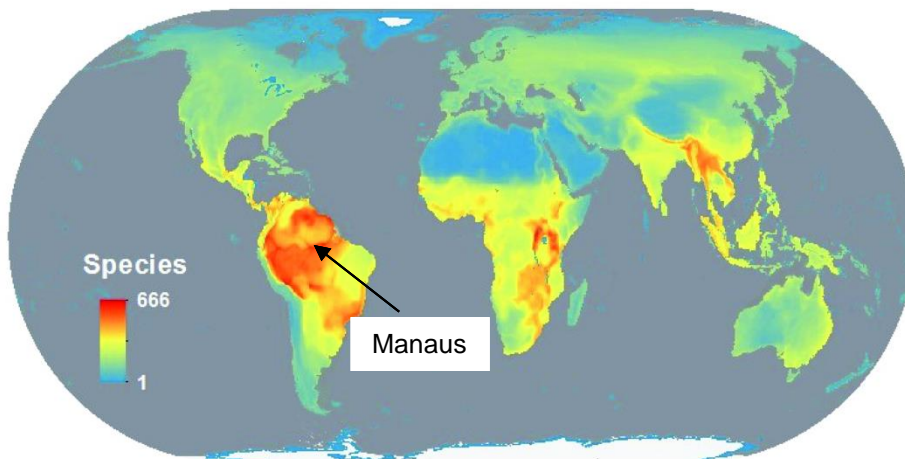


Figure 1.1. Global distribution of bird diversity (taken from Pimm et al. 2014)

In addition to hosting diverse bird communities, the Amazon basin also fueled a human desire to colonize the largely unexplored landscape and exploit its resources (Grann 2009). Early European ambitions were initially tempered by the hostile nature of jungle exploration: disease, infection, inclement weather, difficult terrain, and territorial native peoples (Grann 2009). However, throughout the 19th century, international demand for rubber turned early Amazonian outposts, such as Manaus, Brazil, into full-fledged cities. The infrastructure and thriving economies of Amazonian cities, such as Manaus, provided the economic incentive and human capital to build highway systems and develop hydroelectric energy. The subsequent construction of roads throughout the central Amazon coupled with agricultural subsidies from the government resulted in unparalleled rates of forest clearing throughout the latter half of the 20th century (Figure 1.2). For example, forest clearing associated with agriculture and livestock along a 20 km stretch of BR-174, a major highway north of Manaus built in the 1970s, increased from 622.15 km² of cleared forest in 1978 to 2618.58 km² in 2008 (Rodrigues and Pinheiro 2011). Much of the cleared forest was abandoned due to the abatement of government subsidies, leaving a dynamic landscape ‘matrix’ of remnant forest fragments of varying sizes interspersed with mixed-age regenerating forest and pasture (INPE 2013).

Within the matrix, the speed at which Amazonian forest regenerates is largely dependent on the history of land use. For example, forest succession is quite rapid following natural disturbances, such as wind events, resulting in primary forest characteristics within several decades (Sodhi et al. 2011). However, these processes are often disrupted in human dominated landscapes where pasture is frequently burned in attempt to suppress the growth of woody vegetation. Although the two most common pioneering plant communities in the central Amazon, *Cecropia* spp. and *Vismia* spp., are sensitive to fire, *Vismia* often has an advantage in

burned areas because it can re-sprout immediately following burns (Williamson and Mesquita 2001). Each time pasture is cleared using fire, the more *Vismia* becomes dominant. Over time, frequently burned areas are converted to homogeneous stands of low-growing *Vismia* temporarily arresting forest succession (Williamson and Mesquita 2001).

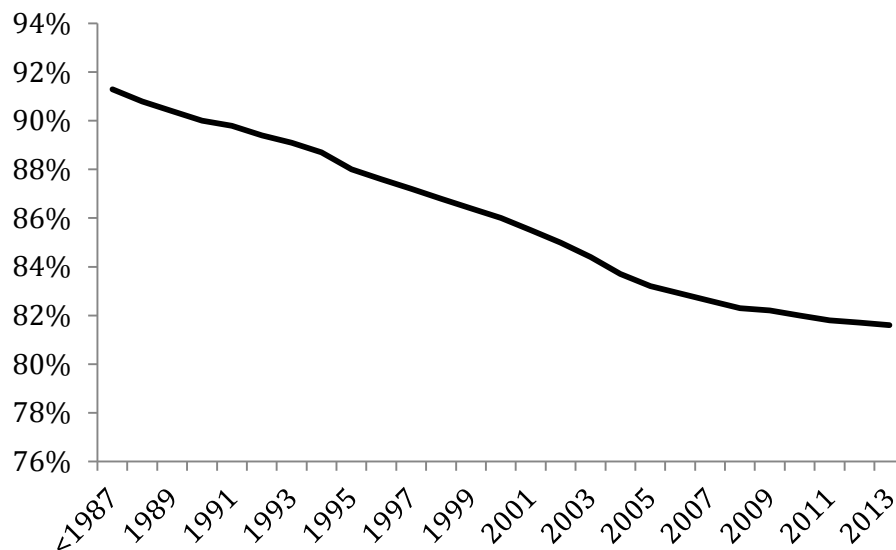


Figure 1.2. Percent of 1970 Brazilian Amazon forest cover remaining (INPE 2013).

VALUE OF DEGRADED LANDSCAPES TO AMAZONIAN BIRDS

The increasingly heterogeneous Amazon landscape may provide varying levels of ecological value to the diverse array of bird species that occupy the region; however, determining the actual value of degraded forest depends on what facet of avian ecology is being measured. There is on-going debate about what constitutes ecological value for birds. Some authors suggest that second growth buffers species from extinction by hosting reduced number of forest-dwelling species and facilitating dispersal through a hostile matrix (Stouffer et al. 2006, Wright and Muller-Landau 2006). Conversely, others noted that species richness and community composition differ between

second growth and primary forest intimating that only a small subset of species found in primary forest subsist in second growth (Barlow et al. 2007, Gardner et al. 2007, Laurance 2007).

Although evidence exists supporting both the benefit and detriment of Amazonian second growth to birds, more recent studies have highlighted the importance of the age of second growth to birds. For example, Mokross et al. (2013) found that Amazonian mixed-species flocks were less cohesive in young second growth when compared to mature second growth. Similarly, Powell et al. (2013) found that the age of second growth was positively correlated with capture rates of forest-dwelling birds at the edge of forest fragments. The relationship between age of second growth and capture rate allowed Powell et al. (2013) to estimate how much time is needed until adjacent second growth yielded capture rates equivalent to that of continuous forest.

To date, the majority of studies have evaluated the ecological value of tropical second growth for birds by comparing species lists between treatments (Sodhi et al. 2011). Although informative, comparisons of abundance and species richness can be misleading because many tropical species do not adhere to an ideal free distribution (Stutchbury and Morton 2001). More commonly, dominant individuals secure territories in high quality habitat and exclude subordinates to low quality habitat where they can occur in high numbers, possibly leading to the erroneous conclusion that presence equates to superior habitat (Van Horn 1983, Johnson 2007). Additionally, species lists cannot detect if an area acts as a population sink; for instance, degraded tropical habitats may attract forest-dwelling birds that ultimately fail to produce enough young to sustain local populations (Hughes et al. 2002). More meaningful parameters such as survival, population growth and age ratios should be estimated to robustly assess the value of degraded tropical forests and account for ideal despotic distributions and source-sink dynamics.

EFFICACY OF ISLAND BIOGEOGRAPHY TO PREDICT COMMUNITY DYNAMICS IN AMAZONIAN FOREST FRAGMENTS

In addition to assessing the ecological value of second growth to tropical birds, determining if biogeographic models can predict species loss in Amazonian forest fragments is an important line of ecological and conservation research (Laurance 2008). Although developed to predict species richness on oceanic archipelagos, the theory of island biogeography has widely been used to explain changes in species richness following forest fragmentation on the mainland (Simberloff and Abele 1976, Hanski and Gilpin 1991, Bierregaard et al. 1992). The popularity of island biogeography is in part due to its elegant simplicity where differences in island size and distance to source population can determine species richness driven by of colonization and extinction (MacArthur and Wilson 1967). However, the efficacy of the island model to predict the response of biological communities to fragmentation has been questioned in large part due to the influence of landscape matrixes on colonization and extinction dynamics (Mendenhall et al. 2014). For example, Amazonian bird communities residing within forest fragments did not suffer from area effects as the surrounding matrix regenerated, as predicted by the island model, suggesting that the assumption of a hostile matrix may be incorrect (Stouffer et al. 2006). Testing the efficacy of Island Biogeography to predict changes in bird communities within fragments is a necessary step towards a greater understanding of how Amazonian heterogeneity affects bird diversity.

OBJECTIVES AND STUDY AREA

The majority of the study was conducted in *terra firme* forest at the Biological Dynamics of Forest Fragments Project (BDFFP), approximately 80 km north of Manaus, Brazil (Figure 1.3). The project began in 1979 by Dr. Thomas Lovejoy in partnership with Instituto Nacional de Pesquisas da Amazônia, and was originally conceived to address the SLOSS (single large or

several small) debate. Over time, the project proved valuable to a wide breadth of ecology, natural history and conservation focused studies. Bird banding began in 1979, prior to forest isolation and continued every year until 1993 when efforts became less frequent. To date, multiple 1, 10 and 100 ha fragments have been isolated and are surrounded by buffers of regenerating forest. In addition to the fragments, vast tracts of second growth of varying ages have resulted from pasture abandonment; expansive tracts of continuous forest are also common. Balbina reservoir, approximately 150 km north of Manaus served as the secondary study site. The Balbina Dam was constructed from 1985 through 1989 adjacent to highway BR 174 along the Uatumã River, which also passes through traditional Waimiri territory. The resulting reservoir flooded 2,360 km² of primary rainforest, resulting in a highly fragmented landscape comprised of over 1500 islands ranging in size from 1 to over 1000 hectares (Fearnside 1989).

The isolated nature of Balbina's islands coupled with the BDFFP's long-term dataset and heterogeneous landscape were critical to the development of this study. To determine the ecological value of second growth and test the efficacy of the island model for tropical birds, I conducted four studies at the BDFFP and Balbina. First, I used capture and census data collected in second growth (dominated by *Cecropia*), continuous forest, forest fragments, and Balbina islands (true islands) to evaluate the efficacy of the island model and measure the influence of succession on bird community assemblages. Second, I used long-term capture data from continuous forest to provide baseline estimates of survival for a diverse set of understory species; these estimates serve as historic benchmarks and were compared with similar estimates throughout the Amazon bioregion. Third, I used capture data to measure differences in survival, population growth, and age ratios between primary forest and second growth (dominated by *Cecropia*) to identify meaningful differences in demographics between treatments. Finally, I

used long-term capture data to measure the influence of second growth age on the survival of birds in 10 and 100 ha forest fragments.

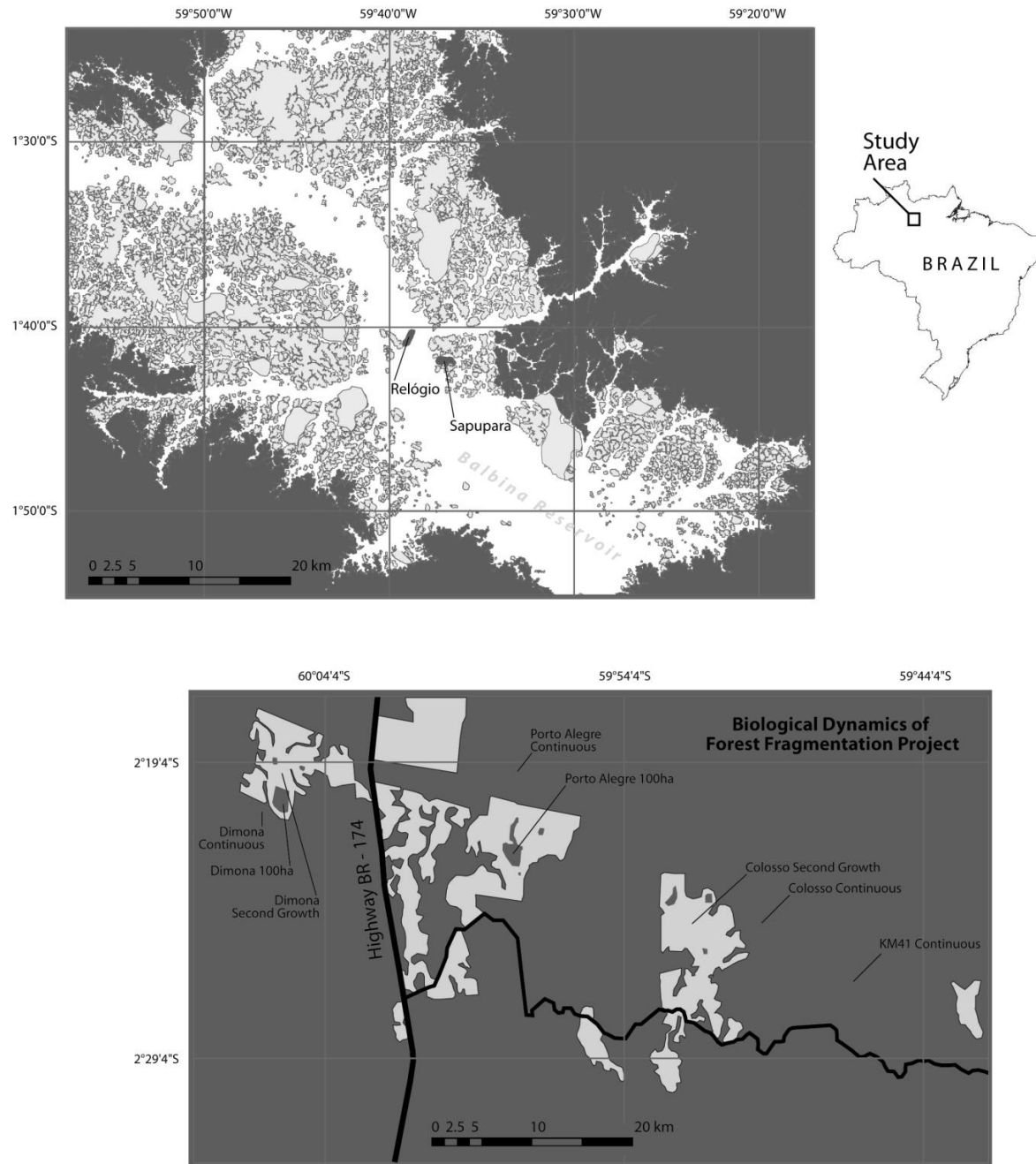


Figure 1.3. Map of study sites at the Balbina reservoir and Biological Dynamics of Forest Fragments Project 80km and 150km north of Manaus, Brazil, respectively.

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CHAPTER 2: IS THE ISLAND MODEL APPROPRIATE FOR AMAZONIAN BIRD COMMUNITIES IN FOREST FRAGMENTS SURROUNDED BY A REGENERATING MATRIX?

INTRODUCTION

Composition and permeability of regenerating forest matrix in deforested Amazonian rainforest often influences source-sink dynamics of local bird populations (Marsden et al. 2003, Bélisle 2005, Umetsu and Pardini 2007, Umetsu et al. 2008, Boscolo et al. 2008, Stouffer et al. 2011, Magrach et al. 2012). As such, the influence of an adjacent matrix on bird communities in isolated habitat patches has been particularly well studied in the central Amazon. For example, Stouffer et al. (2011) demonstrated that birds were able to disperse from source populations through a regenerating forest to recolonize previously depauperate forest fragments, suggesting that species are lost following isolation, but the trajectory of loss does not continue downward when coupled with matrix recovery (Marsden et al. 2003, Ferraz et al. 2007, Laurance 2008, Stouffer et al. 2011). Not only does an adjacent matrix facilitate fragment recolonization, but it may also dampen predicted area effects associated with the theory of island biogeography ('island model' hereafter; Zimmerman and Bierregaard 1986) as demonstrated in the central Amazon where fragments of different sizes yielded similar estimates of species richness, as the adjacent matrix matured (Stouffer et al. 2006). Conversely, bird communities on true islands typically exhibit different biogeographic processes compared to forest fragments in regenerating landscapes. More specifically, true islands bounded by water often host bird communities subject to an initial relaxation (extinction) period through area loss, followed by the establishment of a dynamic balance between area and distance effects on colonization and extinction, as predicted by the island model (Russell et al. 2006). For example, Terborgh et al. (1997) found bird communities on large islands were more diverse than those on small islands in the Guri reservoir

in Venezuela. Differences in biogeographic processes between fragments within a matrix and true islands strongly suggest that the generality of the island model is questionable across the diversity of isolated tropical habitats (Kupfer et al. 2006). Such differences between island model predictions and actual measurements from forest fragments led Mendenhall et al. (2014) to advocate for a ‘countryside’ biogeographic framework, thereby recognizing the mitigating forces of landscape effects, including the matrix, on species richness. In addition to facilitating dispersal, as demonstrated in the central Amazon, a regenerating matrix may also sustain viable populations of forest obligate species.

To date, most research focused on determining the ecological value of a regenerating matrix for birds have examined patterns of species richness; these studies have produced largely contradictory and region-dependent results. For example, Barlow (2007) found fewer species in regenerating matrix relative to primary forest in Brazil, while Blake and Loiselle (2001) documented more species within young matrix relative to primary forest in Costa Rica. The influence of region on patterns of species richness within the matrix was exemplified by Martin et al. (2014) where endemic species in Honduras were found to be less common in the matrix relative to primary forest, when compared with bird communities in similar aged forests in Sulawesi. Dissimilar responses of matrix bird communities probably reflect four differences among the aforementioned studies: (1) differences in avifauna and their respective ability to exploit resources; (2) differences in matrix successional pathways; (3) differences in matrix age; and (4) differences in distance to source populations. Regional dissimilarities are potentially further complicated by the asymmetric response of foraging guilds to the presence of regenerating matrix. In general, frugivorous and nectivorous birds, which are relatively more common in Central American forests, often fare better when subjected to clearing and

subsequent forest regeneration in the Neotropics relative to their insectivorous counterparts that dominate Amazonian forests (Karr et al. 1990, Sekercioglu et al. 2002).

For example, Stouffer et al. (2006) and Powell et al. (2013) demonstrated that the presence of insectivorous birds in Amazonian forest fragments was positively correlated with age of the surrounding matrix, with fewer birds captured in fragments bordered by young forest. In particular, terrestrial insectivores, ant-followers, flock obligates and arboreal insectivores were found to be most sensitive to surrounding matrix age, possibly reflecting an inability of certain foraging guilds to disperse through young second growth to recolonize isolated forest fragments (Stouffer et al. 2006). Antithetically, hummingbirds, gap specialists and some frugivores exhibited increased abundances within fragments surrounded by a young matrix (Stouffer et al. 2006). Apparently many species recolonize forest fragments, even if they do not persist (Stouffer et al. 2011) demonstrating that bird communities within fragments are highly influenced by dispersal, whereas bird communities on true islands, such as within the Guri reservoir, are more strongly influenced by extinction through predation (Terborgh et al. 2001).

A better understanding of how a range of matrix conditions, from open water (islands) to developed second growth, affect bird communities would have significant theoretical and conservation implications. The complex nature of historic and continued degradation within the Amazon basin provides a unique opportunity to conduct such a study. Habitat loss in the Amazon basin is dynamic due to ecological and economic forces, as reflected by hydroelectric development, large-scale pasture abandonment and subsequent forest regeneration (Neff et al. 2006). In this study I worked within the heterogeneous central Amazonian landscape, using multiple methods to describe bird communities on true islands bounded by water, in fragments within a matrix, in second growth of two ages, and in continuous forest. More specifically, my

study aimed to test the following four hypotheses: (1) if islands are an extinction driven system, but fragments surrounded by regenerating forest are colonization driven, then true islands will be less species rich compared to similarly-sized forest fragments; (2) if sensitive foraging guilds (terrestrial insectivores, ant-followers, flock obligates and arboreal insectivores) are dispersal limited, then true islands will have different community structure driven by the lack of sensitive foraging guilds compared to similarly-sized forest fragments within a matrix; (3) if birds are more prone to disperse through older second growth (25 years old) relative to young second growth (15 years old), then young second growth will be significantly less species rich than older second growth; and (4) if sensitive foraging guilds (terrestrial insectivores, ant-followers, flock obligates and arboreal insectivores) are more prone to disperse through older second growth (25 years old) relative to young second growth (15 years old), then young second growth will have a significantly different community structure driven by the lack of sensitive foraging guilds compared to older second growth.

METHODS

The study was conducted in *terra firme* forest at the Biological Dynamics of Forest Fragments (BDFFP), about 80 km north of Manaus, Brazil and on two islands, each about 100 ha in size (Sapopara and Relógio), in the Balbina reservoir, approximately 150 km north of Manaus.

Balbina dam construction was completed in 1989; Sapopara and Relógia have been isolated since then. Forest fragments at BDFFP, including two 100-ha fragments, were isolated from 1980 through 1990. I also worked in 15 and 25 year-old second growth and continuous primary forest at the BDFFP (Figure 1.3). For more information about the study site see Stouffer et al. (2006).

I employed both understory mist-netting and point counts to account for birds in each strata of forest. For example, point counts can detect species that are vocal, conspicuous, or occupy the canopy and midstory. Conversely, mist-netting is useful for detecting quiet or skulking understory species (Ralph et al. 1995). Mist netting and point counts were conducted in five treatments: 100 ha forest fragment (surrounded by at least a 50 m buffer of 15 year old second growth), 100 ha island (surrounded by at least 300 m of open water), older second growth forest (25 years old), young second growth forest (15 years old) and continuous forest. Treatments were aggregated into five sites: Dimona (two transects within a 100ha forest fragment, two transects within older second growth and two transects within continuous forest), Porto Alegre (two transects within a 100 ha forest fragment and two transects within continuous forest), Colosso (two transects within older second growth forest, two transects within young second growth forest and two transects within continuous forest), KM41 (two transects within continuous forest), and Balbina (one transect on each of two 100 ha islands). Each BDFFP site was up to 50 km apart, and Balbina was 70 km to the North of the nearest BDFFP site (Figure 1.3). Despite a distance of 70km between Balbina and the other sites, each site is characterized by *terre firme* forest occurring on ancient soils within the Guinean Shield, resulting in comparable bird communities. My assumption of similar bird communities across the study area is strongly supported by earlier work which documented remarkably similar bird communities throughout the Guinean shield, from Manaus through French Guiana (Willis and Oniki 1988, Johnson et al. 2011).

Each transect was 200 m in length, at least 200 m apart from any neighboring transect, and hosted three point count locations at 0 m, 100 m and 200 m along the transect. Twenty minute point counts were conducted in 2012 during my study area's prolonged dry season, June

through November; each point count occurred between 05:55 and 07:20 am. For each point, the number of individuals per species was conservatively estimated using song, call and visual documentation; flyovers were not included in the analysis. Each point-count station was visited twice on different days, yielding twelve 20 minute point counts per treatment in each area.

Each transect also hosted a line of 16 mist-nets (NEBBA-type ATX, 36 mm mesh, 12 by 2 m), with nets set with the bottom at ground level and opened from 0600 to 1400 for a single day of sampling. All captured birds were banded with uniquely numbered aluminum bands, and then processed to record weight, age, sex, wing chord, and body and flight feather molt. Taxonomy follows Remsen et al. (2011). I mist-netted between June and November in 2010-2013, where I collected 3 days of banding data at 100ha island transects, 4 days of banding data at young second growth transects, and 6 days of banding at 100ha forest fragment transects, continuous forest transects and older second growth transects.

Point count and banding data were organized by number of individuals per species, per count or banding day, by site and treatment. The number of species captured at each transect was divided by associated effort (mist net hours) then multiplied by 100 to yield a standard number of species captured per 100 mist net hours across each transect irrespective of differences in sampling effort. I used program EstimateS (Colwell 2005) to produce Chao1 abundance-based estimates of species diversity and Chao-Jaccard abundance-based similarity indices to compare treatments. The Chao1 diversity index uses the ratio of ‘singletons’ and ‘doubletons’ (species detected only once or twice, respectively) to generate predicted estimates of species richness. Significance between Chao1 estimates are based on non-overlapping 95% confidence intervals generated through a bootstrapping routine in EstimateS. The formula used for Chao1 estimates are based on Chao (1987) where $S_{\text{observations}}$ refers to total number of species observed in all

samples pooled and F_1 and F_2 refer to singletons and doubletons (species detected only once or twice), respectively:

$$\hat{S}_{chao1} = S_{observations} + \frac{F_1^2}{F_2^2}$$

According to Colwell (2005), Chao's abundance-based Jaccard community similarity indices are based on the probability that two randomly chosen individuals, one from each of the two samples, both belong to species shared by both samples (but not necessarily to the same shared species) (Chao et al. 2005). This approach has been shown to substantially reduce the negative bias that undermines the usefulness of traditional similarity indexes, especially with incomplete sampling of rich communities (Chao et al. 2005, Colwell 2005). The formula used for Chao-Jaccard abundance-based similarity indices are based on Chao et al. (2005), and described by Colwell (2005) where Q_1 is the frequency of uniques, Q_2 the frequency of duplicates:

$$\text{var}(\hat{S}_{chao2}) = Q_2 + \left[\frac{1}{2} \left(\frac{Q_1}{Q_2} \right)^2 + \left(\frac{Q_1}{Q_2} \right)^3 + \frac{1}{4} \left(\frac{Q_1}{Q_2} \right)^4 \right]$$

and:

$$\hat{S}_{chao2} = S_{observations} + \frac{Q_1^2}{Q_2}$$

To determine differences in community structure with respect to foraging guild and species among treatments, I separately categorized mist-netting and point count data by species and foraging guild (following Stouffer et al. 2006; Tables A1-A2). I used package Vegan in Program R (Dixon 2003, R Development CoreTeam 2010) to separately ordinate banding and point count data, categorized by species and foraging guild within treatment, via a Detrended Correspondence Analysis (DCA). I statistically examined differences among bird communities within each treatment, by species and foraging guild, via a permutation test using 1000 iterations in package Vegan. Lastly, I used package Car (Fox et al. 2012) in program R to employ a two-

way ANOVA using type III sum of squares to test guild and treatment effects on species abundance for both point count and banding data. I choose type III Sum of Squares ANOVA because it relies on unweighted means that account for correlations between independent variables due to unequal sample sizes.

RESULTS

I recorded 3,339 individual birds representing 180 species during point counts (Table A1). I banded 3,916 individual birds representing 121 species (Table A2). Point count data revealed significantly fewer bird species on true islands compared to all other treatments except young second growth (Figure 2.1). Although not significant, banding data also yielded the lowest number of species on true islands relative to all other treatments. Despite having a slightly higher number of species than true islands, young second growth was species poor compared to all other non-island treatments (Figure 2.1). Community similarity analysis suggested that true islands and young second growth bird communities were most dissimilar relative to all treatment types (Figure 2.2) irrespective of location (Figure A1). Conversely, continuous, forest fragment and older second growth bird communities were most similar irrespective of method (mist-netting or point count). Estimated diversity and community similarity analyses showed that bird communities on true islands and in young second growth forest are most depauperate and dissimilar from communities in continuous forest.

Detrended Correspondence Analysis (DCA) results suggested that, based on mist-net data, true islands and young second growth represented significantly different communities ($p < 0.05$) when classified by foraging guild and species (Figures 2.2-2.3), whereas non-forest, hummingbird and raptor species were most closely associated with young second growth. Based

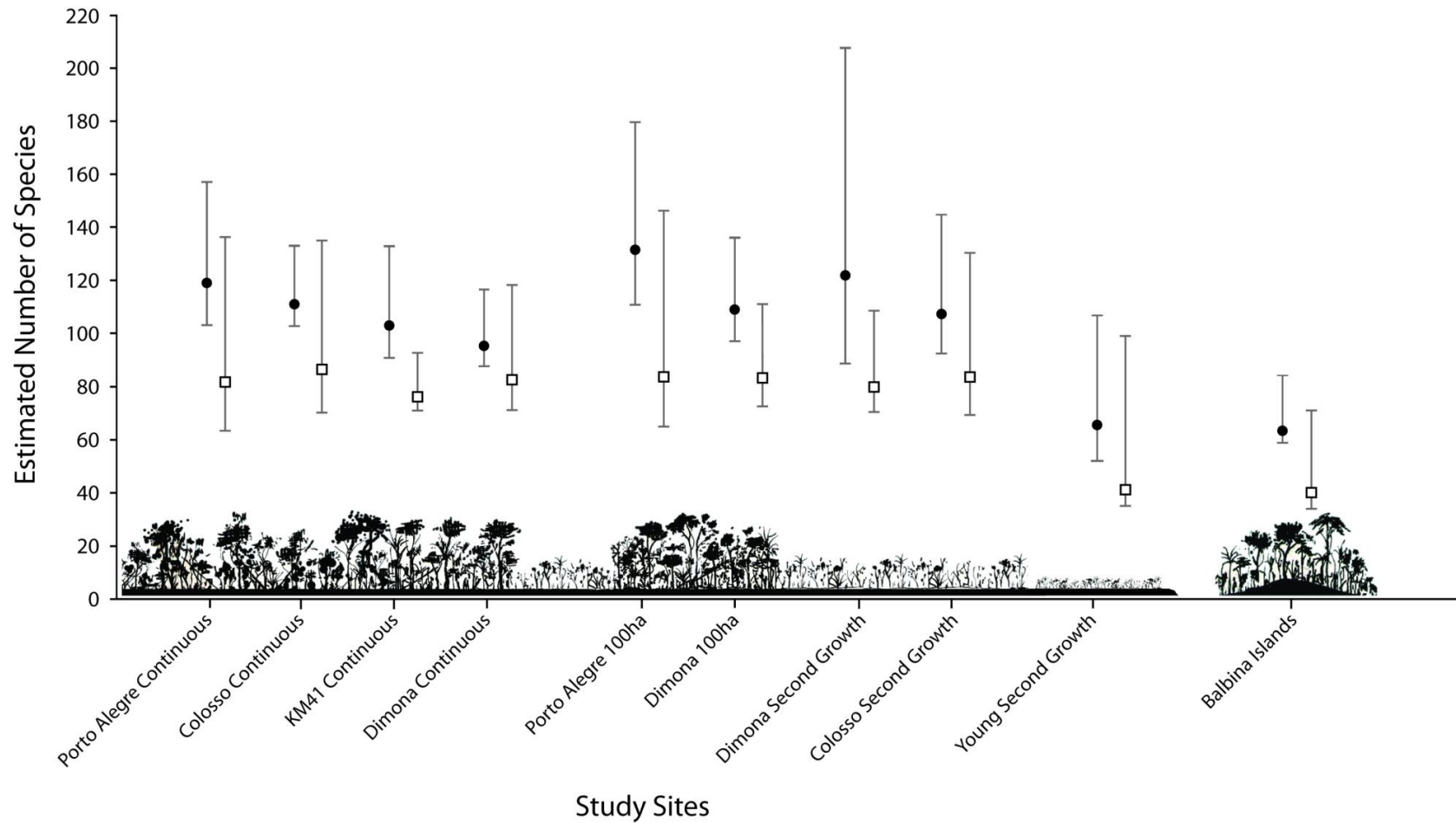


Figure 2.1. Chao1's estimated number of species by treatment (100ha forest fragment, 100ha island, continuous, older second growth forest, and young second growth forest) and region. Filled circles represent point count and open boxes represent banding data. All values are shown with 95% confidence intervals.

