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Fragmentation sensitivity and its consequences on demography and host-ectoparasite dynamics in amazonian birds

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FRAGMENTATION SENSITIVITY AND ITS CONSEQUENCES ON DEMOGRAPHY AND HOST–ECTOPARASITE DYNAMICS IN AMAZONIAN BIRDS

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DEDICATION

I dedicate this manuscript to my wife, my partner in life, and my closest friend, Ceci Johnson, who encourages me to follow my dreams and gives me the inspiration to push forward in good and hard times. I will always appreciate and never forget her unending patience and love through this journey.

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ABSTRACT

The Amazon rainforest is experiencing rapid deforestation due to ranching, agriculture, and urban development, which often leads to remnant patches serving as refugia for forest organisms. By mist-netting passerines in 11 forest fragments (1-, 10-, and 100-ha patches) and nearby continuous forest at the Biological Dynamics of Forest Fragmentation Project near Manaus, Brazil, I conducted a series of studies to identify mechanisms that drive population changes in fragmented landscapes.

First, I examined the age structure of bird populations from six ecological guilds in fragments and continuous forest. Immatures are the dispersing age group in birds, and their relative abundance in fragments was often driven by the age of regenerating second growth surrounding fragments. The relative abundance of adults, the resident age group, in fragments was often driven by patch size. Differences in how guilds responded to fragmentation depended on their dispersal propensity, measured with mark–recapture techniques, with increasing dispersal propensity corresponding to increased relative abundance of immatures in fragments.

Second, I quantified variation in the frequency of molting and breeding simultaneously (called molt–breeding overlap; MBO) among species. I propose that molting and breeding simultaneously requires a consistent or predictable environment, like a humid rainforest understory. Frequent molt–breeding overlap may preclude living in more seasonally fluctuating environments like rainforest fragments. Suboscines, particularly antbirds, had more frequent MBO and were more sensitive to fragmentation than oscine.

Finally, I examined the consequences of fragmentation on host–ectoparasite dynamics. Feather mites, haematophagous mites, and chewing lice showed similar richness and abundance on hosts that occupied either interior forests or fragment edges. In Thamnophilidae and

frugivores, ectoparasite removal caused an increase in body condition, but only for hosts occupying interior forests and not those on fragment edges. Feather mites were beneficial to hosts in interior forest, but became harmful along edges, suggesting that fragmentation can alter delicate host–parasite dynamics in complicated ways. Understanding these relationships may help explain host population declines in fragmented landscapes.

CHAPTER 1: GENERAL INTRODUCTION

BACKGROUND

At nearly the size of the United States, the Amazon basin is home to an incredible amount of biodiversity, including about 20% of the world's bird species. Flying from the Northern Hemisphere into the city of Manaus in Amazonas, Brazil is an amazing sight – with almost nothing but forest, broken only by an occasional meandering river. Manaus is where the waters of the Rio Negro and Rio Solimões meet to form the Amazon River, essentially in the center of the Amazon basin. The intersection of these three rivers serves as a central hub for an ever-increasing human presence in the region.

Although virtually untouched by modern development before 1970, the Amazonian rainforest is now declining at an alarming rate (Skole and Tucker 1993, Laurance et al. 2001, Fearnside 2005). Cattle ranching is one of the predominant causes of deforestation (Uhl and Buschbacher 1985, Fearnside 2005), although agriculture for food and biofuel (Fearnside 2002, Sawyer 2008), logging (Laurance 1998), and urbanization (Fearnside 2002, Laurance et al. 2004) are also responsible for forest loss to a large degree, spurred by the development of roads (Pfaff et al. 2007). This pattern of development often leads to small (< 100 ha), isolated rainforest fragments (Gascon et al. 2000), which can become further degraded by fire and edge effects (Laurance et al. 2002, Barlow et al. 2006). Currently, land prospecting, a growing economy, and especially advances in biofuel technology are stimulating new road development in the Amazon and the rate of deforestation has increased after a period of relatively slow deforestation rates during the 1990's (Fearnside 2005). Although the Brazilian government has established an extensive reserve system, land protection is greater in less-developed regions, and there are

problems with enforcement and deficits of protected private land in regions experiencing high deforestation pressures (Sparovek et al. 2010). At current rates, as much as 2/3 of the Amazonian rainforest could be impacted by 2020 (Laurance et al. 2004). The consequences of deforestation on biodiversity and ecosystem processes are important to understand to develop conservation strategies and policies.

Biological Dynamics of Forest Fragments Project Background

The Biological Dynamics of Forest Fragments Project (BDFFP) is located about 80 km north of Manaus (S 2º30', W 60º; Fig. 1.1). The BDFFP was initiated in 1979 by the World Wildlife Fund-US (WWF) largely because of the ideas, motivation, and effort of Thomas Lovejoy. At the time, Brazilian law required that 50% of forested land remain intact as land owners deforested their land for cattle grazing and agriculture. Taking advantage of this, Lovejoy developed an agreement among the WWF, Brazil's Instituto Nacional de Pesquisas da Amazônica (INPA), the Conselho Nacional de Desenvolvimento Científico e Tecnológico (CNPq), and cooperative ranchers to experimentally isolate fragments as local cattle ranchers cleared their land. This established one of the most important landscape-scale fragmentation experiments on the planet (Bierregaard et al. 2001).

During the early and mid-80's logistical and economic problems prevented about half of the project from becoming realized. Eleven out of the originally planned 24 fragments were isolated between 1980 and 1990 (ten fragments were isolated by 1984; Table 1.1). The surrounding matrix (i.e., surrounding land and unlike the fragment of interest) was used by ranchers for cattle production, but most of this land use ceased within a few years after clearing because governmental incentives for such practices disappeared because of an economic downturn during the 1980s (Fearnside 2005). Since then, secondary succession in the matrix has

been converting the once open pastures into regenerating secondary forest. The speed of regeneration and composition of the returning vegetation is dependent on how intensively the land was used; burning promoted a *Vismia* (Clusiaceae)-dominated second growth whereas clearcutting without burning promoted a *Cecropia* (Cecropiaceae)-dominated second growth (Borges and Stouffer 1999, Lucas et al. 2002), although these once distinct second growth communities have become more similar with age. In most cases, second growth within 100 m of fragments has been occasionally cleared to maintain isolation (Gascon and Bierregaard 2001).

The BDFFP remains as one of the most important projects evaluating the effects of forest fragmentation and over 450 papers have been published in the BDFFP technical series. One of the most unique aspects of this project is that pre-isolation data were collected for several organisms, including birds. Since isolation, monitoring of these and other groups has documented changes in abundance and diversity in response to fragmentation (e.g. Powell and Powell 1987, Bierregaard et al. 1992, 2001, Gascon et al. 1999, Stouffer et al. 2006). The

Table 1.1. Fragment names and characteristics (from Lovejoy et al. 1986, Ferraz et al. 2003, Antongiovanni and Metzger 2005).

Reserve[a]	Year mist-netting began	Year isolated	Isolation distance (m)
1104	1979	1980	120
1112	1981	1983	300
2107	1980	1984	270
2108	1980	1984	480
3114	1982	1983	210
1202	1979	1980	540
1207	1981	1983	70
2206	1980	1984	180
3209	1982	1983	780
2303	1980	1990	150
3304	1982	1983	180

[a] The reserve's first number indicates the ranch where it is located (1 = Esteio; 2 = Dimona; 3 = Porto Alegre). The second number indicates the size of the preserve (1 = 1 ha; 2 = 10 ha; 3 = 100 ha).

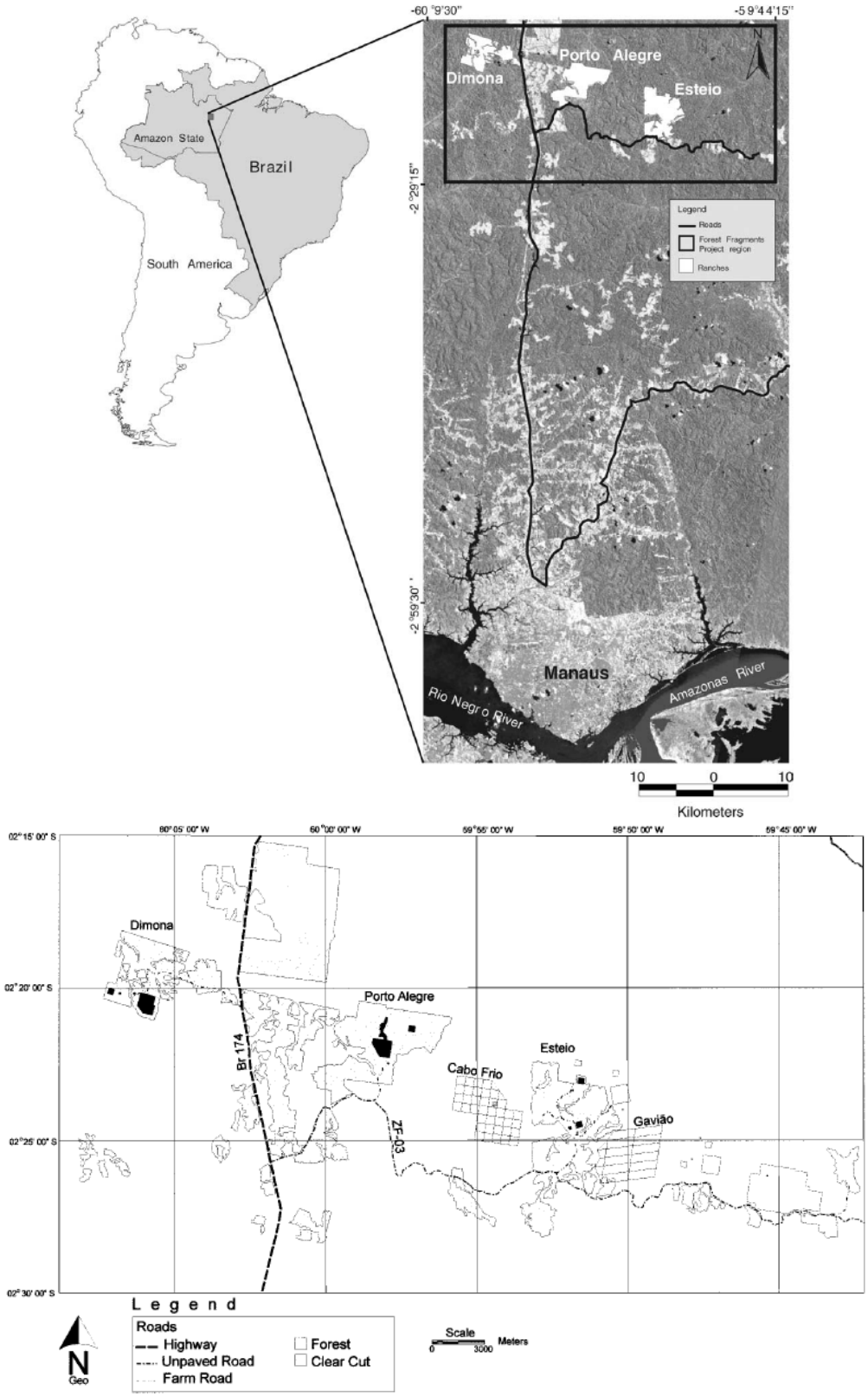

Fig. 1.1. Map of BDFFP within Amazonas, Brazil, ranch locations, and experimental fragment layout from Antongiovanni and Metzger 2005 (top) and Gascon et al. 1999 (bottom).

project has also grown intellectually and today provides one of the most important long-term databases regarding the effects of fragmentation on biodiversity and ecological processes.

A History of Avian Responses to Fragmentation

Long-term avian monitoring with mist-nets has documented changes in abundance and diversity in response to fragmentation based on >60,000 individual bird captures through 2009. Immediately following isolation, a temporary influx of birds was detected in fragments (Lovejoy et al. 1986, Bierregaard and Lovejoy 1989), but as time since isolation passed, individuals and species disappeared from fragments because extinction rates exceeded colonization rates (Ferraz et al. 2003, 2007, Stouffer and Johnson in review). Extinction occurred faster in smaller fragments and some ecological guilds were more susceptible than others (Stouffer and Bierregaard 1995, Stratford and Stouffer 1999, Ferraz et al. 2007). Species that currently persist in small fragments are those for which the matrix enhances dispersal abilities or is incorporated into home ranges (Gascon et al. 1999, Antongiovanni and Metzger 2005, Stouffer et al. 2006, Ferraz et al. 2007, Chapter 2), but they often persist at cost including reduced body condition (Stratford and Stouffer 2001).

Study Site

The landscape surrounding the BDFFP is largely undisturbed *terra firme* lowland rainforest, especially to the north of the BDFFP. The area receives approximately 2500 mm of annual rainfall (ranging from 2000–3500 mm) with a dry season typically lasting from June to November (Stouffer and Bierregaard 1993, Laurance 2001). In the years during and immediately before the study, 2006–08, rainfall ranged from 2682 to 2755 mm (mean: 2714 mm, SE: 22 mm). The site has some topography, especially near streams, and varies in elevation from 50–100 m. Soils are generally nutrient-poor sandy or clay-rich ferrasols, typical of the

region (Sombroek 2000). The predominant vegetative cover is *terre firme* tropical rainforest. The forest canopy is 30–37 m tall with emergents reaching 55 m. The understory is relatively open and is dominated by palms due to the low nutrient soils. At the onset of this study, second growth was widespread connecting fragments to continuous forest 70–780 m away (see Gascon et al. 2001 for more site history details).

DISSERTATION OVERVIEW

Each chapter in my dissertation examines a different aspect of fragmentation sensitivity, with an over-arching goal to understand mechanisms that drive population change in fragmented landscapes. Because responses to fragmentation vary among species and (Stouffer et al. 2006), I focus on multiple species, with each chapter using a slightly different set of species depending on sample sizes available for the particular studies (Appendix A).

In Chapter 2, I examine demographic mechanisms that drive extinction–colonization dynamics for an ecologically diverse group of understory birds. I have developed reliable aging techniques through an understanding of age-related molt patterns and plumage sequences to examine how fragmentation differentially influences immature and adult life stages. I also explicitly quantify dispersal propensities using mark–recapture models and link these rates to empirical observations of how patch, matrix, and landscape variables predict relative abundances of immatures and adults across fragments.

In Chapter 3, I examine variation in molt-breeding overlap among members of the understory bird community and reveal its importance as a trait for predicting fragmentation sensitivity. With >60,000 captures in the BDFFP database, there is an extensive dataset of molting and breeding, and sometimes these life history periods occur simultaneously. Molting and breeding are each energetically demanding, thus I suggest that for an individual to do both

simultaneously requires a predictable, stable, energy-rich environment, such as humid tropical rainforest understory. I also suggest that this strategy is not conducive to living in more seasonal environments, like those in the temperate zone or rainforest fragments, thus the increased frequency of simultaneously molting and breeding in a species should not only increase its risk to fragmentation, but also help to explain why this trait may be most frequently observed in tropical rather than temperate bird species.

In Chapter 4, I examine three groups of avian ectoparasites: feather mites (Astigmata), haematophagous mites (including Mesostigmata, Prostigmata, and Ixodida), and lice (Phthiraptera). I determined the richness and abundance of each group to test whether there were differences associated with fragmentation. Although there are strong arguments for the evolutionary optimization of host-parasite dynamics (Clayton et al. 1999), one might expect fragmentation to shift the balance of these reciprocal relationships either because of excess stress exerted on the host or because low quality hosts are forced into low quality habitats. Hosts in suboptimal habitats could be more susceptible to ectoparasitism because they do not have sufficient resources to expend energy defending themselves from parasites (Quillfeldt et al. 2004). Alternatively, we might expect to see fewer ectoparasites on hosts in suboptimal habitat because lower quality hosts might provide fewer resources for ectoparasites (Tschirren et al. 2007, Bize et al. 2008). In addition, reduced host density may decrease transmission rates of parasites (Vögeli et al. 2011).

In Chapter 5, I present the results of an ectoparasite-removal experiment in which I determined the interactive effects of ectoparasitism and habitat quality on host-ectoparasite dynamics. Although I recovered many ectoparasite taxa likely new to science, the ecology of these organisms at family-level taxonomy is better known, allowing me to model the cumulative

effects of these ectoparasite communities on their hosts exposed to different abiotic and biotic pressures among habitat types.

Ultimately, this work improves upon our understanding of the mechanisms driving population change in fragmented landscapes. Processes that drive extinction–colonization dynamics like dispersal, breeding and molting phenologies, and host–parasite relationships are surely important in other regions, but remain largely understudied (Levins 1969, Hanski 1999, Moore et al. 2008, Lees and Peres 2009, Coulon et al. 2010). I encourage others studying the ecology of fragmented systems to explore these potential mechanisms in other systems.