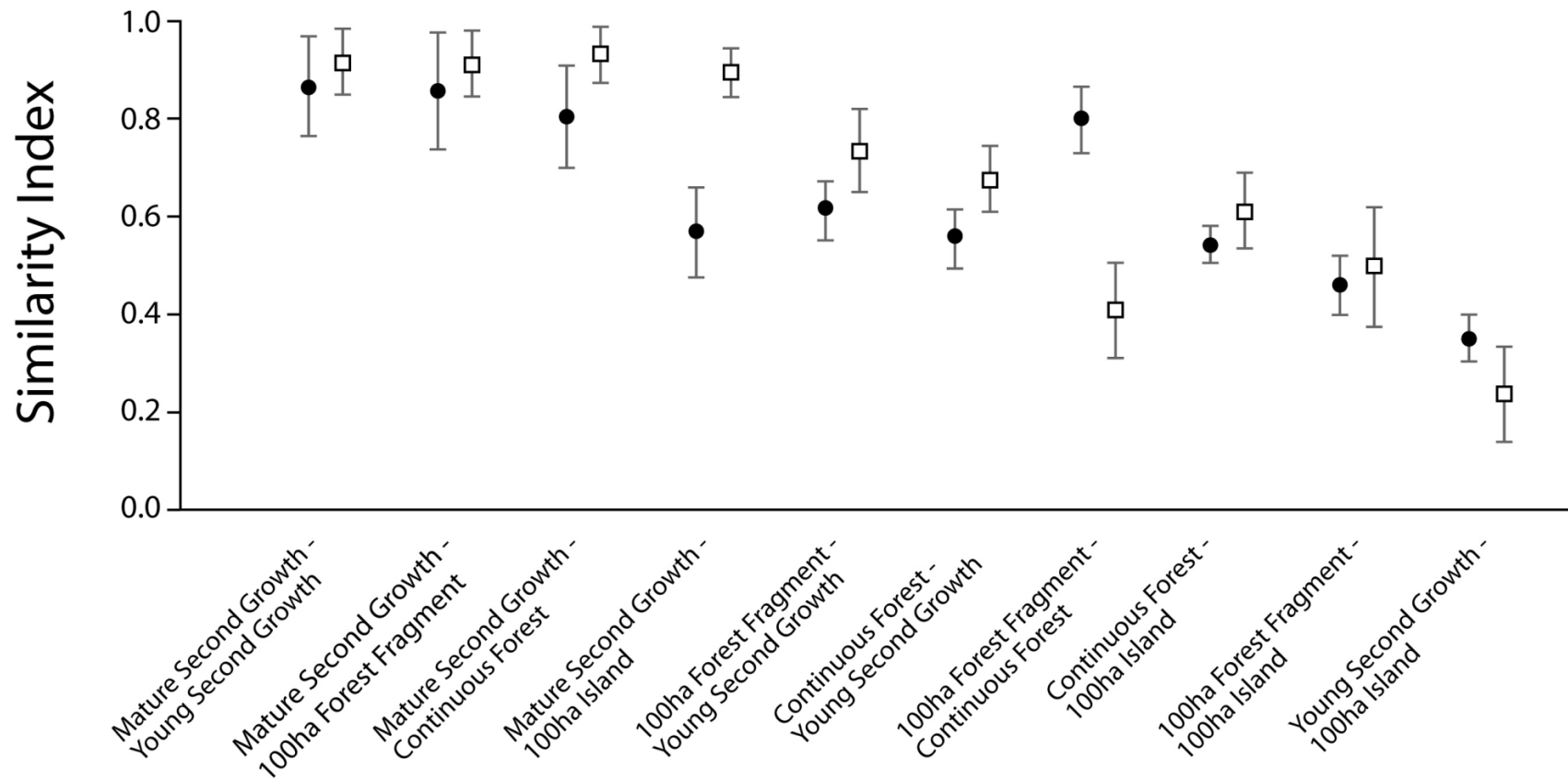


Figure 2.2. Chao's abundance-based Jaccard community similarity indices based on point count data by treatment shown with standard error bars. Filled circles represent point count and open boxes represent banding data. Comparisons are ranked from most to least similar.

on banding data, communities classified by species in forest fragment and continuous forest habitat types approached significance ($p < 0.1$). Guild ordinations based on point count data suggested that true islands also approached significance ($p < 0.1$); when classified by species, forest fragment, older second growth, young second growth and true islands all yielded significantly different bird communities ($p < 0.05$, Figures 2.5-2.6). Similar to banding ordinations, both non-forest and hummingbird foraging guilds were most closely associated with young second growth. My two-way ANOVA using type III Sum of Squares based on foraging guild classification, for point count ($df=48$, $f\text{-stat}=10.04$, $p < 0.001$) and mist-net data ($df=44$, $f\text{-stat}=6.57$, $p < 0.001$) yielded highly significant differences among treatments and guilds. Differences were driven by high number of core frugivores in older second growth, and the absence of flock obligates, flock dropouts and terrestrial insectivores on true islands and in young second growth (Figures A2-A3).

Several species intolerant to second growth (e.g. documented in continuous forest but never in regenerating forest) were found on true islands: *Piaya melanogaster*, *Celeus undatus*, *Tyrannneutes virescens*, and *Ramphotricon ruficauda*. Additionally, two species particularly common in second growth samples were also found on true islands: *Myiarchus ferox* and *Notharchus macrorhynchus* (although, *N. macrorhynchus* is generally more associated with older forest at BDFFP; Cohn-Haft *et al.* 1997). In general, woodpeckers (Picidae) and toucans (Ramphastidae) were well represented on true islands while terrestrial insectivores (e.g. *Formicarius colma*, *Corythopsis torquatus* and *Sclerurus rufigularis*) and obligate flocking species (e.g. *Thamnomanes caesius* and *T. ardesiacus*) were absent from true islands (Tables A1-A2).

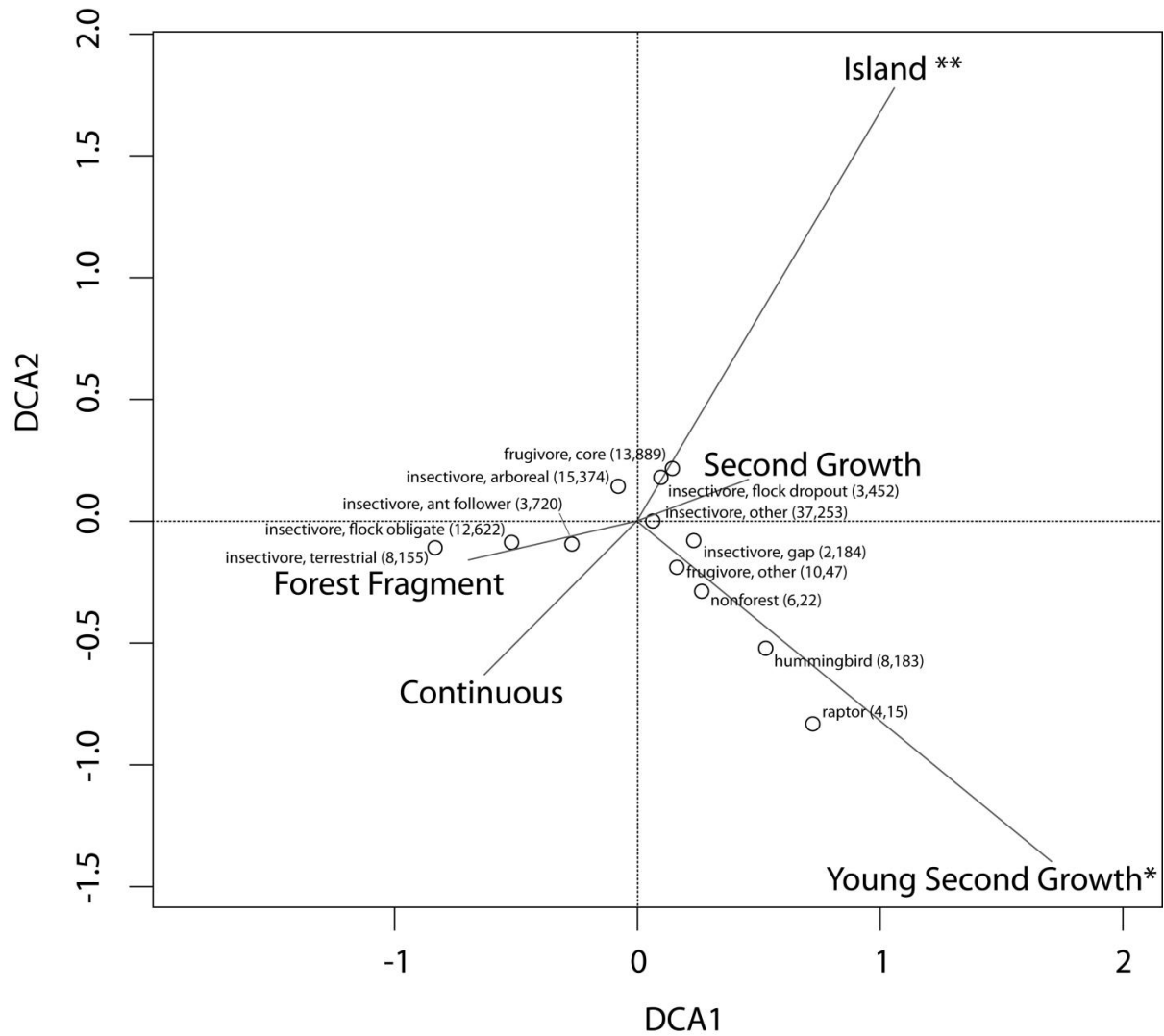


Figure 2.3. Detrended Correspondence Analysis (DCA) ordination of banding data, classified by foraging guild and treatment. Asterisks represent significance levels where: *, **, and *** represent $p < 0.1$, $p < 0.05$ and $p < 0.00$, respectively. Numbers in parentheses represent number of species within foraging guild and total number of individuals captured within each foraging guild.

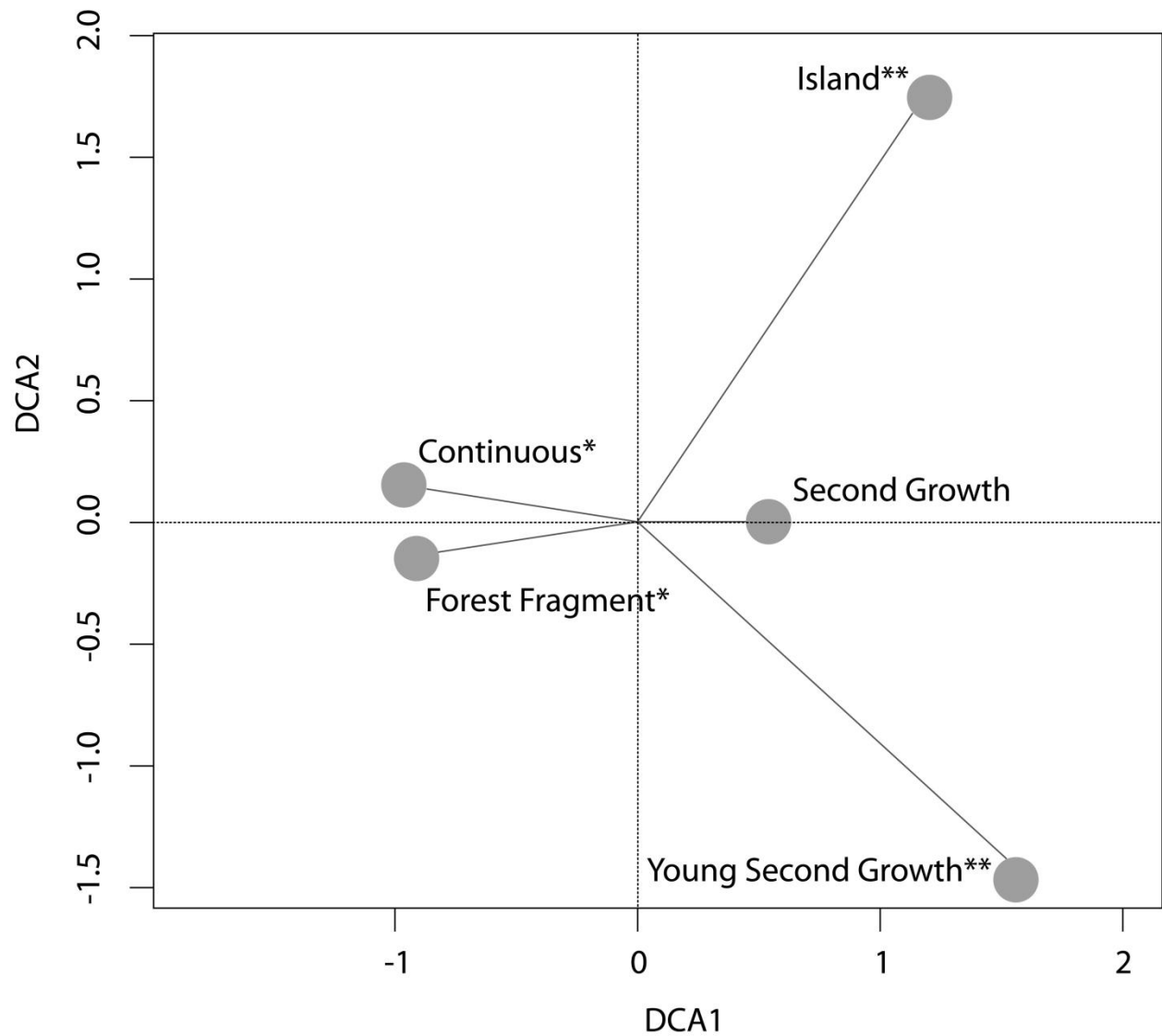


Figure 2.4. Detrended Correspondence Analysis (DCA) ordination of banding data, classified by species and treatment. Asterisks represent significance levels where: *, **, and *** represent $p < 0.1$, $p < 0.05$ and $p < 0.01$, respectively.

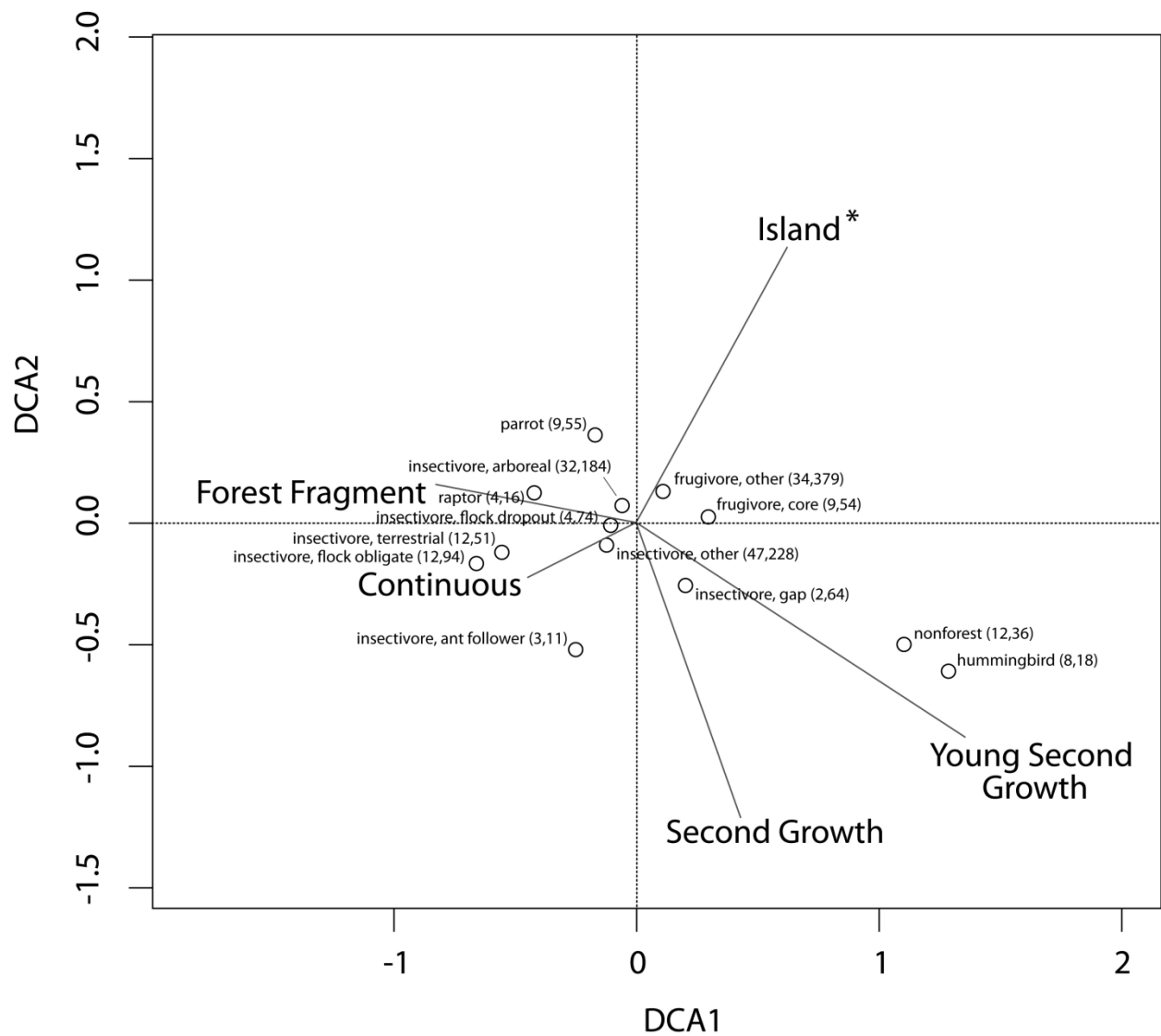


Figure 2.5. Detrended Correspondence Analysis (DCA) ordination of point count data, classified by foraging guild and treatment. Asterisks represent significance levels where: *, **, and *** represent $p < 0.1$, $p < 0.05$ and $p < 0.00$, respectively. Numbers in parentheses represent number of species within foraging guild and total number of individuals counted within each foraging guild.

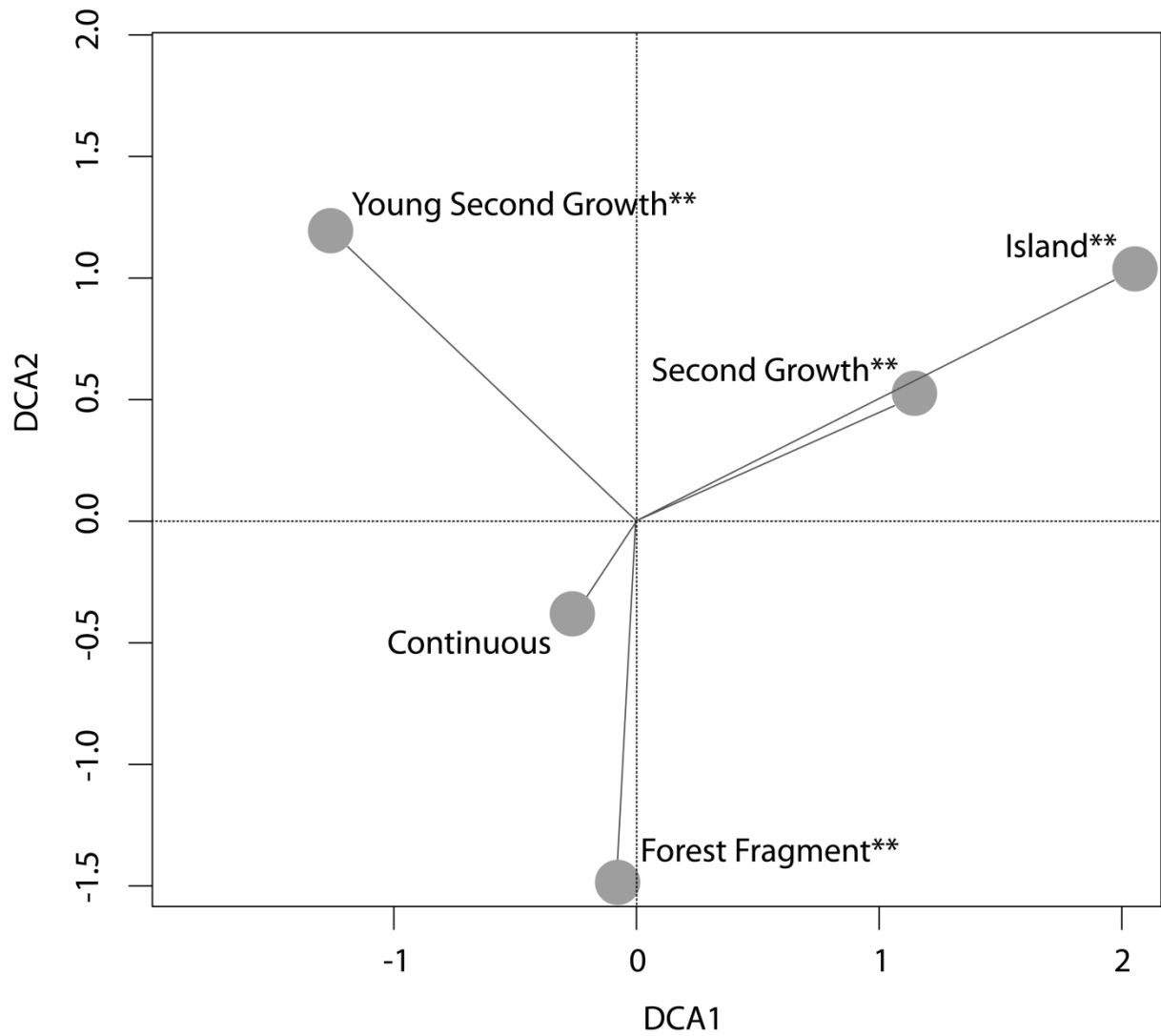


Figure 2.6. Detrended Correspondence Analysis (DCA) ordination of point count data, classified by species and treatment. Asterisks represent significance levels where: *, **, and *** represent $p < 0.1$, $p < 0.05$ and $p < 0.01$, respectively.

DISCUSSION

My study provides two important findings. First, species richness in forest fragments within a regenerating matrix is not driven by extinction dynamics as predicted by the island model. Instead, species richness appears to be dependent on the permeability of the surrounding matrix, which both supports forest species and allows recovery of bird communities in formerly isolated fragments. In contrast, for true islands, small area coupled with the complete absence of an adjacent second growth matrix subjected each island to severe and irreconcilable local extinction events despite the presence of primary forest.

Second, bird communities varied significantly between young (15 year) and older (25 year) second growth; such differences appear to have been driven by the absence of terrestrial insectivores and flocking species, and the abundance of nonforest species, gap-specialists and hummingbirds in young second growth. Young second growth was species poor, with approximately the same number of species as true islands. Despite similar number of species, community structure at the levels of both guild and species were statistically different between true islands and young second growth. Differences in community structure coupled with low species richness suggest two divergent responses to dissimilar system perturbations: second growth bird communities reflect the successional nature of regenerating forest where gap specialists, nonforest species, and hummingbirds are replaced by flocking and insectivorous species as the forest approaches 25 years of age. Conversely, islands are characterized by species capable of major dispersal events and remnant populations of forest-obligate species.

My results support previous assertions that a species' capacity to disperse through matrix to recolonize tropical forest fragments ultimately determines metapopulation persistence in degraded landscapes (Sekercioglu et al. 2002). Interestingly, several species absent from second

growth at BDFFP were detected on true islands. I believe these species are remnants from populations present at the time the reservoir was flooded. Conversely, many solitary ground-dwelling insectivores and core-flocking species that are common in continuous forest and easily detected with both sampling techniques were conspicuously absent from true islands, indicating the inability of these guilds to recolonize islands across open water. This finding is not surprising given previous studies found that these same guilds were less apt to cross open spaces and most prone to go extinct in forest fragments immediately after isolation (Ferraz et al. 2003, Laurance et al. 2004, Stouffer et al. 2006, Stouffer et al. 2009). Although open water is not suitable for many dispersing forest-dwelling birds, the remains of dead trees above the water's surface are common throughout the reservoir and presumably facilitate the dispersal of species capable of utilizing snags (Figure A4). In fact, that is what I found: woodpeckers and toucans used snags on the open water and had relatively high diversity on islands (Table A1).

My results parallel findings from another tropical reservoir where smaller and more isolated islands (1 to 12ha in size and $1\text{km} \leq$ from source populations) had fewer species and fewer transient individuals capable of recolonization, suggesting that communities were altered by biological (remnant mesopredators) and stochastic (extinction) processes leading to a dynamic equilibrium (Terborgh et al. 1997). Relative to Terborgh et al. (1997), however, my island sites were larger (100ha) and farther from source populations, thereby reducing area effects associated with small habitat patches (Terborgh et al. 1997, Stouffer et al. 2006, Stouffer et al. 2009). I believe the depauperate true island diversity estimate probably represents an ongoing extinction debt which will result in future equilibrium characterized by low species richness, including only those birds most capable of dispersing and most resilient to the effects of fragmentation (Ferraz et al. 2003). In general, islands are an extinction driven system, forest

fragments in regenerating matrix are a recolonization driven system, and second growth is a successional driven system at my study sites in the central Amazon.

In addition to informing ecological theory, my study has important conservation implications. For example, I provide evidence of a dynamic relationship between bird communities and degraded tropical landscapes, an understanding that is important for conservation purposes for regions with unparalleled diversity, such as the Amazon basin. Over the last 20 years the Brazilian government subsidized forest clearing to enhance farming opportunities for an expanding populace resulting in the loss of 328,000 km² of Amazonian forest (INPE 2010). In addition to agricultural expansion, the Brazilian government authorized the construction of 30 additional hydroelectric dams in the Amazon basin, resulting in, on average, one new dam being constructed every four months over the next seven years (Eletrobrás 1987, Ministério de Minas e Energia 2011). The threat of massive Amazon forest loss due to hydroelectric development is considerable given that a single dam in the central Amazon, Balbina, flooded 2360 km² of tropical rainforest (Fearnside 1989). Dams lead to hilltop islands surrounded by water, a much more static landscape than when forest is removed for agriculture. Such differences mean that islands and isolated habitats behave differently and represent a larger threat to the preservation of biodiversity than habitat patches within a matrix. These ecological, economic and political realities coupled with my results suggest that many more bird communities will be subject to the deleterious effects of ecological decay associated with hydroelectric development.

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CHAPTER 3: VARIATION IN TROPICAL BIRD SURVIVAL ACROSS LONGITUDE AND GUILDS: A CASE STUDY FROM THE AMAZON¹

INTRODUCTION

Variation in demography can influence the dynamics and structure of biological communities (Carnicer et al. 2012). Changes in species richness across latitudes have been attributed to many potential mechanisms, including demography, where fewer extinction events may result in more diverse communities (Carnicer et al. 2007, Mittelbach et al. 2007). These hypothetical relationships between demography and diversity suggest that populations in species-rich tropical communities might exhibit different demographic characteristics, such as higher survival, relative to their temperate counterparts in species-poor areas. Additionally, well documented differences in clutch size between tropic and temperate bird communities support a ‘trade-off’ paradigm, where survival in the tropics must be relatively high in order to compensate for small clutch size (Martin 1996).

Data supporting the “high survival in tropical birds” paradigm are mixed. For example, apparent survival estimates from tropical resident landbirds in Trinidad and Puerto Rico are high (Snow 1962, Snow and Lill 1974, Faaborg and Arendt 1995), but the generality of this result was questioned based on negligible differences in apparent landbird survival between Central and North America (Karr et al. 1990). More recently, differences in apparent survival between

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tropical and temperate latitudes have been documented in old and new world bird communities, further obscuring demographic trends (Johnson et al. 1997, Peach et al. 2001, McGregor et al. 2007). Differences in immigration and emigration within bird communities are generally unaccounted for and can also influence apparent survival estimates, potentially concealing meaningful differences across latitudes.

In addition to potential differences in structure and demography between communities, variation in demography within communities also exists and may be driven by variation in species' life history strategies such as degree of association with mixed-species flocks or nest architecture. For example, Cruz-Angon et al. (2008) found significantly higher apparent survival for two tropical bird species when they participated in mixed-species flocks. Blake and Loiselle (2008) used six years of banding data from the western Amazon to make similar comparisons between flocking and non-flocking apparent survival estimates and found no significant difference between flock guilds. In addition to flock membership, Martin (1988) and Jullien and Clobert (2000) suggested that variations in nest architecture may influence survival because such differences are subject to correspondingly varying amounts of predation.

Our ability to quantify relationships between survival and variation in diversity or life history strategies in the Neotropics remains elusive in part because of inconsistent survival estimates across guilds and locations. Perhaps these inconsistencies are not surprising, considering how few sites have been well sampled across vast tropical areas. Conversely, the network of bird banding stations in North America has revealed demographic variation within species throughout temperate North America (Desante and Saracco 2009) illustrating our need for comparable information from the tropics to appreciate patterns at a broader scale. In addition to identifying variation in demography across tropical landscapes, apparent survival estimates

also inform conservation by providing historic benchmarks of demography in a rapidly changing environment. Here I provide apparent survival estimates of 31 understory bird species based on ten years of constant effort bird banding data from multiple plots within primary forest in central Amazonia. I compare my results with survival estimates for the same species captured in western and eastern Amazonia. In addition to broad geographic comparisons, I determined flocking guild, nest type, and mass for my 31 study species from the central Amazon and examined how these life history characters influenced demographic variation. My results represent one of the largest analyses of Neotropical bird survival ever conducted, and are especially valuable because they represent a long-term sample from multiple sites in the heart of the Amazon.

METHODS

Study Site

The study was conducted in contiguous *terra firme* rainforest at the Biological Dynamics of Forest Fragments Project (BDFFP) site approximately 80km north of Manaus, Brazil (Figure 1.3). The understory at BDFFP is relatively open and dominated by palms. Canopy height at BDFFP averages 30-35 m with emergent trees as high as 55 m, which is short relative to some western Amazonian forests. The study site receives an average of about 2500 mm of precipitation/year with annual peaks from January to April and a pronounced dry season from July to November (Gascon and Bierregaard 2001).

Bird Captures

All banding data were collected from continuous forest, divided into 13 plots of 1-, 10-, and 100-ha. All plots were located 0.5 to 30 km from the nearest plot. Some plots were later isolated as fragments, but data reported here were all collected prior to isolation. My study focused on plots that were sampled (birds banded) at least three times a year, for at least four consecutive years,

from 1979 through 1988; other plots at the BDFFP that did not meet these criteria and were excluded from the analysis. Importantly, my results are from multiple sites over a 10 year period, thereby reducing the influence of a single site or a single year on subsequent results.

Plots were sampled with either one line of 8 nets (1-ha plots), one line of 16 nets (10-ha plots), or up to five lines of 16 nets, with each line separated by several hundred meters (100-ha plots). Mist-nets (NEBBA-type ATX, 36-mm mesh, 12 x 2m) were set with the bottom of the net at ground level and were kept open from 0600 to 1400 for a single day of sampling, with sampling at each site typically occurring at one to four month intervals. No nets were moved and only data derived from net captures were used in this study (no color-band resighting was included in the analysis). All captured birds were banded with uniquely numbered aluminum bands, and then processed to record weight, age, sex, wing chord, and body and flight feather molt. Taxonomy follows Remsen et al. (2011).

Analysis

Based on number of captures, I selected 33 species with sufficient data for survival estimates (reduced to 31 species after goodness-of-fit tests, see *Results*). Cormack-Jolly-Seber (CJS) models were used to estimate apparent annual survival, with time intervals for each site adjusted to account for unequal sampling effort (White and Burnham 1999). Six candidate models were formulated for each of the 31 species (Table 1). In addition to varying apparent annual survival (ϕ) and apparent annual recapture probability (p), I included Time-Since-Marking models (TSM) where survival in the first interval (ϕ_1) differed from survival during the second (ϕ_2) and subsequent capture intervals (Cooch and White 2013). TSM models can account for survival deflation due to the effects of transient individuals moving through the study area (Pradel et al. 1997). Estimates for the first survival interval (ϕ_1) were not used in comparisons with other

studies. All demographic analysis and goodness-of-fit tests were conducted in Program MARK (White and Burnham 1999).

Table 3.1. Descriptions of Cormack-Jolly-Seber (CJS) models used to estimates survival of birds captured between 1979 and 1988 in contiguous forest 80 km north of Manaus, Brazil. Notations and descriptions include the survival parameter (Surv.), recapture probability parameter (Recap.), number of parameters associated with each model (Par.) and number of species for which the associated model had the lowest QAICc value (No.).

Surv.	Recap.	Par.	No.	Model Description
$\phi(\cdot)$	$p(\cdot)$	2	18	Constant survival; constant recapture
$\phi(2./.)$	$p(t)$	11	6	Time-since-marking model (TSM) with two classes for survival (first and subsequent intervals after marking) with survival constant for each class; time-dependent recapture
$\phi(\cdot)$	$p(t)$	10	5	Constant survival; time-dependent recapture
$\phi(2./.)$	$p(\cdot)$	3	4	Time-since-marking model (TSM) with two classes for survival (first and subsequent intervals after marking) with survival constant for each class; constant recapture
$\phi(t)$	$p(\cdot)$	10	0	Time-dependent survival; constant recapture
$\phi(t)$	$p(t)$	18	0	Time-dependent survival; time-dependent recapture

Model fit was evaluated in two ways: (1) testing for trap happiness/shyness and (2) quantifying data overdispersion. Program RELEASE goodness-of-fit (GOF) was used to test for trap happy/shy individuals; program Release performs two separate GOF tests (three if comparing groups, which I did not): test 2 measures the probability that an individual known to be alive at occasion (*i*) is seen again dependent on whether it was marked at or before occasion (*i*), and test 3 measures whether, among those animals seen again, does when they were seen depend on whether they were marked on or before occasion (*i*) (Cooch and White 2013). Importantly, program RELEASE results are not unequivocal, and failure to reject the null hypothesis may reflect a lack of power to detect meaningful differences in net shyness. The

overdispersion factor (\hat{c}) was calculated for each species by dividing the deviance of each species' global model by the deviance estimated via a boot-strapping goodness-of-fit routine (using 1000 iterations). The resulting \hat{c} value was used to augment corrected Akaike Information Criterion (AICc) values, thereby providing quasi-corrected AIC (QAICc) values for model selection purposes. Top models were selected if they were at least two QAICc values less than, and had fewer parameters relative to the next most competitive model (Arnold 2010). All top models with the same number of parameters within two QAICc values were subsequently averaged in program MARK.

When possible, results from my study were compared with previously published survival estimates and associated standard errors for the same species from Peru, Ecuador and French Guiana (Francis et al. 1999, Jullien and Clobert 2000, Blake and Loiselle 2008); note that although French Guiana is not in the Amazon Basin it is immediately adjacent to the watershed and shares a similar forest type and avian community and is, therefore, referred to as 'Amazonian' in this study. I compared survival among eastern, central, and western Amazonia for 17 species shared at two or more sites. To more generally compare differences among all localities, I define non-overlapping standard error values as representative of significantly different survival estimates.

I also grouped my 31 study species into solitary, facultative and obligate flocking guilds based on Jullien and Clobert's (2000) categorizations (which included flock drop-outs at my site, such as *Xiphorhynchus pardalotus*, as obligate flocking species), then used the Delta Method to provide averaged survival estimates and associated standard errors for each guild (Powell 2007). Because life history differences can vary with body size (Jullien and Clobert 2000) and nest architecture (Martin 1988), I associated average body mass (derived from averaging body mass

using my banding data) with nest architecture (derived from a literature review, see Table 3.2) and flocking guild (Table 3.2). Influence of life history characteristics on the apparent annual survival of 31 study species was modeled by fitting generalized linear mixed models using Markov chain Monte Carlo techniques provided by the R package MCMCglmm (Hadfield 2010). Flock guild (three factors), nest architecture (five factors) and mass (continuous) were included as fixed effects. To account for phylogeny I used a phylogenetic hypothesis for all bird species (Jetz et al. 2012) and, since no consensus tree is provided, I sampled 100 trees containing my focal species from the posterior distribution of trees generated by Jetz et al. (2012). By sampling across the posterior distribution I also accounted for phylogenetic uncertainty. I ran one model for each of the 100 trees and averaged p-values and coefficients. Each model was run for 100,000 generations with the first 5,000 generations discarded as burn-in to ensure sufficient convergence; I also ensured that the autocorrelation among samples was less than 0.1. To determine whether phylogeny influenced the relationship between apparent annual survival and life-history characters, I compared the deviance information criterion (DIC) of the phylogenetic model with the DIC of a model with the same fixed effects but in which species were treated as a random effect, rather than phylogeny.

RESULTS

For all study species combined, I used 8,248 capture records. Most species yielded low estimates of over-dispersion ($\hat{c} < 2.0$) except for *Myrmotherula menetriesii* ($\hat{c} = 3.24$) and *Tachyphonus surinamus* ($\hat{c} = 3.13$). Program RELEASE goodness-of-fit tests yielded non-significant values ($p\text{-value} < 0.05$) for all species except *Mionectes macconnelli* and *Dixiphia pipra* ($p\text{-value} < 0.05$), indicating trap shyness, which could bias my estimates downward; these species were subsequently removed from the study.

Table 3.2. Survival estimates for 31 species captured in continuous forest 80 km north of Manaus, Brazil. Notation indicates guild classification: Solitary (sol), obligate flocking (obl), and facultative flocking (fac). Further notation indicates whether models were subsequently averaged (*), or whether species' top model did not include TSM (†). The first time interval represents transient survival ($\phi 1$) and the second represents resident survival ($\phi 2$). 'Nest' refers to nest architecture taken from Jullien and Clobert (2000): Bur (burrow), Th (tree hole), Glo (global), Op (open nest), Hs (hollow stub) Subscripts refer to the following references: (1) Hilty and Brown 1986; (2) Jullien and Clobert 2000; (3) Skutch 1985; (4) Tostain et al. 1992; (5) Skutch 1981; (6) Jullien and Cariveau 2001; (7) Oniki and Willis 1979; (8) not described, but *see* Denton and Blue-Smith 2000.

Species	Nest	Mass (g)	Caps/Recaps	$\phi 1$	SE	$\phi 2$	SE
Galbulidae							
<i>Galbula albirostris</i> (sol)	Bur ¹	17.4	103/8	0.304	0.311	0.915	0.181
Furnariidae							
<i>Certhiasomus stictolaemus</i> (obl)	Th ¹	16.0	194/106	-	-	0.652	0.042
<i>Xiphorhynchus pardalotus</i> (obl)	Th ³	36.7	235/99	-	-	0.749	0.053
<i>Glyphorhynchus spirurus</i> * (obl)	Th ¹	13.3	522/171	-	-	0.561	0.117
<i>Automolus infuscatus</i> (obl)	Bur ²	31.0	254/65	-	-	0.554	0.059
<i>Sclerurus ruficularis</i> * (sol)	Bur ¹	20.9	117/51	0.427	0.076	0.730	0.091
<i>Xenops minutus</i> (obl)	Th ³	12.0	112/24	-	-	0.650	0.107
Thamnophilidae							
<i>Pernostola rufifrons</i> † (sol)	Glo ¹	28.3	222/54	-	-	0.402	0.069
<i>Thamnomanes ardesiacus</i> (obl)	Op ²	16.9	338/132	0.427	0.051	0.650	0.051
<i>Thamnomanes caesi</i> us (obl)	Op ²	16.7	342/42	-	-	0.653	0.105
<i>Myrmotherula longipennis</i> (obl)	Op ¹	7.9	247/72	-	-	0.493	0.055
<i>Myrmotherula menetriesii</i> (obl)	Op ¹	7.9	146/6	-	-	0.553	0.301
<i>Myrmotherula axillaris</i> (obl)	Op ¹	7.4	131/25	-	-	0.575	0.099
<i>Isleria guttata</i> (sol)	Op ¹	10.0	115/34	0.319	0.080	0.711	0.118
<i>Epinecrophyllos gutturalis</i> (obl)	Glo ³	8.4	216/46	-	-	0.391	0.076
<i>Hypocnemis cantator</i> (sol)	Op ¹	17.6	190/36	-	-	0.516	0.082
<i>Willisornis poecilonotus</i> (sol)	Th ⁴	15.9	632/201	-	-	0.487	0.035
<i>Pithys albifrons</i> (obl)	Op ²	19.4	792/252	0.414	0.038	0.543	0.041
<i>Gymnopithys rufigula</i> † (obl)	Hs ¹	28.6	443/141	-	-	0.531	0.041

Table 3.2. Continued. Survival estimates for 31 species captured in continuous forest 80 km north of Manaus, Brazil. Notation indicates guild classification: Solitary (sol), obligate flocking (obl), and facultative flocking (fac). Further notation indicates whether models were subsequently averaged (*), or whether species' top model did not include TSM (†). The first time interval represents transient survival ($\phi 1$) and the second represents resident survival ($\phi 2$). 'Nest' refers to nest architecture taken from Jullien and Clobert (2000): Bur (burrow), Th (tree hole), Glo (global), Op (open nest), Hs (hollow stub) Subscripts refer to the following references: (1) Hilty and Brown 1986; (2) Jullien and Clobert 2000; (3) Skutch 1985; (4) Tostain et al. 1992; (5) Skutch 1981; (6) Jullien and Cariveau 2001; (7) Oniki and Willis 1979; (8) not described, but see Denton and Blue-Smith 2000.

Species	Nest	Mass (g)	Caps/ Recaps	$\phi 1$	SE	$\phi 2$	SE
Formicariidae							
<i>Formicarius colma</i> (sol)	Hs ¹	40.9	171/31	-	-	0.430	0.109
Tyrannidae							
<i>Corythopis torquatus</i> (sol)	Glo ¹	14.7	175/51	-	-	0.401	0.062
<i>Platyrinchus saturatus</i> (sol)	Op ³	10.0	57/128	-	-	0.603	0.070
<i>Platyrinchus coronatus</i> (sol)	Op ³	8.4	148/40	-	-	0.632	0.087
<i>Myiobius barbatus</i> † (obl)	Glo ³	10.3	250/50	-	-	0.540	0.079
Tityridae							
<i>Schiffornis turdina</i> (sol)	Op ⁵	32.1	189/99	0.487	0.077	0.760	0.068
Pipridae							
<i>Dixiphia serena</i> (sol)	Op ²		162/34	-	-	0.528	0.099
Troglodytidae							
<i>Microcerculus bambla</i> (sol)	Bur ⁶	16.1	83/18	-	-	0.309	0.108
Poliophtilidae							
<i>Microbates collaris</i> (sol)	Op ⁷	10.3	198/63	0.320	0.051	0.714	0.094
Turdidae							
<i>Turdus albicollis</i> (sol)	Op ³	47.7	304/110	0.419	0.056	0.684	0.070
Vireonidae							
<i>Hylophilus ochraceiceps</i> * (sol)	Op ¹	9.6	158/49	-	-	0.581	0.076
Thraupidae							
<i>Tachyphonus surinamus</i> † (fac)	Op ⁸	19.5	108/11	-	-	0.679	0.348

Models with constant survival and recapture probabilities had the most support for most species indicating a lack of power to detect variation across years (Table 3.1). In total, 21 of the 31 species had more than one top model within two QAICc values of each other (Table B1). Only *Glyphorhynchus spirurus* had a competitive model with time-dependent survival. Despite variation in survival from 0.423 to 0.725, standard errors from all years overlapped broadly (Table 3.3); for *Glyphorhynchus spirurus* I used a constant time model to estimate the single survival estimate for subsequent comparisons. Based on top and averaged models, the average annual survival estimate for all species was 0.59, with a standard error of 0.10. Out of the 31 species, *Galbula albirostris* had the highest annual survival estimate ($\phi = 0.92$, SE=0.18) and *Microcerculus bambla* had the lowest annual survival estimate ($\phi = 0.31$, SE=0.11).

Table 3.3. Time dependent survival estimates (ϕ) and associated standard errors (SE) for *Glyphorhynchus spirurus* captured between 1979 and 1988 in contiguous forest 80 km north of Manaus, Brazil *G. spirurus* was the only species with time dependency in its top model.

Year	ϕ	SE
1980	0.725	0.219
1981	0.479	0.134
1982	0.636	0.132
1983	0.526	0.065
1984	0.535	0.059
1985	0.636	0.131
1986	0.490	0.096
1987	0.580	0.091
1988	0.423	0.175

I found no relationship between apparent annual survival relative to life history characteristics and mass after accounting for phylogeny. The model that did not include phylogeny as a random effect had the highest DIC ($\Delta\text{DIC} = 8.8$) indicating that phylogeny affected apparent annual survival. I therefore only present results of the phylogenetically corrected model but note that both models recovered similar results. Specifically, nest

architecture, flock guild and mass had no significant effect on apparent annual survival (pMCMC > 0.05, Table 3.4), although nest architecture was significant when considering an alpha level of 0.1 (pMCMC = 0.09).

Table 3.4. We found no relationship between apparent annual survival relative to life history characteristics and mass after accounting for phylogeny. Posterior means, 95% Confidence Intervals and pMCMC-values are average across 100 models using 100 different phylogenetic trees sampled from a posterior distribution of trees.

Variable	Posterior Mean	95% Confidence Interval	pMCMC
Nest Architecture	-0.032	[-0.067; 0.004]	0.087
Flock Guild	0.017	[-0.069; 0.103]	0.689
Mass (g)	0.002	[-0.003; 0.006]	0.474

I identified 18 species from this study (Brazil) that had previously published annual survival estimates from Ecuador, Peru, and/or French Guiana (Figure 3.1). For several species, parameter estimates were nearly identical among sites (e.g. *Gymnopathys rufigula*, *Willisornis poecilinotus*, *Thamnomanes ardesiacus*, and *Lepidothrix serena*). However, I identified eight species with non-overlapping survival estimate standard errors across South America. French Guiana accounted for six of these differences, with the highest estimates for four species and the lowest estimates for two species (Figure 3.1). *Pithys albifrons* showed broad geographic variation with non-overlapping standard errors: survival was highest in eastern ($\phi = 0.80$, SE=0.06), intermediate in central ($\phi = 0.54$, SE=0.04) and lowest in western Amazonia ($\phi = 0.42$, SE=0.06; Figure 3.2). Although only yielding non-overlapping standard error values for French Guiana compared to Brazil and Ecuador, *Automolus infuscatus* showed a similar trend of increasing survival from east to west. Conversely, *Turdus albicollis* and *Glyphorhynchus spirurus* showed lower survival in French Guiana compared to Brazil and Ecuador. *Myiobius barbatus* and *Thamnomanes caesi* showed increasing survival from east to west, although only French

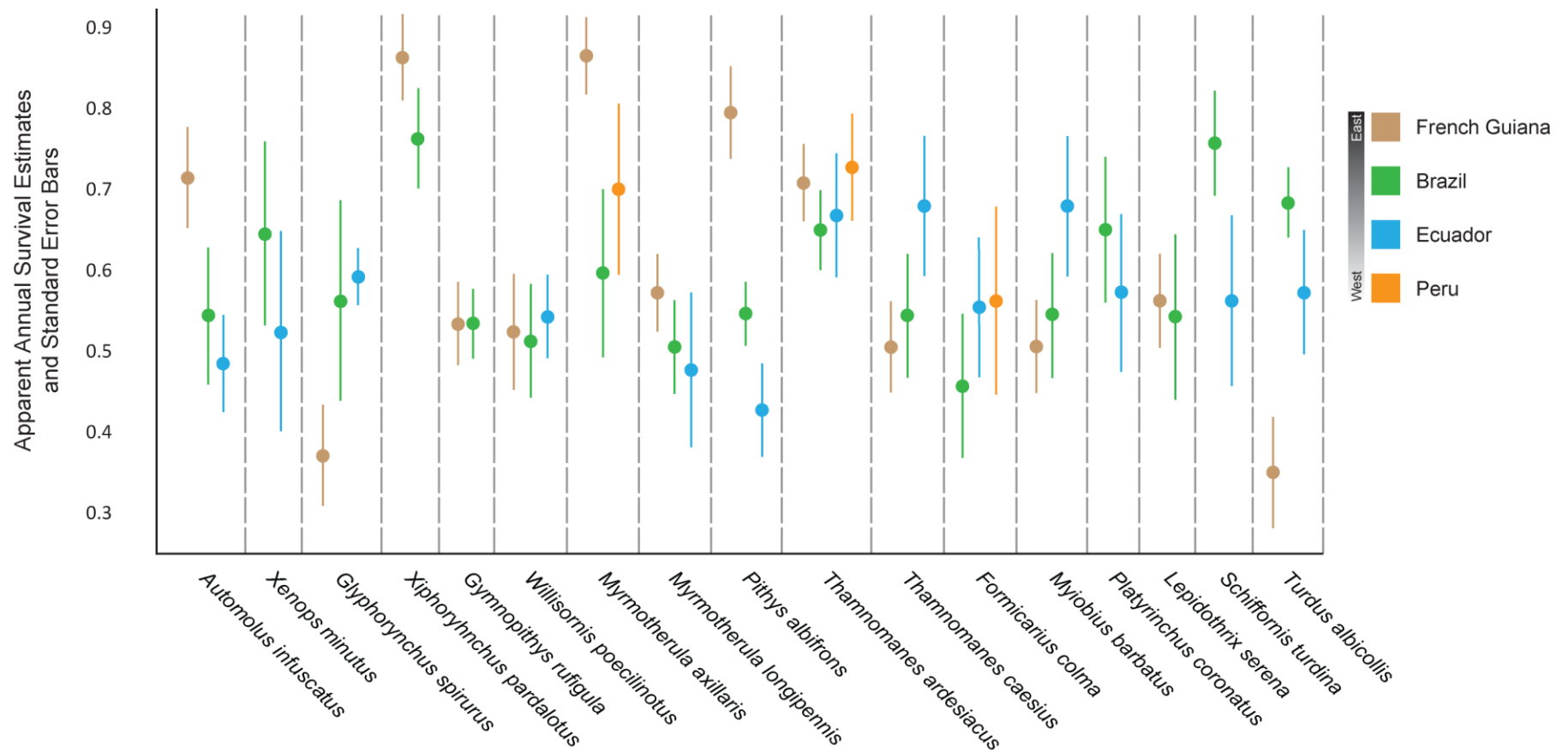


Figure 3.1. Comparison of annual survival estimates and associated standard errors for 17 species that co-occur in multiple locations throughout Central and South America. Ecuador data from Blake and Loiselle (2008); French Guiana data from Jullien and Clobert (2000); Peru data from Francis et al. (1999); Brazil data from this study.

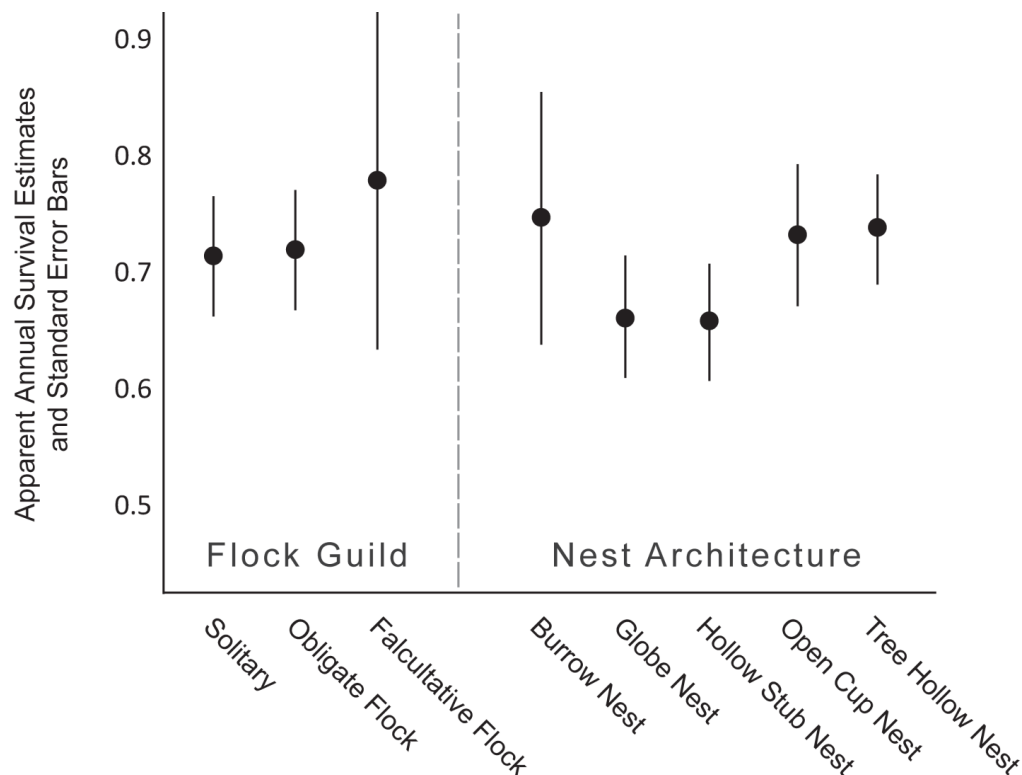


Figure 3.2. Averaged annual survival estimates and associated standard errors by flocking and nest architecture for birds captured between 1979 and 1988 in contiguous forest 80 km north of Manaus, Brazil. Values were derived from the classification of 31 species into guilds.

Guiana and Ecuador differed significantly from each other for these species.

DISCUSSION

Survival estimates from long-term monitoring efforts in continuous forest are especially valuable because they serve as historical benchmarks that can be compared to other sites as the Neotropics become increasingly disturbed. My average survival estimate for 31 Central Amazonian species from undisturbed forest in the 1970s and 1980s ($\phi = 0.59$, $SE = 0.10$), over two decades ago, was concordant with a previously published average survival estimate for 31 western Amazonian

species ($\phi = 0.58$, $SE = 0.02$; Blake and Loiselle 2008) and 17 eastern Amazonian species ($\phi = 0.63$, $SE = 0.06$; Jullien and Clobert 2000). Despite similarities in survival estimates, differences in recapture rates (recaptures/individuals) were lower at my central Amazon study site (29%) relative to the western Amazon (57%) and eastern Amazon (51%). Differences in recapture rates may be driven by site differences in local demography or natural history (e.g. abundance, home range size), study design (e.g. nets dispersed on a grid in Ecuador and linearly in Brazil) or habitat heterogeneity. The relatively low recapture rates at my site probably reduced statistical power to detect differences among guilds and across time.

I found no significant difference in survival among flock guilds (Figure 3.2). My results reaffirm Blake and Loiselle's (2008) findings that flocking behavior may not significantly improve annual survival in Amazonia. However, flocking birds foraging without an accompanying flock may exhibit lower survival, as demonstrated by two species (*Chlorospingus ophthalmicus* and *Basileuterus culicivorus*) that join flocks during the nonbreeding season in Mexico (Cruz-Angon et al. 2008). Year-round flocking behavior of resident Amazonian birds makes such comparisons difficult without manipulation. Similarly, I found no significant relationship between mass and survival; this result was surprising given previously documented allometric scaling of bird survival and mass (McCarthy et al. 2008). My results suggest that other attributes, such as nest architecture, may more strongly influence avian survival in the Amazon or, conversely, I lacked the statistical power or sample size necessary to associate mass and survival within an Amazonian understory bird community. I did detect a moderately significant difference in apparent survival when accounting for nest architecture where species that nest in burrows (*Microcerculus bambla* and *Tachyphonus surinamus*) exhibited higher apparent survival.

I believe my results make sense given that nest architecture probably influences survival in regions with extremely high levels of nest predation, like the Amazon (Ryder et al. 2008). High nest predation has been shown to limit local population viability (Low et al. 2010), and differences in nest predation may manifest as variation in survival across landscapes leading to changes in community structure. Further study is needed to verify the influence of life history characteristics on survival in Amazonian birds.

Eight of 18 species compared across South America had non-overlapping apparent survival estimate standard errors, yielding two general patterns of survival: survival was highest in western Amazonia (*Glyphorynchus spirurus*, *Myiobius barbatus*, *Thamnomanes caesius* and *Turdus albicollis*) or highest in eastern Amazonia (*Pithys albifrons*, *Automolus infuscatus* and *Myrmotherula axillaris*), but rarely higher or lower at my site in central Amazonia. In general, my results do not support a single gradient where species residing in more diverse communities, such as the western Amazon, exhibit higher survival. The strongest variation across the Amazon was exhibited by an obligate ant-follower, *Pithys albifrons*: highest in the east, intermediate in central, and lowest annual survival in the western Amazon. Intraspecific differences in apparent survival may be due to variation in life history characteristics across landscapes where nest predation, for example, may be higher in western populations of *Pithys albifrons* relative to eastern ones. Conversely, survival may be governed by unknown local effects where detected differences in species survival across the Amazon reflect unrelated processes. I believe a focused effort describing variation in survival, using the same study design, of additional wide-ranging species (e.g. *Cyphorhinus arada*, *Dendrocolaptes certhia*) across the Amazon is another necessary step towards understanding relationships between demography, community structure and diversity in the Neotropics.

Early studies of survival among Neotropical birds, often based on short-term samples or studies of lekking species, led to the suggestion that tropical birds generally show higher survival than comparable temperate species (Karr et al. 1990). However, it is important to consider that methodological differences between studies (mark-recapture vs. mark-resighting) can yield dissimilar probabilities of encountering an individual after it has been marked; typically studies that color-band individuals, and then resight them, provide relatively higher probabilities of reencountering individuals than passive mist-netting (Sandercock 2006). Differences in recapture/resighting probability also influence statistical power and my ability to discern biologically meaningful differences in survival across guilds and time. Clearly, a rigorous comparison of estimated survival from netting and resighting from the same locality for non-lekking species is needed (S. Sillett pers. com.).

I recommend two additional priorities for future research that can make use of banding data to identify ecologically meaningful phenomena with conservation implications. First, areas with high survival and population growth may be most valuable for preserving populations or forest biodiversity more broadly. Empirical studies have correlated environmental changes with population dynamics at local scales, which in turn influence broader patterns of species richness (Thomas et al. 1994, Sæther et al. 2008, Oliver et al. 2010, Carnicer et al. 2012). Variation in survival, population growth and extinction within a metacommunity at local scales can probably influence regional patterns of species richness as well, where core areas of stable survival and population growth are less likely to go extinct and more likely to be a source of dispersing individuals (Carnicer et al. 2012). If spatial variation in multiple species' survival and population growth are concordant within a metacommunity, such local demographic hotspots are, therefore, more likely to be species rich. I believe identifying local areas of stable survival and population

growth aid in preserving community-level viability and inherently more diverse areas in an increasingly fragmented Amazon.