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CHAPTER 2: DEMOGRAPHIC STRUCTURE OF AMAZONIAN UNDERSTORY BIRDS IN A FRAGMENTED LANDSCAPE

INTRODUCTION

Forest fragmentation has profound consequences on biotic communities including the invasion of non-forest species (Gascon et al. 1999, With 2002), a reduction in floral and faunal biomass (Laurance et al. 1997), and the loss of biodiversity (Willis 1974, Fahrig 2003). Early fragmentation research used island biogeographic theory (IBT; MacArthur and Wilson 1967) to predict rates of community-wide species loss through patch size and isolation effects (Terborgh 1974, Diamond 1975, Simberloff and Abele 1976). Species loss in forest fragments does not necessarily adhere to IBT because species loss is non-random in a human-modified landscape; there is often a predictable order of which species are lost, unlike the equivalency assumed in IBT (Ney-Nifle and Mangel 2000, Ewers and Didham 2006, Laurance 2008). Furthermore, IBT is difficult to directly apply to fragmentation studies because matrix quality can moderate the negative effects of patch size and isolation (Gascon et al. 1999, Graham and Blake 2001, Antongiovanni and Metzger 2005, Kupfer et al. 2006, Stouffer et al. 2006).

Metapopulation theory (Levins 1969, Hanski 1999) is a useful tool for examining population dynamics in fragmented landscapes and has advantages over IBT (Laurance 2008), although metapopulation and IBT models are perhaps better thought of as specific variations of a more general spatially realistic model (Hanski 2010). Here, individual species' responses to fragmentation can be modeled while adjusting species-specific immigration and emigration rates to account for both the distance between patches and the quality of the intervening matrix (Vandermeer and Carvajal 2001). Even so, a temporally and spatially changing matrix, as realistically occurs in human-modified landscapes, is difficult to model (Hein et al. 2003,

Malanson et al. 2007) and can lead to inaccurate predictions of population and community changes within patches (Schultz and Crone 2002, Ferraz et al. 2003). Revealing mechanisms of recovery is further complicated by the possibility that the intervening matrix may not only modify dispersal abilities (Hein et al. 2003, Hodgson et al. 2007, Lees and Peres 2009, Prevedello and Vieira 2010), but could also influence reproductive output within patches (Robinson et al. 1995, Rodewald 2002, Keyser 2002, Young et al. 2008, Robinson 2009). Due to inherent difficulties of quantifying dispersal and fecundity in Neotropical birds, we know little about how population processes can promote recovery or persistence in forest fragments (Fahrig 2003, Ewers and Didham 2006, Kupfer et al. 2006). Here I provide new insights into how fragmentation affects avian demographic structuring and the underlying mechanistic role of dispersal in a group of understory lowland Amazonian rainforest birds.

Understanding Neotropical forest bird population dynamics in fragmented systems is particularly problematic for several reasons. First, high species richness, with many rare species, makes it difficult to sample more than a small subset of species. As a result, demographic parameters are extremely difficult to estimate based on breeding activity because nests are so rare and fail high rates (Chalfoun et al. 2002). While it might be possible to study common species, these are often less sensitive to fragmentation and may misrepresent rarer species in the community. An alternative approach for understanding population demographics is to measure the relative abundance of age groups (Newton 1999, Rohwer 2004, Iverson et al. 2004, Harris et al. 2008), but this will only become practical as resources become available for aging and sexing Neotropical birds (Ryder and Wolfe 2009). Second, dispersal ability, although widely assumed to be critical to the recovery of bird populations in forest fragments (Tilman et al. 1997, Stouffer and Bierregaard 2007), has received almost no empirical study in the Neotropics (but see

Castellón and Seiving 2006, Moore et al. 2008), but likely depends on habitat quality and organism age (Greenwood and Harvey 1982).

The Biological Dynamics of Forest Fragmentation Project (BDFFP) in Amazonian Brazil is an ideal place to study the effects of forest fragmentation on the population dynamics of Neotropical birds. Here, forest fragments are replicated for each of three size categories (1, 10, and 100 ha) surrounded by second growth in various stages of regeneration and embedded within an otherwise undisturbed swath of continuous forest (Gascon and Bierregaard 2001). Recent advances in the understand of plumage and molt sequences now allows us to accurately age birds, and thus quantify the demographic makeup of many species at the BDFFP (Ryder and Durães 2005, Ryder and Wolfe 2009, E. I. Johnson, unpublished data).

Previous work at the BDFFP has shown that species in small fragments are susceptible to local extinctions (Stratford and Stouffer 1999, Ferraz et al. 2003, 2007), while regenerating second growth is responsible for the more recent trend of biodiversity recovery (Ferraz et al. 2007, Stouffer et al. 2006, 2009). Two non-mutually exclusive mechanisms could be responsible for this recovery, based on metapopulation theory (Hanski 1999). First, birds occupying fragments may utilize regenerating matrix and its resources to maintain breeding territories and increase local reproductive output, stabilizing isolated populations (Hanski 1994). Local reproductive success could be revealed by comparing densities and ratios of adults and immatures across fragment sizes (Newton 1999, Rohwer 2004, Iverson et al. 2004, Harris et al. 2008). Second, dispersal propensity may facilitate recolonization or maintain isolated populations in forest fragments, again reflected by patterns of age ratios. Dispersal in non-migratory passerines is thought to primarily take place soon after fledging (i.e. natal dispersal *sensu* Greenwood and Harvey 1982), which may result in an accumulation of young birds in

isolated forest fragments after they disperse from high quality natal habitat (e.g. continuous forest). The relative importance of these mechanisms (i.e. breeding success and dispersal ability) likely varies among species. Conversely, birds that remain absent from fragments likely show both reduced breeding success in fragments and poor dispersal.

I expected that differences in the relative abundance of adults and immatures between fragmented and continuous forest populations would reflect a combination of bird age-specific responses to fragment size, second growth age in the matrix, and proximity to continuous forest as well as species-specific dispersal abilities. I expected that adult relative abundance would be most dependent on patch size rather than matrix age or proximity to continuous forest because this age class is largely sedentary as they maintain a constant home range or territory. If immature relative abundance was driven by local reproductive output, then I expected patch size would best predict immature relative abundance; however, if immature relative abundance was instead driven by colonization through dispersal, then matrix and landscape characteristics would better predict their relative abundance. Greater species-specific dispersal propensities were predicted to decrease the importance of second growth age and proximity to continuous forest, but not patch characteristics. To test these predictions, I first assessed the relative abundance of adults and immatures in three sizes of forest fragments and continuous forest control plots. I then determined the relative importance of patch size, matrix age, and proximity to continuous forest on the relative abundance of adults and immatures. Finally, I quantified dispersal propensity using mark–recapture techniques and related it to the distribution of age classes and their responses to patch, matrix, and landscape characteristics in six guilds of understory Amazonian birds. This study provides insight into the mechanisms that drive occupancy and recolonization dynamics of birds in human-modified landscapes.

METHODS

Bird Sampling

In 2007 I sampled each of the 11 forest fragments and in 2008 I sampled two continuous forest plots. I sampled each of these 13 sites six times at monthly intervals during the dry season with mist nets (NEBBA type ATX, 36-mm mesh size, 12 x 2 m) set at ground-level. One line of eight nets was used in 1-ha fragments; one line of 16 nets was used in 10-ha fragments; three lines of 16 nets were used in 100-ha fragments and 100-ha continuous forest plots. Differences in net-arrangement among study sites could arguably affect capture rates (a proxy for relative abundance), but preisolation capture rates from these 1-, 10-, and 100- plots showed strong congruence indicating that capture rates were minimally affected by differences in net arrangement (Stouffer et al. 2006). A line of four nets was also placed along each of four borders around 1- and 100-ha fragments and continuous forest plots, but only along three borders of 10-ha fragments (this made it logistically possible to sample all nets in one day, which was important for completing six monthly replicates during the dry season). Each interior line was netted for one day at a time from 0600–1400. A subset of forest fragments was also sampled either once or twice each in June and July 2009. Two additional 100-ha continuous forest sites were sampled twice each in 2008 at bimonthly intervals. I used a different mist net arrangement at these sites; mist nets were placed along six parallel trails spaced 200 m apart, with six lines of four nets each placed every 200 m along each of the six trails (144 nets/plot). Captured birds were banded with a uniquely numbered aluminum band issued through The Brazilian National Center for Bird Conservation (CEMAVE) and aged using molt and plumage criteria (E. I. Johnson, unpublished data; see Methods: Target Species).

Capture rates are not perfect measures of bird density and instead reflect a combination of bird density and bird activity in the understory (Remsen and Good 1996). I do not compare capture rates across species or guilds, but instead compare capture rates across fragment sizes and bird age categories, thus measure changes in relative density. Although there may be biases in capture rates due to fragment size (from edge avoidance) or bird age (due to movement tendencies), I account for these potential biases in several ways. First, I excluded same-day recaptures. This minimizes inflated capture rates due to potential increased edge avoidance in small fragments. Second, I conducted an additional analysis of age ratios based on the number of individuals captured, not including recaptures. Concordance between the two analyses, one including recaptures and the other only considering individuals once, would suggest that capture rates are not biased by movements. Third, I conducted a mark–recapture analysis, which not only models parameters of interest (survival and transience), but also tests for recapture probability and capture heterogeneity among sites.

Target Species

I studied 22 target species with juvenal and Formative I plumages (*sensu* Howell et al. 2003) that are distinct from definitive plumages (Fig. 2.1; E. I. Johnson, unpublished data). This allowed me to accurately age individuals and categorize them as immature (<1 year old) or adult (>1 years old). Study species typically breed during the late dry season (August–December) and molt follows breeding (Chapter 3). First fledglings of the breeding season are usually observed in September at the study site, making skull ossification in passerines and bill corrugations in hummingbirds useful only until about March (Pyle 1997). Because my study season initiated in June, species with identical Formative I and Basic II plumages could not be included in my target set of species.

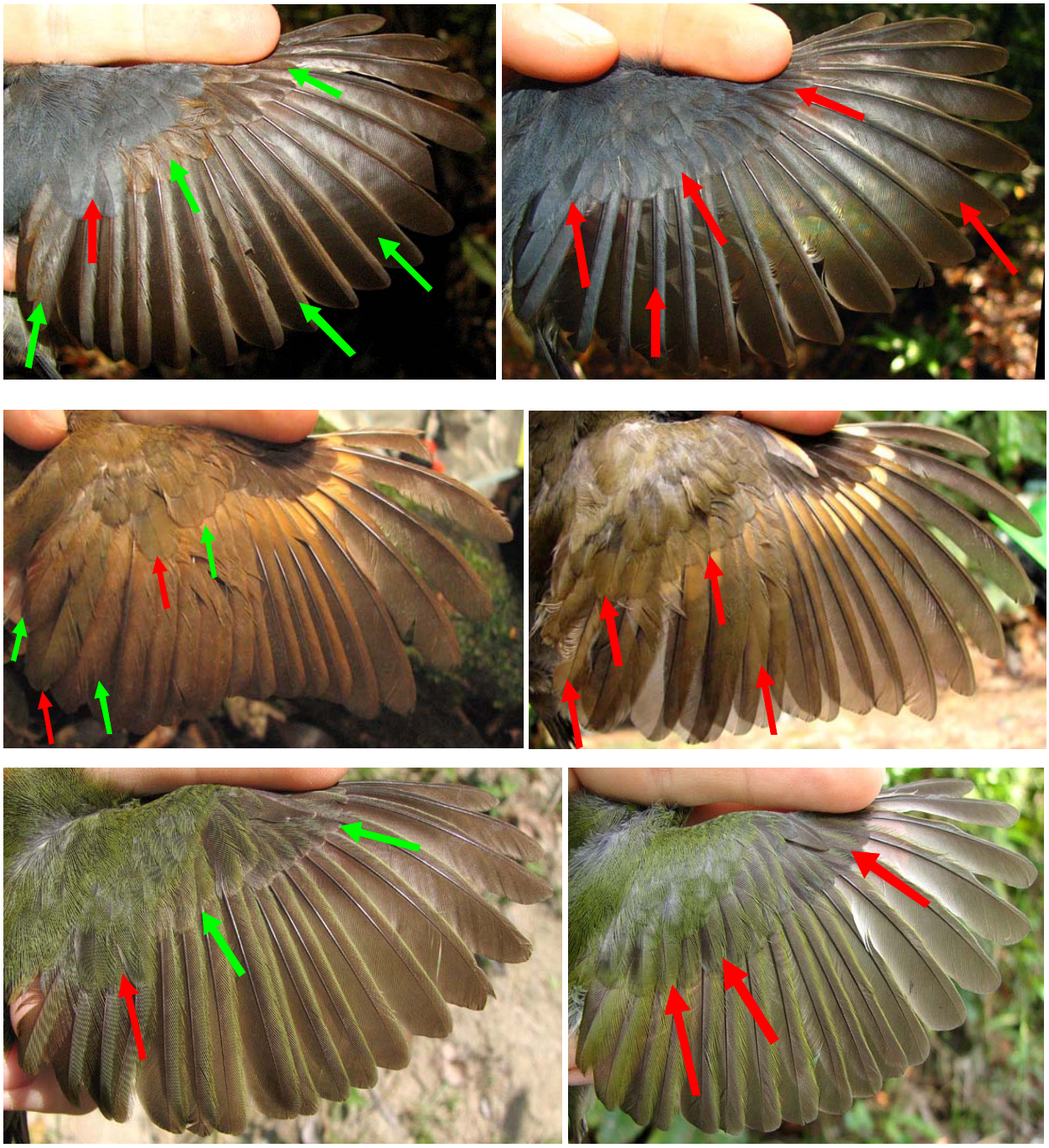


Fig. 2.1. Spread wings of *Thamnomanes ardesiacus* (top), *Formicarius colma* (middle), and *Pipra pipra* (bottom) illustrating aging criteria. Newly replaced formative feathers (red arrows) contrasting with retained juvenal feathers (green arrows) creates a molt limit indicating an immature (left) in contrast to adults (right), which replace all feathers during their molt.

Analyses

I conducted three analyses: 1) quantifying demographic structure through age ratios and capture rates of adults and immatures in fragments and continuous forest, 2) examining the effects of patch, matrix, and landscape characters on the relative abundance of adults and immatures, and 3) modeling variation in transience and survival as a function of fragment size and bird age with mark–recapture techniques. For the first two analyses, I divided the 22 target species into six foraging guilds previously shown to have varying sensitivity to forest fragmentation, pooling data within each guild (Stouffer and Bierregaard 1995, 2007, Stouffer et al. 2006). For the third analysis, I used ten target species and three additional species lacking plumage-based aging criteria; these 13 species were the most frequently captured during the study (>50 individuals captured). I present least square means, back-transformed for ease of interpretation when necessary.

Demographic Structure.—I conducted two analyses to reveal the how fragment size affects demographic structuring of the six guilds, repeated for the ten target species with sufficient data. First, I pooled samples across fragments of the same size, creating a 4×2 contingency table of fragment size by bird age with cells containing the number of individuals in each category. I analyzed these data using the likelihood ratio G-test except when ≥25% of the cells had expected values of <5; I then used the Fisher's exact test (proc freq, SAS Institute 2003). I also conducted all possible pairwise comparisons correcting for the inflated type I error rate as in Sokal and Rohlf (1981: 728). The most appropriate analysis for these data would consider variation among fragments of the same size, but most guilds and species in individual fragments had low sample sizes, creating high variance in proportions of immatures, which resulted in low power for detecting statistical differences. Not presented here, I conducted such

an analysis using logistic regression (proc glimmix, SAS Institute 2003) on the binary dependent variable bird age (adult or immature) with fragment size as a fixed dependent categorical variable and plot as a random dependent variable. It showed congruence with the results of the likelihood ratio G-test, except it was more conservative in assigning statistical significance due to low power, thus I only present results from the likelihood G-test.

For the second analysis of demographic structuring, I calculated capture rates of adults and immatures by dividing the number of captures by the number of mist-net hours (1 mist-net opened for 1 hour = 1 mist-net hour) and multiplying by 1000 for ease of interpretation. I used a two-way ANOVA (proc mixed, SAS Institute 2003) with capture rate as the dependent variable, bird age and fragment size as fixed independent variables, and plot as a random independent variable. I separately examined the effects of fragment size on immature and adult capture rates using analyses of simple main effects (Sokal and Rohlf 1981). When necessary I log-transformed capture rates to improve fit of univariate normality and I present least square means, back-transformed when necessary for ease of interpretation.

Sensitivity to Landscape Variable*s*.—Stouffer et al. (2006) showed that multiple landscape variables, in addition to fragment size, were important in explaining capture rates and that these responses varied across guilds. I extend this rationale here by not only testing that guilds respond differently to landscape variables, but also whether age groups respond differently to landscape variables as well. Following Stouffer et al. (2006), I considered six landscape variables including log-transformed fragment size, two related to the second growth (age of the oldest second growth along the shortest path to continuous forest and age of the fragment border), and two related to nearby continuous forest (amount of continuous forest within 800 m of the fragment and linear distance to continuous forest). Using maximum-

likelihood least squares multiple linear regression, I determined the effect of these variables on capture rates in forest fragments (for continuous forest data, these landscape variables are not applicable). I then constructed an additional 62 candidate maximum-likelihood least squares regression models with all possible combinations of variables. Using an information theoretic approach, I ranked the 63 candidate models and the null model (i.e. intercept only) according to lowest Akaike Information Criterion corrected for small sample size (AIC_c), which penalizes by the number of parameters used. I calculated ΔAIC_c by substracting the each model's AIC_c from the best model. I then calculated model likelihoods using

$$e^{-0.05*\Delta AIC_c},$$

and model weights (ω_i) by dividing its likelihood by the sum of all models' likelihoods. I considered models with $\Delta AIC_c < 4$ to be equally parsimonious and used multimodel inference to assess the relative importance of each of the six landscape variables (Burnham and Anderson 2002). I considered important variables to be significant in models with $\Delta AIC_c < 4$ that ranked higher than the null model. I conducted this information theoretic analysis twice for each species, once each for immatures and adults.