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CHAPTER 4: ASSESSING AVIAN SURVIVAL AND POPULATION GROWTH TO DETERMINE THE ECOLOGICAL VALUE OF AMAZON SECOND GROWTH TO BIRD COMMUNITIES

INTRODUCTION

The Amazon basin is home to over 1,300 known species of birds, encompassing approximately 10% of known global avian diversity (Gill and Donsker 2013). Given the immense amount of diversity in the Amazon, the area has significant global conservation value that may be under threat as the basin continues to be developed (Wearn et al. 2012). Agricultural development is the largest contributor of forest clearing in the Amazon, resulting in the destruction of 328,000 km² of primary forest in Brazil alone within the last 20 years (more than twice the size of the state of Florida), a great deal of which has been abandoned resulting in a patchwork of variably-aged regenerating matrixes and forest fragments (INPE 2010). The dynamic Amazonian landscape tends to complicate conservation strategies for birds because it is not known if regenerating forest most often functions as population sources or sinks (Gardner et al. 2007). While second growth clearly does not provide the same habitat quality as primary forest for many birds, contemporary research suggests that second growth can provide considerable ecological value for a diversity of primary forest obligate species (although *see* Barlow et al. 2007). For example, many forest obligate species recolonized second growth forest after several decades of regeneration (Antongiovanni and Metzger 2005, Powell et al. 2013) and when second growth surrounds isolated forest fragments, the regenerating matrix can mitigate extinction or ‘relaxation’ as predicted by the species area relationship (Stouffer et al. 2006, Stouffer et al. 2011). Similarly, patches of remnant forest within a regenerating matrix can provide increased

survival for sensitive species (Sekercioglu et al. 2007) and serve as valuable stopover and wintering habitat for a diversity of migratory birds (Blake and Loiselle 2001, Wolfe et al. 2013).

Collectively, these studies suggest that regenerating tropical forest within heterogeneous landscapes can provide ecological value to birds by facilitating dispersal, which can promote the use of even small forest fragments that could not otherwise support stable populations. Second growth may also provide the resources necessary to sustain bird communities similar to the ones found in primary forest (*see* chapter 2). Despite such optimism, many of these studies relied on comparing species lists to measure community-level dynamics which may not be appropriate for ascertaining source-sink dynamics (although *see* Sekercioglu et al 2007). For example, most understory Neotropical birds exhibit territorial behavior whether they occur in mixed-species flocks, leks, family groups or pairs (Stutchbury and Morton 2001). The territorial nature of resident tropical birds presumably results in ideal despotic distributions, where dominant (typically older) birds displace subordinate (typically younger) individuals into marginal habitat. Displaced subordinate individuals in poor quality habitat can occur at higher densities relative to their dominant counterparts in better quality habitat (Bernstein et al. 1991, Johnson 2007) resulting in an erroneous assumption that more individuals equates to superior habitat (Van Horne 1983) . In addition to the potential influence of ideal despotic distributions on the habitat use of Neotropical birds, the effects of forest regeneration appears to vary with foraging guild affiliation (Gray et al. 2007). In particular, terrestrial insectivores and flock obligates are less likely to use second growth either for dispersal or as part of a home range that includes old growth forest (Powell et al. 2013, Mokross et al. 2014). Sensitive foraging guilds' slow response to habitat changes appear to be largely dependent on forest age, where terrestrial insectivores in the central Amazon were predicted to reach complete 'recovery' in second growth after 60 years

of regeneration (Powell et al. 2013). The presence and structure of second growth can also influence the behavior of Neotropical birds as well. For example, Mokross et al. (2013) demonstrated that mixed-species foraging flocks were less cohesive and flock attendance sharply decreased in second growth relative to primary forest. Conversely, frugivorous and gap-specialist species are more apt to occupy and readily move through regenerating matrixes (Stouffer 2006, Gray 2007). The asymmetric response of foraging guilds to forest succession, changes in complex interspecific interactions coupled with the potential for ideal despotic distributions can complicate the evaluation of second growth habitat quality for tropical birds.

To evaluate the ecological value of second growth, I focused on estimating three demographic parameters: (1) determine differences in age structure between second growth and primary forest to ascertain potential ideal despotic distributions for a diversity of species and foraging guilds (*sensu* Marra 2000, Rohwer 2004). Unfortunately, the seemingly simple task of classifying Neotropical birds into discrete age categories has been hindered by a nearly ubiquitous absence of field methodologies necessary to separate juvenile, young and adult birds. Recent advances in age-specific patterns of molt and plumage maturation for a variety of Neotropical birds, coupled with new age-classification schemas designed for tropical avifauna, are beginning to usher in a new era of population-level studies (Wolfe et al. 2010, Johnson et al. 2011, Johnson and Wolfe 2014). (2) Measure variation in survival between second growth and primary forest (Sekercioglu et al. 2007, Gardner et al. 2009) and (3) measure differences in population growth between second growth and primary forest. By assessing the age structure and differences in avian survival and population growth across a disturbance gradient, we can begin to identify source-sink dynamics and potential ideal despotic distributions within a heterogeneous Amazonian landscape. Here, I used four years of capture-recapture data from

multiple primary and second growth forest plots in the central Amazon to gauge the ecological value of second growth for a diversity of species and dietary guilds.

METHODS

The study was conducted in *terra firme* forest at the Biological Dynamics of Forest Fragments (BDFFP), approximately 80 km north of Manaus, Brazil (Figure 1.3). I sampled in two landscape treatments: primary forest and 25 year old second growth. Within second growth, I employed six transects grouped in two areas whereas in primary forest I used 12 transects in continuous forest and six transects in 100 ha forest fragments grouped into four areas (*see* Figure 3.1). Each transect hosted 16 mist-nets (36-mm mesh, 12 x 3 m) arranged in a line and each transect was separated by several hundred meters from its nearest neighboring transect. Mist nets were set with the bottom trammel at ground level and were kept open from either 06:00 to 14:00, or 06:00 to 13:00 for a single day of sampling. Birds were banded over a four year period from 2010 through 2013 (for primary forest transects), and 2011 through 2013 (for second growth transect sites) during the area's dry season (June through October). All transects were operated in a pulse-like fashion, where each transect was sampled two to three times within a two week period, per year. No nets were moved and only data derived from net captures were used in this study (no color-band resighting was included in the analysis). All captured birds were banded with uniquely numbered aluminum bands, and then processed to record weight, age, sex, wing chord, and body and flight feather molt.

I only used species with 10 or more individuals captured in the study. Of the 52 species used, I classified age for 25 species that have been documented to undergo partial preformative molts thereby allowing us to separate first (approximately 0-12 months of age) from definitive cycle birds (approximately over 12 months of age; *sensu* Wolfe et al. 2010). The remaining 27

species in the study undergo complete preformative molts and I was unable to differentiate first cycle from definitive birds unless an individual was in juvenal plumage. The number of individuals captured for each species, in each treatment (primary or second growth forest) was standardized by 100 mist net hours. Captured birds within their first ('young' hereafter) and definitive ('adult' hereafter) cycles were separated and grouped by treatment. I used a series of χ^2 tests in program R (R Development Core Team 2010) to determine if each age group (young or adult) for each species was captured more or less than expected in primary or second growth forest. To examine the influence of forest type and foraging guild affiliation on age ratios and capture rate, I grouped each species into one of 11 foraging guilds following Stouffer et al. (2006) (Table 4.1) and used package nlme (Pinheiro et al. 2010) in program R to conduct two separate ANOVAs, where capture rate and age ratio (percent of adult birds captured) served as response variables, and guild and forest type served as fixed factors, with species included as a random effect. Tukey's range test was used *post hoc* to determine if capture rates and age ratios of each foraging guild differed significantly between second growth and primary forest.

To conduct mark-recapture analyses, I selected six species with sufficient data to generate robust estimates of survival and population growth for each treatment. Two flock obligates, *Thamnomanes caesioides* and *T. ardesiacus*, did not individually provide enough data for robust estimates and were subsequently lumped into a seventh species category, *Thamnomanes spp.* I removed all juvenal individuals from the dataset to limit the influence of transients on subsequent estimates; each species was grouped by treatment (second growth and primary forest) and effort was collapsed by year. Because each transect was operated in a pulse-like fashion (within two week intervals), I strictly adhered to closed population assumptions during my

Table 4.1. List of study species with number of captured (n) and chi-squared results detailing whether young and adult birds were captured more often than expected in second growth (SG) or primary forest (PF); significance values denoted by * < 0.10, ** < 0.01, *** < 0.001. Study species with indiscernible age categories (differentiating young from old) were denoted by N/A. Foraging guild affiliation is denoted as follows: (In,Fob) - Insectivore, Flock Obligate; (In,Fld) - Insectivore, Flock-dropout; (In,Ar) - Insectivore, Arboreal; (In,Te) - Insectivore, Terrestrial; (In,Anf) - Insectivore, Ant-follower; (In,O) - Insectivore, Other; (In,Ga) - Insectivore, Gap; (Fr,Co) - Frugivore, Core; (Fr,Ot) - Frugivore, Other; (No) - Non-forest.

Species	n	Chi-squared Test		
		Adult p-value	Young p-value	Total p-value
<i>Galbula albirostris</i> (In, Ot)	56	N/A	N/A	SG
<i>Malacoptila fusca</i> (In, Ot)	25	N/A	N/A	PF**
<i>Frederickena viridis</i> (In, Ot)	18	N/A	N/A	PF*
<i>Thamnophilus murinus</i> (In, Ot)	43	SG	SG	SG
<i>Thamnomanes ardesiacus</i> (In, Fob)	164	PF***	PF	PF
<i>Thamnomanes caesius</i> (In, Fob)	173	PF	PF	PF
<i>Epinecrophylla gutturalis</i> (In Fob)	79	PF***	SG	SG*
<i>Myrmotherula axillaris</i> (In, Fld)	69	SG	SG**	SG
<i>Myrmotherula longipennis</i> (In, Fob)	103	PF***	PF***	PF
<i>Myrmotherula menetriesii</i> (In, Fob)	43	N/A	N/A	SG**
<i>Hypocnemis cantator</i> (In, Ga)	102	SG**	PF	PF
<i>Percnostola rufifrons</i> (In, Ga)	149	N/A	N/A	PF
<i>Schistocichla leucostigma</i> (In, Ot)	23	SG	PF**	SG
<i>Myrmeciza ferruginea</i> (In, Ot)	21	PF	PF**	PF*
<i>Pithys albifrons</i> (In, Anf)	758	N/A	N/A	PF**
<i>Gymnopithys rufigula</i> (In, Anf)	240	N/A	N/A	PF*
<i>Hylophylax naevia</i> (In, Ar)	10	PF**	PF*	PF
<i>Willisornis poecilinotus</i> (In, Ar)	260	PF***	PF	PF**
<i>Conopophaga aurita</i> (In, Te)	24	N/A	N/A	PF
<i>Formicarius colma</i> (In, Te)	124	PF***	PF**	PF
<i>Sclerurus rufigularis</i> (In, Te)	28	N/A	N/A	SG
<i>Certhiasomus stictolaemus</i> (In, Obl)	70	N/A	N/A	PF*
<i>Dendrocincla fuliginosa</i> (In, Ar)	58	N/A	N/A	SG*
<i>Dendrocincla merula</i> (In, Anf)	53	N/A	N/A	SG
<i>Glyphorhynchus spirurus</i> (In, Fld)	603	N/A	N/A	PF*
<i>Dendrocolaptes certhia</i> (In, Ot)	23	N/A	N/A	PF
<i>Xiphorhynchus pardalotus</i> (In, Fld)	127	N/A	N/A	SG

Table 4.1. List of study species with number of captured (n) and chi-squared results detailing whether young and adult birds were captured more often than expected in second growth (SG) or primary forest (PF); significance values denoted by * < 0.10, ** < 0.01, *** < 0.001. Study species with indiscernible age categories (differentiating young from old) were denoted by N/A. Foraging guild affiliation is denoted as follows: (In,Fob) - Insectivore, Flock Obligate; (In,Fld) - Insectivore, Flock-dropout; (In,Ar) - Insectivore, Arboreal; (In,Te) - Insectivore, Terrestrial; (In,Anf) - Insectivore, Ant-follower; (In,O) - Insectivore, Other; (In,Ga) - Insectivore, Gap; (Fr,Co) - Frugivore, Core; (Fr,Ot) - Frugivore, Other; (No) - Non-forest.

Species	n	Chi-squared Test		
		Adult p-value	Young p-value	Total p-value
<i>Xenops minutus</i> (In, Fob)	38	N/A	N/A	PF
<i>Philydor erythrocerus</i> (In, Ot)	14	N/A	N/A	PF*
<i>Clibanornis rubiginosus</i> (In, Ar)	14	N/A	N/A	PF**
<i>Automolus ochrolaemus</i> (In, Ar)	25	N/A	N/A	SG***
<i>Automolus infuscatus</i> (In, Fob)	91	N/A	N/A	SG
<i>Corythopsis torquata</i> (In, Te)	41	N/A	N/A	SG
<i>Mionectes macconnelli</i> (Fr, Co)	149	N/A	N/A	PF
<i>Rhynchocyclus olivaceus</i> (In, Ot)	21	N/A	N/A	PF
<i>Platyrinchus saturatus</i> (In, Ar)	40	PF***	PF*	PF*
<i>Platyrinchus coronatus</i> (In, Ar)	59	PF**	PF	PF
<i>Onychorhynchus coronatus</i> (In, Ot)	14	PF***	PF	PF
<i>Myiobius barbatus</i> (In, Fob)	81	N/A	N/A	SG
<i>Terenotriccus erythrurus</i> (In, Ot)	33	N/A	N/A	PF
<i>Attila spadiceus</i> (Fr, Ot)	23	PF	SG	SG*
<i>Lepidothrix serena</i> (fr,co)	66	SG*	SG	SG*
<i>Manacus manacus</i> (No)	14	SG**	SG***	SG
<i>Dixiphia pipra</i> (Fr, Co)	567	SG***	SG***	SG*
<i>Ceratopipra erythrocephala</i> (Fr, Co)	121	SG***	SG***	SG
<i>Schiffornis turdina</i> (Fr, Co)	38	N/A	N/A	PF
<i>Hylophilus muscicapinus</i> (In Fob)	15	N/A	N/A	PF
<i>Hylophilus ochraceiceps</i> (In, Fob)	46	N/A	N/A	SG
<i>Microcerculus bambla</i> (In, Ar)	10	PF*	SG	PF*
<i>Cyphorhinus arada</i> (In, Te)	22	PF**	PF*	PF
<i>Microbates collaris</i> (In, Ar)	38	PF***	PF**	PF
<i>Turdus albicollis</i> (Fr, Co)	119	PF	SG***	SG
<i>Tachyphonus surinamus</i> (Fr, Co)	74	N/A	N/A	PF

sampling periods. Pradel models were used in program MARK (White and Burnham 1999) to evaluate a series of eight models per species, where survival (Φ), population growth (λ) and recapture probability (p) varied by treatment (second growth and primary forest) and a null parameter (.) (Table C1). Importantly, Pradel models use a time-reversal approach to estimate recruitment and survival to derive an explicit estimate of population growth without directly measuring abundance (Cooch and White 2006). The data overdispersion factor (\hat{c}) was calculated for each species by dividing the deviance of each species' global model by the deviance estimated via a bootstrapping goodness-of-fit routine (using 1000 iterations); all subsequent \hat{c} values were below 2.0 and acceptable for model fit. Program RELEASE goodness-of-fit (GOF) was used to test for trap happy/shy individuals (Cooch and White 2013). All program RELEASE tests yielded non-significant values ($p > 0.05$). All models were ranked by their corrected Akaike Information Criterion (AICc), and all models with the same number of parameters within the top 0.95 AICc weight were averaged in program MARK (Arnold 2010).

RESULTS

I captured 1417 individuals in second growth and 3343 individuals in primary forest. Adults were captured more often than expected in primary forest ($p < 0.05$) for 12 of the study species. Each of these 12 species was insectivorous. Conversely, adults were captured more often than expected in second growth ($p < 0.05$) for five species; each of these five species was categorized as either a frugivore, non-forest or gap specialist (Table 4.1). With respect to young birds, five species exhibited a significantly larger proportion of captures in second growth and eight species exhibited a significantly larger proportion of captures in primary forest. In general, frugivores, non-forest and gap specialists were more often captured in second growth and insectivores in primary forest. When age classes (young and adult) were combined, the trend of flocking,

arboreal and terrestrial insectivores being captured more often in primary forest, and frugivores, non-forest and gap specialists in second growth generally held true (Table 4.1). I also found a significant difference in the capture rate of foraging guild between second growth and primary forest ($df = 1,9$, $F = 2.45$, $p = 0.024$), although the Tukey's range test failed to detect significant differences within foraging guild comparisons. Differences in the age ratios of foraging guilds between second growth and primary forest were nearly significant ($df = 1,9$, $F = 2.29$, $p = 0.075$), where the Tukey's range test identified a significant difference in age ratios within terrestrial insectivores between second growth (more young) and primary forest (more adult) ($p = 0.007$).

Each species yielded multiple competitive models (within two AICc values of the top model) which included treatment (primary and second growth forest) as a grouping parameter (Table C1). Averaged estimates of survival were found to be higher in primary forest for four of the seven species representing the following guilds: flock obligates, flock dropout, arboreal insectivore and core frugivore (Figure 4.1, Table C2). Conversely, both obligate ant followers and the gap specialist exhibited higher survival in second growth when compared to primary forest. Population growth was estimated to be above stable, indicative of growing populations for all species in both second growth and primary forest (Figure 4.2). However, population growth was elevated in primary forest for *Thamnomanes spp.* (flock obligate), and *Glyphorhynchus spirurus* (flock dropout). The two obligate ant followers (*Pithys albifrons* and *Gymnopithys rufigula*) exhibited virtually no difference in population growth between treatments, and the core frugivore (*Dixiphia pipra*) and gap specialist (*Percnostola rufifrons*) exhibited elevated population growth in second growth (Figures C1 and C2).

Figure 4.1. Comparison of survival estimates for seven central Amazonian birds captured in second growth and primary forest. Foraging guild affiliation is denoted by (In,Fob) - Insectivore, Flock Obligate; (In,Fld) – Insectivore, Flock-dropout; (In,Ar) – Insectivore, Arboreal; (In,Anf) – Insectivore, Ant-follower; (In,Ga) – Insectivore, Gap; (Fr,Co) – Frugivore, Core.

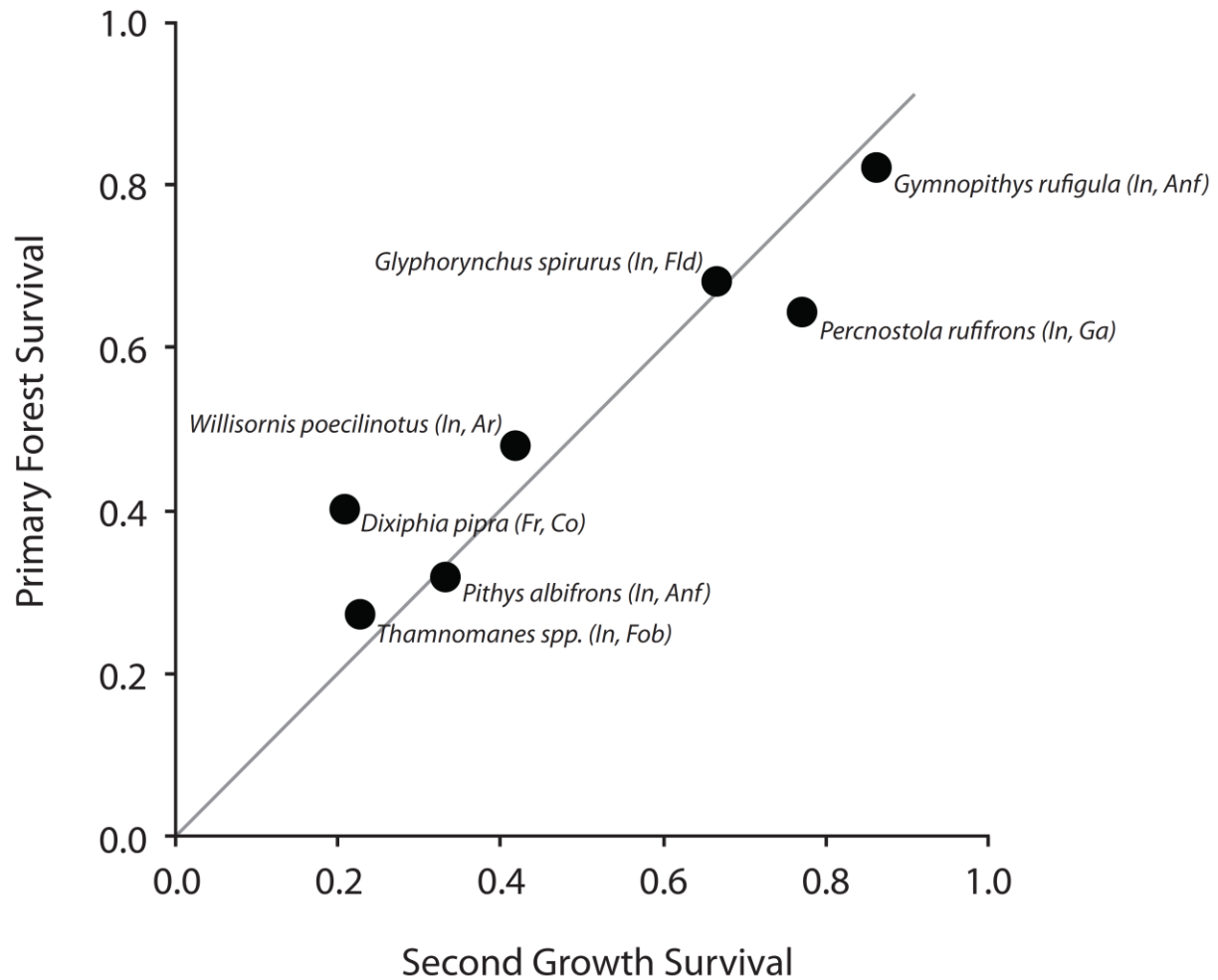
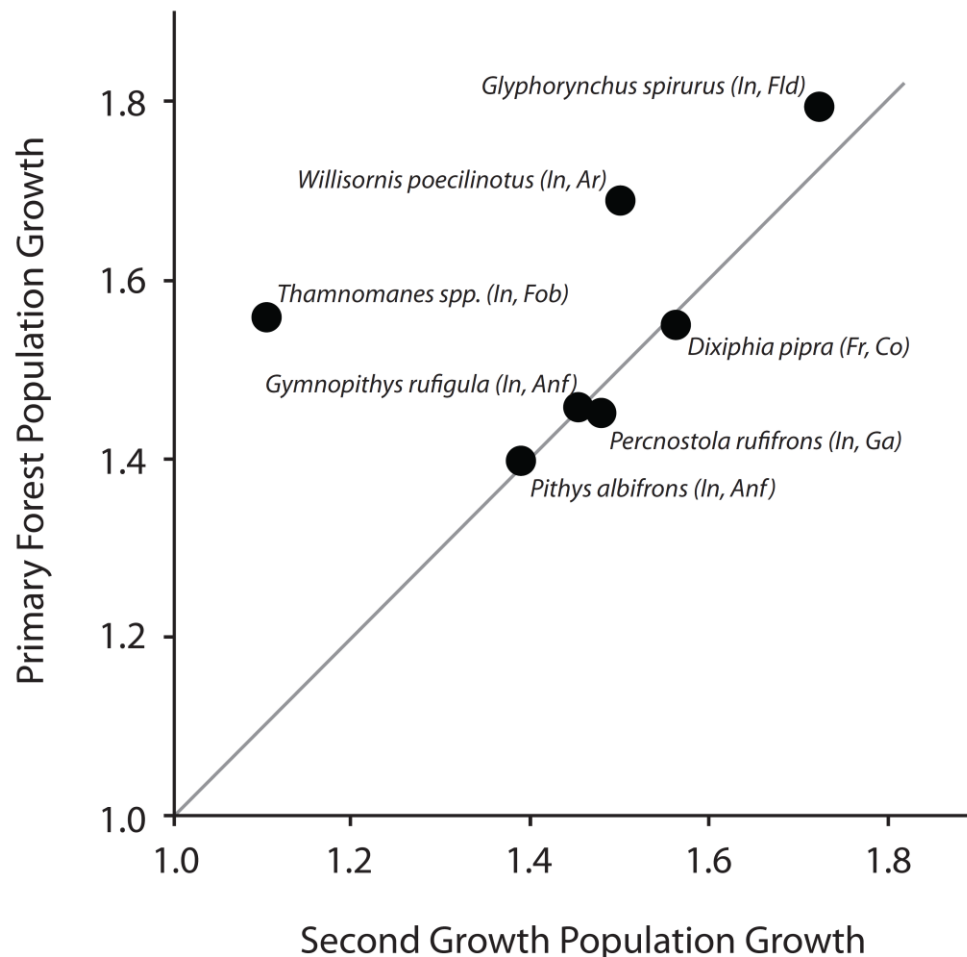


Figure 4.2. Comparison of population growth estimates for seven central Amazonian birds captured in second growth and primary forest. Foraging guild affiliation is denoted by (In,Fob) - Insectivore, Flock Obligate; (In,Fld) – Insectivore, Flock-dropout; (In,Ar) – Insectivore, Arboreal; (In,Anf) – Insectivore, Ant-follower; (In,Ga) – Insectivore, Gap; (Fr,Co) – Frugivore, Core.



DISCUSSION

The majority of previous studies focused on measuring the ecological value of second growth for birds have relied on measures of abundance, often neglecting more meaningful demographic parameters. Here, I provide species specific age structure, survival and population growth estimates for a diversity of dietary guilds in primary forest and 25 year-old second growth in the central Amazon. The ecological value of second growth at my study site was dynamic and

covaried with respect to foraging guild. I found evidence for despotic distributions in 12 insectivorous species where adult birds were statistically more likely to be captured in primary forest than second growth; however, these relationships were guild dependent as exemplified by ‘reverse’ despotic distributions where adults of five frugivorous and gap specialist species were statistically more likely to be captured in second growth. The asymmetrical response of foraging guild to the presence of second growth epitomizes the importance of considering life history characteristics when evaluating the habitat quality of tropical landscapes. Within heterogeneous tropical forests, dissimilar habitat preferences among foraging guilds may culminate in competing interests where gap specialists and frugivorous species more effectively exploit resources in regenerating matrixes while forest-dwelling insectivores profit from occupying mature tropical forest. Competing interests among foraging guilds are malleable through time: as forest succession approaches primary forest-like conditions, second growth becomes less valuable for one community while increasing in value for the other.

The multifaceted response of birds to Amazonian forest degradation is further supported by previous work which documented the absence of insectivorous birds in 15-year old second growth (Wolfe et al. 2014), suggesting a rapid successional process in regenerating matrixes between 15 and 25 years at my study site. More specifically, the inability of flock obligates and terrestrial insectivores to recolonize cleared forest fragments within a young regenerating matrix (Stouffer et al. 2006) coupled with the absence of these same foraging guilds in 15-year old second growth (Wolfe et al. 2014) indicates an avoidance of early successional regenerating forest; however, after 25 years, many forest-dwelling species have colonized second growth. Potential despotic distributions operating between second growth and primary forest are reinforced by my finding that terrestrial insectivore age structure varied significantly between

treatments, such that adult birds were proportionately captured more often in primary forest, relative to young birds in second growth. These results appear to coincide with Powell et al.'s (2013) estimate that second growth may fully recover as measured by movement of understory birds after 60 years of growth.

Survival and population growth estimates largely supported inference from the age structure and foraging guild analysis where arboreal insectivore and flock obligates exhibited increased survival and population growth in primary forest relative to second growth. The single flock dropout analyzed, *Glyphorynchus spirurus*, exhibited only a marginal increase in survival and population growth in primary forest which is concordant with recent telemetry studies suggesting that the species readily uses second growth at similar rates as primary forest after several decades of growth (Powell et al. 2013). Somewhat surprisingly, my two ant followers that have previously been shown to avoid clearings and young forest (Bierregaard and Lovejoy 1989), showed no appreciable difference in population growth or survival between treatments indicating that this guild may be one of the first of the previously identified 'sensitive groups' to fragmentation to not only traverse second growth, but successfully utilize the regenerating matrix after 25 years of growth (Stouffer et al. 2006). In general, I found all species yielded stable population growth estimates ($\lambda > 1$); however, given the relatively short duration of the study (four years) I may not have detected demographic oscillations associated with birds in second growth or primary forest (Wolfe and Ralph 2013, Wolfe et al 2014).

The ecological value of regenerating forest to birds is variable through time and highly dependent on avian foraging guild. Frugivores, gap specialists and ant followers may exact maximum benefit after several decades of succession, slowly giving way to forest-obligate insectivores. During this transitional period, dispersing or subordinate insectivores may

increasingly try to occupy regenerating forest which may reach full recovery after 60 years (Powell et al. 2013).

Differences in opinion regarding what parameter constitutes ecological value for birds has resulted in on-going debate, where some authors suggest that second growth buffers species from extinction by hosting reduced numbers of forest-obligate species and facilitating dispersal through a hostile matrix (Stouffer et al. 2006, Wright and Muller-Landau 2006). Conversely, others noted that species richness and community composition differ between second growth and primary forest suggesting that only a small subset of species found in primary forest subsist in regenerating forest (Barlow et al. 2007, Gardner et al. 2007, Laurance 2007). My findings suggest that the habitat quality of 25-year old Amazonian second growth is ecologically valuable to different foraging guilds and subject to maturation, providing different exploitative opportunities over the course of several decades for different bird communities. An extensive amount of work in my study area has focused on the ability of second growth to facilitate recolonization of previously depauperate forest fragments; here, I suggest that 25-year old second growth not only assists dispersal, but also provides the resources necessary to sustain many of the same birds found in primary forest. Although my work has demonstrated the ecological value of second growth for a diversity of species and foraging guilds in the short-term, I suggest a long-term mark-recapture effort in young, mature and old regenerating Amazonian forest to create a hierarchical framework of ecological value. Such a framework will inevitably help prioritize and conserve the habitats necessary to sustain biodiversity and sensitive tropical bird populations.

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CHAPTER 5: THE EFFECTS OF A REGENERATING MATRIX ON SURVIVAL OF BIRDS IN AMAZONIAN FOREST FRAGMENTS

INTRODUCTION

Bird populations in tropical forest fragments are often considered dynamic (i.e. subject to frequent species turnover) relative to their counterparts in pristine forest (Laurence et al. 2011). The dynamic nature of bird populations in forest fragments is in part governed by the condition of the surrounding matrix where presence of corridors, history of land-use, matrix age, and distance to source populations can moderate avian dispersal into remnant fragments (Stouffer and Bierregaard 2007, Sodhi et al. 2011). Dispersal is necessary to maintain connectivity between fragments and buffer bird populations from extinction; thus, condition of the surrounding matrix not only moderates dispersal, but determines the balance between extinction and colonization in forest fragments (Renjifo 2001, Ewers and Didham 2006). Matrix-mediated changes in bird populations within forest fragments can occur rapidly, or unfold over longer periods of time, as documented in the central Amazon (Stouffer et al. 2011).

At the Biological Dynamics of Forest Fragmentation Project near Manaus, Brazil, the relationship between central Amazonian bird populations within fragments and the surrounding matrix was measured over a 30 year period, where the fragmentation of pristine forest led to a rapid increase in bird capture rates, indicative of higher abundance following isolation (Bierregaard and Lovejoy 1989). Increased capture rates probably reflect a “crowding effect” where birds sought refuge from deforestation by moving into remnant habitat patches (Bierregaard et al. 1992, Debinski and Holt 2000). After several months of elevated bird abundance, the number of captures in forest fragments exhibited decline, culminating in the disappearance of several species from fragments (Bierregaard and Lovejoy 1989, Bierregaard et

al. 1992). The pattern of rapid increase in abundance followed by decline within fragments suggests that a formerly open system had become closed after clearing, thereby eliminating dispersal and expediting local extinction events. After years of matrix regeneration, many of the previously absent species not only returned to recolonize Amazonian forest fragments (Stouffer et al. 2011), but also established themselves within adjacent second growth (*see* chapter 2). Once established, these pioneering bird populations in fragments and second growth may be subject to source-sink dynamics where vulnerable species periodically perish and are subsequently replaced by individuals from superior habitats with higher survival and reproductive surpluses (Sodhi et al. 2011). Clearly, the transition of Amazonian forest fragments from depauperate patches to potential sources may principally depend on the condition of the surrounding matrix (Renjifo 2001, Ewers and Didham 2006, Stouffer and Bierregaard 2007, Kennedy 2010). This dynamic role of developing matrix revealed at the BDFFP suggests that bird survival in fragments is likely mediated by the matrix. Therefore, exploring critical links between the survival of tropical birds within forest fragments and the condition of the surrounding matrix should be an essential focus of conservation biology in tropical latitudes.

To date, few studies have examined avian survival in forest fragments relative to the condition of the surrounding matrix. One such study found that Ovenbird (*Seiurus aurocapillus*) apparent survival in Canada was considerably lower (34%) in small fragments (>15 ha) in an agricultural landscape than in forestry fragments (56%) and continuous forest (62%) (Bayne and Hobson 2002). Low apparent survival may have been driven by heightened dispersal out of the agricultural landscape, where birds incapable of successfully nesting left the area (Bayne and Hobson 2002). Additionally, differences in apparent survival between treatments suggest that edge effects, or changes in population dynamics at the boundary of two habitats, associated with

a low-contrast forestry matrix did not yield as negative of an impact as those associated with a high-contrast agricultural matrix (Bayne and Hobson 2002). Clearly, not all edge effects are equal: amount of contrast between matrix and habitat yield an asymmetrical influence on avian survival within forest fragments (Stouffer and Bierregaard 1995, Bayne and Hobson 2002, Stouffer et al. 2006). The asymmetrical influence of edge effects associated with fragmented landscapes has been implicated in the decline of plant and animal populations throughout the globe (Debinski and Holt 2000). Thus, tropical birds in fragments surrounded by a young matrix may be subject to the deleterious synergy of edge effects and dispersal limitation (Gilpin and Soulé 1986).

Deleterious edge effects and dispersal limitation may be particularly acute in tropical systems where insectivorous and flocking birds are often more sedentary, closely tied to forest-like characteristics, and incapable of dispersing long distances (Stouffer and Bierregaard 1995, Sodhi et al. 2004, Laurance et al. 2004, Moore et al. 2008). These sensitive tropical birds may avoid edges where heightened exposure to wind, sun, increased air temperature, increased soil temperature and storm damage can result in the death of trees they rely upon, as well as modifications to the microclimates they prefer (Saunders et al. 1991, Camargo and Kapos 1995, Murica 1995, Laurance and Curran 2008). The cumulative threat of edge-induced mortality is significant; approximately half of the world's tropical forests are degraded and in some stage of regeneration (Wright 2005). Thus, assessing the influence of matrix composition and associated edge effects on tropical bird survival within habitat fragments is of critical importance. Here I used long-term capture data from a 10 and 100 ha forest fragment in the central Amazon to test the following hypothesis: if the age of the adjacent matrix influences survival of sensitive avian

foraging guilds (flocking, arboreal insectivores and ant-followers), then survival estimates of sensitive foraging guilds will be positively correlated with matrix age.

METHODS

The study was conducted in *terra firme* Amazonian rainforest at the Biological Dynamics of Forest Fragments (BDFFP), approximately 80 km north of Manaus, Brazil (Figure 1.3). The BDFFP consists of 1, 10 and 100 ha forest fragments as part of the largest and longest operating landscape fragmentation experiment on Earth (for a history of the project *see* Bierregaard 2001). Here, I use the BDFFP's long-term bird banding database that encompasses data collected within fragments from 1979, before isolation occurred through 2013. Mist-nets (12 m, 36 mm mesh), with the bottom trammel set at ground level, were used to capture birds. The number of nets differed among fragments; a single line of 16 nets was used in 10 ha fragments, and three single lines of 16 nets were used in 100 ha fragments. I considered one complete sample a single day of netting that began at 0600 until 1400 hours. All captured birds except hummingbirds were banded with uniquely numbered aluminum bands, and then processed to record weight, age, sex, wing chord, and body and flight feather molt. To ascertain the effects of matrix condition on avian survival, I only used data from fragments if sampling occurred during three discrete time periods: (1) pre-isolation, (2) less than five years of matrix regeneration, and (3) more than five years of matrix regeneration. Fragments that were only sampled during two time periods, pre-isolation and less than five years of matrix regeneration, were not used in the analysis. The amount of time between individual sampling events varied over time; fragments were generally sampled at least every 6 weeks during the course of this study from 1979 through 1992, although fragments were sampled more often for about 1 year before and after initial isolation (Stouffer et al. 2006). In this study, I only used data from two fragments, a single 10 ha (Cidade Powell) and

100 ha (Porto Alegre) fragment, that met my stringent data selection criteria based on: (1) at least three samples per year, (2) three discrete stages of matrix condition, and (3) enough capture data to yield robust survival estimates.

I chose six study species based on their unique foraging guild (Table 5.1) and high number of captures/recaptures to ensure that I could examine the effects of matrix condition on survival. Capture histories for each species were constructed by pooling all samples within a calendar year into a single occasion then grouping birds by fragment and transiency. I defined transients as individuals that were only captured once within a single year and residents were birds captured more than once within a single year. Transient models can account for survival deflation due to the effects of floater individuals moving through the study area (Pradel et al. 1997). I used Cormack-Jolly-Seber models in Program MARK (White and Burnham 2001) to estimate annual survival for each species where apparent survival (Φ) and recapture probability (p) parameters jointly varied by time (t), time independence ($.$), group, which included fragment and transiency (g), and group-time interactions ($g*t$). To determine the influence of matrix condition on study species survival, I formulated linear time trends within program MARK's design matrix representative of three stages of matrix succession; time trends were calculated for each fragment's unique isolation and re-isolation history: (1) pre-isolation, (2) less than 5 years of matrix regeneration, and (3) more than five years of matrix regeneration. I associated time trends (representative of three levels of matrix growth) with the grouping variable (g - matrix) for the survival parameter only. Thus, each study species had a total of eight candidate *a priori* models (Table D1).

Table 5.1. Candidate Cormack-Jolly-Seber models for six central Amazonian bird species captured in 100 and 10 ha fragments, ranked by Akaike Information Criterion (AIC_c). Top models are shown with corresponding null models for comparative purposes. Included for each model are AIC_c weights (w_i) and deviance. Numbers within parentheses refer to number of individuals and total captures, respectively. Foraging guild affiliation is denoted as follows: (In,Fob) - Insectivore, Flock Obligate; (In,Fld) – Insectivore, Flock-dropout; (In,Ar) – Insectivore, Arboreal; (In,Anf) – Insectivore, Ant-follower; (In,Ga) – Insectivore, Gap; (Fr,Co) – Frugivore, Core.

Model	ΔAIC_c	w_i	Deviance
<i>Dixiphia pipra</i> Fr, Co (344/496)			
Phi(g - matrix)p(g*t)	0.00	1.00	265.58
Phi(.) p(.)	214.47	0.00	618.59
<i>Glyphorynchus spirurus</i> In,Fld (131/271)			
Phi(g - matrix)p(g*t)	0.00	1.00	402.13
Phi(.) p(.)	164.72	0.00	780.39
<i>Percnostola rufifrons</i> In,Ga (79/129)			
Phi(transient - forest age)p(g*t)	0.00	1.00	213.23
Phi(.) p(.)	136.66	0.00	458.60
<i>Pithys albifrons</i> In,Anf (239/535)			
Phi(g - matrix) p(g*t)	0.00	1.00	124.29
Phi(.) p(.)	130.59	0.00	346.68
<i>Thamnomanes ardesiacus</i> In,Fob (112/265)			
Phi(g - matrix)p(g*t)	0.00	1.00	279.68
Phi(.) p(.)	170.02	0.00	572.07
<i>Willisornis poecilinotus</i> In,Ar (176/524)			
Phi(g - matrix)p(t)	0.00	1.00	491.81
Phi(.) p(.)	161.86	0.00	703.25

I evaluated model fit two ways: 1) testing for trap happiness/shyness, and 2) quantifying over-dispersion. Program RELEASE goodness-of-fit (GOF) was used to test for trap happy/shy individuals in program MARK (Cooch and White 2014). Importantly, program RELEASE results are not unequivocal, and failure to reject the null hypothesis may reflect a lack of power to detect meaningful differences in net shyness. I calculated the over-dispersion factor (\hat{c}) for each species by dividing the deviance of each species' global model by the deviance estimated via a boot-strapping goodness-of-fit routine (using 1000 iterations). Top models were selected if they were at least two Akaike information criterion (AICc) values less than, and had fewer parameters relative to the next most competitive model (Arnold 2010). Taxonomy follows Remsen et al. (2011).

RESULTS

From 1979-1993 I recorded 1857 captures in the two experimental fragments representing 932 individual birds of the six study species (Table 5.1). The single gap specialist, *Percnostola rufifrons*, was the least frequently captured species while the single core frugivore and arboreal insectivore, *Dixiphia pipra* and *Willisornis poecilonotus*, were the most commonly captured species. Program RELEASE yielded non-significant values ($p < 0.05$) for models associated with each study species, indicating no identifiable trap shyness. Additionally, models associated with each species yielded $\hat{c} < 2$, indicative of adequate model fit. All six study species exhibited nearly the same top competitive model which included a grouping variable (fragment and transiency) and matrix condition (time trend representative of three stages of matrix regeneration) associated with annual survival (Table 5.1, Table D1). Recapture probabilities in each top model included a group and time interaction ($g*t$) except for *Willisornis poecilonotus* which yielded a time dependent recapture probability parameter (t). Top models were

unequivocal (all delta AICc >28) (Table D1) and delta AICc > 128 from the null model (Table 5.1).

The six study species exhibited three responses to matrix clearing and subsequent regeneration. The arboreal insectivore (*Willisornis poecilonotus*), obligate ant-follower (*Pithys albifrons*) and obligate flocking species (*Thamnomanes ardesiacus*) all suffered a significant decline in apparent survival within the first five years after isolation, followed by a marginal recovery in the following 5 year period of matrix regeneration in both the 100 ha and 10 ha fragments (Figure 5.1, Table 5.2). Conversely, the flock drop-out (*Glyphorynchus spirurus*) and core frugivore (*Dixiphia pipra*) showed virtually no change over the course of the study (Figure 5.2, Table 5.2). The gap specialist (*Pernostola rufifrons*) responded positively to isolation as demonstrated by a dramatic increase in survival within the first five years after isolation, followed by a slight decrease in apparent survival during the subsequent 5 year period of matrix regeneration in both the 100 ha and 10 ha fragments (Figure 5.2, Table 5.2). Although four of the six study species did exhibit lower survival in the 10 ha fragment than the 100 ha fragment, I believe evidence for a possible area effect was negligible considering I only included two fragments and that pre-isolation survival estimates had similar differences for these same species (Table 5.2).

Table 2. Apparent survival estimates with standard errors for six central Amazonian bird species captured in 100 and 10 ha fragments.

Species and matrix age	Phi	SE	Phi	SE
<i>Glyphorhynchus spirurus</i>	100 ha Fragment		10 ha Fragment	
< 5 year matrix regeneration	0.65	0.11	0.41	0.15
> 5 year matrix regeneration	0.64	0.11	0.39	0.15
Preisolation	0.63	0.13	0.38	0.16
<i>Pithys albifrons</i>	100 ha Fragment		10 ha Fragment	
< 5 year matrix regeneration	0.45	0.09	0.47	0.06
> 5 year matrix regeneration	0.57	0.11	0.60	0.07
Preisolation	0.69	0.14	0.71	0.12
<i>Dixiphia pipra</i>	100 ha Fragment		10 ha Fragment	
< 5 year matrix regeneration	0.61	0.12	0.52	0.09
> 5 year matrix regeneration	0.55	0.13	0.46	0.10
Preisolation	0.50	0.18	0.41	0.15
<i>Percnostola rufifrons</i>	100 ha Fragment		10 ha Fragment	
< 5 year matrix regeneration	0.49	0.15	0.79	0.17
> 5 year matrix regeneration	0.33	0.14	0.66	0.21
Preisolation	0.20	0.13	0.50	0.24
<i>Thamnomanes ardesiacus</i>	100 ha Fragment		10 ha Fragment	
< 5 year matrix regeneration	0.63	0.07	0.45	0.19
> 5 year matrix regeneration	0.69	0.08	0.51	0.18
Preisolation	0.74	0.11	0.58	0.18
<i>Willisornis poecilonotus</i>	100 ha Fragment		10 ha Fragment	
< 5 year matrix regeneration	0.61	0.05	0.42	0.08
> 5 year matrix regeneration	0.67	0.05	0.48	0.08
Preisolation	0.73	0.06	0.55	0.09

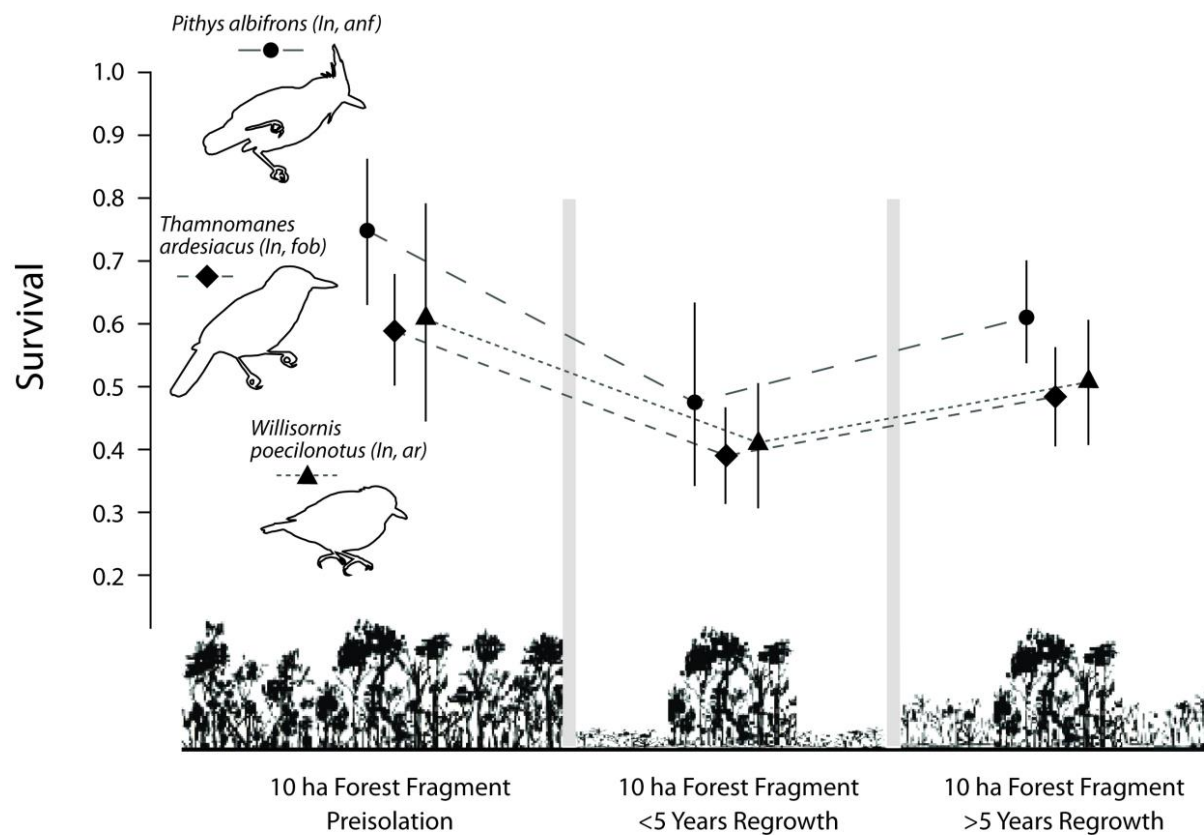


Figure 5.1. Apparent survival estimates with standard errors for three central Amazonian bird species captured in a 10 fragment. Survival varies as a function of age of the surrounding matrix. Foraging guild affiliation is denoted as follows: (In,Fob) - Insectivore, Flock Obligate; (In,Ar) – Insectivore, Arboreal; (In,Anf) – Insectivore, Ant-follower.

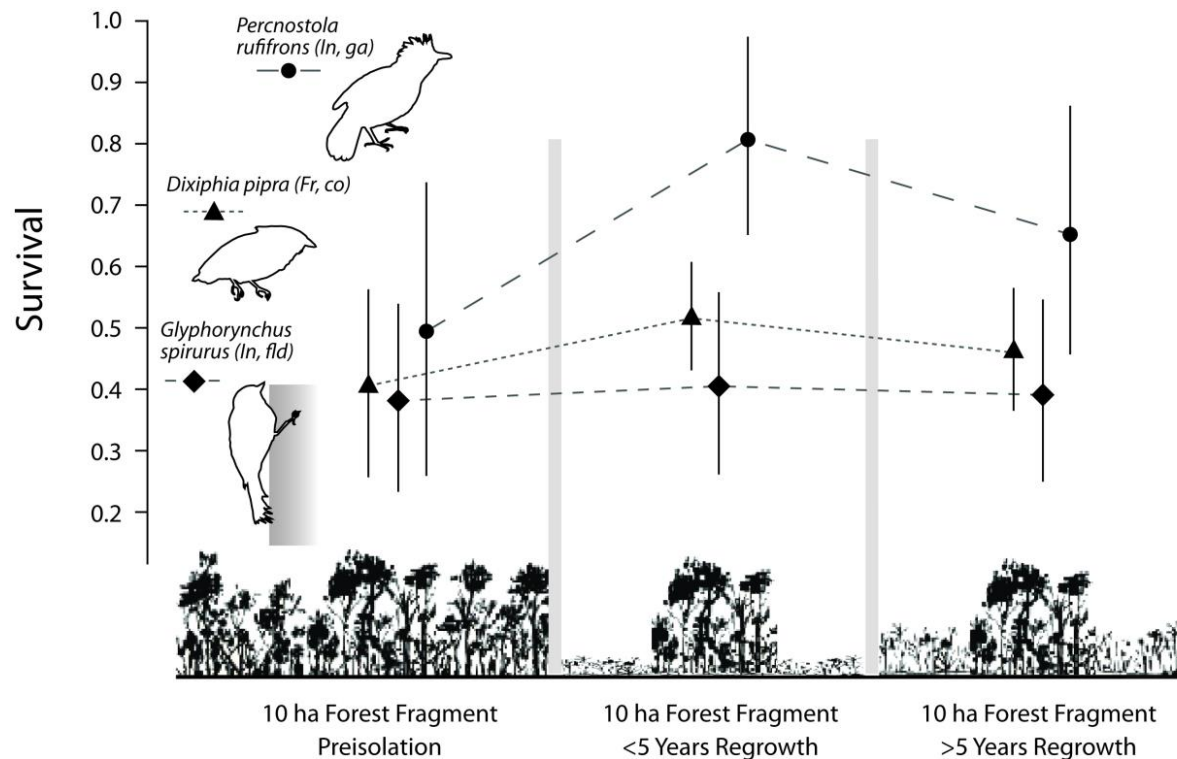


Figure 5.2. Apparent survival estimates with standard errors for three central Amazonian bird species captured in a 10 fragment. Survival varies as a function of age of the surrounding matrix. Foraging guild affiliation is denoted as follows: (In,Fld) – Insectivore, Flock-dropout; (In,Ga) – Insectivore, Gap; (Fr,Co) – Frugivore, Core.

DISCUSSION

Bird populations in forest fragments are often subject to source-sink dynamics (Renjifo 2001, Ewers and Didham 2006) where the condition of the surrounding matrix may tip the balance in favor of reproductive surplus or population decline (Ewers and Didham 2006, Sodhi et al. 2011). In this study I demonstrated that apparent survival of tropical birds residing in forest fragments was closely associated with the condition of the adjacent matrix. The flock obligate, arboreal insectivore and obligate ant-follower species (*Pithys albifrons*, *Thamnomanes ardesiacus* and *Willisornis poecilonotus*) all exhibited dramatic reductions in apparent survival within the first 5 years after initial isolation (Figure 5.1). The reduction in apparent survival coincided with their decreased abundance within fragments (Bierregaard and Lovejoy 1989). Considering these

forest-dwelling insectivores species are averse to crossing roads and clearings (Stouffer and Bierregaard 1995) I suspect that documented decreases in apparent survival does not represent dispersal events through a barren matrix, but rather a substantial reduction in actual survival. Reductions in survival may be a direct result of high-contrast edge effects where tree mortality, changes in insect communities, and changes in ambient soil and air temperature wielded irreconcilable negative forces on birds residing in forest fragments. Area effects may also be reducing apparent survival, at least for *Thamnomanes ardesiacus* and *Willisornis poecilonotus*, where survival was substantially higher in the 100 ha fragment relative to the 10 ha fragment. However, both *Thamnomanes ardesiacus* and *Willisornis poecilonotus* exhibited lower survival in the 10 ha fragment prior to isolation, thereby confounding my ability to ascertain the influence of area on these species.

Although young matrix was associated with lower survival among the flock obligate, arboreal insectivore and obligate ant follower species (*Pithys albifrons*, *Thamnomanes ardesiacus* and *Willisornis poecilonotus*), I found the reverse effect with *Percnostola rufifrons*, the single gap specialist (Figure 5.2). *Percnostola rufifrons* exhibited a dramatic increase in survival during the first 5 years after isolation. Being a gap specialist, *Percnostola rufifrons* has acquired evolutionary adaptations to life on the edge. For example, when compared to other study species within the family Thamnophilidae, *Percnostola rufifrons* has dark plumage (being predominantly black in males but not in females), which may provide extra protection against feather degradation due to solar exposure and abrasion (Bortolotti 2006). Further analyses exploring differences in survival relative to sex can test this hypothesis. *Percnostola rufifrons* is also the only known Neotropical passerine to exhibit a third molt (the presupplemental molt), within their first year of life (Johnson and Wolfe 2014); the insertion of an extra molt may

mitigate the rigors of living in a potentially hostile environment by expediting the replacement of degraded plumage. Other adaptations associated with *Percnostola rufifrons* that have yet to be documented may also include an ability to disperse over open areas, thereby buffering against local extinction by increasing metapopulation connectivity. In addition to the three study species that exhibited a strong decrease and one that exhibited a strong increase in survival relative to the condition of the surrounding matrix, two other species, *Glyphorynchus spirurus* and *Dixiphia pipra*, appeared to show only a small increase in survival associated with a young matrix; this finding supports previous work suggesting that *Glyphorynchus spirurus* and *Dixiphia pipra* may select edge as their preferred foraging habitat (Powell et al. 2014).

I believe that the increase in survival among the gap specialist (*Percnostola rufifrons*) represents a real increase in survival associated with edge and regenerating forest habitats. I also believe that the static response of *Glyphorynchus spirurus* and *Dixiphia pipra* represents an ability to subsist along forest edge. Young regenerating tropical forest is dynamic and subject to more sun and varying levels of soil moisture than primary forest (Wolfe et al. 2014). The combination of increased solar exposure and oscillating periods of soil moisture can elevate primary productivity (Brown et al. 1990) in regenerating tropical forest resulting in more insect and fruit resources for birds not adverse to foraging along edge (e.g. *Glyphorynchus spirurus*, *Dixiphia pipra* and *Percnostola rufifrons*). These same regenerating tropical forests may also be water limited and highly unstable during droughts when fruits and insects become scarce (Wolfe and Ralph 2015). Although my study indicated that *Glyphorynchus spirurus*, *Dixiphia pipra* and *Percnostola rufifrons* may exhibit higher apparent survival near edge, previous studies suggest that bird populations in regenerating forest may be subject to boom-bust cycles as a result of precipitation regimes (Wolfe et al. 2014b). I suggest that *Glyphorynchus spirurus*, *Dixiphia*

pipra and *Pernostola rufifrons* may be adept to living with unstable resources unlike sensitive species, *Pithys albifrons*, *Thamnomanes ardesiacus* and *Willisornis poecilonotus*, which may be averse to foraging along edge and reliant on more stable resources found in continuous forest.

The influence of regenerating matrix on the apparent survival of birds residing in Amazonian forest fragments is variable: detrimental to forest dwelling species, beneficial to a gap specialist and inconsequential to others. Insectivorous birds that rely upon mature forest are of special conservation concern (Şekercioğlu et al. 2002), and my study suggests that young regenerating matrix (>5 years) has little, if any ecological value for these sensitive species. However, each of the sensitive study species (*Pithys albifrons*, *Thamnomanes ardesiacus* and *Willisornis poecilonotus*) were found to readily disperse through and occupy older (25 year old) second growth (see Chapter 2). Thus, young regenerating matrixes should be viewed as having ecological value for certain species, while hosting unrealized potential for others. My study in association with previous findings (Stouffer et al. 2011, Powell et al. 2014) suggests that many sensitive birds residing in forest fragments will first exhibit increased metapopulation connectivity as the matrix regenerates, followed by the maturation of available core territories within the matrix itself. Thus, the conservation value of tropical forest must not be solely based on a contemporary snapshot of available habitat, but rather take into account the future ecological value of regenerating forest in human-dominated landscapes.

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APPENDIX A: GUILD ASSIGNMENTS AND RESULTS FROM CHAPTER 2

Table A1. Species and number of individuals per 240 point count minutes in treatments by region. Codes in parentheses indicate foraging guild where (In,Fob) - Insectivore, Flock Obligate; (In,Fld) – Insectivore, Flock-dropout; (In,Ar) – Insectivore, Arboreal; (In,Te) – Insectivore, Terrestrial; (In,Anf) – Insectivore, Ant-follower; (In,O) - Insectivore, Other; (In,Ga) – Insectivore, Gap; (Fr,Co) – Frugivore, Core; (Pa) – Parrot; (Ra) – Raptor; (Fr,Ot) – Frugivore, Other; (Hu) – Hummingbird; (No) – Non-forest.

Species	Porto Alegre Continuous	Colosso Continuous	KM41 Continuous	Dimona Continuous	Porto Alegre 100 Hectares	Dimona 100 Hectares	Dimona Second Growth	Colosso Second Growth	Young Second Growth	Balbina Islands
<i>Tinamus major</i> (In,Te)	0	1	0	0	1	3	0	0	0	0
<i>Crypturellus soui</i> (No)	0	0	0	0	0	0	1	1	0	0
<i>Crypturellus variegatus</i> (In,Te)	2	4	2	0	0	1	1	0	0	3
<i>Penelope marail</i> (Fr,Ot)	0	3	0	1	2	1	1	2	0	0
<i>Crax alector</i> (Fr,Ot)	3	0	0	0	0	0	0	0	0	0
<i>Odontophorus gujanensis</i> (In,Ot)	0	0	0	1	1	0	0	0	1	0
<i>Harpagus bidentatus</i> (Ra)	1	0	0	1	0	0	0	0	0	0
<i>Buteogallus urubitinga</i> (Ra)	0	0	0	0	0	0	0	0	0	3
<i>Leucopternis melanops</i> (Ra)	0	1	0	0	0	0	0	0	0	0
<i>Psophia crepitans</i> (Fr,Ot)	10	0	0	0	0	0	0	0	0	0
<i>Columba plumbea</i> (Fr,Ot)	1	9	2	8	0	8	8	16	2	6
<i>Columba subvinacea</i> (Fr,Ot)	1	0	1	2	0	1	1	2	0	5
<i>Piaya cayana</i> (In,Ot)	0	0	0	0	0	0	0	0	1	0
<i>Piaya melanogaster</i> (In,Ot)	1	0	0	1	0	0	0	0	0	3
<i>Dromococcyx pavoninus</i> (In,Ot)	0	0	0	1	0	0	0	0	0	0
<i>Glaucidium hardyi</i> (In,Ot)	0	0	0	0	0	0	0	2	0	0
<i>Topaza pella</i> (Hu)	0	0	0	0	0	0	0	0	1	0
<i>Florisuga mellivora</i> (Hu)	0	1	0	0	0	0	0	0	0	0
<i>Phaethornis ruber</i> (Hu)	0	0	0	0	0	0	0	0	0	1
<i>Phaethornis bourcieri</i> (Hu)	0	0	0	0	1	0	0	0	2	0
<i>Phaethornis superciliosus</i> (Hu)	0	0	0	0	0	2	0	3	4	0
<i>Heliothryx auritus</i> (Hu)	0	0	0	0	0	0	0	0	0	1
<i>Campylopterus largipennis</i> (Hu)	0	0	0	0	0	0	0	0	1	0
<i>Thalurania furcata</i> (Hu)	0	0	0	1	0	0	0	0	5	0
<i>Trogon melanurus</i> (Fr,Ot)	5	7	3	2	2	0	1	4	0	4
<i>Trogon viridis</i> (Fr,Ot)	4	9	5	8	2	8	8	7	3	13
<i>Trogon violaceus</i> (Fr,Ot)	1	2	3	2	1	2	0	3	0	2

Table A1. Species and number of individuals per 240 point count minutes in treatments by region. Codes in parentheses indicate foraging guild where (In,Fob) - Insectivore, Flock Obligate; (In,Fld) – Insectivore, Flock-dropout; (In,Ar) – Insectivore, Arboreal; (In,Te) – Insectivore, Terrestrial; (In,Anf) – Insectivore, Ant-follower; (In,O) - Insectivore, Other; (In,Ga) – Insectivore, Gap; (Fr,Co) – Frugivore, Core; (Pa) – Parrot; (Ra) – Raptor; (Fr,Ot) – Frugivore, Other; (Hu) – Hummingbird; (No) – Non-forest.