Transience and Survival.— I do not know the fate of individuals through empirical observations, so I used mark–recapture modeling techniques to estimate transience and apparent survival. Mark–recapture models used maximum-likelihood to estimate apparent survival, which is not a measure of true survival: it is the probability that a given bird left the population due to mortality or permanent emigration. By simultaneously estimating transience, defined as the proportion of newly marked individuals that permanently leave the sampling area, these models not only provide a more accurate interpretation of survival probability, but also offer a measure of relative dispersal propensity among species (Pradel et al. 1997).

Using data from the six samples of 11 fragments and two continuous forest plots (excluding samples from 2009 and continuous forest plots with only two replicates), I constructed capture histories for all individuals of each of the 13 study species. I analyzed capture histories in a Cormack–Jolly–Seber (CJS) mark–recapture analysis (Lebreton et al. 1992) using the "sin link" function in program MARK (White and Burnham 1999). The global model included variation in apparent survival (Φ) and recapture probability (ρ) by fragment size (*grp*: 1-, 10-, 100-ha fragments, continuous forest), time (*t*: sampling interval 1–5), and their interaction (*grp*×*t*), expressed as: $\Phi_{grp \times t}$, $\rho_{grp \times t}$. By considering variation in ρ among fragment sizes I compared apparent survival and transience estimates among fragment sizes despite differences in the arrangement of nets between fragment size classes. The presence of both transients and residents in a population violates an assumption of the CJS model, so I tested fit of the global model to CJS assumptions using the program U-CARE to assess the goodness–of–fit (GOF) and estimate $\hat{c}$ (a measure of over- or under-dispersion in the data; Choquet et al. 2005). Specifically, U-CARE provides directional tests for the presence of transients (TEST 3.SR) and trap dependence (TEST 2.CT).

I constructed an additional 15 reduced-parameter candidate models to constrain variation in Φ and/or ρ by *grp* and/or *t* and eight time–since–marking (TSM) models (Table 2.1). TSM models incorporate two apparent survival parameters, one for the first sampling interval after the initial capture of newly marked individuals (Φ^1) and a second for previously marked individuals in subsequent intervals (Φ^{2+}). Thus, if $\Phi^1 < \Phi^{2+}$, there is evidence for transient individuals in the population. I ranked the 24 candidate models according to lowest AIC_c and calculated Akaike weights (ω_i) as described above. Multiple models were often equally parsimonious (see Results) so I used model averaging (weighted by ω_i) across all 24 candidate models to generate apparent

survival parameter estimates (Burnham and Anderson 2002). I also determined the importance of the six competing apparent survival parameters (CJS models: Φ_{grp}, Φ_t, $\Phi_{grp \times t}$, $\Phi_.$, and TSM models: $\Phi_{grp/2t.}$, $\Phi_{./2t}$; Table 2.1) by summing model weights for each apparent survival parameter (multimodel inference; Burnham and Anderson 2002). Finally, I estimated the proportion of transients among newly marked individuals for each group variable with the formula:

$$\tau_{grp} = 1 - \Phi^{1}_{t,grp}/\Phi^{2+}_{t} \; \forall \; t \text{ (Pradel et al. 1997).}$$

I analyzed the data a second time using the same 24 candidate models, but using bird age (immature and adult) as the *grp* variable for the ten species with aging criteria. It was not possible to conduct a single analysis using fragment size and bird age, because the data become too sparse to evaluate eight groups, resulting in poor model fit and uncertain parameter estimates.

Table 2.1. Cormack–Jolly–Seber (CJS) and time–since–marking (TSM) model notation and description used to estimate apparent survival (Φ) and recapture probabilities (ρ) near Manaus, Brazil. All possible combinations of Φ and ρ allowed for the comparison of 24 candidate models in the mark–recapture analyses. The group (*grp*) variable represents fragment size or bird age.

Apparent survival		Recapture	
Parameter	Description	Parameter	Description
Φ_{grp}	CJS: Group-dependent survival	ρ_{grp}	Group-dependent recapture
Φ_t	CJS: Time-dependent survival	ρ_t	Time-dependent recapture
$\Phi_{grp \times t}$	CJS: Group- and time-dependent survival	$\rho_{grp \times t}$	Group- and time-dependent recapture
$\Phi_.$	CJS: Constant survival	$\rho_.$	Constant recapture
$\Phi_{grp/2t}$	TSM: two classes of survival (first and subsequent interval following marking) and group-dependent		
$\Phi_{./2t}$	TSM: two classes of survival		

RESULTS

During this study I captured 2656 individuals of the 25 target species 3621 times in 29,967 mist-net hours. For 22 species for which I developed aging criteria, I successfully aged 95% (1970 of 2082 individuals); this group became my sample for demographic analyses.

Demographic Structure

Age Ratios.—The proportion of immatures varied across guilds, among species within guilds, and across fragment sizes, indicating great variation in how fragmentation affects demographic structuring across study species (Fig. 2.2). The highest proportion of immatures (≥50%) was observed in the frugivores *Pipra pipra* and *Turdus albicollis*, and the ant-follower *Pithys albifrons* in 1-ha fragments (Figs. 2.1a,b). The lowest proportion of immatures (<5%) was observed in the frugivore *T. albicollis* in continuous forest and the gap specialist *Hypocnemis cantator* in 1-ha fragments (Figs. 2.1a,e). Only the ant-follower *Gymnopithys rufigula* had <20% of immatures across all forest sizes (Fig. 2.2b); all other species (and guilds) had >35% immatures in at least one fragment size class (Fig. 2.2).

I detected significant differences in the proportion of immatures in three of six guilds (frugivores, ant-followers, and gap specialists) and five of seven species in these guilds represented (*P. pipra*, *T. albicollis*, *P. albifrons*, *Percnostola rufifrons*, and *H. cantator*). For frugivores and ant-followers, the proportion of immatures increased with decreasing fragment size (Figs. 2.2a,b) whereas for gap specialists, the proportion of immatures decreased with decreasing fragment size (Fig. 2.2e). Only the frugivore *Lepidothrix serena* and ant-follower *G. rufigula* did not follow the pattern of their guilds – the proportion of immature *L. serena* and *G. rufigula* did not change with fragment size (Table 2.2, Figs. 2.2a,b). For the other three guilds (flock dropouts, flock obligates, and other insectivores) and their species, the proportion of immatures did not change across fragment sizes (Table 2.2, Figs. 2.2c,d,f).

Capture Rates.— In all six guilds, adult capture rates were significantly higher than immatures (Fig. 2.3) and there was considerable age- and guild-level variation in response to fragment size (Table 2.3). Changes in the proportion of immatures (Figs. 2.2a,b) was driven by

Table 2.2. Statistical comparisons of the proportion of immatures among forest fragments and continuous forest near Manaus, Brazil. Significant differences ($P < 0.05$) are in bold. Differences among pairwise comparisons are indicated by letters ordered by highest proportion (A) to lowest proportion (B or C). See Fig. 2.2 for size effects.

Guild	Age Ratios: Log Likelihood G-test					
Species	G_3	P	1-ha	10-ha	100-ha	Forest
Frugivore	**45.95**	**<0.001**	A	AB	B	C
Pipra pipra	**23.83**	**0.002**	A	AB	B	BC
Lepidothrix serena	0.68	0.878	A	A	A	A
Turdus albicollis	**11.97**	**0.008**	A	B	BC	C
Ant-follower	**23.12**	**<0.001**	A	AB	A	B
Pithys albifrons	**25.56**	**<0.001**	A	AB	A	B
Gymnopithys rufigula	2.13	0.545	A	A	A	A
Flock Obligate	6.79	0.079	A	A	A	A
Thamnomanes caesius	2.24	0.525	A	A	A	A
Thamnomanes ardesiacus	4.37	0.225	A	A	A	A
Flock Dropout (*Myrmotherula axillaris*)	4.82	0.185	A	A	A	A
Gap Specialist	**8.88**	**0.031**	B	AB	A	AB
Percnostola rufifrons	**8.09**	**0.044**	B	B	A	B
Hypocnemis cantator	**9.32**	**0.025**	B	AB	AB	A
Other Insectivore	1.45	0.694	A	A	A	A

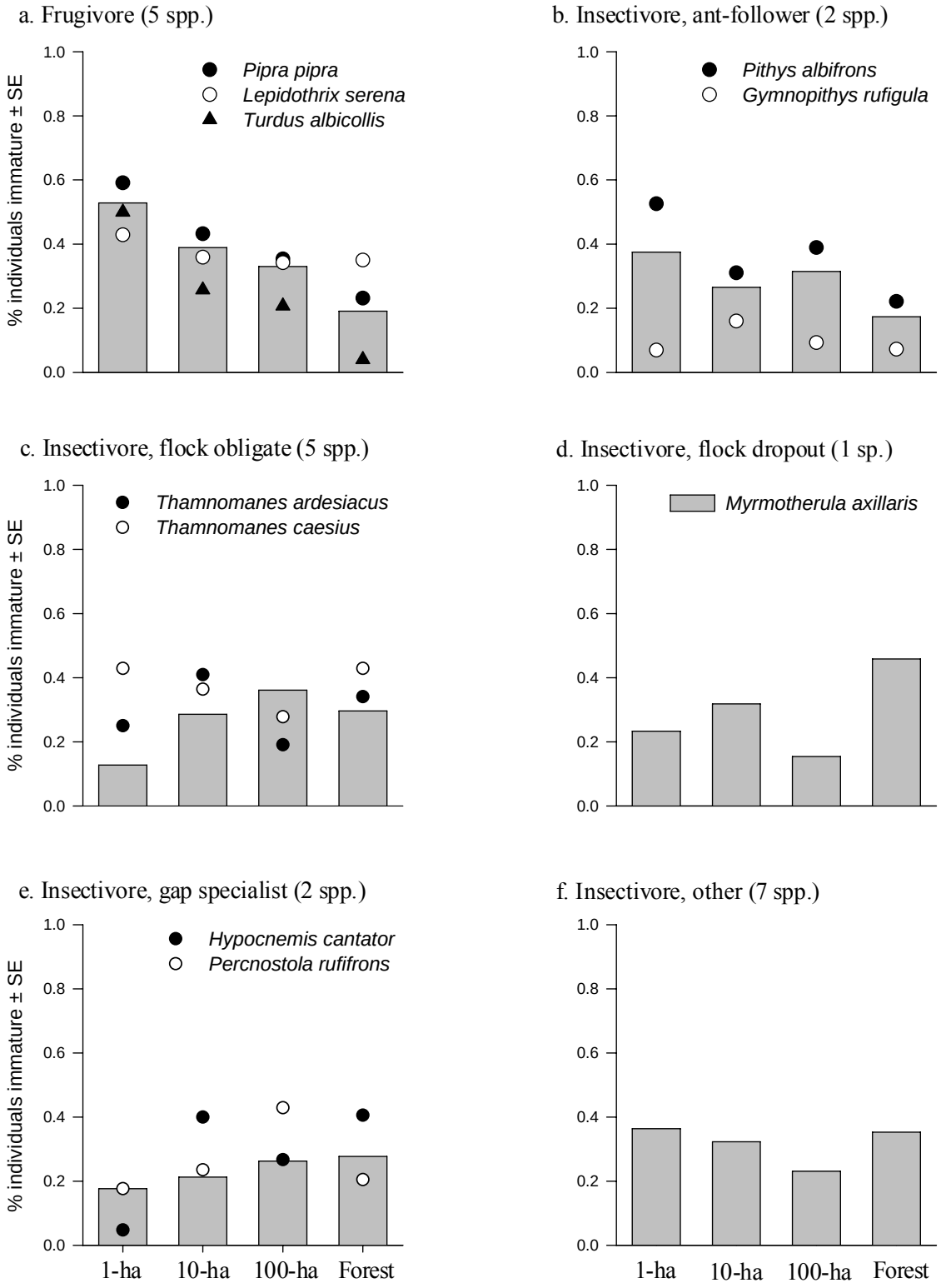


Fig. 2.2. The proportion of captured individuals that were immature in fragments and continuous forest for six guilds (gray bars) representing 22 species near Manaus, Brazil. Ten species with large sample sizes (>50 individuals) are also represented individually (circles and triangles). See Table 2.2 for test statistics and pairwise comparisons.

Table 2.3. 2-way ANOVA results testing for differences in capture rates between adults and immatures (Age), among forest fragments (Frag), and their interaction (Age × Frag) for six guilds representing 22 species near Manaus, Brazil. See Fig. 2.3 for size effects.

	Age		Frag		Age × Frag	
Guild	$F_{1,11}$	P	$F_{3,11}$	P	$F_{3,11}$	P
Frugivore (5 spp.)	**23.36**	**<0.001**	**5.31**	**0.017**	**4.45**	**0.028**
Pipra pipra	**11.26**	**0.006**	**4.96**	**0.020**	**9.15**	**0.003**
Lepidothrix serena	2.14	0.172	2.57	0.107	0.15	0.927
Turdus albicollis	**9.38**	**0.011**	2.00	0.172	1.63	0.239
Ant-follower (2 spp.)	**33.65**	**<0.001**	1.95	0.180	**5.36**	**0.016**
Pithys albifrons	**17.37**	**0.002**	2.37	0.126	**6.04**	**0.011**
Gymnopithys rufigula	**55.21**	**<0.001**	1.14	0.375	1.89	0.189
Flock obligate (5 spp.)	**21.44**	**<0.001**	**5.47**	**0.015**	1.71	0.223
Thamnomanes caesius	**8.06**	**0.016**	1.34	0.312	0.39	0.764
Thamnomanes ardesiacus	**23.03**	**<0.001**	**4.96**	**0.021**	2.02	0.170
Flock dropout (*Myrmotherula axillaris*)	**13.47**	**0.004**	1.36	0.305	1.90	0.188
Gap specialist (2 spp.)	**49.59**	**<0.001**	0.21	0.890	2.74	0.094
Percnostola rufifrons	**17.33**	**0.002**	0.42	0.743	0.84	0.502
Hypocnemis cantator	**37.75**	**<0.001**	1.24	0.341	**9.32**	**0.002**
Other insectivore (7 spp.)	**24.24**	**<0.001**	**7.17**	**0.006**	1.17	0.367

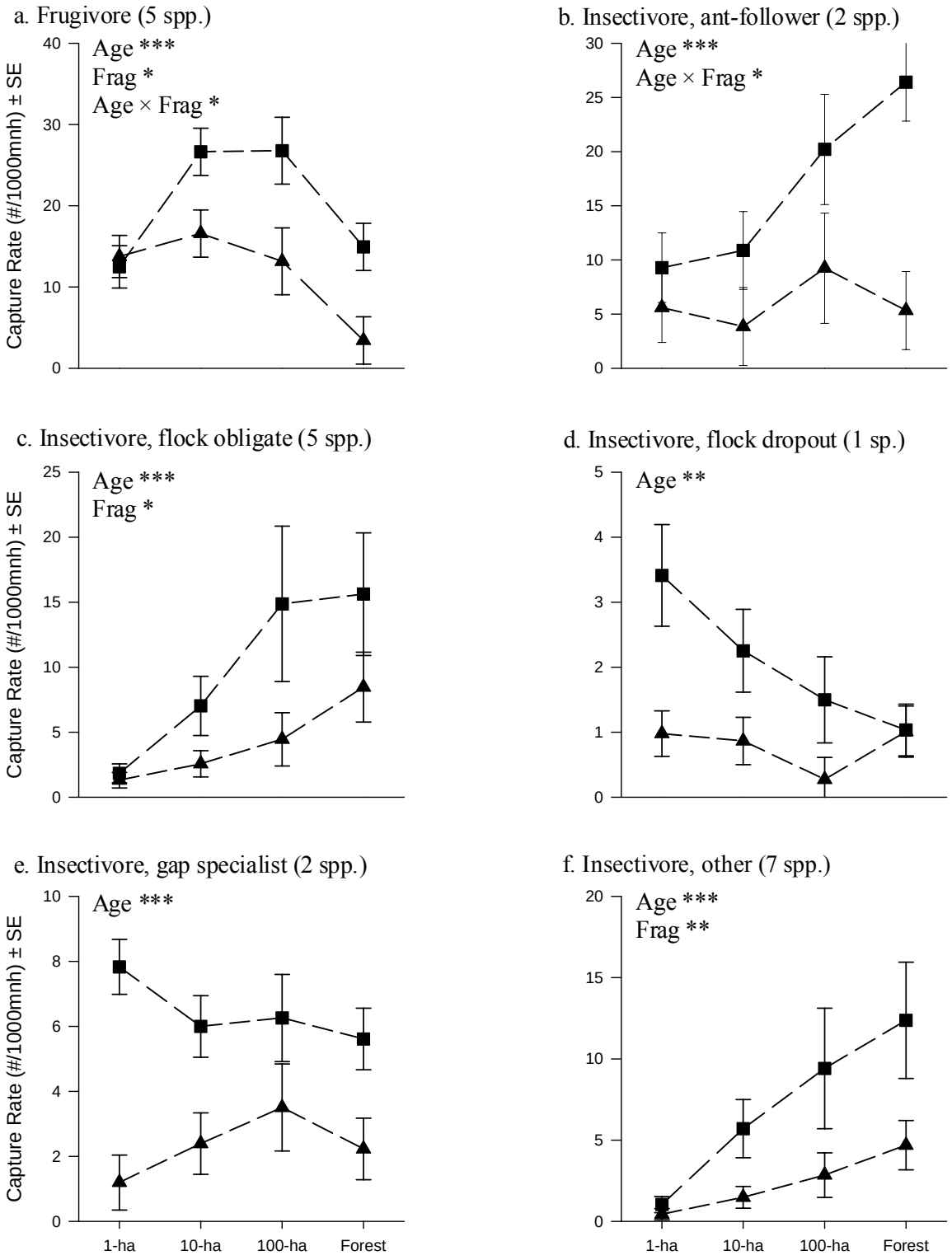


Fig. 2.3. Capture rates of immatures (triangles) and adults (squares) in forest fragments and continuous forest for six guilds representing 22 species near Manaus, Brazil. Significant bird age (Age), fragment size (Frag), and interaction (Age × Frag) effects are from a 2-way ANOVA (*: $P < 0.05$; **: $P < 0.01$; ***: $P < 0.001$). See Table 2.3 for test statistics.