Species	Porto Alegre Continuous	Colosso Continuous	KM41 Continuous	Dimona Continuous	Porto Alegre 100 Hectares	Dimona 100 Hectares	Dimona Second Growth	Colosso Second Growth	Young Second Growth	Balbina Islands
<i>Trogon rufus</i> (Fr,Ot)	5	1	1	4	2	0	4	0	0	3
<i>Momotus momota</i> (Fr,Ot)	0	4	4	8	1	2	1	5	1	7
<i>Galbula albirostris</i> (In,Ot)	0	4	0	0	0	0	0	1	0	0
<i>Galbula leucogastra</i> (In,Ot)	0	0	0	0	0	1	0	0	0	0
<i>Galbula dea</i> (In,Ot)	1	1	1	0	3	1	1	1	0	0
<i>Jacamerops aureus</i> (In,Ar)	1	0	0	2	0	2	2	0	0	0
<i>Notharchus macrorhynchos</i> (In,Ar)	0	0	0	0	0	0	0	0	0	1
<i>Bucco tamatia</i> (In,Ot)	0	3	0	0	0	0	0	0	0	0
<i>Bucco capensis</i> (In,Ot)	0	0	0	0	1	0	0	0	0	0
<i>Malacoptila fusca</i> (In,Ot)	0	0	0	1	1	0	0	0	0	0
<i>Nonnula rubecula</i> (In,Ar)	0	0	0	0	0	0	2	0	0	0
<i>Monasa atra</i> (In,Ot)	0	0	3	0	1	0	0	8	0	0
<i>Capito niger</i> (Fr,Ot)	0	1	0	2	1	2	2	3	0	0
<i>Ramphastos tucanus</i> (Fr,Ot)	4	9	4	8	10	2	7	14	5	9
<i>Ramphastos vitellinus</i> (Fr,Ot)	5	8	4	1	4	2	1	13	1	5
<i>Selenidera piperivora</i> (Fr,Ot)	0	0	0	0	0	0	0	0	2	2
<i>Picumnus exilis</i> (In,Ar)	1	0	0	0	0	0	0	0	0	0
<i>Melanerpes cruentatus</i> (No)	1	3	3	0	0	0	0	2	4	6
<i>Veniliornis cassini</i> (In,Ar)	0	1	0	1	0	1	0	0	0	0
<i>Piculus flavigula</i> (In,Ar)	1	2	2	4	2	1	3	0	0	7
<i>Piculus chrysochloros</i> (In,Ar)	1	0	0	1	0	0	0	0	0	0
<i>Celeus undatus</i> (In,Ar)	8	3	1	3	4	1	0	0	0	3
<i>Celeus flavus</i> (In,Ar)	1	0	0	0	0	0	0	0	0	0
<i>Celeus torquatus</i> (In,Ar)	0	0	0	1	0	0	0	0	0	2
<i>Dryocopus lineatus</i> (In,Ar)	1	0	0	0	3	2	1	4	4	2
<i>Campephilus rubricollis</i> (In,Ar)	7	6	1	6	4	4	1	0	1	0
<i>Micrastur gilvicollis</i> (Ra)	4	7	1	1	3	1	0	1	0	0

Table A1. Species and number of individuals per 240 point count minutes in treatments by region. Codes in parentheses indicate foraging guild where (In,Fob) - Insectivore, Flock Obligate; (In,Fld) – Insectivore, Flock-dropout; (In,Ar) – Insectivore, Arboreal; (In,Te) – Insectivore, Terrestrial; (In,Anf) – Insectivore, Ant-follower; (In,O) - Insectivore, Other; (In,Ga) – Insectivore, Gap; (Fr,Co) – Frugivore, Core; (Pa) – Parrot; (Ra) – Raptor; (Fr,Ot) – Frugivore, Other; (Hu) – Hummingbird; (No) – Non-forest.

Species	Porto Alegre Continuous	Colosso Continuous	KM41 Continuous	Dimona Continuous	Porto Alegre 100 Hectares	Dimona 100 Hectares	Dimona Second Growth	Colosso Second Growth	Young Second Growth	Balbina Islands
<i>Ibycter americanus</i> (Ra)	2	3	1	0	7	1	1	2	0	0
<i>Touit purpuratus</i> (Pa)	0	2	0	0	0	0	0	0	0	0
<i>Brotogeris chrysoptera</i> (Pa)	3	0	0	0	2	1	0	0	0	0
<i>Pyrilia caica</i> (Pa)	3	6	1	1	0	1	3	1	0	4
<i>Pionus fuscus</i> (Pa)	1	2	0	0	1	0	0	2	0	3
<i>Pionus menstruus</i> (Pa)	2	2	0	0	0	0	0	3	0	3
<i>Amazona autumnalis</i> (Pa)	1	3	2	1	3	0	0	1	0	0
<i>Amazona farinosa</i> (Pa)	7	1	0	0	8	2	0	1	0	5
<i>Derophtus accipitrinus</i> (Pa)	1	1	0	0	1	2	0	0	0	0
<i>Ara spp.</i> (Pa)	2	4	0	2	2	10	0	2	0	5
<i>Euchrepomis spodiopila</i> (In,Ot)	0	0	1	1	0	0	0	0	0	0
<i>Cymbilaimus lineatus</i> (In,Ot)	9	7	8	3	2	1	0	5	0	1
<i>Frederickena viridis</i> (In,Ot)	0	0	5	0	2	0	0	0	0	0
<i>Thamnophilus murinus</i> (In,Ot)	5	7	6	1	7	7	10	9	2	6
<i>Thamnophilus punctatus</i> (No)	0	0	0	0	0	0	0	4	4	0
<i>Thamnomanes ardesiacus</i> (In,Fob)	3	4	5	5	8	7	3	1	0	0
<i>Thamnomanes caesi</i> us (In,Fob)	7	5	4	7	10	7	6	3	1	0
<i>Isleria guttata</i> (In,Ar)	0	0	0	0	0	0	0	0	0	1
<i>Epinecrophylla gutturalis</i> (In,Fob)	0	0	0	0	3	0	2	0	0	0
<i>Myrmotherula brachyura</i> (In,Ot)	6	2	1	5	3	2	1	5	1	1
<i>Myrmotherula axillaris</i> (In,Fld)	1	2	1	1	5	1	0	0	1	6
<i>Myrmotherula longipennis</i> (In,Fob)	0	0	1	3	5	1	0	1	0	0
<i>Herpsilochmus dorsimaculatus</i> (In,Fld)	2	8	3	6	6	7	11	1	0	1
<i>Hypocnemis cantator</i> (In,Ga)	10	2	5	11	1	3	12	17	4	5
<i>Cercomacra cinerascens</i> (In,Ar)	15	5	8	4	8	5	0	5	2	2
<i>Cercomacra tyrannina</i> (No)	0	0	0	0	0	0	0	4	3	0
<i>Percnostola rufifrons</i> (In,Ga)	3	2	7	7	7	10	5	15	1	7

Table A1. Species and number of individuals per 240 point count minutes in treatments by region. Codes in parentheses indicate foraging guild where (In,Fob) - Insectivore, Flock Obligate; (In,Fld) – Insectivore, Flock-dropout; (In,Ar) – Insectivore, Arboreal; (In,Te) – Insectivore, Terrestrial; (In,Anf) – Insectivore, Ant-follower; (In,O) - Insectivore, Other; (In,Ga) – Insectivore, Gap; (Fr,Co) – Frugivore, Core; (Pa) – Parrot; (Ra) – Raptor; (Fr,Ot) – Frugivore, Other; (Hu) – Hummingbird; (No) – Non-forest.

Species	Porto Alegre Continuous	Colosso Continuous	KM41 Continuous	Dimona Continuous	Porto Alegre 100 Hectares	Dimona 100 Hectares	Dimona Second Growth	Colosso Second Growth	Young Second Growth	Balbina Islands
<i>Schistocichla leucostigma</i> (In,Ot)	0	0	7	0	0	0	0	0	0	0
<i>Myrmeciza ferruginea</i> (In,Ot)	2	3	4	2	3	2	1	1	0	0
<i>Myrmornis torquata</i> (In,Te)	0	1	0	0	0	0	0	0	0	0
<i>Pithys albifrons</i> (In,Anf)	1	6	2	2	0	2	3	1	0	0
<i>Gymnopithys rufigula</i> (In,Anf)	0	5	0	1	1	1	3	1	0	0
<i>Hylophylax naevia</i> (In,Ar)	0	0	0	1	0	0	0	0	0	0
<i>Willisornis poecilinotus</i> (In,Ar)	4	0	0	3	7	1	1	0	0	0
<i>Conopophaga aurita</i> (In,Te)	1	5	1	0	0	0	0	0	0	0
<i>Grallaria varia</i> (In,Te)	8	11	4	6	4	11	0	8	0	0
<i>Hylopezus macularius</i> (In,Te)	0	1	0	0	1	0	0	0	0	0
<i>Myrmothera campanisona</i> (In,Ot)	1	2	0	0	0	5	0	2	0	0
<i>Formicarius colma</i> (In,Te)	7	7	2	0	3	8	0	4	0	0
<i>Formicarius analis</i> (In,Ot)	5	13	7	0	0	0	1	1	0	0
<i>Sclerurus mexicanus</i> (In,ot)	0	0	1	0	0	0	0	0	0	0
<i>Sclerurus caudacutus</i> (In,Te)	0	0	0	0	0	1	0	0	0	0
<i>Certhiasomus stictolaemus</i> (In,Fob)	1	4	0	2	1	4	0	0	0	0
<i>Sittasomus griseicapillus</i> (In,Ot)	2	2	2	3	2	6	5	0	0	0
<i>Deconychura longicauda</i> (In,Ot)	2	6	1	1	4	1	0	0	0	0
<i>Dendrocincla merula</i> (In,Anf)	0	0	0	1	0	0	0	0	0	0
<i>Dendrocincla fuliginosa</i> (In,Ar)	1	2	2	4	5	1	2	7	1	5
<i>Glyphorynchus spirurus</i> (In,Fld)	6	7	7	5	5	3	8	8	1	2
<i>Dendrocolaptes certhia</i> (In,Ot)	3	1	3	6	4	2	1	4	4	1
<i>Dendrocolaptes picumnus</i> (In,Ot)	2	0	0	0	0	1	0	0	0	0
<i>Hylexetastes perrotii</i> (In,Ot)	5	1	3	3	1	2	0	0	0	0
<i>Xiphorhynchus pardalotus</i> (In,Fld)	3	6	6	5	9	4	4	4	0	8
<i>Campylorhamphus procurvovides</i> (In,Ot)	0	0	0	0	0	0	0	1	0	0
<i>Lepidocolaptes albolineatus</i> (In,Ot)	0	0	0	0	1	0	0	0	0	0

Table A1. Species and number of individuals per 240 point count minutes in treatments by region. Codes in parentheses indicate foraging guild where (In,Fob) - Insectivore, Flock Obligate; (In,Fld) – Insectivore, Flock-dropout; (In,Ar) – Insectivore, Arboreal; (In,Te) – Insectivore, Terrestrial; (In,Anf) – Insectivore, Ant-follower; (In,O) - Insectivore, Other; (In,Ga) – Insectivore, Gap; (Fr,Co) – Frugivore, Core; (Pa) – Parrot; (Ra) – Raptor; (Fr,Ot) – Frugivore, Other; (Hu) – Hummingbird; (No) – Non-forest.

Species	Porto Alegre Continuous	Colosso Continuous	KM41 Continuous	Dimona Continuous	Porto Alegre 100 Hectares	Dimona 100 Hectares	Dimona Second Growth	Colosso Second Growth	Young Second Growth	Balbina Islands
<i>Xenops minutus</i> (In,Fob)	0	0	0	2	0	0	0	0	0	0
<i>Philydor pyrrhodes</i> (In,Ot)	0	0	0	0	1	0	0	0	0	0
<i>Clibanornis rubiginosus</i> (In,Ar)	0	2	2	0	0	0	0	0	0	0
<i>Automolus ochrolaemus</i> (In,Ar)	0	0	2	1	0	0	1	6	3	0
<i>Automolus infuscatus</i> (In,Fob)	5	4	3	1	5	2	1	0	0	0
<i>Tyrannulus elatus</i> (In,Ar)	0	0	1	0	0	1	0	1	0	3
<i>Myiopagis gaimardii</i> (In,Ar)	1	5	1	4	0	2	2	0	0	11
<i>Myiopagis caniceps</i> (In,Ar)	0	0	0	0	1	1	0	0	0	0
<i>Ornithion inerme</i> (In,Ar)	1	3	0	0	2	1	0	0	0	0
<i>Camptostoma obsoletum</i> (In,Ot)	0	0	0	0	0	0	0	0	0	1
<i>Zimmerius gracilipes</i> (In,Ot)	6	4	4	1	4	5	6	1	0	3
<i>Phylloscartes virescens</i> (In,Ot)	1	0	1	0	0	0	0	0	0	0
<i>Mionectes macconnelli</i> (Fr,Co)	0	0	0	0	0	0	0	0	1	0
<i>Myiornis ecaudatus</i> (In,Ar)	1	0	1	0	0	0	1	0	0	0
<i>Lophotriccus vitosus</i> (In,Ar)	4	1	5	4	1	0	0	0	0	0
<i>Hemitriccus zosterops</i> (In,Ot)	10	12	6	5	8	4	2	6	0	5
<i>Todirostrum pictum</i> (In,Ar)	0	1	0	0	1	0	0	0	0	0
<i>Rhynchocyclus olivaceus</i> (In,Ot)	0	1	0	0	0	0	0	1	0	0
<i>Tolmomyias assimilis</i> (In,Ot)	3	3	3	2	1	8	6	3	0	0
<i>Tolmomyias poliocephalus</i> (In,Ot)	1	1	0	0	1	1	4	6	3	0
<i>Platyrinchus saturatus</i> (In,Ar)	0	0	0	1	0	0	0	0	0	0
<i>Platyrinchus coronatus</i> (In,Ar)	8	6	0	3	5	3	1	0	0	0
<i>Platyrinchus platyrhynchos</i> (In,Ot)	0	0	1	0	0	0	0	0	0	0
<i>Myiobius barbatus</i> (In,Fob)	0	0	0	1	0	0	1	0	0	0
<i>Terenotriccus erythrurus</i> (In,Ot)	0	2	0	0	1	0	0	0	4	0
<i>Myiozetetes cayanensis</i> (No)	0	0	0	0	0	0	0	0	2	0
<i>Conopias parvus</i> (In,Ar)	2	0	2	0	3	1	5	2	1	5

Table A1. Species and number of individuals per 240 point count minutes in treatments by region. Codes in parentheses indicate foraging guild where (In,Fob) - Insectivore, Flock Obligate; (In,Fld) – Insectivore, Flock-dropout; (In,Ar) – Insectivore, Arboreal; (In,Te) – Insectivore, Terrestrial; (In,Anf) – Insectivore, Ant-follower; (In,O) - Insectivore, Other; (In,Ga) – Insectivore, Gap; (Fr,Co) – Frugivore, Core; (Pa) – Parrot; (Ra) – Raptor; (Fr,Ot) – Frugivore, Other; (Hu) – Hummingbird; (No) – Non-forest.

Species	Porto Alegre Continuous	Colosso Continuous	KM41 Continuous	Dimona Continuous	Porto Alegre 100 Hectares	Dimona 100 Hectares	Dimona Second Growth	Colosso Second Growth	Young Second Growth	Balbina Islands
<i>Tyrannus melancholicus</i> (No)	0	0	0	0	0	0	0	1	1	0
<i>Rhytipterna simplex</i> (Fr,Ot)	7	12	5	2	4	0	1	9	0	4
<i>Myiarchus ferox</i> (No)	0	0	0	0	0	0	0	1	2	1
<i>Ramphotrigon ruficauda</i> (In,Ot)	0	0	1	3	0	0	0	0	0	5
<i>Attila spadiceus</i> (Fr,Ot)	5	9	0	1	7	1	3	7	3	0
<i>Phoenicircus carnifex</i> (Fr,Ot)	2	2	0	1	0	1	4	2	2	0
<i>Haematoderus militaris</i> (Fr,Ot)	0	0	1	0	1	0	0	0	0	0
<i>Perissocephalus tricolor</i> (Fr,Ot)	0	0	1	1	0	0	1	0	0	0
<i>Lipaugus vociferans</i> (Fr,Ot)	8	8	34	30	4	31	5	7	3	32
<i>Xipholena punicea</i> (Fr,Ot)	0	1	1	0	1	0	0	0	0	0
<i>Tyrannetes virescens</i> (Fr,Ot)	0	3	1	0	0	2	0	0	0	14
<i>Corapipo gutturalis</i> (Fr,Co)	0	3	0	0	0	2	0	0	0	0
<i>Lepidothrix serena</i> (Fr,Co)	0	6	0	0	3	3	8	1	0	0
<i>Manacus manacus</i> (No)	0	0	0	0	0	0	0	0	1	0
<i>Dixiphia pipra</i> (Fr,Co)	0	1	0	0	0	1	1	1	0	15
<i>Ceratopipra erythrocephala</i> (Fr,Co)	0	1	0	0	0	3	4	11	1	0
<i>Tityra cayana</i> (Fr,Ot)	2	6	0	0	4	0	0	2	0	4
<i>Schiffornis turdina</i> (Fr,Co)	1	5	1	2	0	0	0	0	0	0
<i>Laniocera hypopyrra</i> (In,Ot)	6	0	2	0	0	0	0	0	0	0
<i>Pachyramphus marginatus</i> (In,Ot)	0	5	0	0	1	0	0	2	0	0
<i>Pachyramphus surinamus</i> (In,Ot)	1	2	3	0	1	4	0	1	0	0
<i>Cyclarhis gujanensis</i> (In,Ot)	0	0	0	0	0	0	1	5	1	0
<i>Vireolanius leucotis</i> (In,Ar)	7	6	7	1	6	8	1	0	0	0
<i>Vireo olivaceus</i> (No)	0	0	0	0	0	0	0	1	0	0
<i>Hylophilus muscicapinus</i> (In,Fob)	2	5	2	5	11	10	8	2	1	0
<i>Hylophilus ochraceiceps</i> (In,Fob)	3	4	2	2	6	3	1	0	0	0
<i>Pheugopedius coraya</i> (No)	0	0	0	0	0	0	1	6	1	0

Table A1. Species and number of individuals per 240 point count minutes in treatments by region. Codes in parentheses indicate foraging guild where (In,Fob) - Insectivore, Flock Obligate; (In,Fld) – Insectivore, Flock-dropout; (In,Ar) – Insectivore, Arboreal; (In,Te) – Insectivore, Terrestrial; (In,Anf) – Insectivore, Ant-follower; (In,O) - Insectivore, Other; (In,Ga) – Insectivore, Gap; (Fr,Co) – Frugivore, Core; (Pa) – Parrot; (Ra) – Raptor; (Fr,Ot) – Frugivore, Other; (Hu) – Hummingbird; (No) – Non-forest.

Species	Porto Alegre Continuous	Colosso Continuous	KM41 Continuous	Dimona Continuous	Porto Alegre 100 Hectares	Dimona 100 Hectares	Dimona Second Growth	Colosso Second Growth	Young Second Growth	Balbina Islands
<i>Cyphorhinus arada</i> (In,Te)	0	0	0	0	0	1	0	0	0	0
<i>Microbates collaris</i> (In,Ar)	0	0	2	5	2	2	1	1	0	0
<i>Ramphocaenus melanurus</i> (Fr,Ot)	1	3	2	2	7	1	5	1	0	8
<i>Turdus albicollis</i> (Fr,Co)	0	1	0	0	1	1	0	0	0	11
<i>Lamprospiza melanoleuca</i> (Fr,Ot)	0	1	0	0	0	7	0	0	0	0
<i>Tachyphonus surinamus</i> (Fr,Co)	0	0	0	0	1	1	1	2	0	0
<i>Ramphocelus carbo</i> (No)	0	0	0	0	0	0	0	1	0	0
<i>Tangara varia</i> (Fr,Ot)	0	0	1	0	0	0	3	0	0	0
<i>Tangara chilensis</i> (Fr,Ot)	0	0	0	0	1	0	0	0	0	0
<i>Dacnis lineata</i> (Fr,Ot)	0	0	0	0	0	0	3	1	0	0
<i>Cyanerpes caeruleus</i> (Fr,Ot)	0	0	0	0	0	0	0	1	0	0
<i>Coereba flaveola</i> (Fr,Ot)	0	0	0	2	0	0	0	0	0	2
<i>Saltator grossus</i> (Fr,Ot)	6	0	1	1	1	0	1	1	0	0
<i>Caryothraustes canadensis</i> (Fr,Ot)	1	2	2	1	3	2	0	4	0	3
<i>Psarocolius viridis</i> (Fr,Ot)	4	6	2	2	4	0	3	1	1	0
<i>Cacicus spp.</i> (Fr,Ot)	0	0	1	0	0	0	0	0	0	3
<i>Icterus cayanensis</i> (Fr,Ot)	0	0	0	0	0	0	0	0	1	0
<i>Euphonia cayennensis</i> (Fr,Co)	1	2	0	0	2	0	0	0	0	0

Table A2. Species and number of individuals per 100 mist-net hours in treatments by region. Codes in parentheses indicate foraging guild where (In,Fob) - Insectivore, Flock Obligate; (In,Fld) – Insectivore, Flock-dropout; (In,Ar) – Insectivore, Arboreal; (In,Te) – Insectivore, Terrestrial; (In,Anf) – Insectivore, Ant-follower; (In,O) - Insectivore, Other; (In,Ga) – Insectivore, Gap; (Fr,Co) – Frugivore, Core; (Pa) – Parrot; (Ra) – Raptor; (Fr,Ot) – Frugivore, Other; (Hu) – Hummingbird; (No) – Non-forest.

Species	Porto Alegre Continuous	Colosso Continuous	KM41 Continuous	Dimona Continuous	Porto Alegre 100 Hectares	Dimona 100 Hectares	Dimona Second Growth	Colosso Second Growth	Young Second Growth	Balbina Islands
<i>Crypturellus variegatus</i> (In,Te)	0	1	0	0	0	0	0	0	0	0
<i>Harpagus bidentatus</i> (Ra)	0	0	0	0	0	0	0	0	2	0
<i>Leucopternis melanops</i> (Ra)	0	0	0	0	0	1	0	0	0	0
<i>Geotrygon montana</i> (In,Te)	0	1	0	3	2	1	0	1	0	0
<i>Glaucidium hardyi</i> (In,Ot)	0	0	1	0	0	0	0	1	0	0
<i>Nyctidromus albicollis</i> (No)	0	0	0	0	0	0	2	0	0	0
<i>Florisuga mellivora</i> (Hu)	1	0	0	0	1	0	1	1	0	0
<i>Phaethornis bourcierii</i> (Hu)	3	7	5	3	3	2	7	7	6	0
<i>Phaethornis superciliosus</i> (Hu)	2	2	2	4	0	8	9	14	13	0
<i>Heliothryx auritus</i> (Hu)	0	0	0	0	1	0	0	0	0	0
<i>Campylopterus largipennis</i> (Hu)	0	1	2	0	1	2	8	7	10	0
<i>Thalurania furcata</i> (Hu)	1	1	3	4	0	2	3	7	6	4
<i>Amazilia versicolor</i> (Hu)	0	0	0	0	0	0	1	4	2	0
<i>Amazilia fimbriata</i> (Hu)	0	0	0	0	0	0	0	1	0	0
<i>Trogon viridis</i> (Fr,Ot)	0	0	0	0	0	0	0	1	0	0
<i>Trogon rufus</i> (Fr,Ot)	0	0	0	0	0	0	0	3	0	0
<i>Chloroceryle aenea</i> (No)	0	0	0	1	0	0	0	0	0	0
<i>Momotus momota</i> (Fr,Ot)	1	0	6	1	0	1	1	3	0	0
<i>Galbula albirostris</i> (In,Ot)	5	3	1	2	3	4	11	4	0	0
<i>Jacamerops aureus</i> (In,Ar)	0	0	0	0	0	1	0	0	2	0
<i>Bucco tamatia</i> (In,Ot)	0	0	0	0	0	0	1	1	0	0
<i>Bucco capensis</i> (In,Ot)	0	1	0	0	1	0	0	0	0	0
<i>Malacoptila fusca</i> (In,Ot)	5	4	2	4	1	1	0	0	0	0
<i>Nonnula rubecula</i> (In,Ar)	1	1	0	0	0	1	2	0	0	0
<i>Monasa atra</i> (In,Ot)	0	0	0	0	0	0	0	2	0	0
<i>Veniliornis cassini</i> (In,Ot)	0	0	0	0	1	0	0	0	0	0
<i>Celeus flavus</i> (In,Ar)	0	0	0	0	0	0	1	0	0	0

Table A2. Species and number of individuals per 100 mist-net hours in treatments by region. Codes in parentheses indicate foraging guild where (In,Fob) - Insectivore, Flock Obligate; (In,Fld) – Insectivore, Flock-dropout; (In,Ar) – Insectivore, Arboreal; (In,Te) – Insectivore, Terrestrial; (In,Anf) – Insectivore, Ant-follower; (In,O) - Insectivore, Other; (In,Ga) – Insectivore, Gap; (Fr,Co) – Frugivore, Core; (Pa) – Parrot; (Ra) – Raptor; (Fr,Ot) – Frugivore, Other; (Hu) – Hummingbird; (No) – Non-forest.

Species	Porto Alegre Continuous	Colosso Continuous	KM41 Continuous	Dimona Continuous	Porto Alegre 100 Hectares	Dimona 100 Hectares	Dimona Second Growth	Colosso Second Growth	Young Second Growth	Balbina Islands
<i>Campephilus rubricollis</i> (In,Ar)	0	0	0	1	0	0	0	0	0	0
<i>Micrastur ruficollis</i> (Ra)	0	0	0	0	0	0	0	1	0	0
<i>Micrastur gilvicollis</i> (Ra)	0	1	2	3	1	0	2	1	2	0
<i>Cymbilaimus lineatus</i> (In,Ot)	0	0	1	0	0	0	0	1	0	0
<i>Frederickena viridis</i> (In,Ot)	2	0	2	3	2	1	0	0	0	0
<i>Thamnophilus murinus</i> (In,Ot)	0	4	3	3	2	1	7	1	0	0
<i>Thamnomanes ardesiacus</i> (In,Fob)	11	16	10	15	13	8	8	9	0	0
<i>Thamnomanes caesioides</i> (In,Fob)	8	16	11	13	14	11	11	13	0	0
<i>Iseria guttata</i> (In,Ar)	0	0	1	0	0	1	0	0	0	17
<i>Epinecrophyllos gutturalis</i> (In,Fob)	5	3	9	4	8	7	3	4	0	0
<i>Myrmotherula axillaris</i> (In,Fld)	3	1	5	1	3	2	1	9	8	29
<i>Myrmotherula longipennis</i> (In,Fob)	14	10	9	8	10	4	8	1	2	0
<i>Myrmotherula menetriesii</i> (In,Fob)	0	8	4	4	3	2	2	3	0	0
<i>Hypocnemis cantator</i> (In,Ga)	7	4	11	4	4	5	13	8	10	8
<i>Cercomacra cinerascens</i> (In,Ar)	0	0	0	0	1	0	0	0	0	0
<i>Cercomacra tyrannina</i> (No)	0	0	0	0	0	0	0	0	2	0
<i>Percnostola rufifrons</i> (In,Ga)	11	3	8	6	9	8	13	25	4	4
<i>Schistocichla leucostigma</i> (In,Ot)	0	1	3	3	0	1	3	1	0	0
<i>Myrmeciza ferruginea</i> (In,Ot)	2	2	4	0	2	3	1	0	0	0
<i>Pithys albifrons</i> (In,Anf)	31	74	83	48	55	40	75	36	13	0
<i>Gymnopithys rufigula</i> (In,Anf)	5	16	21	17	22	12	17	14	0	0
<i>Hylophylax naevia</i> (In,Ar)	0	1	2	5	0	0	0	0	0	0
<i>Willisornis poecilinotus</i> (In,Ar)	18	19	32	25	23	12	18	8	0	0
<i>Conopophaga aurita</i> (In,Te)	3	2	0	1	0	0	3	0	0	0
<i>Myrmothera campanisona</i> (In,Ot)	0	0	0	0	0	1	0	0	0	0
<i>Formicarius colma</i> (In,Te)	14	12	5	6	10	5	0	4	0	0
<i>Formicarius analis</i> (In,Ot)	0	1	1	2	0	0	1	0	0	0

Table A2. Species and number of individuals per 100 mist-net hours in treatments by region. Codes in parentheses indicate foraging guild where (In,Fob) - Insectivore, Flock Obligate; (In,Fld) – Insectivore, Flock-dropout; (In,Ar) – Insectivore, Arboreal; (In,Te) – Insectivore, Terrestrial; (In,Anf) – Insectivore, Ant-follower; (In,O) - Insectivore, Other; (In,Ga) – Insectivore, Gap; (Fr,Co) – Frugivore, Core; (Pa) – Parrot; (Ra) – Raptor; (Fr,Ot) – Frugivore, Other; (Hu) – Hummingbird; (No) – Non-forest.

Species	Porto Alegre Continuous	Colosso Continuous	KM41 Continuous	Dimona Continuous	Porto Alegre 100 Hectares	Dimona 100 Hectares	Dimona Second Growth	Colosso Second Growth	Young Second Growth	Balbina Islands
<i>Sclerurus mexicanus</i> (In,Ot)	1	2	0	0	0	0	0	0	2	0
<i>Sclerurus ruficularis</i> (In,Te)	1	0	2	2	5	4	1	0	0	0
<i>Sclerurus caudacutus</i> (In,Te)	1	0	0	0	1	0	0	0	0	0
<i>Certhiasomus stictolaemus</i> (In,Fob)	5	3	7	11	10	8	2	0	0	0
<i>Sittasomus griseicapillus</i> (In,Ot)	0	0	0	0	0	0	1	0	0	0
<i>Deconychura longicauda</i> (In,Ot)	1	2	4	1	0	1	0	0	0	0
<i>Dendrocincla merula</i> (In,Anf)	0	10	10	3	3	2	5	0	0	0
<i>Dendrocincla fuliginosa</i> (In,Ar)	4	2	3	0	9	4	5	7	6	13
<i>Glyphorhynchus spirurus</i> (In,Fld)	36	41	33	10	30	16	58	50	6	4
<i>Dendrocolaptes certhia</i> (In,Ot)	1	1	0	0	0	0	2	1	0	0
<i>Hylexetastes perrotii</i> (In,Ot)	2	1	0	0	0	0	2	0	0	0
<i>Xiphorhynchus pardalotus</i> (In,Fld)	2	6	7	8	10	4	12	13	0	4
<i>Campylorhamphus procurviroides</i> (In,Ot)	1	1	1	0	1	0	0	2	0	4
<i>Xenops minutus</i> (In,Fob)	3	0	4	1	6	2	4	3	0	0
<i>Philydor erythrocerum</i> (In,Ot)	0	1	2	2	1	1	2	0	0	0
<i>Philydor pyrrhodes</i> (In,Ot)	0	0	0	1	0	0	0	0	0	0
<i>Clibanornis rubiginosus</i> (In,Ar)	3	4	2	0	0	0	0	1	0	0
<i>Automolus ochrolaemus</i> (In,Ar)	1	0	1	0	0	0	3	2	2	0
<i>Automolus infuscatus</i> (In,Fob)	5	8	6	4	9	4	8	5	2	0
<i>Synallaxis rutilans</i> (In,Ot)	0	0	0	3	0	0	0	1	0	0
<i>Corythopsis torquatus</i> (In,Te)	4	13	0	7	3	0	0	1	0	0
<i>Mionectes oleagineus</i> (Fr,Co)	0	0	0	0	0	0	0	0	0	1
<i>Mionectes macconnelli</i> (Fr,Co)	11	8	12	14	13	7	15	4	0	0
<i>Hemitriccus zosterops</i> (In,Ot)	0	3	0	0	0	0	0	1	0	0
<i>Rhynchocyclus olivaceus</i> (In,Ot)	1	0	3	0	1	0	3	4	0	0
<i>Tolmomyias assimilis</i> (In,Ot)	0	0	0	0	0	1	0	1	0	0
<i>Platyrinchus saturatus</i> (In,Ar)	4	4	2	9	3	1	0	0	0	0

Table A2. Species and number of individuals per 100 mist-net hours in treatments by region. Codes in parentheses indicate foraging guild where (In,Fob) - Insectivore, Flock Obligate; (In,Fld) – Insectivore, Flock-dropout; (In,Ar) – Insectivore, Arboreal; (In,Te) – Insectivore, Terrestrial; (In,Anf) – Insectivore, Ant-follower; (In,O) - Insectivore, Other; (In,Ga) – Insectivore, Gap; (Fr,Co) – Frugivore, Core; (Pa) – Parrot; (Ra) – Raptor; (Fr,Ot) – Frugivore, Other; (Hu) – Hummingbird; (No) – Non-forest.

Species	Porto Alegre Continuous	Colosso Continuous	KM41 Continuous	Dimona Continuous	Porto Alegre 100 Hectares	Dimona 100 Hectares	Dimona Second Growth	Colosso Second Growth	Young Second Growth	Balbina Islands
<i>Platyrinchus coronatus</i> (In,Ar)	6	9	1	6	0	4	3	0	0	0
<i>Platyrinchus platyrhynchos</i> (In,Ot)	0	0	1	0	0	0	0	0	0	0
<i>Onychorhynchus coronatus</i> (In,Ot)	0	0	2	2	1	0	0	0	0	0
<i>Myiobius barbatus</i> (In,Fob)	4	9	10	5	8	1	2	2	0	0
<i>Terenotriccus erythrurus</i> (In,Ot)	0	1	3	0	3	0	6	3	6	0
<i>Rhytipterna simplex</i> (Fr,Ot)	0	1	0	0	0	1	0	0	0	0
<i>Ramphotrigon ruficauda</i> (In,Ot)	0	0	0	1	0	0	0	0	0	0
<i>Attila spadiceus</i> (Fr,Ot)	0	6	2	0	0	0	1	1	2	0
<i>Phoenicircus carnifex</i> (Fr,Ot)	0	0	0	0	0	0	1	0	2	0
<i>Lipaugus vociferans</i> (Fr,Ot)	0	1	1	2	0	1	0	1	0	0
<i>Corapipo gutturalis</i> (In,Fob)	0	3	0	0	3	1	1	0	0	0
<i>Lepidothrix serena</i> (Fr,Co)	8	6	3	1	9	7	8	8	0	0
<i>Lepidothrix serena</i> (Fr,Co)	4	4	15	2	5	1	20	14	0	0
<i>Manacus manacus</i> (No)	0	0	2	0	0	0	3	1	0	0
<i>Dixiphia pipra</i> (Fr,Co)	32	33	27	18	23	19	77	70	21	21
<i>Ceratopipra erythrocephala</i> (Fr,Co)	4	0	1	1	1	1	31	25	0	0
<i>Schiffornis turdina</i> (Fr,Co)	3	11	6	5	0	1	1	0	0	0
<i>Laniocera hypopyrra</i> (In,Ot)	0	0	0	1	0	1	0	0	0	0
<i>Pachyramphus marginatus</i> (In,Ot)	0	0	0	0	0	0	0	1	0	0
<i>Piprites chloris</i> (In,Ot)	0	0	0	1	0	0	0	0	0	0
<i>Hylophilus muscicapinus</i> (In,Fob)	0	9	1	0	4	1	0	0	0	0
<i>Hylophilus ochraceiceps</i> (In,Fob)	6	6	4	5	4	1	2	0	0	0
<i>Microcerculus bambla</i> (In,Ar)	0	0	3	1	0	1	0	2	0	0
<i>Pheugopedius coraya</i> (No)	0	0	2	0	1	1	0	3	0	0
<i>Cyphorhinus arada</i> (In,Te)	0	0	4	6	0	5	1	0	0	0
<i>Microbates collaris</i> (In,Ar)	0	1	9	7	7	1	0	0	0	0
<i>Turdus albicollis</i> (Fr,Co)	6	8	6	18	3	4	14	10	0	29

Table A2. Species and number of individuals per 100 mist-net hours in treatments by region. Codes in parentheses indicate foraging guild where (In,Fob) - Insectivore, Flock Obligate; (In,Fld) – Insectivore, Flock-dropout; (In,Ar) – Insectivore, Arboreal; (In,Te) – Insectivore, Terrestrial; (In,Anf) – Insectivore, Ant-follower; (In,O) - Insectivore, Other; (In,Ga) – Insectivore, Gap; (Fr,Co) – Frugivore, Core; (Pa) – Parrot; (Ra) – Raptor; (Fr,Ot) – Frugivore, Other; (Hu) – Hummingbird; (No) – Non-forest.

Species	Porto Alegre Continuous	Colosso Continuous	KM41 Continuous	Dimona Continuous	Porto Alegre 100 Hectares	Dimona 100 Hectares	Dimona Second Growth	Colosso Second Growth	Young Second Growth	Balbina Islands
<i>Tachyphonus cristatus</i> (In,Ot)	0	0	0	1	0	0	0	0	0	0
<i>Tachyphonus surinamus</i> (Fr,Co)	1	8	4	3	3	1	3	8	4	21
<i>Lanio fulvus</i> (In,Fob)	1	0	1	0	0	0	0	0	0	0
<i>Tangara varia</i> (Fr,Co)	0	0	0	0	0	1	0	0	0	0
<i>Sporophila angolensis</i> (No)	0	0	1	0	0	1	0	0	0	0
<i>Coereba flaveola</i> (Fr,Ot)	0	0	0	2	1	0	0	0	0	0
<i>Saltator maximus</i> (Fr,Ot)	0	0	0	0	0	0	1	0	0	0
<i>Saltator grossus</i> (Fr,Ot)	1	0	0	0	0	0	0	0	0	0
<i>Arremon taciturnus</i> (In,Ot)	0	0	0	1	0	0	1	1	0	0
<i>Cyanocopsa cyanoides</i> (Fr,Co)	1	0	2	0	1	1	0	1	0	0
<i>Oporornis agilis</i> (In,Ot)	0	0	0	0	0	0	0	0	0	1
<i>Myiothlypis rivularis</i> (In,Ot)	1	0	0	5	0	0	0	0	0	0
<i>Euphonia cayennensis</i> (Fr,Co)	0	0	0	0	0	1	0	0	0	0

Figure A1. Chao's abundance-based Jaccard community similarity indices based on point count data by treatment (100 ha forest fragment, 100 ha island, continuous, older second growth forest and young second growth forest) and region, shown with standard error bars. Filled circles represent point count and open boxes represent banding data. Comparisons are ranked from most to least similar.

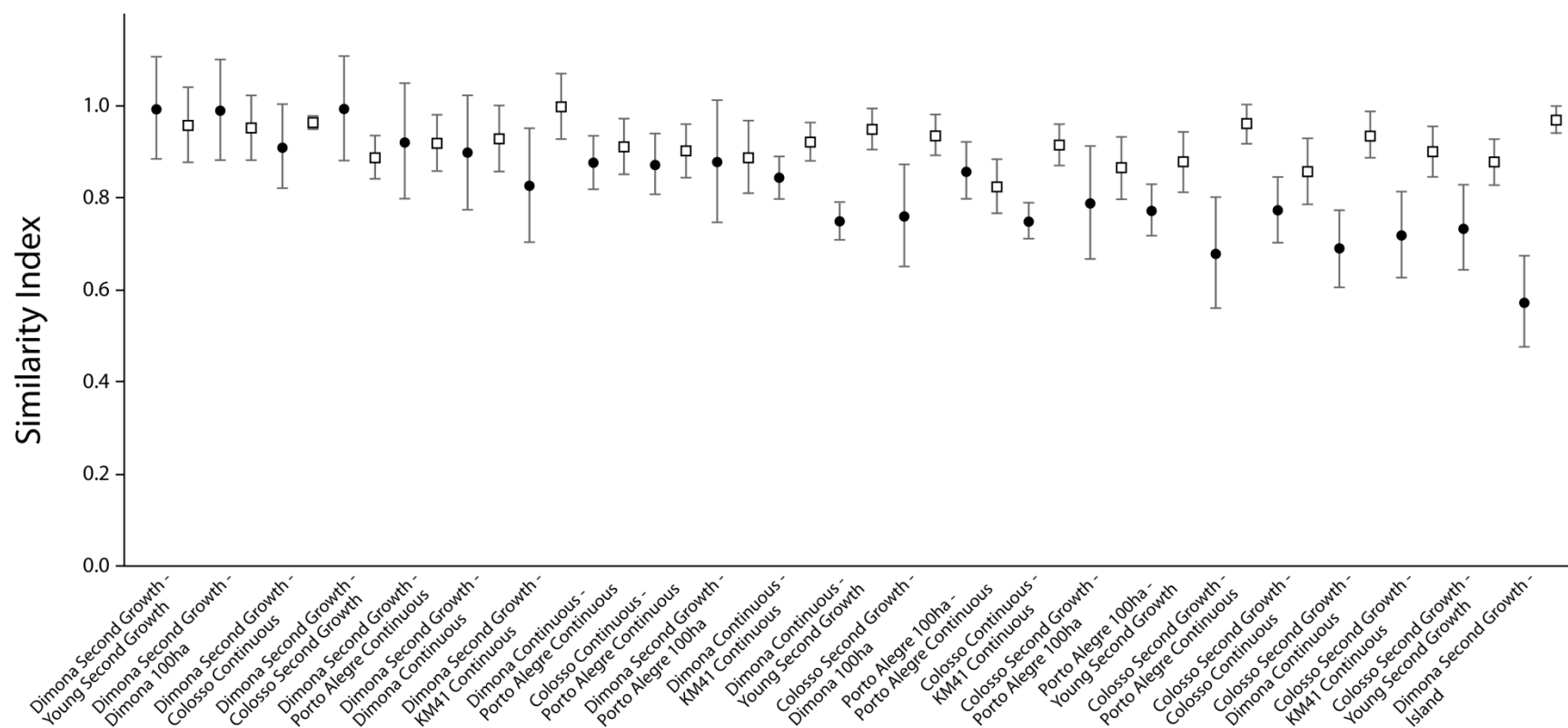


Figure A1. Continued. Chao's abundance-based Jaccard community similarity indices based on point count data by treatment (100 ha forest fragment, 100 ha island, continuous, older second growth forest and young second growth forest) and region, shown with standard error bars. Filled circles represent point count and open boxes represent banding data. Comparisons are ranked from most to least similar.

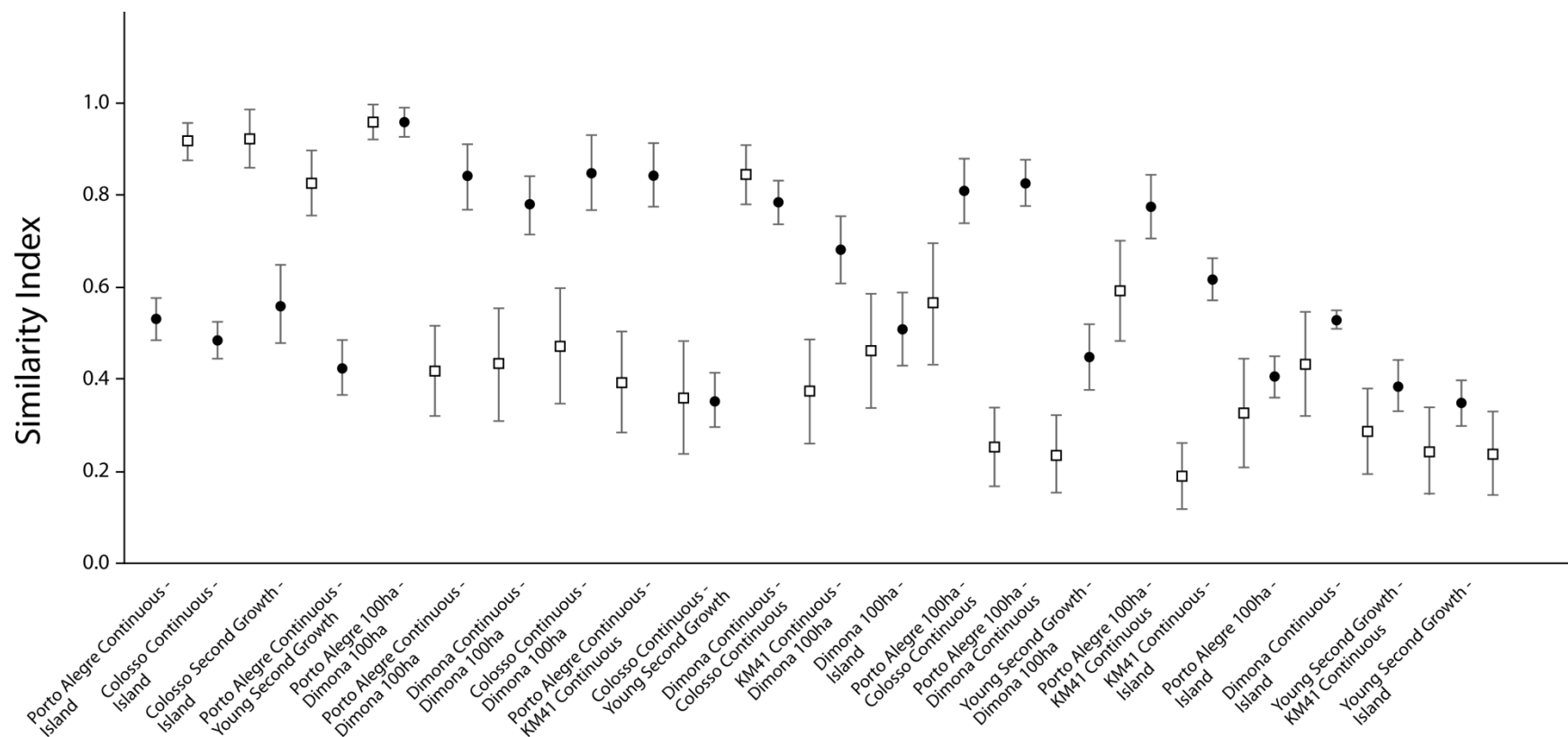


Figure A2. Whisker and box plots illustrating minimum, quartiles, median, and maximum of individuals in each foraging guild per 100 mist-net hours by treatment.

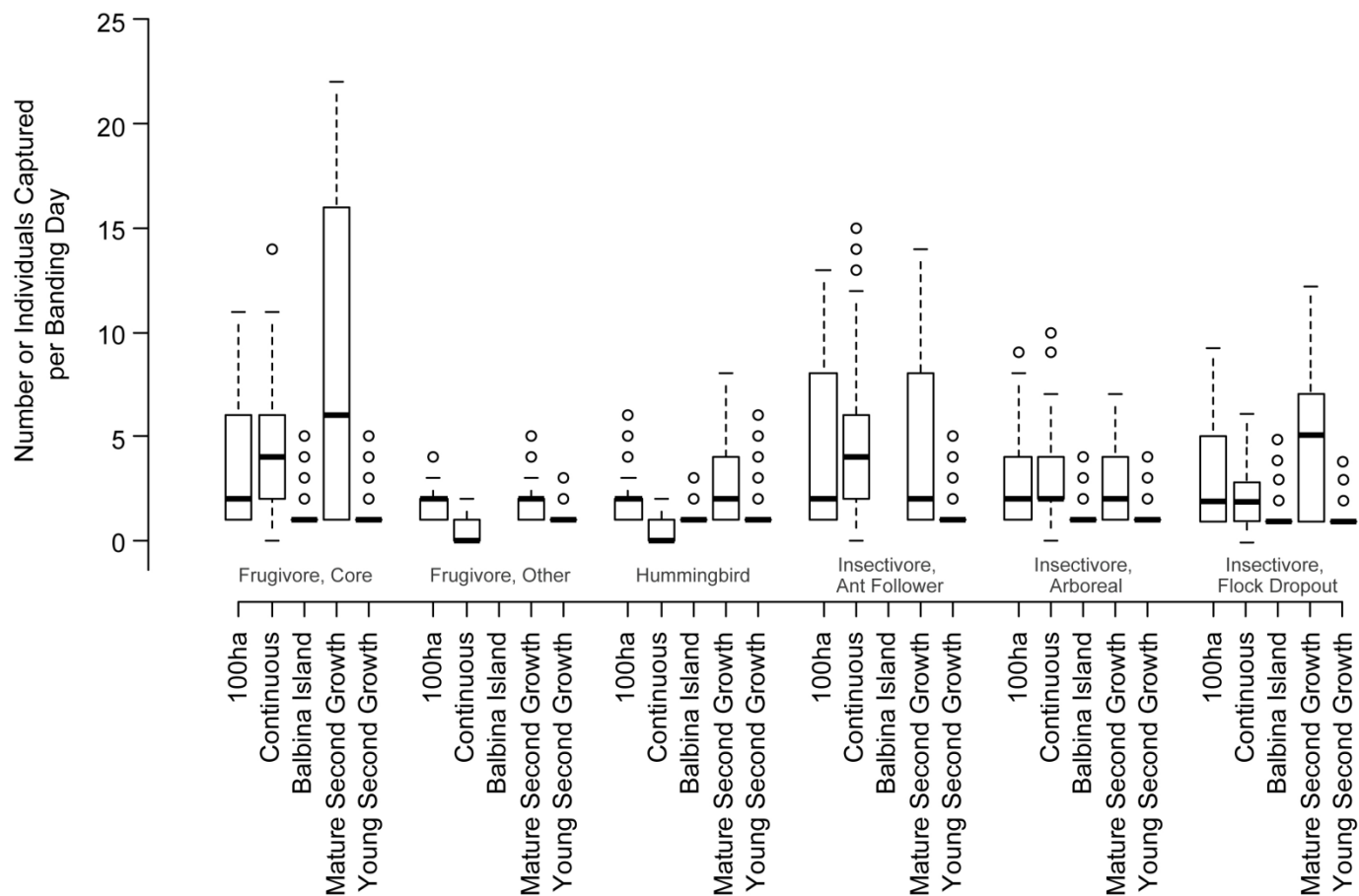


Figure A2 continued. Whisker and box plots illustrating minimum, quartiles, median, and maximum of individuals in each foraging guild per 100 mist-net hours by treatment.

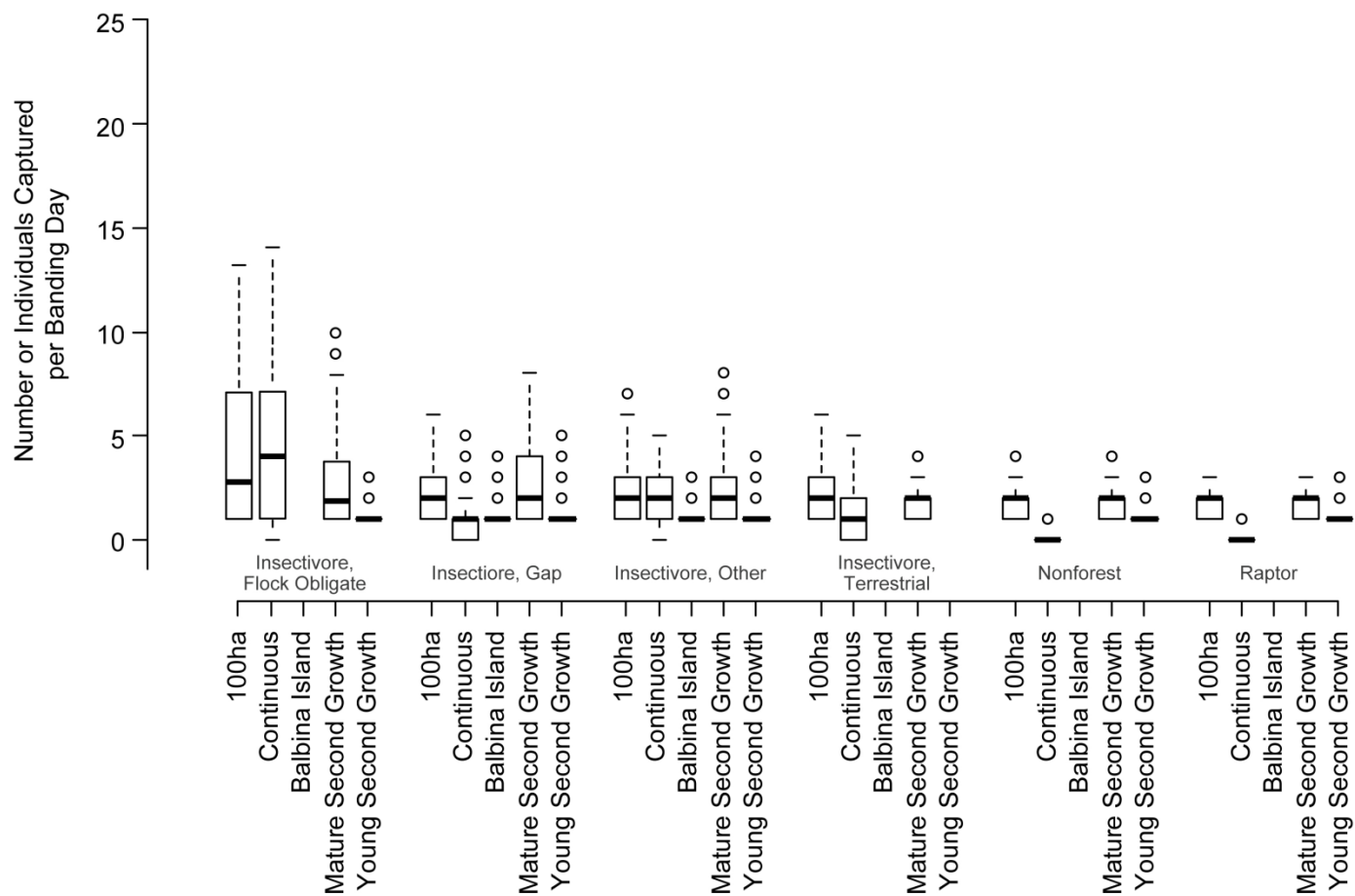


Figure A3. Whisker and box plots illustrating minimum, quartiles, median, and maximum of individuals in each foraging guild per 240 point count minutes by treatment.

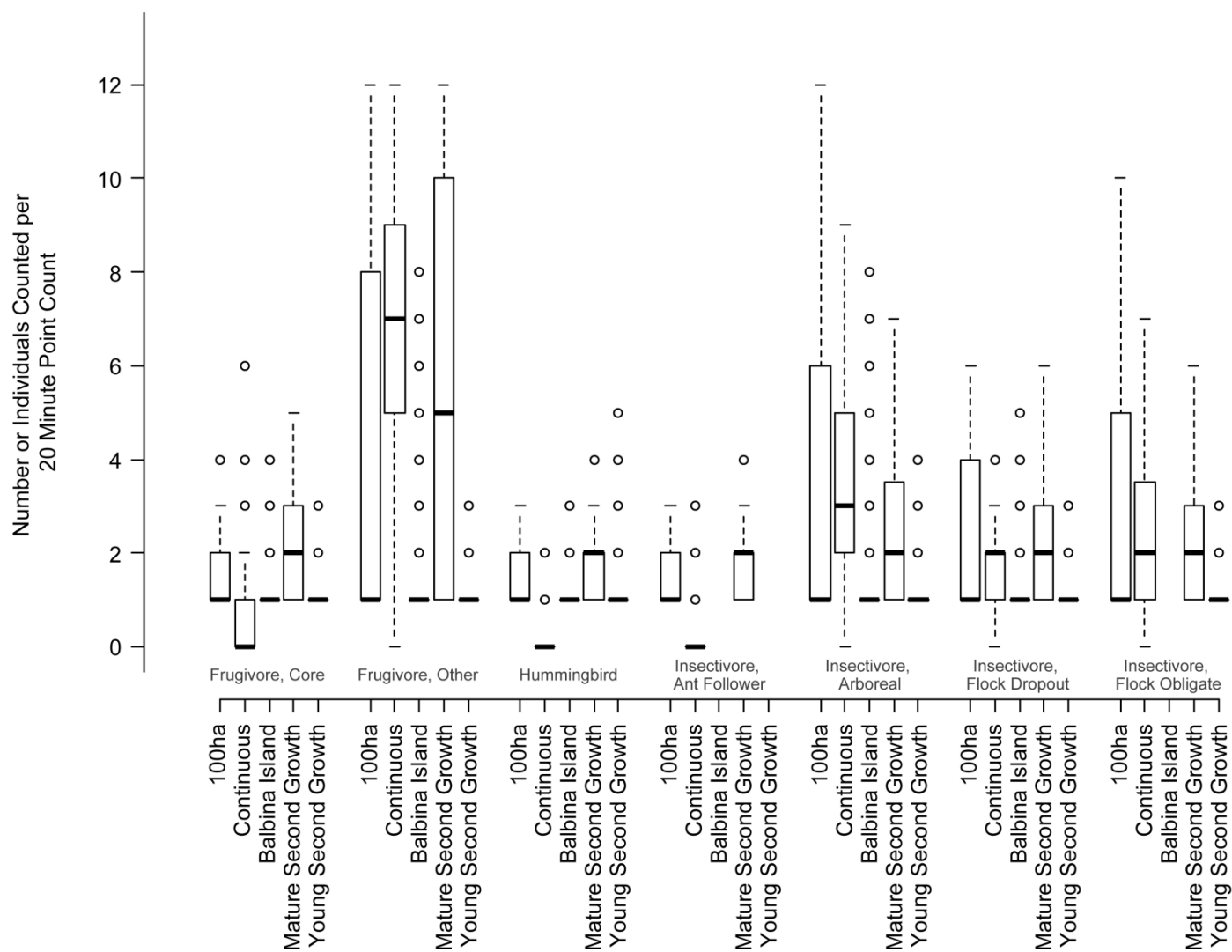


Figure A3 continued. Whisker and box plots illustrating minimum, quartiles, median, and maximum of individuals in each foraging guild per 240 point count minutes by treatment.