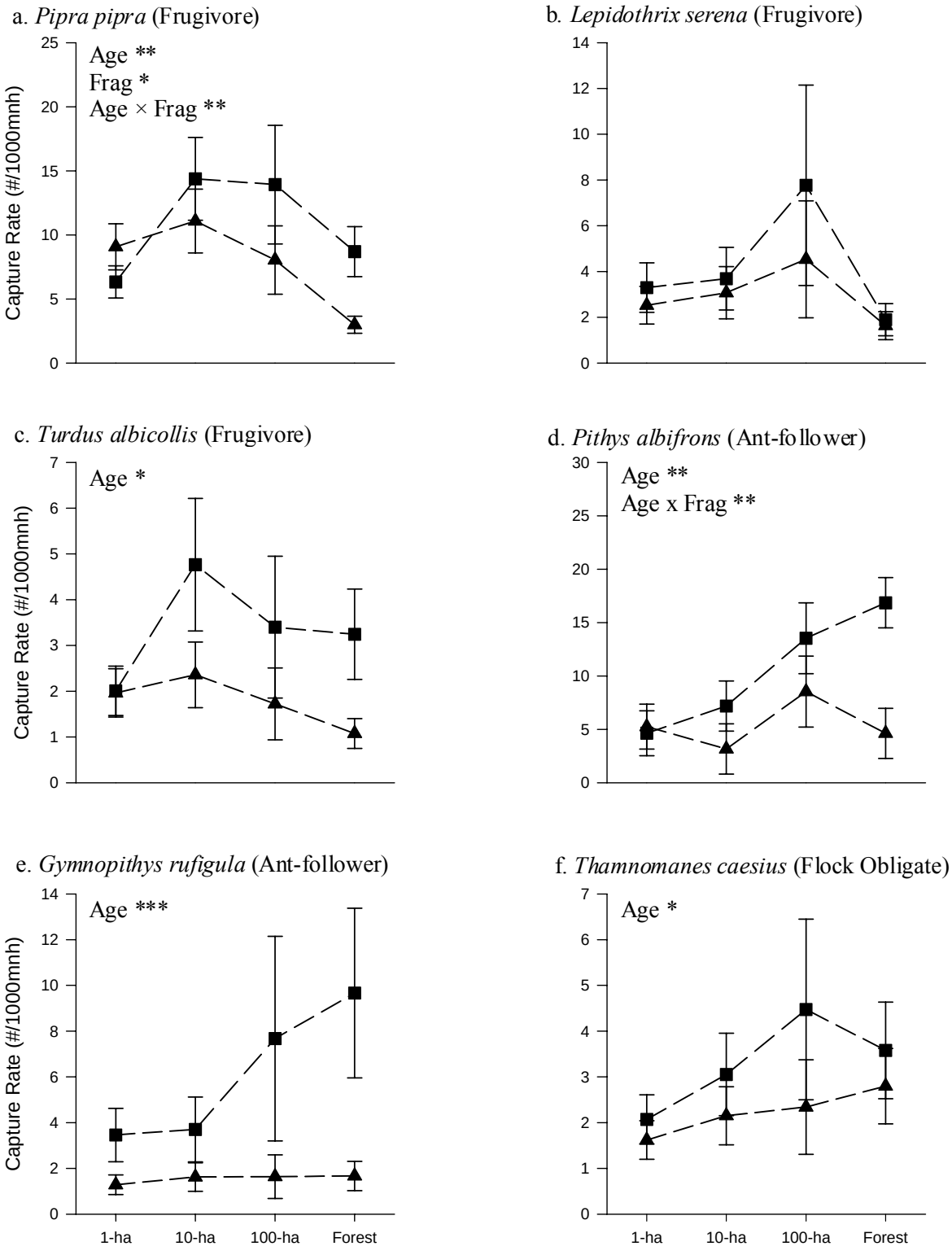
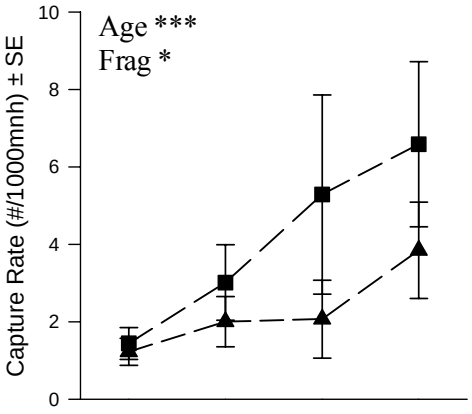


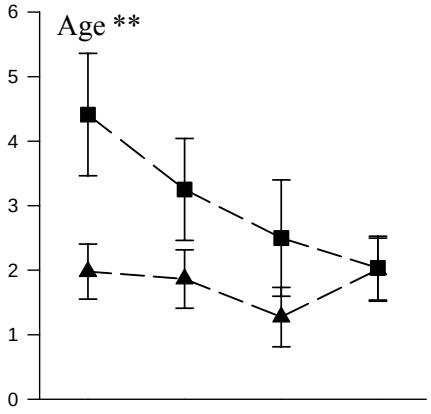
Fig. 2.4. Capture rates of immatures (triangles) and adults (squares) in forest fragments and continuous forest for ten species near Manaus, Brazil. Significant bird age (Age), fragment size (Frag), and interaction (Age × Frag) effects are from a two-way ANOVA (*: $P < 0.05$; **: $P < 0.01$; ***: $P < 0.001$). See Table 2.3 for test statistics.

Fig. 2.4 Continued

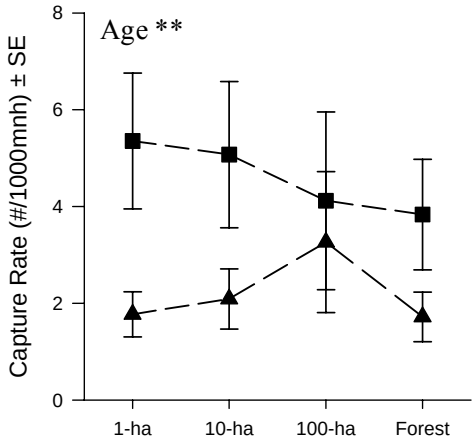
g. *Thamnomanes ardesiacus* (Flock Obligate)



h. *Myrmotherula axillaris* (Flock dropout)



i. *Percnostola rufifrons* (Gap Specialist)



j. *Hypocnemis cantator* (Gap Specialist)

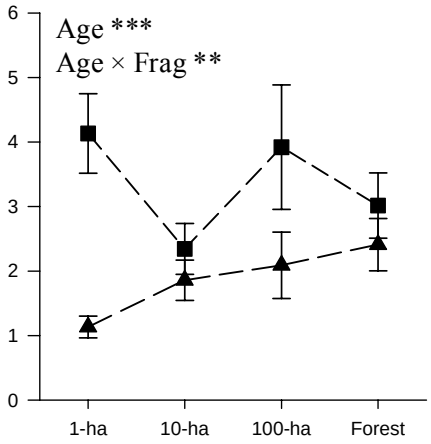


Table 2.4. Model variables, ΔAIC_c, and ω_i for models that ranked better than the null model for each age group and guild. See Table 2.5 for model-averaged parameter estimates and explanation of variable names. NULL = model with no independent variables (intercept only).

Guild	Age	Model	ΔAIC_c	ω_i
Frugivore	Immature	NULL	0.0	0.48
		63 models	≥3.5	≤0.09
	Adult	FragSize	0.0	0.29
		FragSize + BordAge	1.1	0.17
		NULL	2.2	0.10
		61 models	≥2.2	≤0.10
Ant-follower	Immature	BordAge	0.0	0.44
		NULL	2.2	0.15
		62 models	≥3.7	≤0.07
	Adult	NULL	0.0	0.27
		63 models	≥0.3	≤0.22
Flock Obligate	Immature	2grthAge + FragSize + BordAge	0.0	0.72
		14 models	4.1–11.5	≤0.09
		NULL	11.6	0.00
		48 models	≥11.7	0.00
	Adult	FragSize + BordAge	0.0	0.80
		6 models	6.2–9.5	≤0.04
		NULL	9.6	0.01
		56 models	≥9.7	≤0.01
Flock dropout	Immature	DistContFor	0.0	0.28
		NULL	1.6	0.12
		62 models	≥2.0	≤0.10
	Adult	NULL	0.0	0.36
		63 models	≥1.3	≤0.19
Gap specialist	Immature	FragSize + 2grthAge	0.0	0.83
		9 models	6.3–11.3	≤0.04
		NULL	12.9	0.00
		53 models	≥13.3	0.00
	Adult	NULL	0.0	0.35
		63 models	≥1.1	≤0.20
Other insectivore	Immature	FragAge + FragSize	0.0	0.36
		AmtContFor + DistContFor + FragSize	0.9	0.23
		FragSize	1.7	0.15
		NULL	3.8	0.05
		60 models	≥4.1	≤0.05
	Adult	FragSize	0.0	0.32
		NULL	1.6	0.14
		62 models	≥1.9	≤0.11

Table 2.5. Combined Akaike weights ($\sum\omega_i$) of six landscape variables that indicate their relative importance in explaining capture rates of adults and immatures for six guilds in forest fragments near Manaus, Brazil. Variables in bold are significant variables in models with $\Delta AIC_c < 4$ that ranked higher than the null model (Table 2.4). Model averaged parameter estimates and unconditional standard errors are provided for important variables.

	FragSize		FragAge		2grthAge		BordAge		DistContFor		AmtContFor	
Guild	Imm	Ad	Imm	Ad	Imm	Ad	Imm	Ad	Imm	Ad	Imm	Ad
Frugivore	0.09	**0.66**	0.12	0.08	0.10	0.06	0.10	0.25	0.10	0.10	0.10	0.20
Ant-follower	0.09	0.25	0.09	0.08	0.09	0.08	**0.69**[a]	0.40	0.10	0.09	0.09	0.09
Flock obligate	**0.83**	**0.97**	0.02	0.03	**0.79**[b]	0.05	**0.99**[c]	**0.92**[d]	0.03	0.03	0.02	0.04
Flock dropout	0.16	0.29	0.14	0.10	0.13	0.09	0.11	0.10	**0.54**[e]	0.13	0.26	0.09
Gap specialist	**0.94**	0.18	0.05	0.09	**0.99**[f]	0.25	0.03	0.09	0.03	0.10	0.03	0.09
Other insectivore	**0.90**	**0.69**	**0.46**[g]	0.14	0.04	0.11	0.04	0.26	**0.31**[h]	0.07	**0.29**[i]	0.09

[a] slope = 0.58 ± 0.22; [b] slope = 0.25 ± 0.07; [c] slope = 0.33 ± 0.06; [d] slope = 0.57 ± 0.15; [e] slope = 0.15 ± 0.06; [f] slope -0.30 ± 0.06; [g] slope = 0.40 ± 0.16; [h] slope = -0.26 ± 0.12; [i] slope = -0.03 ± 0.02

FragSize = log fragment size (range: 1–3 ha; avg 1.7; SE 0.2; see Fig. 2.3)

FragAge = time since isolation (range: 17–27 years; avg: 23.6; SE: 0.8)

2grthAge = age of second growth giving <1 km path to forest (range: 13–24 years; avg: 20.0; SE: 1.3)

BordAge = age of the second growth immediately surrounding fragments (range: 7–24 years; avg: 14.4; SE: 1.9)

DistContFor = linear distance to nearest continuous forest (range: 10.6–75.4 x 10 m; avg: 31.5; SE: 6.0)

AmtContFor = amount of continuous forest within 800 m of the fragment (range: 0–2,129 x 1000 m^2; avg: 43.8; SE: 11.4).

an increase in immature capture rates with decreasing fragment size for frugivores ($F_{3,11} = 3.9$, $P = 0.041$; Fig. 2.3a), but a decrease in adult capture rates with decreasing fragment size in ant-followers ($F_{3,11} = 5.1$, $P = 0.018$; Fig. 2.3b). Although age ratios did not change for flock obligates and other insectivores (Figs. 2.2c,f), decreasing fragment size significantly decreased capture rates of both adults and immatures (Figs. 2.3c,f, Table 2.3). In flock dropouts and gap specialists there was no effect of fragmentation and no interaction between bird age and fragment size (Figs. 2.3d,e).

Species capture rates matched their respective guild in most, but not all, cases (Table 2.3, Figs. 2.3,2.4). First, capture rates of the frugivores *L. serena* and *T. albicollis* did not increase with decreasing fragment size, nor was there an interaction with fragment size and bird age as in the frugivore guild (Table 2.3, Figs. 2.4b,c). Second, in the ant-follower *G. rufigula*, there was no interaction between fragment size and bird age (Table 2.3, Fig. 2.4e). Finally, in the flock obligate *Thamnomanes caesius*, there was no change in capture rates across fragment sizes (Table 2.3, Fig. 2.4f). To summarize, in these cases where capture rates of species did not match their guild, it was due to the lack of a pattern, rather than an alternate pattern, suggesting that either lower samples in species decreased the ability to detect a pattern or that some species were less sensitive to fragmentation than other members of their guild.

Sensitivity to Landscape Variables

I analyzed capture rates in an information theoretic framework to describe how fragment size, matrix characters, and landscape parameters explain capture rates of adults and immatures in the six guilds (see Table 2.4 for a list of top-rankling models). Capture rates increased with fragment size for adult frugivores, flock obligates, and other insectivores (Table 2.5). Other landscape variables generally had low weights for predicting adult capture rates except in flock

obligates, which increased with older fragment borders. Larger fragments resulted in higher capture rates for immature flock obligates, gap specialists, and other insectivores. Flock obligates also positively responded to increasing fragment border age and second growth age, but immature gap specialists decreased with increasing second growth age. Immature other insectivores increased in older fragments and decreased with increasing proximity to and abundance of nearby continuous forest, suggesting fragments acted as a refuge in more isolated fragments. Immature ant-followers were more frequently captured in fragments surrounded by older borders (Table 2.5).

Mark–Recapture Analysis

Fragment Size as *grp* Variable.—I analyzed differences in apparent survival and transience across fragment sizes for 13 species serving as representative members for the six guilds. For only one species, *G. rufigula*, apparent survival varied across fragment sizes (Table 2.6), but seemingly it varied at random with survival higher in 10-ha fragments and continuous forest than in 1- and 100-ha fragments with standard errors overlapping (Fig. 2.5).

Combined Akaike weights ($\sum\omega_i$) of time–since–marking (TSM) models ranked as the most important models in all three frugivores, one of two ant-followers, two of three flock dropouts, and one of two gap specialists, suggesting transience was important in these species and guilds (Table 2.6, Figs. 2.5a–d,h,i,l). In four of these, TSM models weights were >4 times as likely as the next competing parameter (Table 2.6). One of these seven species, the ant-follower *P. albifrons*, also showed increasing transience with decreasing fragment size; 84% of newly marked individuals were transients in 1-ha fragments and 21% were transients in continuous forest, but survival probabilities of residents did not change with fragment size (Fig. 2.5d, Table 2.6). The test for transience in program U-CARE also indicated that transience

violated CJS assumptions for five of these seven species (Table 2.7). For the other two of these seven species, the flock dropout *M. axillaris* and gap specialist *H. cantator*, models indicated that a high proportion of newly-marked individuals were transient (τ-hat$_{M.\ axillaris}$ = 30–32%, τ-hat$_{H.\ cantator}$ = 25–27%), but tests were not significant (Table 2.7); these species had the lowest sample sizes of all those considered for this analysis. Transience was not determined to be important in flock obligates and other insectivores (Table 2.6, Figs. 2.5f,g,m).