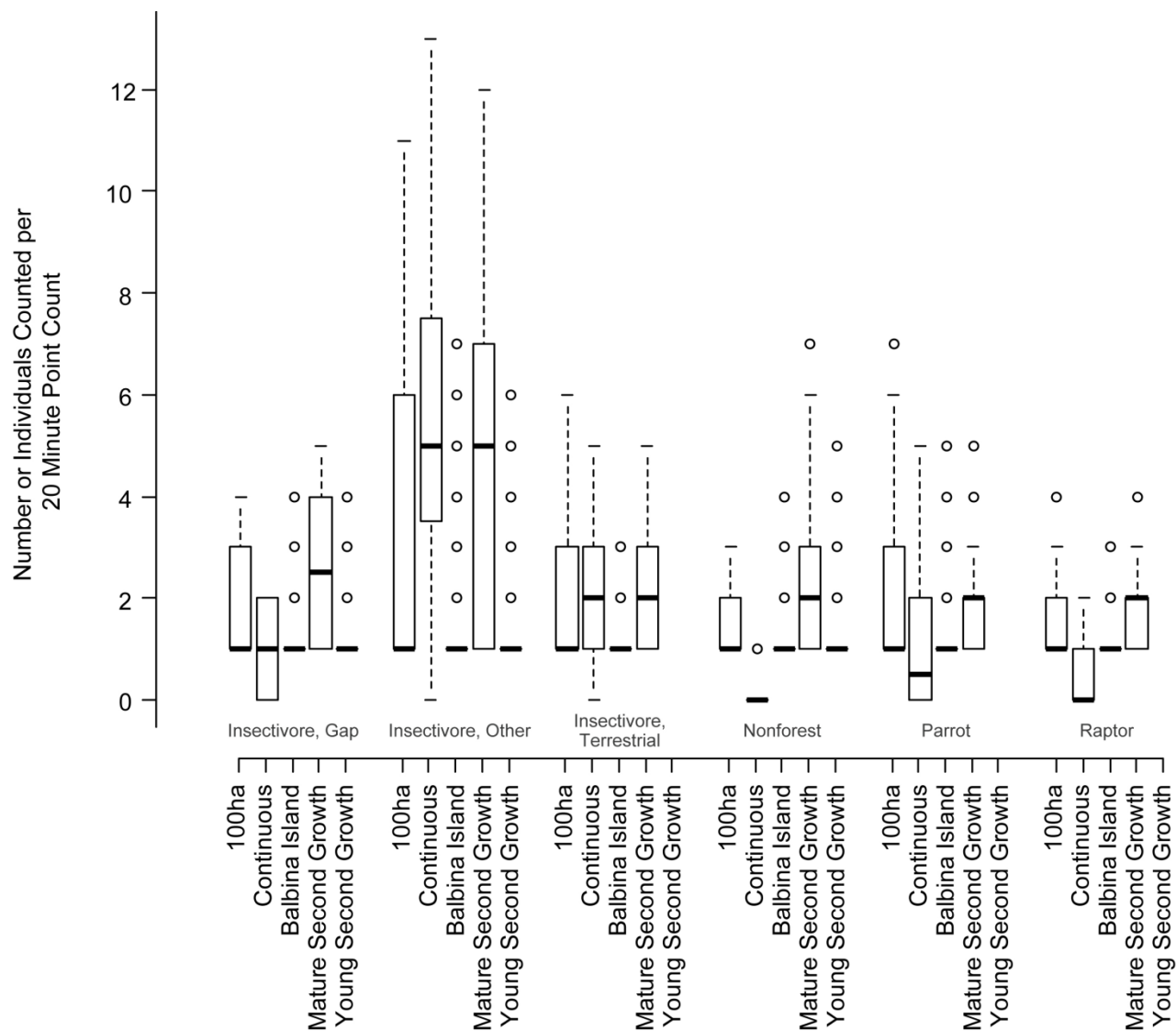


Figure A4. Standing dead trees above the water's surface adjacent to a forested island in the Balbina reservoir, 150km north of Manaus, Brazil.



APPENDIX B: MODEL RANKING FROM CHAPTER 3

Table B1. Most competitive CMJ models of study species captured between 1979 and 1988 in contiguous forest 80 km north of Manaus, Brazil. CJS models for each study species, within two QAICc values of the top model, are shown with associated model weights (w_i) and number of parameters (k).

Species	Model	ΔQAICc	w_i	k
<i>Galbula albirostris</i>	$\phi(2./.) p(.)$	0.00	0.83	3
<i>Glyphorhynchus spirurus</i>	$\phi(.) p(t)$	0.00	0.43	10
	$\phi(t) p(.)$	0.94	0.27	10
	$\phi(2./.) p(t)$	1.54	0.20	11
<i>Certhiasomus stictolaemus</i>	$\phi(.) p(t)$	0.00	0.39	10
	$\phi(2./.) p(t)$	0.87	0.25	11
	$\phi(.) p(.)$	1.27	0.21	2
<i>Xiphorhynchus pardalotus</i>	$\phi(.) p(.)$	0.00	0.58	2
	$\phi(2./.) p(.)$	0.66	0.41	3
<i>Automolus infuscatus</i>	$\phi(.) p(.)$	0.00	0.61	2
	$\phi(2./.) p(.)$	1.81	0.25	3
<i>Sclerurus rufigularis</i>	$\phi(2./.) p(t)$	0.00	0.50	11
	$\phi(2./.) p(.)$	0.92	0.32	3
<i>Xenops minutus</i>	$\phi(.) p(.)$	0.00	0.59	2
	$\phi(2./.) p(.)$	1.96	0.22	3
<i>Percnostola rufifrons</i>	$\phi(.) p(.)$	0.00	0.50	2
<i>Thamnomanes ardesiacus</i>	$\phi(2./.) p(.)$	0.00	0.84	3
<i>Thamnomanes caesius</i>	$\phi(.) p(.)$	0.00	0.68	2
	$\phi(2./.) p(.)$	1.85	0.27	3
<i>Myrmotherula longipennis</i>	$\phi(.) p(.)$	0.00	0.67	2
	$\phi(2./.) p(.)$	1.78	0.28	3
<i>Myrmotherula menetriesii</i>	$\phi(.) p(.)$	0.00	0.72	2
	$\phi(2./.) p(.)$	1.95	0.27	3
<i>Myrmotherula axillaris</i>	$\phi(.) p(.)$	0.00	0.63	2
	$\phi(2./.) p(.)$	1.25	0.34	3
<i>Isleria guttata</i>	$\phi(2./.) p(t)$	0.00	0.66	11
<i>Epinecrophylla gutturalis</i>	$\phi(.) p(.)$	0.00	0.58	2
	$\phi(2./.) p(.)$	1.28	0.31	3

Table B1. Continued. Most competitive CMJ models of study species captured between 1979 and 1988 in contiguous forest 80 km north of Manaus, Brazil. CJS models for each study species, within two QAICc values of the top model, are shown with associated model weights (w_i) and number of parameters (k).

Species	Model	ΔQAICc	w_i	k
<i>Hypocnemis cantator</i>	$\phi(.) p(t)$	0.00	0.51	10
	$\phi(2./.) p(t)$	1.75	0.21	11
<i>Willisornis poecilinotus</i>	$\phi(.) p(t)$	0.00	0.50	10
	$\phi(2./.) p(t)$	0.22	0.45	11
<i>Pithys albifrons</i>	$\phi(2./.) p(t)$	0.00	0.73	11
<i>Gymnopithys rufigula</i>	$\phi(.) p(t)$	0.00	0.72	10
<i>Formicarius colma</i>	$\phi(.) p(.)$	0.00	0.67	2
	$\phi(2./.) p(.)$	1.54	0.31	3
<i>Corythopsis torquatus</i>	$\phi(.) p(.)$	0.00	0.41	2
	$\phi(2./.) p(.)$	1.12	0.24	3
	$\phi(.) p(t)$	1.66	0.18	10
<i>Mionectes macconnelli</i>	$\phi(2./.) p(.)$	0.00	0.71	3
<i>Platyrrinchus saturatus</i>	$\phi(.) p(.)$	0.00	0.52	2
	$\phi(2./.) p(.)$	0.35	0.44	3
<i>Platyrrinchus coronatus</i>	$\phi(.) p(.)$	0.00	0.55	2
	$\phi(2./.) p(.)$	1.13	0.31	3
<i>Myiobius barbatus</i>	$\phi(.) p(.)$	0.00	0.72	2
<i>Schiffornis turdina</i>	$\phi(2./.) p(t)$	0.00	0.75	3
<i>Dixiphia pipra</i>	$\phi(2./.) p(.)$	0.00	0.94	3
<i>Lepidothrix serena</i>	$\phi(.) p(.)$	0.00	0.69	2
	$\phi(2./.) p(.)$	1.76	0.29	3
<i>Turdus albicollis</i>	$\phi(2./.) p(t)$	0.00	0.00	11
<i>Microcerculus bambla</i>	$\phi(.) p(.)$	0.00	0.59	2
	$\phi(2./.) p(.)$	0.78	0.40	3
<i>Microbates collaris</i>	$\phi(2./.) p(t)$	0.00	0.83	11
<i>Hylophilus ochraceiceps</i>	$\phi(.) p(.)$	0.00	0.57	2
	$\phi(2./.) p(.)$	1.70	0.24	3
<i>Tachyphonus surinamus</i>	$\phi(.) p(.)$	0.00	0.72	2

APPENDIX C: ESTIMATES AND MODEL RANKINGS FROM CHAPTER 4

Table C1. Candidate Pradel models for seven central Amazonian bird species captured in second growth and primary forest, ranked by Akaike Information Criterion (AIC_c). Included for each model are AIC_c weights (w_i) and number of parameters (K).

Model	ΔAIC_c	w_i	K
<i>Percnostola rufifrons</i>			
Phi(.) p(.) Lambda(.)	0.00	0.33	3
Phi(g) p(.) Lambda(.)	1.20	0.18	4
Phi(.) p(g) Lambda(.)	1.86	0.13	4
Phi(.) p(.) Lambda(g)	2.03	0.12	4
Phi(g) p(g) Lambda(.)	2.79	0.08	5
Phi(g) p(.) Lambda(g)	3.15	0.07	5
Phi(.) p(g) Lambda(g)	3.87	0.05	5
Phi(g) p(g) Lambda(g)	4.79	0.03	6
<i>Glyphorynchus spirurus</i>			
Phi(.) p(.) Lambda(.)	0.00	0.33	3
Phi(.) p(.) Lambda(g)	1.03	0.20	4
Phi(g) p(.) Lambda(.)	2.01	0.12	4
Phi(.) p(g) Lambda(.)	2.05	0.12	4
Phi(g) p(.) Lambda(g)	2.97	0.08	5
Phi(.) p(g) Lambda(g)	3.09	0.07	5
Phi(g) p(g) Lambda(.)	3.67	0.05	5
Phi(g) p(g) Lambda(g)	4.65	0.03	6
<i>Gymnopathys rufigula</i>			
Phi(.) p(.) Lambda(.)	0.00	0.37	3
Phi(.) p(g) Lambda(.)	1.75	0.15	4
Phi(g) p(.) Lambda(.)	2.08	0.13	4
Phi(.) p(.) Lambda(g)	2.10	0.13	4
Phi(g) p(g) Lambda(.)	2.87	0.09	5
Phi(.) p(g) Lambda(g)	3.85	0.05	5
Phi(g) p(.) Lambda(g)	4.21	0.04	5
Phi(g) p(g) Lambda(g)	5.01	0.03	6
<i>Willisornis poecilinotus</i>			
Phi(.) p(.) Lambda(.)	0.00	0.26	3
Phi(.) p(.) Lambda(g)	0.34	0.22	4
Phi(g) p(.) Lambda(.)	1.62	0.12	4
Phi(g) p(.) Lambda(g)	1.70	0.11	5
Phi(.) p(g) Lambda(.)	1.93	0.10	4
Phi(.) p(g) Lambda(g)	2.09	0.09	5
Phi(g) p(g) Lambda(.)	3.09	0.06	5
Phi(g) p(g) Lambda(g)	3.24	0.05	6

Table C1. Continued. Candidate Pradel models for seven central Amazonian bird species captured in second growth and primary forest, ranked by Akaike Information Criterion (AIC_c). Included for each model are AIC_c weights (w_i) and number of parameters (K).

Model	ΔAIC_c	w_i	K
<i>Dixiphia pipra</i>			
Phi(g) p(.) Lambda(.)	0.00	0.34	4
Phi(.) p(g) Lambda(.)	0.80	0.23	4
Phi(g) p(g) Lambda(.)	1.66	0.15	5
Phi(g) p(.) Lambda(g)	1.97	0.13	5
Phi(.) p(g) Lambda(g)	2.74	0.09	5
Phi(g) p(g) Lambda(g)	3.64	0.05	6
Phi(.) p(.) Lambda(.)	5.61	0.02	3
Phi(.) p(.) Lambda(g)	7.37	0.01	4
<i>Pithys albifrons</i>			
Phi(.) p(.) Lambda(.)	0.00	0.38	3
Phi(.) p(.) Lambda(g)	1.85	0.15	4
Phi(.) p(g) Lambda(.)	2.03	0.14	4
Phi(g) p(.) Lambda(.)	2.04	0.14	4
Phi(g) p(g) Lambda(.)	3.86	0.06	5
Phi(.) p(g) Lambda(g)	3.89	0.06	5
Phi(g) p(.) Lambda(g)	3.91	0.05	5
Phi(g) p(g) Lambda(g)	5.75	0.02	6
<i>Thamnomanes spp.</i>			
Phi(.) p(.) Lambda(g)	0.00	0.39	4
Phi(g) p(.) Lambda(g)	1.18	0.22	5
Phi(.) p(g) Lambda(g)	1.44	0.19	5
Phi(g) p(g) Lambda(g)	2.97	0.09	6
Phi(.) p(.) Lambda(.)	3.80	0.06	3
Phi(g) p(.) Lambda(.)	5.40	0.03	4
Phi(.) p(g) Lambda(.)	5.60	0.02	4
Phi(g) p(g) Lambda(.)	7.12	0.01	5

Table C2. Averaged parameter estimates (including all models within 0.95 of the AIC_c weight) for seven central Amazonian bird species captured in second growth and primary forest.

Parameter	Estimate	SE
<i>Glyphorynchus spirurus</i>		
Apparent Survival Parameter (ϕ) Primary Forest	0.68	0.17
Apparent Survival Parameter (ϕ) Second Growth	0.66	0.17
Recapture Parameter (p) Primary Forest	0.35	0.11
Recapture Parameter (p) Second Growth	0.36	0.12
Population Size Rate of Change (λ) Primary Forest	1.80	0.13
Population Size Rate of Change (λ) Second Growth	1.72	0.13
<i>Gymnopathys rufigula</i>		
Apparent Survival Parameter (ϕ) Primary Forest	0.82	0.24
Apparent Survival Parameter (ϕ) Second Growth	0.86	0.28
Recapture Parameter (p) Primary Forest	0.18	0.09
Recapture Parameter (p) Second Growth	0.16	0.08
Population Size Rate of Change (λ) Primary Forest	1.46	0.11
Population Size Rate of Change (λ) Second Growth	1.45	0.14
<i>Willisornis poecilinotus</i>		
Apparent Survival Parameter (ϕ) Primary Forest	0.48	0.17
Apparent Survival Parameter (ϕ) Second Growth	0.41	0.19
Recapture Parameter (p) Primary Forest	0.49	0.21
Recapture Parameter (p) Second Growth	0.53	0.26
Population Size Rate of Change (λ) Primary Forest	1.69	0.15
Population Size Rate of Change (λ) Second Growth	1.50	0.24
<i>Pernostola rufifrons</i>		
Apparent Survival Parameter (ϕ) Primary Forest	0.64	0.32
Apparent Survival Parameter (ϕ) Second Growth	0.77	0.39
Recapture Parameter (p) Primary Forest	0.20	0.14
Recapture Parameter (p) Second Growth	0.19	0.12
Population Size Rate of Change (λ) Primary Forest	1.45	0.14
Population Size Rate of Change (λ) Second Growth	1.48	0.15

Table C2. Continued. Averaged parameter estimates (including all models within 0.95 of the AIC_c weight) for seven central Amazonian bird species captured in second growth and primary forest.

Parameter	Estimate	SE
<i>Dixiphia pipra</i>		
Apparent Survival Parameter (ϕ) Primary Forest	0.40	0.14
Apparent Survival Parameter (ϕ) Second Growth	0.21	0.16
Recapture Parameter (p) Primary Forest	0.36	0.15
Recapture Parameter (p) Second Growth	0.42	0.33
Population Size Rate of Change (λ) Primary Forest	1.55	0.08
Population Size Rate of Change (λ) Second Growth	1.57	0.09
<i>Pithys albifrons</i>		
Apparent Survival Parameter (ϕ) Primary Forest	0.32	0.11
Apparent Survival Parameter (ϕ) Second Growth	0.33	0.14
Recapture Parameter (p) Primary Forest	0.43	0.16
Recapture Parameter (p) Second Growth	0.41	0.17
Population Size Rate of Change (λ) Primary Forest	1.40	0.07
Population Size Rate of Change (λ) Second Growth	1.39	0.09
<i>Thamnomanes spp.</i>		
Apparent Survival Parameter (ϕ) Primary Forest	0.28	0.17
Apparent Survival Parameter (ϕ) Second Growth	0.23	0.16
Recapture Parameter (p) Primary Forest	0.40	0.27
Recapture Parameter (p) Second Growth	0.43	0.31
Population Size Rate of Change (λ) Primary Forest	1.56	0.13
Population Size Rate of Change (λ) Second Growth	1.11	0.17

Figure C1. Survival estimates with associated standard errors for seven central Amazonian birds captured in second growth and primary forest. Foraging guild affiliation is denoted by (In,Fob) - Insectivore, Flock Obligate; (In,Fld) – Insectivore, Flock-dropout; (In,Ar) – Insectivore, Arboreal; (In,Anf) – Insectivore, Ant-follower; (In,Ga) – Insectivore, Gap; (Fr,Co) – Frugivore, Core.

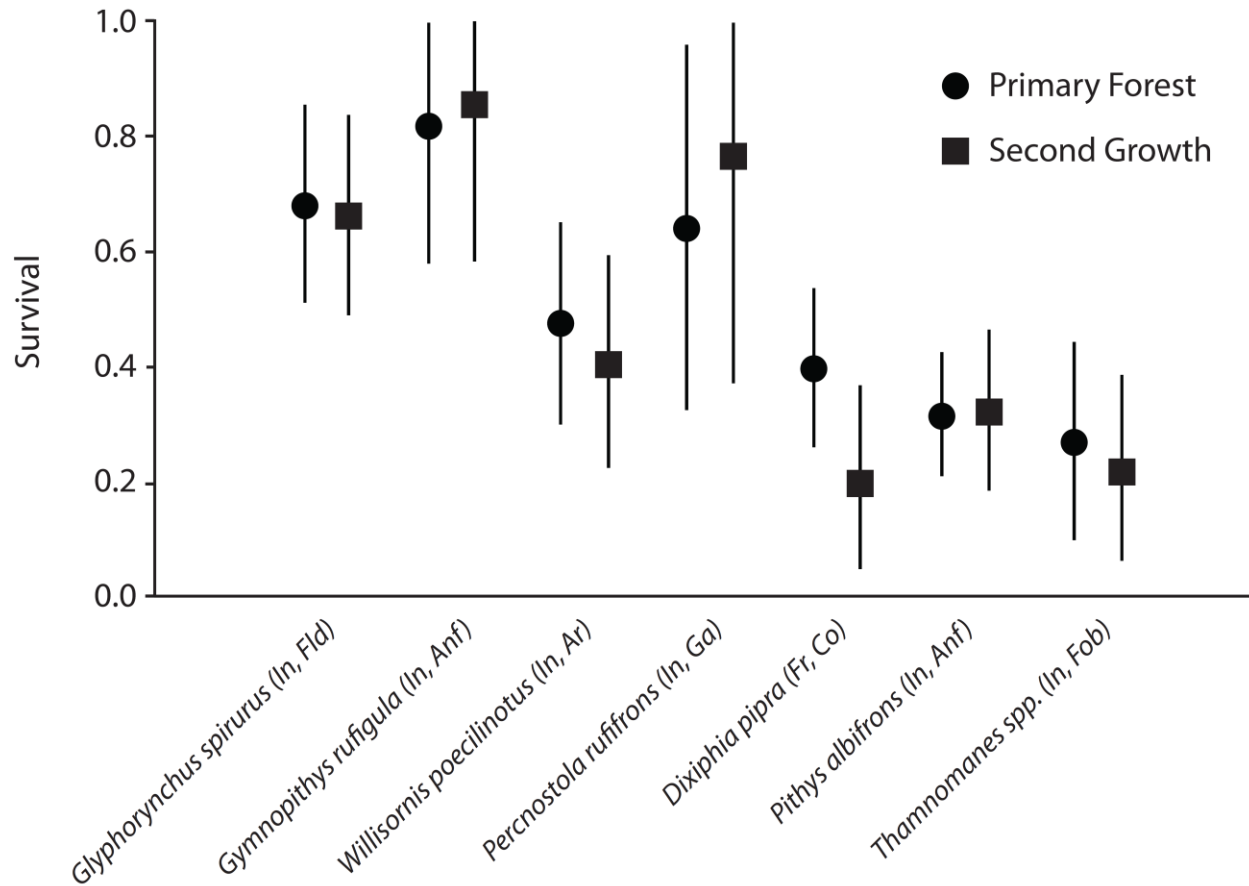
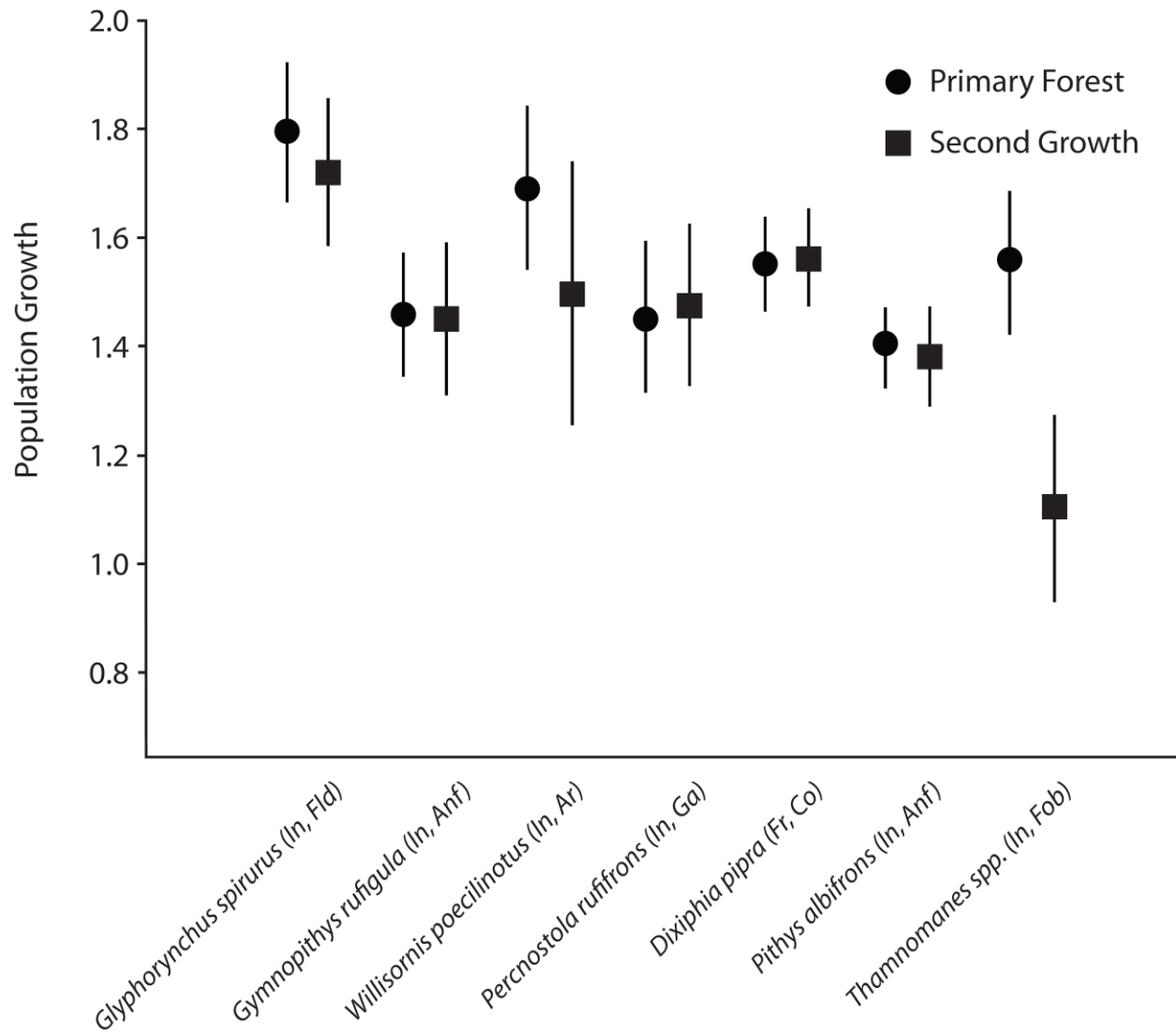


Figure C2. Population growth estimates with associated standard errors for seven central Amazonian birds captured in second growth and primary forest. Foraging guild affiliation is denoted by (In,Fob) - Insectivore, Flock Obligate; (In,Fld) – Insectivore, Flock-dropout; (In,Ar) – Insectivore, Arboreal; (In,Anf) – Insectivore, Ant-follower; (In,Ga) – Insectivore, Gap; (Fr,Co) – Frugivore, Core.



APPENDIX D: MODEL RANKING FROM CHAPTER 5

Table D1. Candidate Cormack-Jolly-seber models for six central Amazonian bird species captured in 100 and 10 ha fragments, ranked by Akaike Information Criterion (AIC_c). Included for each model are AIC_c weights (w_i) and deviance. Numbers within parentheses refer to number of individuals and total captures, respectively.

Model	ΔAIC_c	w_i	Deviance
<i>Dixiphia pipra</i>			
Phi(g - matrix)p(g*t)	0.00	1.00	265.58
Phi(g - matrix)p(t)	120.35	0.00	468.49
Phi(g - matrix)p(g)	137.43	0.00	485.57
Phi(g - matrix)p(.)	158.05	0.00	527.33
Phi(g) p(g)	164.25	0.00	490.77
Phi(t) p(t)	166.88	0.00	523.53
Phi(.) p(.)	214.47	0.00	618.59
Phi(g*t) p(g*t)	352.26	0.00	192.14
<i>Glyphorynchus spirurus</i>			
Phi(g - matrix)p(g*t)	0.00	1.00	402.13
Phi(t) p(t)	99.56	0.00	665.64
Phi(g - matrix)p(t)	112.17	0.00	658.95
Phi(g - matrix)p(g)	140.44	0.00	678.51
Phi(g) p(g)	150.10	0.00	679.39
Phi(.) p(.)	164.72	0.00	780.39
Phi(g - matrix)p(.)	165.81	0.00	738.24
Phi(g*t) p(g*t)	712.77	0.00	261.75
<i>Percnostola rufifrons</i>			
Phi(g - matrix)p(g*t)	0.00	1.00	213.23
Phi(g*t) p(g*t)	76.06	0.00	143.44
Phi(g - matrix)p(t)	108.46	0.00	372.28
Phi(g - matrix)p(.)	120.44	0.00	405.45
Phi(g - matrix)p(g)	121.45	0.00	385.28
Phi(t) p(t)	129.65	0.00	406.23
Phi(.) p(.)	136.66	0.00	458.60
Phi(g) p(g)	151.80	0.00	393.96

Table D1. Candidate Cormack-Jolly-seber models for six central Amazonian bird species captured in 100 and 10 ha fragments, ranked by Akaike Information Criterion (AIC_c). Included for each model are AIC_c weights (w_i) and deviance. Numbers within parentheses refer to number of individuals and total captures, respectively.

Model	ΔAIC_c	w_i	Deviance
<i>Pithys albifrons</i>			
Phi(g - matrix) p(g*t)	0.00	1.00	124.29
Phi(g - matrix) p(t)	60.27	0.00	230.74
Phi(g - matrix) p(.)	93.48	0.00	282.94
Phi(t) p(t)	101.20	0.00	269.53
Phi(g - matrix) p(g)	104.46	0.00	272.79
Phi(g) p(g - matrix)	121.00	0.00	285.03
Phi(.) p(.)	130.59	0.00	346.68
Phi(g) p(g)	141.39	0.00	288.01
<i>Thamnomanes ardesiacus</i>			
Phi(g - matrix)p(g*t)	0.00	1.00	279.68
Phi(g - matrix)p(t)	71.46	0.00	417.53
Phi(g - matrix)p(g)	104.08	0.00	452.29
Phi(g - matrix)p(.)	111.56	0.00	478.76
Phi(g) p(g)	134.45	0.00	458.90
Phi(t) p(t)	143.56	0.00	498.14
Phi(.) p(.)	170.02	0.00	572.07
Phi(g*t) p(g*t)	242.21	0.00	210.68
<i>Willisornis poecilinotus</i>			
Phi(g - matrix)p(t)	0.00	1.00	491.81
Phi(g - matrix)p(g)	28.83	0.00	522.76
Phi(g - matrix)p(.)	72.87	0.00	583.59
Phi(t) p(t)	87.57	0.00	581.50
Phi(.) p(.)	161.86	0.00	703.25
Phi(g) p(g)	283.61	0.00	679.39
Phi(g*t) p(g*t)	846.28	0.00	261.75
Phi(g - matrix)p(g*t)	921.43	0.00	560.81

APPENDIX E: PERMISSION FROM OIKOS TO REPRINT PREVIOUSLY PUBLISHED CHAPTER 3



Oikos Technical Editor

Aug 26 (2 days ago) ☆



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Best wishes
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! Note! A sloppy hand often reflects a sloppy mind!

TIP of the day from the Editor: Read the Instructions for authors BEFORE you submit!!

VITA

Jared Desomond Wolfe was born in Sacramento, CA in 1980. He attended Sacramento City College from 1998 until 2000 when he left to pursue a Bachelor of Science degree at Humboldt State University in Conservation Biology and Applied Vertebrate Ecology. Before and during his undergraduate Jared worked as a field biologist for private, academic, governmental and non-profit organizations throughout the western hemisphere, from Alaska to Ecuador. Jared returned to complete a Master of Science in Wildlife Biology at Humboldt State University in 2007 under Dr. Mathew D. Johnson studying migrant bird stopover ecology in Tortuguero, Costa Rica. Jared shifted his research focus to resident tropical birds in the central Amazon under the tutelage of his PhD advisor Dr. Phil C Stouffer in 2010. After spending four field seasons in the central Amazon, Jared is scheduled to finish his PhD in 2014.