Bird Age as *grp* Variable.—I examined differences in survival and transience between adults and immatures for ten species that could be aged. Monthly apparent survival probabilities of residents ranged from 0.39 ± 0.51 to 0.98 ± 0.09 in immatures and 0.81 ± 0.19 to 1.00 ± 0.11 in adults (Fig. 2.6). In all species, except *L. serena*, *T. caesius*, *P. rufifrons*, and *H. cantator*, models indicated adult apparent survival was greater than immature apparent survival ($\omega_{\Phi grp}$ and $\omega_{\Phi g/2t}$; Table 2.8, Fig. 2.6). In these four exceptions, models indicating adult apparent survival was similar to immature apparent survival were not clearly superior and only had weights twice as high (at best) as models that indicated adult survival was greater than immature survival. For all species, except the frugivore *P. pipra*, rates of transients were similar between adults and immatures (Table 2.7), but this was largely because of reduced resident apparent survival in immatures (Fig. 2.6). In the ant-follower *P. albifrons* and the flock dropout *M. axillaris*, although transience estimates were lower in adults (Table 2.7), apparent survival of resident immatures was considerably lower than in adults (Figs. 2.6d,h).

DISCUSSION

Interpreting Age Structuring and Transience

These data improve upon recent studies of population dynamics in forest fragments that considered matrix effects on capture rates (Stouffer et al. 2006) and occupancy and

Table 2.6. Summarized results from mark–recapture analyses of 13 species near Manaus, Brazil. Fragment size is the *grp* variable. Akaike weights ($\sum\omega_i$) are the combined weights of models with the same apparent survival parameter; each survival parameter was modeled with four candidate recapture probability parameters (ρ_{grp}, ρ_t, $\rho_{grp\times t}$, and $\rho_.$). The most likely model for each species is indicated in bold.

	CJS models				TSM models	
Species	$\sum\omega_{\Phi grp}$	$\sum\omega_{\Phi t}$	$\sum\omega_{\Phi grp\times t}$	$\sum\omega_{\Phi.}$	$\sum\omega_{\Phi g/2t}$	$\sum\omega_{\Phi./2t}$
Frugivore						
Pipra pipra	0.002	0.000	0.000	0.002	0.155	**0.841**
Lepidothrix serena	0.111	0.005	0.000	0.162	0.009	**0.713**
Turdus albicollis	0.018	0.015	0.000	0.402	0.001	**0.565**
Ant-follower						
Pithys albifrons	0.007	0.002	0.000	0.001	**0.967**	0.023
Gymnopithys rufigula	**0.584**	0.003	0.000	0.229	0.036	0.147
Flock obligate						
Thamnomanes caesius	0.063	0.010	0.000	**0.671**	0.001	0.256
Thamnomanes ardesiacus	0.223	0.043	0.000	**0.510**	0.050	0.174
Flock dropout						
Myrmotherula axillaris	0.217	0.002	0.000	0.216	0.025	**0.540**
Glyphorynchus spirurus	0.015	0.011	0.000	0.090	0.004	**0.881**
Xiphorhynchus pardalotus	0.062	0.023	0.000	**0.519**	0.001	0.395
Gap specialist						
Percnostola rufifrons	0.037	0.017	0.000	**0.669**	0.001	0.276
Hypocnemis cantator	0.071	0.017	0.000	0.420	0.001	**0.490**
Other insectivore						
Willisornis poecilinota	0.197	0.010	0.000	**0.556**	0.019	0.218

Table 2.7. The proportion of newly marked individuals (τ-hat) that were transients, defined as the proportion of newly marked individuals that permanently leave the sampling area, for 13 species with their sample size (N = number of individual bird capture histories), listed by guild, by fragment size and by bird age near Manaus, Brazil. The *P*-values from 1-sided tests for transience in program U-CARE are also presented; violations of the CJS assumption of no transience, i.e. τ-hat ≠ 0, are in bold ($P < 0.05$).

		τ-hat by fragment size					τ-hat by bird age		
Species	N	1 ha	10 ha	100 ha	Forest	*P*	Imm	Ad	*P*
Frugivore									
Pipra pipra	346	**0.58**	**0.54**	**0.56**	**0.55**	**0.001**	**0.58**	**0.35**	**0.001**
Lepidothrix serena	100	0.28	0.28	0.28	0.31	0.197	**0.15**	**0.17**	**0.021**
Turdus albicollis	57	0.25	0.25	0.25	0.25	0.081	**0.11**	**0.15**	**0.050**
Ant-follower									
Pithys albifrons	282	**0.84**	**0.41**	**0.44**	**0.21**	**0.031**	**0.21**	**0.33**	**0.003**
Gymnopithys rufigula	101	0.05	0.03	0.04	0.03	0.254	0.20	0.05	0.286
Flock obligate									
Thamnomanes caesius	72	0.07	0.07	0.07	0.07	0.182	0.00	0.11	0.185
Thamnomanes ardesiacus	77		-0.02	0.01	0.03	0.274	-0.05	0.00	0.397
Flock dropout									
Myrmotherula axillaris	55	0.30	0.31	0.33	0.32	0.314	-0.15	0.31	0.161
Glyphorynchus spirurus	229	**0.18**	**0.18**	**0.17**	**0.17**	**0.010**			
Xiphorhynchus pardalotus	56	**0.13**	**0.14**	**0.14**	**0.14**	**0.009**			
Gap specialist									
Percnostola rufifrons	75	0.03	0.03	0.03	0.03	0.158	0.02	0.02	0.398
Hypocnemis cantator	54	0.26	0.27	0.25	0.26	0.500	0.19	0.26	0.069
Other insectivore									
Willisornis poecilinota	95	0.01	0.01	0.02	0.02	0.393			

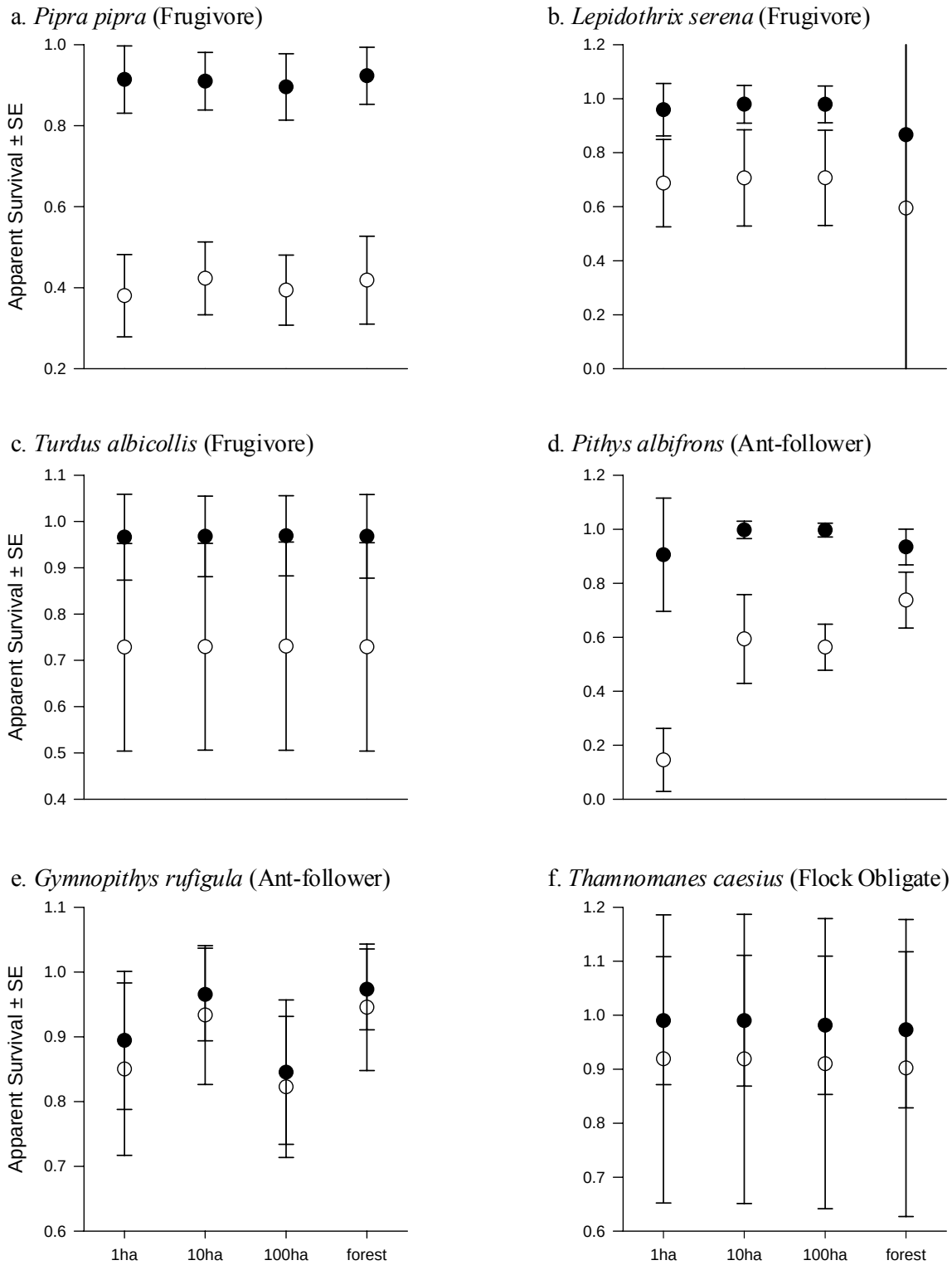
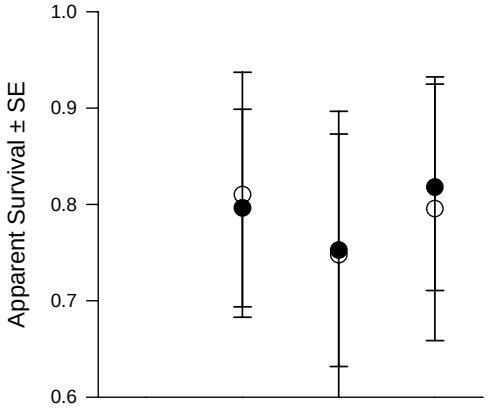


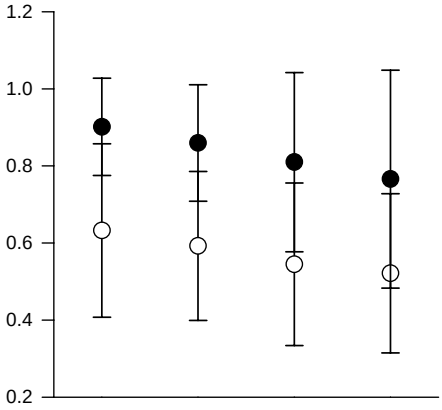
Fig. 2.5. Model averaged apparent survival probabilities for 1-, 10-, and 100-ha fragments and continuous forest near Manaus, Brazil separated by residents (closed circles) and the first interval survival for a mixture of residents and transients (open circles) for representative species in each guild.

Fig. 2.5 Continued

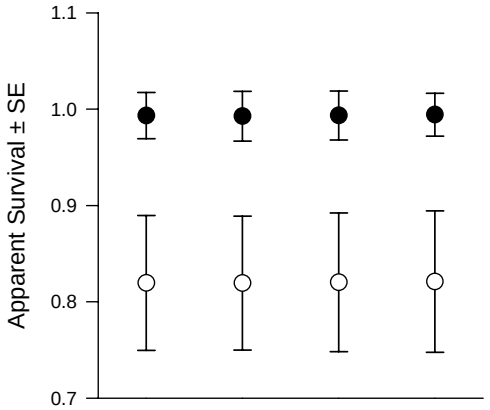
g. *Thamnomanes ardesiacus* (Flock Obligate)



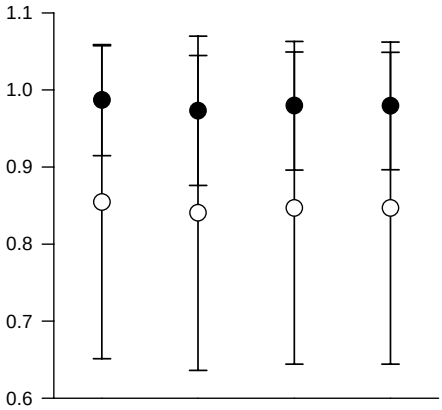
h. *Myrmotherula axillaris* (Gap Specialist)



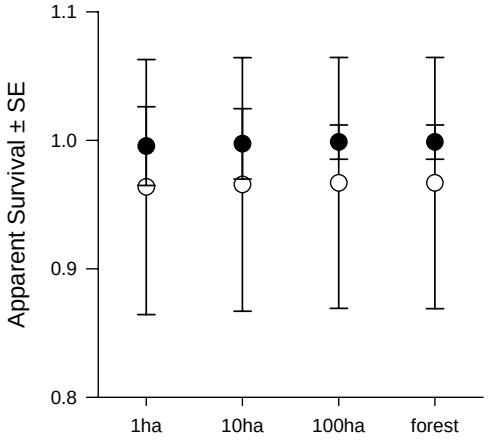
i. *Glyphorynchus spirurus* (Flock Dropout)



j. *Xiphorhynchus pardalotus* (Flock Dropout)



k. *Percnostola rufifrons* (Gap Specialist)



l. *Hypocnemis cantator* (Gap Specialist)

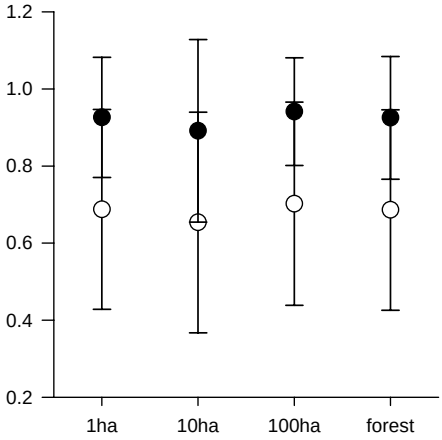


Fig. 2.5 Continued

m. *Willisornis poecilinota* (Other Insectivore)

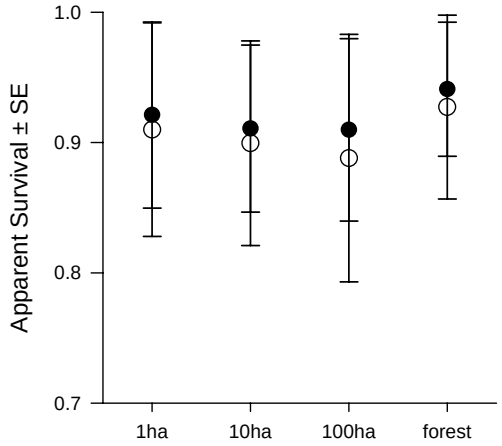


Table 2.8. Summarized results from mark–recapture analyses of ten species with aging criteria near Manaus, Brazil. Bird age is the *grp* variable. Akaike weights ($\sum\omega_i$) are the combined weights of models with the same apparent survival parameter; each survival parameter was modeled with four candidate recapture probability parameters (ρ_{grp}, ρ_t, $\rho_{grp\times t}$, and $\rho_.$). The most likely model for each species is indicated in bold.

	CJS models				TSM models	
Species	$\sum\omega_{\Phi grp}$	$\sum\omega_{\Phi t}$	$\sum\omega_{\Phi grp\times t}$	$\sum\omega_{\Phi.}$	$\sum\omega_{\Phi g/2t}$	$\sum\omega_{\Phi./2t}$
Frugivore						
Pipra pipra	0.057	0.002	0.001	0.005	**0.868**	0.067
Lepidothrix serena	0.235	0.009	0.000	0.201	0.122	**0.433**
Turdus albicollis	**0.525**	0.004	0.000	0.120	0.180	0.171
Ant-follower						
Pithys albifrons	0.075	0.001	0.012	0.000	**0.908**	0.004
Gymnopithys rufigula	**0.471**	0.008	0.000	0.211	0.169	0.141
Flock obligate						
Thamnomanes caesius	0.225	0.007	0.000	**0.476**	0.108	0.184
Thamnomanes ardesiacus	**0.400**	0.034	0.001	0.368	0.072	0.125
Flock dropout						
Myrmotherula axillaris	0.323	0.001	0.000	0.090	**0.350**	0.235
Gap specialist						
Percnostola rufifrons	0.233	0.022	0.000	**0.515**	0.037	0.193
Hypocnemis cantator	0.178	0.014	0.000	0.321	0.086	**0.401**

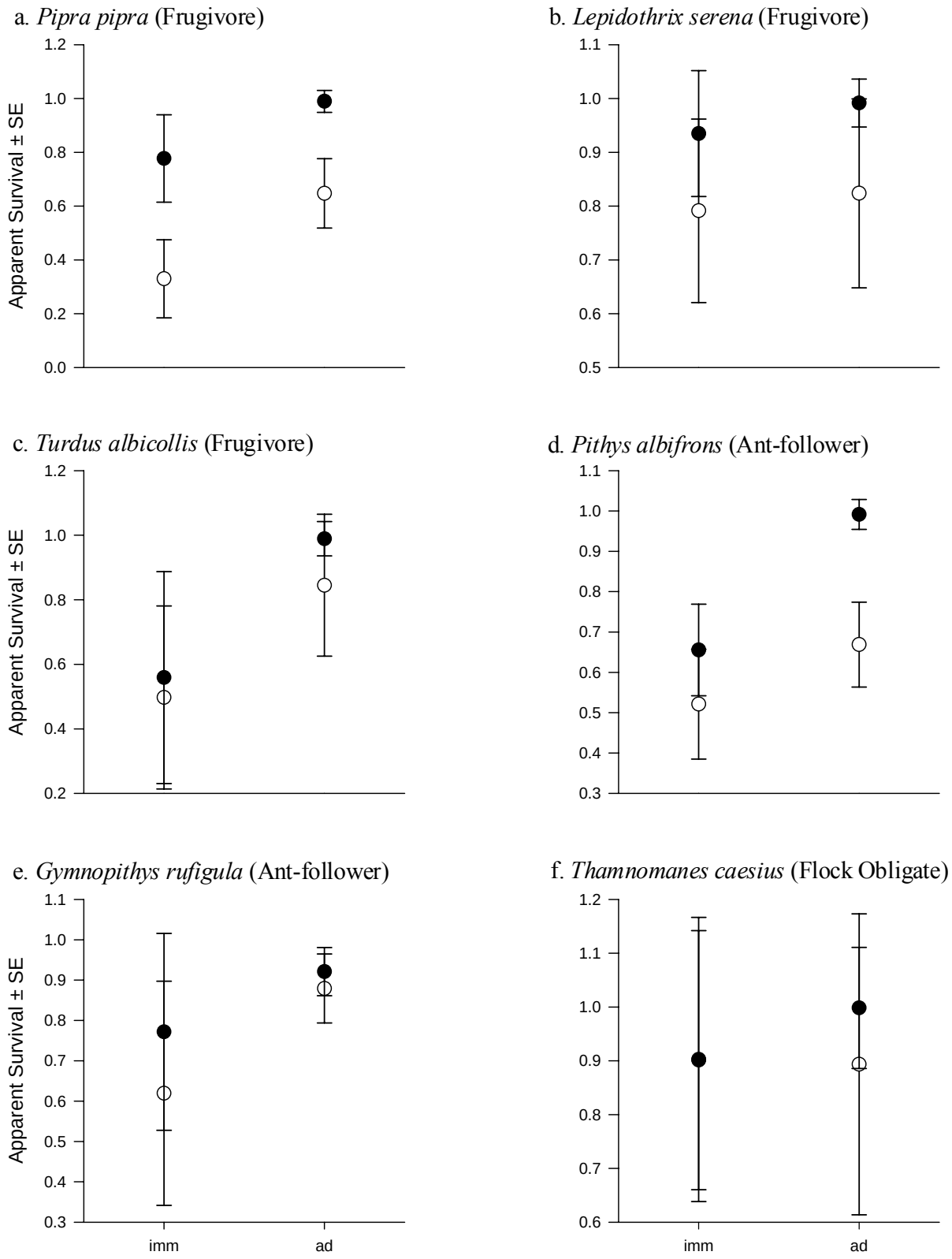
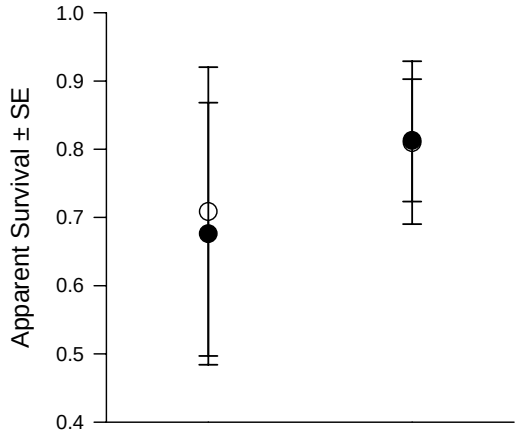


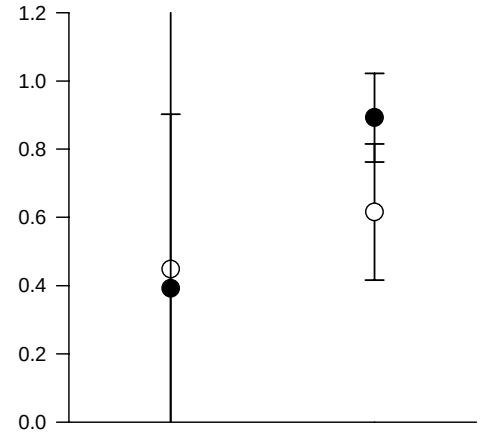
Fig. 2.6. Model averaged apparent survival probabilities for immatures and adults near Manaus, Brazil separated by residents (closed circles) and the first interval survival for a mixture of residents and transients (open circles) for representative species in each guild.

FIG. 2.6 Continued

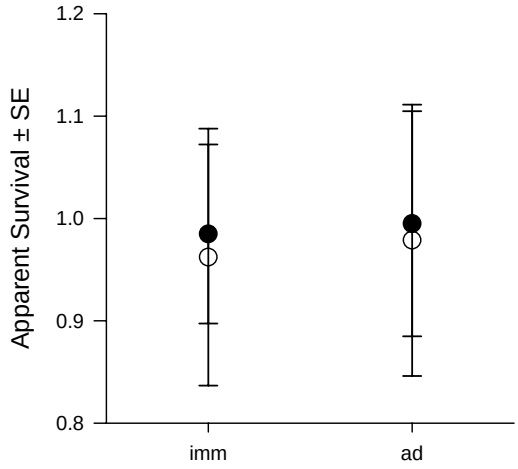
g. *Thamnomanes ardesiacus* (Flock Obligate)



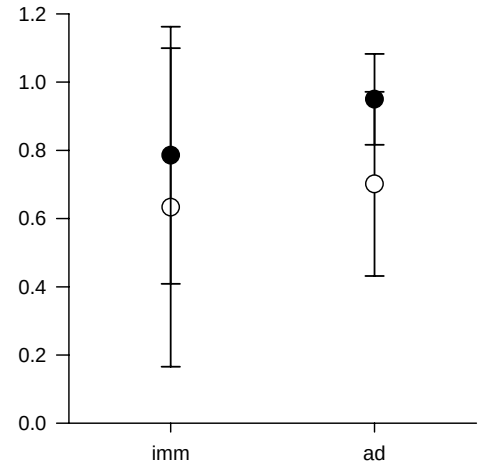
h. *Myrmotherula axillaris* (Gap Specialist)



i. *Percnostola rufifrons* (Gap Specialist)



j. *Hypocnemis cantator* (Gap Specialist)



recolonization dynamics among fragments (Ferraz et al. 2007). By describing where immatures and adults occur in the landscape, identifying which landscape variables are important in explaining variation in immature and adult relative abundance, and quantifying the relative importance of transience between age groups and across fragment sizes, we can infer the process leading to variation in age ratios and capture rates in the landscape. I did not explicitly examine local reproductive output, but instead used age ratios, relative abundance, and transience probabilities to infer its importance (Newton 1999, Rohwer 2004, Iverson et al. 2004, Harris et al. 2008). For example, I assumed that for species with poor dispersal ability and consistent age ratios across patch sizes, local reproductive output is an important mechanism for regulating isolated populations.

I found considerable variation in age-dependent responses to fragmentation, which contributes a more detailed understanding of guild-level responses to fragmentation (Stouffer et al. 2006). Fragmentation-sensitivity defined only as the change in relative abundance with patch size is clearly an over-simplification of a species' sensitivity (Van Horne 1983, Henry et al. 2007) because it does not differentiate between the capacity of dispersing immatures to colonize distant fragments from both local persistence and reproductive output.

As predicated, adult capture rates were more often influenced by patch size than by other landscape characteristics including second growth age and proximity to continuous forest. In contrast, immature capture rates in fragments were often associated with older second growth in the matrix. In immature flock obligates and other insectivores increasing patch size was also important to maintain increased relative abundance; neither dispersal nor local reproductive output was sufficient to maintain immature relative abundance in smaller fragments. Immature gap specialists showed a negative relationship to patch size despite moderate dispersal

propensities, suggesting that local reproductive output was decreased. These results suggest that some species persist in fragments as local breeding populations, whereas others occur only because of dispersal of immatures from other habitats. These results represent a major improvement over studies based on simple tallies of individuals or species among fragments, as I identify age- and species-specific mechanisms that lead to patterns of relative abundance in different sized forest fragments.

I categorize the six guilds into four major groups based on how they respond to this human-modified landscape: 1) good dispersers (i.e. high transience) not sensitive to fragmentation; 2) good dispersers sensitive to fragmentation; 3) poor dispersers sensitive to fragmentation; and 4) moderate dispersers not sensitive to fragmentation.

1. Good Dispersers Not Sensitive to Fragmentation.—Adult frugivore capture rates remained constant with fragment size, but immature capture rates increased markedly as fragment size decreased. It is unlikely that the four-fold increase in immature capture rates was the result of increased fecundity in small fragments; a more parsimonious explanation supported by the data suggests a combination high dispersal abilities and low sensitivity to matrix characteristics. Fragment edges are relatively dense with fruit compared to the surrounding second growth and forest interior and therefore the edge attracts frugivores (Loiselle and Blake 1993, Galetti et al. 2003, Ries and Sisk 2004) and particularly dispersing immatures. Manakins, the most common frugivores captured, may wander locally for years before breeding (Graves et al. 1983, Théry 1992), which may explain why even adults showed relatively high transience.

2. Good Dispersers Sensitive to Fragmentation.—Ant-followers best fit into this category. *Pithys albifrons* had high rates of transience ($0.21 < \tau < 0.85$) but adults and immatures were both sensitive to the age of the 100-m-wide border immediately surrounding fragments. In other

words, *P. albifrons* adults would apparently not cross narrow open spaces, despite otherwise high tolerance of older second growth. Immatures showed higher transience than adults and apparently regularly dispersed into fragments, but were also limited by narrow open spaces (Table 2.5). I did not detect high transience in *Gymnopithys rufigula*, although the pattern of adult and immature capture rates was similar to *P. albifrons*. Low "resident" apparent survival in *G. rufigula* suggests they this does not accurately portray actually survival and that *G. rufigula* may instead be likely to persist for >1 sampling interval and then disperse (see also Discussion: Sampling Considerations).

Ant-followers are known to be sensitive to fragmentation (Willis 1974, Harper 1989, Stouffer and Bierregaard 1995, Boswell et al. 1998), but I show that only adult abundance declines with decreasing fragment size in this landscape with 7–24 year old second growth. *Eciton burchelli* (Hymenoptera: Formicidae) army ants will use older and taller secondary forests and utilize small fragments (Roberts et al. 2000); my data suggest that birds utilizing these swarms may be primarily immature. These data show that dispersing birds (especially immatures) have the ability to reach forest fragments in this landscape, but that they are sensitive to patch size and the narrow cleared areas around fragments, and thus do not persist in small fragments.

3. Poor Dispersers Sensitive to Fragmentation.—Flock obligate and other insectivore guilds had the lowest proportion of transients ($0.00 < \tau < 0.07$). Furthermore, these were the only two guilds for which fragment size was an important landscape predictor for both immature and adult capture rates, suggesting that they are highly sensitive to patch size (see also Bierregaard and Stouffer 1995). The immatures of these two guilds responded differently to other landscape variables, however. Older second growth increased immature flock obligate

capture rates suggesting that immatures sometimes disperse to fragments, but this process never compensates numerically for loss of adults. Instead, immature other insectivores respond to fragment quality (using age as a proxy for fragment deterioration; Laurance et al. 1997). They were more abundant in recently isolated fragments with little continuous forest nearby (Table 2.5), suggesting that the few dispersing birds are not affected by matrix quality, but instead use fragments as a temporary refuge when high quality forest is not available.

4. Moderate Dispersers Not Sensitive to Fragmentation.—I grouped gap specialists and flock dropouts into this fourth category. These guilds had intermediate levels of dispersal ($0.03 < \tau < 0.33$) and were relatively insensitive to fragment size, except for immature gap specialists which were much less abundant in 1-ha fragments. These species regularly nest in the smallest fragments and surrounding second growth (P. C. Stouffer personal observation), but I suggest that a decrease in nesting success coupled with low dispersal rates may be responsible for fewer immatures in small fragments, especially for *Hypocnemis cantator* in 1-ha fragments. Interestingly, immature capture rates also decreased with increasing second growth age, which may reflect a natural response to a habitat decreasing in suitability, or older second growth may be facilitating nest predator movements and decreasing nest success (Gates and Gysel 1978, Schlaepfer et al. 2002). A better understanding of nest success in fragmented tropical landscapes is an important consideration for future research (Chalfoun et al. 2002).

Within-guild Variation

In some cases, species deviated from the general patterns of their guild. For example, the manakins wither large sample sizes, *Pipra pipra* and *Lepidothrix serena*, had different demographic and dispersal patterns. Differences in transience rates may reflect the time it takes each species to reach definitive plumage (i.e. breeding maturity); because *P. pipra* takes three

years to reach definitive plumage, there is a greater proportion of non-breeding individuals than in *L. serena*, which takes two years to reach definitive plumage (Ryder and Durães 2005, E. I. Johnson, unpublished data). Age ratios across fragment sizes of *P. pipra* drive the frugivore pattern, but demographics were similar for *Turdus albicollis*, a thrush that breeds in its second year. Therefore, we might conclude that maturity time does not directly contribute to demographic responses to fragmentation and that instead there are real differences in how these manakin species respond to landscape characteristics.

The two gap specialists, *H. cantator* and *Percnostola rufifrons*, also responded differently to fragmentation, although neither appeared to be particularly sensitive to fragment size *per se*. For these species, it is difficult to separate fragmentation effects from local habitat heterogeneity because of their preference for gap-like conditions. Our understanding of population-level responses to fragmentation will benefit from more focused studies at the species-level.

The two *Thamnomanes* spp. flock obligates were highly consistent in their demographic response to fragmentation, although *T. ardesiacus* capture rates decreased at a faster rate with decreasing fragment size than *T. caesius*. Core flock species are highly codependent and it is not surprising that their demographic responses to fragmentation are consistent across species. The average mixed-species flock home range is close to 10-ha at the BDFFP (Develey and Stouffer 2001). The presence of coherent mixed-flocks in 10-ha fragments is a recent phenomenon, as these were largely absent from fragments for about a decade following isolation (Stouffer and Bierregaard 1995). Flocks' recent occurrence corresponds with an increase in older second growth surrounding fragments, which is often used by the single flock present in each 10-ha fragment (K. Mokross, unpublished data). In some areas, second growth has become tall enough to sustain mixed-flocks, increasing their presence in 1-ha fragments as well.

Sampling Considerations

Analyzing raw capture rate data as a response to fragmentation does not consider capture probability, which may differ according to the spatial arrangement of nets as a consequence of fragment size. I minimized problems associated with this by excluding same-day recaptures from the analysis. Even so, recapture probabilities might be expected to be greater in small fragments when interior forest species actively avoid edges, thereby inflating capture rates; however, this should make comparisons of capture rates across fragment sizes conservative measures of sensitivity to fragmentation.

I advise caution when interpreting my estimates of monthly survival for residents. These estimates were generated considering six replicates within a breeding season instead of the preferred method of gathering multiple years of data. Even so, monthly survival probabilities were generally high (>0.95), despite several exceptions (Figs. 2.5, 2.6), and within the known range of survival probabilities of other Neotropical birds (e.g. Brawn et al. 1995, Jullien and Clobert 2000, Blake and Loiselle 2008). Although my study design was not intended to generate true survival estimates, a monthly sampling interval is appropriate for detecting transience across bird guilds, age groups, and fragment sizes assuming the duration of stay is shorter than the sampling interval (Chase et al. 1997, Pradel et al. 1997). Estimates only consider birds that disappeared during the first monthly interval after marking, making estimates conservative. If individuals are resident for >1 interval and then disperse, this will not appear in my analysis as transience and instead decreases apparent survival probability estimates of residents; apparent survival estimates of residents should therefore at least partially reflect site persistence. Even so, this modeling technique improves precision in apparent survival estimates of residents and can

reveal the importance of transience, even if conservatively (Chase et al. 1997, Belda et al. 2007, Blake and Loiselle 2008, Ruiz-Gutierrez et al. 2008).

Importantly, for most species I examined, apparent survival probabilities of adult residents were about 0.95, suggesting that underestimating dispersal was not a problem. In *T. ardesiacus* and *G. rufigula*, however, monthly apparent survival estimates of residents were consistently below 0.95 as were immatures of most species; a monthly survival estimate of 0.95 extrapolates to an annual survival estimate of 0.54 whereas a monthly survival estimate of 0.90 extrapolates to an annual survival estimate of only 0.28. These survival estimates are very low compared to other Neotropical birds (e.g. Jullien and Clobert 2000, Parker et al. 2006, Blake and Loiselle 2008), suggesting it is possible that transience was indeed higher for these species, but went undetected. As an ant-follower, *G. rufigula* is expected to have relatively high rates of transience, as in *P. albifrons*. The larger *G. rufigula* is dominant over the smaller *P. albifrons* (Willis and Oniki 1978) and may spend less time searching or make fewer large movements than their smaller counterpart, which may at least partially account for my estimation of low transience. In *T. ardesiacus* and several other species, estimates of transience for immatures were lower than for adults, contrary to expectations (Greenwood and Harvey 1982, Jullien and Thiollay 1998). In most of these circumstances, apparent survival estimates of immature residents were lower than in adults, which may be interpreted as lower actual survival. Additionally, I likely underestimated transience in these species because non-territorial immatures may spend >1 month prospecting new habitats, especially where adult density is reduced (such as in isolated fragments), rather than continuously dispersing widely in search of appropriate future breeding habitat.

I used second growth age as a proxy for structure, but second growth dynamics are also influenced by fire history and distance to mature forest at the study sites (Borges and Stouffer 1999, Laurance et al. 2006). Using second growth age as a proxy for structure therefore misses some of its complex variation. Even so, second growth age was a useful variable for understanding immature capture rates in four of six guilds I examined, but certainly more could be learned about how variation in second growth structure influences avian population dynamics in fragmented landscapes. Second growth characteristics at the study site are minimally affected by local variation in climate and edaphic properties (Laurance et al. 2006), but variation in these factors are much greater across the Neotropics and may be important in understanding second growth regeneration dynamics elsewhere (Ganade and Brown 2002, Silva et al. 2006). I therefore caution against extrapolating second growth stand age at this site to have equivalent consequences on avian population dynamics at other sites.

Although this study was not intended to examine evolutionary relationships of demographic responses among the study organisms, some preliminary patterns emerged. A phylogenetic interpretation of the results might suggest that antbirds in particular are sensitive to fragmentation, as they constituted the majority of ant-followers, flock obligates, and other insectivores in my analyses. Although fragmentation sensitivity is likely at least partially phylogenetically constrained, two antbird gap specialists were captured with increasing frequency in small fragments, suggesting considerable variability within Thamnophilidae. Ecological strategies have been repeatedly shown to have a deterministic force in driving fragmentation sensitivity (Stouffer and Bierregaard 1995, Barlow et al. 2007, Arraiga-Weiss et al. 2008). For example, Neotropical terrestrial insectivores are highly sensitive to fragmentation and include a taxonomically varied group, including *Sclerurus* spp. (Furnariidae), *Mymornis*

torquata (Thamnophilidae), *Formicarius* spp. (Formicariidae), *Grallaria varia* (Grallariidae), *Conopophaga* spp. (Conopophagidae), *Corythopis torquatus* (Tyrannidae), *Cyphorhinus arada* (Troglodytidae; Stouffer 2007). This ecological guild is also highly fragmentation-sensitive in Afrotropical and Asian rainforest ecosystems, although it also largely consists of a variety of other taxa (Johns 1996, Waltert et al. 2005). In the next chapter, I explore a previously understudied life history trait as it relates to fragmentation sensitivity and provide additional discussion about the evolutionary inertia of fragmentation sensitivity among understory Amazonian birds.

Conclusions

Although this study was conducted in a best-case-scenario landscape, with extensive continuous forest within 1 km of fragments connected by 7–24 year old second growth, only flock dropouts and gap specialists (3 of 22 species I examined) were demographically unaffected by fragmentation. Fragmentation had severe impacts on the demographic structure in several species (ant-following insectivores and frugivores) or caused significant population declines in others (flock obligates and other understory insectivores). The aging second growth matrix played a significant role in facilitating immature dispersal and compensated for small fragment size for breeding adults, and thus is critical to maintain fragmented populations (Stouffer et al. 2006). In the most sensitive insectivores (ant-followers and flock obligates), even narrow strips of cleared vegetation can limit dispersal, a result consistent with previous studies of the effects of Amazonian forest roads (Develey and Stouffer 2001, Laurance et al. 2004, Lees and Peres 2009).

Given contemporary rates of deforestation, forest fragments and second growth may become critical to the preservation of tropical forest species (Wright and Muller-Landau 2006, Bowen et al. 2007, Arroyo-Rodriguez et al. 2009, Gardner et al. 2009, Letcher and Chazdon

2009, but see Brook et al. 2006). Additional demographic studies should be conducted in other fragmented Neotropical systems to better understand mechanistic processes underlying population dynamics in a variety of landscapes. Quantifying the relative importance of nearby continuous forest, matrix age and extent, and patch size on natal dispersal and breeding area sensitivity on bird populations is critical for making sound conservation decisions to maximize biodiversity in human-modified landscapes. These results provide a first examination of the importance of these landscape variables on demographic processes that underlie extinction–colonization dynamics in Amazonian bird populations.

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CHAPTER 3: VARIATION IN MOLT-BREEDING OVERLAP AMONG AMAZONIAN BIRDS AND ITS CONSEQUENCES IN A FRAGMENTED LANDSCAPE

INTRODUCTION

The annual cycle in birds is potentially subject to rigorous evolutionary pressures, such that each species' life history is a result of physiological, behavioral, and demographic adaptations to abiotic and biotic factors (Dawson et al. 2000, Ricklefs and Wikelski 2002, Moreno 2004). Trade-offs between fecundity, plumage replacement and maintenance, immunocompetence, and daily energy expenditure, for example, are presumably optimized through natural selection to maximize fitness. Life history events are therefore presumably timed and regulated to balance energy intake with energy expenditure.

Life history events in birds that demand especially high energy expenditure include breeding, molting, and migration, and these periods are often separated temporally (Kjellén 1994, Murphy 1996). Breeding requires a significant amount of energy to enlarge gonads, produce eggs, incubate, and feed nestlings and fledglings, and therefore successful breeding can reduce future survival and fecundity (Drent and Daan 1980, Gustafsson and Sutherland 1988, Nilsson and Svensson 1996, Thomson et al. 1998). Feather production during molt requires specific amino acids and increases basal metabolic rates by up to 111% (Newton 1966, Lindström et al. 1993, Murphy 1996). High reproductive investment can delay molt or decrease feather quality (Siikamäki et al. 1994, Nilsson and Svensson 1996, Dawson et al. 2000), and molting early can reduce fecundity, but increase parental survival (Morales et al. 2007). During feather replacement, flight performance, thermoregulatory capacity, and immunity to pathogens can be reduced (Swaddle et al. 1996, Chai 1997, Moreno-Rueda 2010). Because of costs associated with molting, most migratory species rarely molt and migrate simultaneously, while

others temporarily arrest molt until migration is completed (Stresemann and Stresemann 1966, Pyle 1997, Leu and Thompson 2002, Pérez and Hobson 2006).

For species that do not migrate, pressure to quickly molt and breed is reduced. Paradoxically, despite being free from pressures of migrating, many tropical birds molt and breed simultaneously, referred to as molt–breeding overlap (MBO hereafter; Snow and Snow 1964, Foster 1975, Avery 1985, Marini and Durães 2001). The causes and consequences of MBO are poorly understood. In this chapter, I explore the frequency of MBO in a variety of lowland understory Amazonian passerines and its consequences in a fragmented landscape, where novel stresses associated with fragmentation may reduce daily net energy acquisition and therefore preclude the ability to molt and breed simultaneously.

The physiological regulation of breeding and molting has been studied more intensively in temperate bird species, few of which show MBO, than in tropical species with frequent MBO (e.g. Murphy 1996, Dawson 2006 and references therein). Here, I briefly summarize the regulation of molting and breeding based on species that do not typically molt and breed simultaneously. The onset of breeding is associated with increasing daylength (photosensitivity), and this leads to a stimulation of reproductive hormones, including gonadotropin-releasing hormone, testosterone, and prolactin, which can be modified based on non-photic cues (e.g. temperature) and parental behavior (Dawson and Goldsmith 1982, 1984, 1985, Hall 1987, Wingfield et al. 1992, Sharp et al. 1998, Dawson 2006, 2008). Absolute photorefractoriness, or the termination of reproductive activity despite continued long daylength, coincides with the onset of a postnuptial molt (Nicholls et al. 1988). This period typically begins during the near-independence of fledglings from the last clutch of the breeding season as gonads regress (Dawson 2006 and references therein).

The physiological switch from photosensitivity to photorefractoriness probably involves an increase in gonadotropin-inhibiting hormone coinciding with the first decrease in prolactin concentrations following its peak near the termination of breeding (Bentley et al. 2003, Dawson 2006, Dawson et al. 2009). In most temperate species, this physiological switch corresponds with the cessation of breeding and initiation of molt, but the exact physiological mechanisms that regulate temporally distinct molting schedules are still largely unknown (Hau et al. 2008). MBO occasionally occurs in multiple-clutch or late breeders of temperate species that follow the above breeding and molting physiology (Morton and Morton 1990, Svensson and Nilsson 1997, Zaias and Breitwisch 1990, Hemborg 1999, Morales et al. 2007, Flockhart 2010). This suggests that it is physiologically possible to at least partially decouple the onset of molt from the termination of breeding; some tropical species with frequent MBO may indicate an increased capacity to independently regulate breeding and molting.

Although changes in photoperiod are relative subtle in the tropics, a few well-studied studied tropical species indeed show surprisingly striking sensitivity to small changes in daylength and exhibit high photosensitivity as in temperate species (Hau et al. 1998, 2008, Gwinner and Scheuerlein 1999, Beebe et al. 2005). Light intensity associated with wet and dry seasons possibly act synergistically with photoperiod (Gwinner and Scheuerlein 1998). A photosensitive tropical thamnophilid, the Spotted Antbird (*Hylophylax naevioides*) does not exhibit photorefractoriness such that enlarged gonads do not inhibit molt (Beebe et al. 2005). Species that live in unpredictable temperate environments, like crossbills (*Loxia* spp.), Zebra Finches (*Taeniopygia guttata*), Columbiformes, and some Ploceidae, show "relative" photorefractoriness, where breeding can reinitiate soon after gonads partially regress (Lofts and Murton 1968, Sossinka 1974, Dittami 1986, Hahn 1995, Hahn et al. 2004). Absent or reduced

photorefractoriness may also be advantageous and common in wet tropical forests where the onset of the rainy season may vary unpredictably from year to year, which may be linked to increased frequency of MBO.

Compared to temperate species, the physiological demands of simultaneously molting and breeding may be lower for tropical species because of their slower-paced lifestyle (Foster 1974, Franklin et al. 1999, Wingfield 2005). Tropical birds typically lay fewer eggs per clutch (usually just two; Skutch 1969, 1985, Kulesza 1990, Young 1994, Martin et al. 2000), have reduced maximum gonad size and hormonal concentrations (Stutchbury and Morton 2001, Wikelski et al. 2003a, Goymann et al. 2004, Hau et al. 2010), have a lower metabolic rate (Ricklefs 1976, Weathers 1979, Wikelski et al. 2003b, Jetz et al. 2008), and a prolonged molt (Helm and Gwinner 1999, Ryder and Wolfe 2009). High nest predation rates resulting in multiple nesting attempts (Skutch 1949, 1985, Kulesza 1990, Ferretti et al. 2005, Roper 2005, but see Snow and Snow 1963, Oniki 1979, Martin 1995, Robinson et al. 2000) coupled with decreased seasonality and more constant resource availability (Lack 1947, Ashmole 1963, Cody 1966, Ricklefs 1980, Martin 1996) may at least partially explain this reduced-paced life style such that MBO may not severely reduce fecundity or fitness in tropical species (Foster 1974), as it does for temperate Pied Flycatchers (*Ficedula hypoleuca*; Slagsvold and Dale 1996, Hemborg and Lundberg 1998, Hemborg 1999, Hemborg et al. 2001).

These generalizations of tropical birds oversimplify their diversity of life history strategies, which include a diversity of social systems and foraging strategies (Terborgh et al. 1990, Stutchbury and Morton 2001). Furthermore, there is a strong environmental gradient between canopy and understory microclimates within tropical a forest, such that species occuping different strata experience and respond to different evolutionary pressures (Burney and

Brumfield 2009). The understory is typified by a relatively constant daily and annual temperature, light intensity, and humidity relative to the canopy, which experiences considerably more dramatic fluctuations (Endler 1993, Laurance et al. 2002, Walther 2002). Therefore, we should expect to see variation in the frequency of MBO among tropical taxa. Rainforest fragmentation can severely alter the microclimate such that forest fragments are subject to greater daily and seasonal variation in humidity, temperature, and wind than continuous forest, thus mimicing a more seasonal environment (Kapos 1989, Kapos et al. 1993, Laurance et al. 2002). Food resources for interior rainforest birds may be negatively impacted or become less predictable in this altered abiotic state (Laurance et al. 2002), thus decreasing the likelihood that simultaneously molting and breeding would be feasible. MBO might be a costly life history trait in such environments where resource availability changes dramatically and perhaps unpredictably with daily and seasonal fluctuations in abiotic conditions.

In this chapter, I examine patterns and consequences in MBO among species in a fragmented landscape. First, I predicted that there would be variation in the frequency of MBO among species corresponding to their ecology and taxonomy. Second, I predicted that increased frequency of MBO would correlate with longer molt durations, longer and increasingly overlapping molting and breeding seasons, and decreased flexibility in timing of molt initiation. Third, I predicted that because MBO may be disadvantageous in seasonal environments, species with higher frequencies of MBO would be more sensitive to fragmentation. Given that Amazonian rainforest fragments experience more seasonal abiotic fluctuations (Kapos 1989, Kapos et al. 1993, Laurance et al. 2002) as in temperate forests, I discuss the implications MBO in seasonal environments and consider its role in explaining contemporary biogeographical patterns among New World passerines.

METHODS

Assessing Molting and Breeding Status

Since the mist-netting program began at the BDFFP in 1979, primary feather molt had been noted, as "no", "symmetrical", or "asymmetrical" and which primary feather was molting (p1–p10) was also recorded. With >60,000 capture records through 2009, this provides an invaluable resource for describing the timing and duration of molt for a variety of species.

Breeding status of captured individuals was not assessed at the beginning of the BDFFP mist-netting project. Instead, the presence–absence of brood patches was first assessed on 18 Aug 1982 and continued until 4 Apr 1986; it was again reinstated on 1 Jul 2000. Starting on 27 Dec 1985, a 5-level coding system was collected until 1 Jul 2000. The 5-level system is as follows: 1) feathered abdomen with no brood patch; 2) unfeathered abdoment with no brood patch; 3) a potentially forming brood patch, but not yet active; 4) an active brood patch with swollen veins and loose skin; 5) an old, dry, inactive brood patch. I used #4 to indicate the presence of a brood patch ("yes") and the other four codes to indicate its absence ("no"). Thus, since 1982 breeding status had been recorded in one form or another. Cloacal protuberance data were collected starting 1 Jul 2000, but I did not use this information for determining breeding status because of its brevity of collection and uncertainty in its accuracy.

Assessing Molt–Breeding Overlap

I considered MBO to occur when molting primary feathers on the wing occurred simultaneously with an active brood patch. Although other metrics have been used in the literature to assess MBO, such as using gonad size, body molt, and molt overlapping fledgling (e.g. Foster 1975, Nilsson and Svensson 1996, Marini and Durães 2001), my assessment is among the most conservative and least subjective.

Data Quality Control

Because a multitude of observers with varying levels of experience have collected data for the BDFFP database, I evaluated the validity of molting and breeding data by comparing older data with 6405 captures (about 10% of the database) that I recorded between 10 Jun 2007 and 9 Aug 2009. First, I visually compared yearly and monthly frequencies of breeding and molting to look for inconsistencies throughout the database. The proportion of birds found to be breeding and molting, as well as the frequency of MBO, in my 2007–09 data were similar to the pre-2007 data, with a few exceptions. Birds were far too often indicated as breeding from 25 Mar to 15 Aug 1983, 9 Oct to 13 Oct 1983, and 24 Feb to 17 Jun 1985. Molt status data appeared to be accurate during these periods, so I only excluded breeding status data from these dates. Second, I examined recapture histories to evaluate whether molt status on recaptured birds corresponded to expectations from previous and subsequent captures. I excluded asymmetrical molt, defined as only one wing undergoing primary molt. Finally, I excluded molting and breeding records for within-month recaptures.

Analyses

Molt–Breeding Overlap by Taxonomy and Ecological Guild.—I quantified the proportion of captures with MBO among all 87 Passeriformes, presented as the percentage of captures with brood patches that were simultaneously molting by species, subfamily, family, and suborder. I did not examine non-passerines because they collectively represent few captures and some have ambiguous (e.g. Trochilidae and Columbidae) or unknown brood patch development. I compared MBO frequencies at family-level and higher taxonomic levels for one analysis and among ecological guilds (Appendix A) using Chi-square contingency tests (proq freq, SAS Institute 2003). I focused subsequent analyses on 31 species with ≥15 observed brood patches.

Population-level Molting and Breeding Phenology.—I assessed monthly frequencies of captures with brood patches or primary molt. I averaged the monthly population-level overlap (PO) by using the minimum value for proportion of captures either breeding or molting. For example, if 5.5% of captures were molting and 2.3% were breeding, I considered PO of molting and breeding to overlap 2.3%. This does not measure MBO at the individual level, but may correlate with individual MBO (see *Correlates of molt–breeding overlap*).

Correlates of Molt–Breeding Overlap.—I determined whether MBO was predicted by PO of molting and breeding seasons, average molt duration, variability in the timing of molt initiation using general linear models (simple linear regressions and ANOVAs).

Because greater molting and breeding season PO may increase the probability that individual birds would experience MBO, I tested whether PO predicts MBO frequency using a general linear model.

I determined molt duration by examining recaptured individuals as they progressed through their wing molt. Because actively molting feathers were noted, I could extrapolate how fast that molt would complete for each individual. I then averaged rates across all individuals to estimate molt duration for each species. I tested the hypothesis that longer average molt duration increases the frequency of MBO.

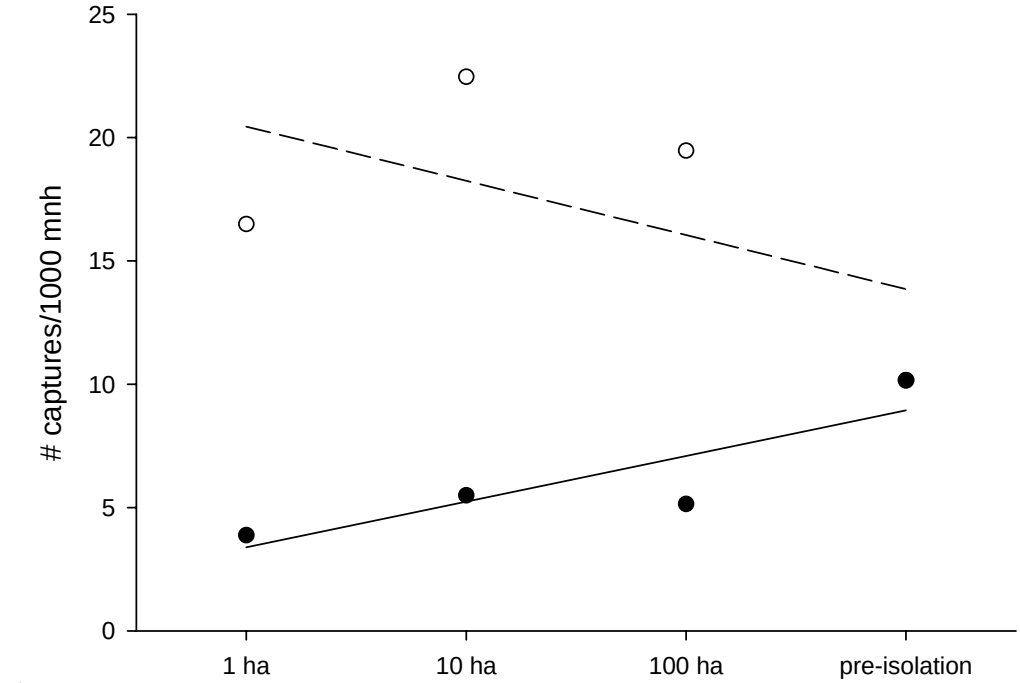
I assessed the variability in the timing of molt initiation using the same birds as the previous analysis, but extrapolating back to estimate the date of wing molt initiation. This analysis tests the hypothesis that increased variation in molt initiation decreases the frequency of MBO because birds that can initiate molt at any time will be able to avoid MBO, compared to species that are constrained in the timing of molt initiation.

I looked at feather growth rates of individual birds to determine whether relatively slow feather growth rates within species increased the probability of MBO. Horizontal faint dark–light bars in feathers represent 24 hours of growth, thus provides a permanent record of their daily growth rate (Michener and Michener 1938, Grubb 1989). I measured daily growth rates of outer rectrices (R6) from birds with brood patches captured from 1991–2009. I standardized growth rates by using residuals of each species' mean and then pooling at the guild level for statistical analysis using nine species with >10 individuals with brood patches and a collected feather. To facilitate comparisons across species, I used residuals from the species' average growth rate as a continuous independent variable in a logistic regression (proc logistic, SAS Institute 2003) to determine its ability to predict the probably of having MBO.

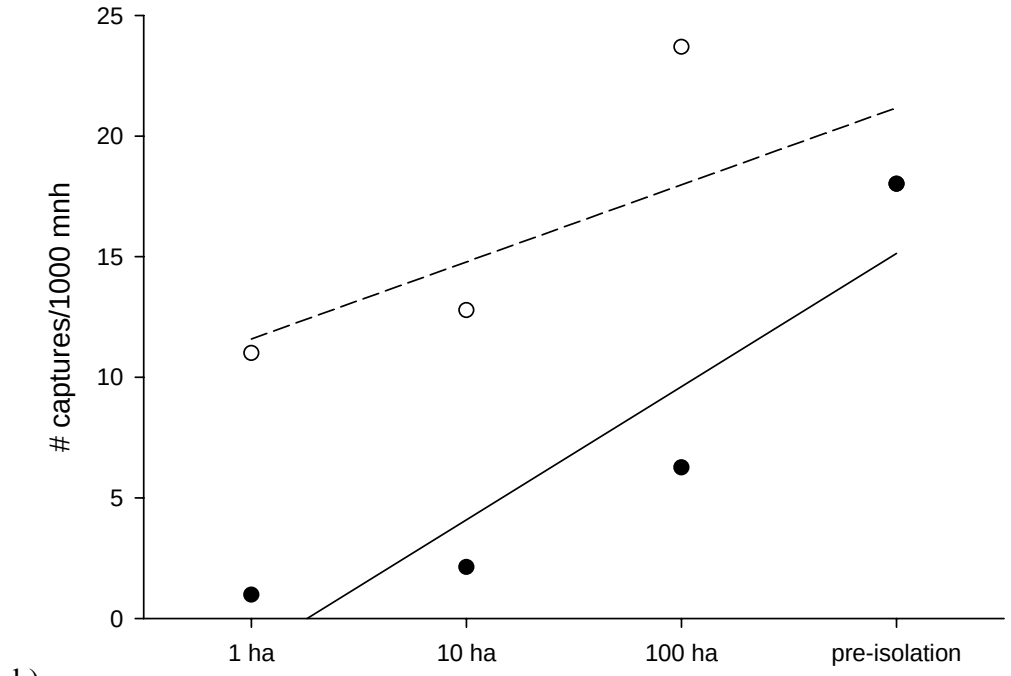
Molt–Breeding Overlap and Fragmentation Sensitivity.—Before I tested whether increased MBO is associated with increased fragmentation sensitivity, I tested heterogeneity in MBO among fragment sizes to determine whether species can adjust MBO frequency to different physical cues between forests and fragments.

I used four indices to measure fragmentation sensitivity: 1) maximum post-isolation decline (i.e., slope of capture rates across fragment sizes when capture rates were at their minimum; Fig. 3.1), 2) maximum post-isolation recovery (i.e., slope of capture rates across fragment sizes with regenerating second growth; Fig. 3.1), 3) preisolation capture rates (an indicator of rarity; see Table 1.1 for fragment isolation dates), and 4) dispersal ability (i.e. transience from Chapter 2). Increasing fragmentation sensitivity is indicated with more positive capture rate slopes across fragment sizes (Fig. 3.1) and lower transience (Chapter 2).

I considered a factor analysis to reduce the number of fragmentation-sensitivity variables and the optimal solution retained three factors; maximum decline and preisolation capture rates



a)



b)

Fig. 3.1. Calculating fragmentation sensitivity defined as the slope in capture rates slope across fragment sizes when capture rates post-isolation were at their minimum (solid lines) and maximum (dashed lines) for (a) *Glyphorynchus spirurus* and (b) *Pithys albifrons*. More positive slopes indicate a greater sensitivity to fragmentation. The slope was calculated with fragment sizes on the x-axis transformed to a log-scale (0–3).

loaded onto a single factor (E. I. Johnson, unpublished data). I interpreted the three factors to mean that each variable represented a unique biological process. To retain the maximum amount of information in these variables, I used the raw variables in a multiple linear regression model to understand how they collectively predicted MBO. Preisolation capture rate was strongly collinear with maximum decline, so I chose to include only maximum decline in the multiple regression model. This interpretation was supported by examining Pearson's partial correlation coefficients among the four fragmentation-sensitivity variables (proc corr, SAS Institute 2003).

When necessary, percentage data were arcsine-transformed and other variables were log-transformed to meet assumptions of parametric statistics. I present least-square means and standard errors unless otherwise stated.

When in the Molt Cycle Does Breeding Occur?.—For species of Furnariidae, Thamnophilidae, and Formicariidae, I counted the number of individual with brood patches by the extent of primary feather molt (p1–10). Molt on both wings were noted, so when the molt extent differed on each side, I added half a bird to feather molt category. Given that brood patches for single-brooded birds may last no longer than four weeks and molt often follows breeding (del Hoyo 1992–2010), we might expect MBO to occur at the beginning of the molt cycle (i.e. with molting p1) if there was a physiological drive to regulate molt and breeding for their independence. Alternatively, if MBO occurs throughout the molt cycle, we might instead conclude that molt and breeding are physiologically decoupled.

RESULTS

Molt–Breeding Overlap by Taxonomy and Ecological Guild

The BDFFP database includes 26871 records of 87 species of Passeriformes from 1979–2009 where the presence–absence of wing molt and brood patch was assessed (Appendix B).

Most of these records were for suboscines (90.4%), with only 6.9% from 10-primaried oscines and 2.7% from 9-primaried oscines. The most frequently captured species were in the Thamnophilidae (41.9%), followed by Furnariidae (27.5%), Pipridae (9.1%), and Tyrannidae (7.3%).

An active brood patch was observed in 1472 (5.5%) of captured individuals and of these, 187 (12.7%) were simultaneously undergoing symmetrical primary feather molt, which I considered to be MBO (Appendix B). The occurrence of MBO varied among species and higher-level taxa, being significantly more frequent in suboscines (13.3%) than in oscines (6.4%; $\chi^2_1 = 4.6$, $P = 0.032$; Fig. 3.2). The frequency of MBO differed significantly among suboscine families, not including families with <15 individuals observed with brood patches ($\chi^2_1 = 98.2$, $P < 0.001$; Fig. 3.2). Among suboscines, MBO was most frequent in the Thamnophilidae and least frequent in the Tyrannidae and Pipridae. Within oscines, MBO was more frequent in 10-primaried oscines, especially in the Polioptilidae (15.2%), than 9-primaried oscines, but the differences between 10- and 9-primaried oscines were not significant ($\chi^2_1 = 1.8$, $P = 0.19$), nor were pairwise differences among oscine families (Fig. 3.2). In only one occasion was MBO observed in a 9-primaried oscine (*Cyanocompsa cyanoides*; Appendix B).

Ecological guilds had differing levels of MBO ($\chi^2_7 = 81.0$, $P < 0.001$). Ant-followers had the highest frequency of MBO (31%), followed by gap specialists, terrestrial insectivores, other insectivores, and flock obligates with 13–17% MBO frequency. Flock dropouts, frugivores, and non-forest species had <7% MBO frequency (Fig. 3.3).

Population-level Molting and Breeding Phenology

Across all 87 species of passerines, the breeding season at the BDFFP is essentially year-round, peaking in late dry season and early wet season (September–January; Fig 3.4). The

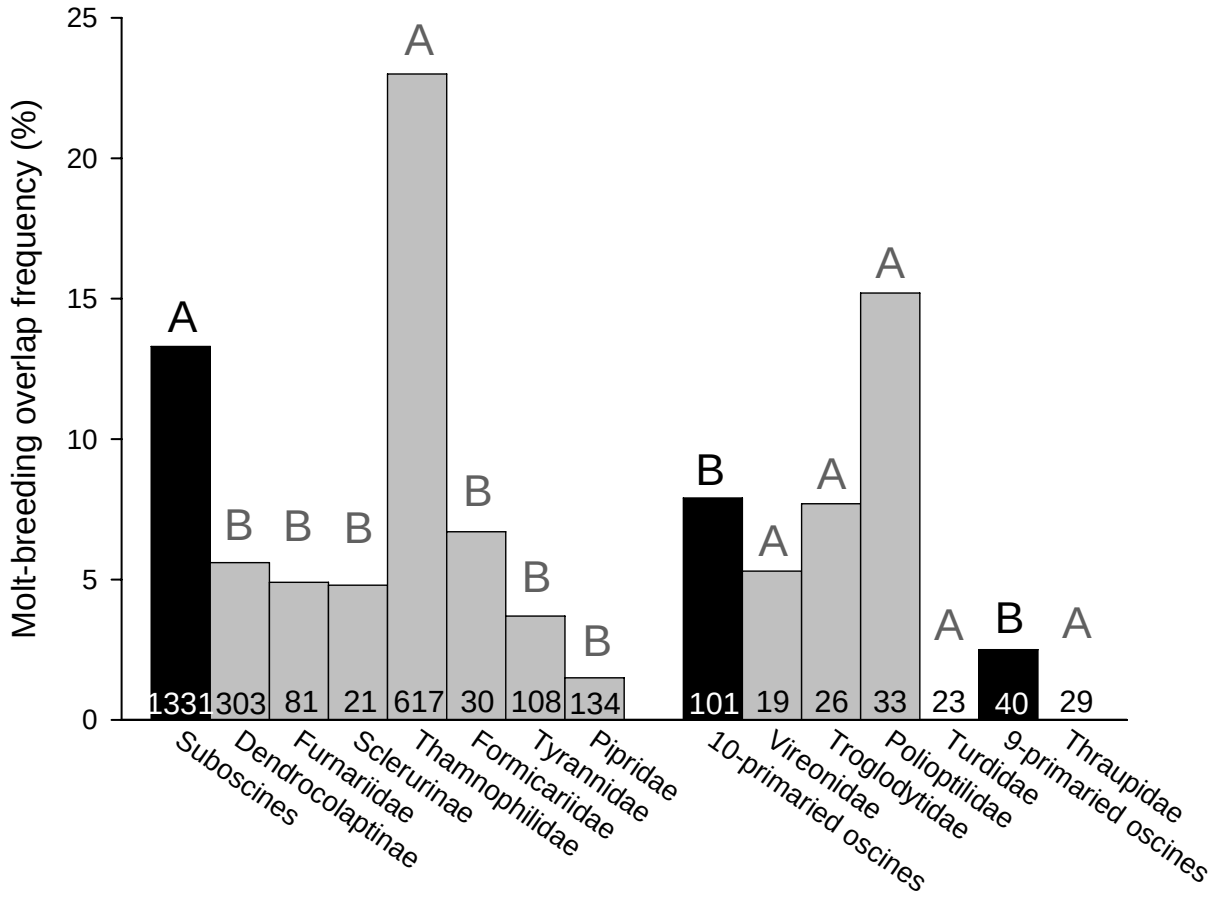


Fig. 3.2. Frequency of molt–breeding overlap by order and family (or subfamily among Furnariidae). Numbers inside bars indicate the number of individuals captured with brood patches. Letters above bars represent differences among post hoc pairwise comparisons; comparisons are made across the three suborders (black) and among families within suboscines and within 10- and 9-primaried oscines (gray).

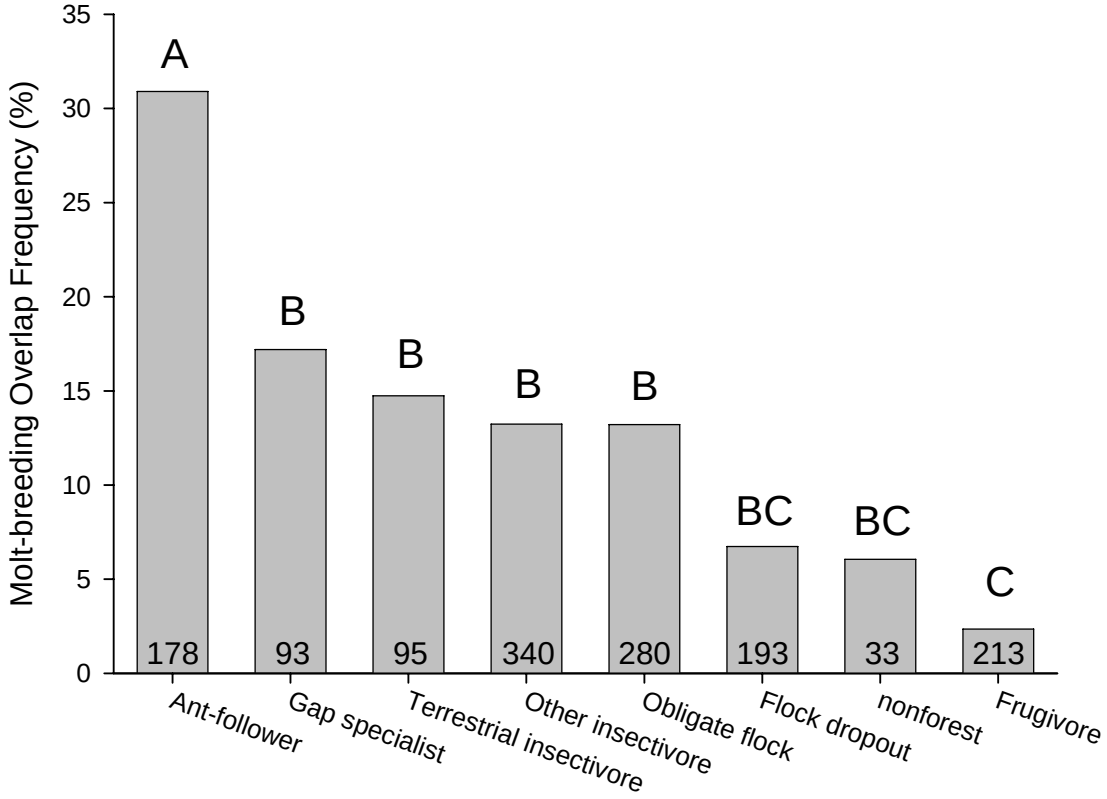


Fig. 3.3. Frequency of molt–breeding overlap by guild. Letters above bars represent differences among post hoc pairwise comparisons and the numbers within the bars represents the number of individuals with brood patches.

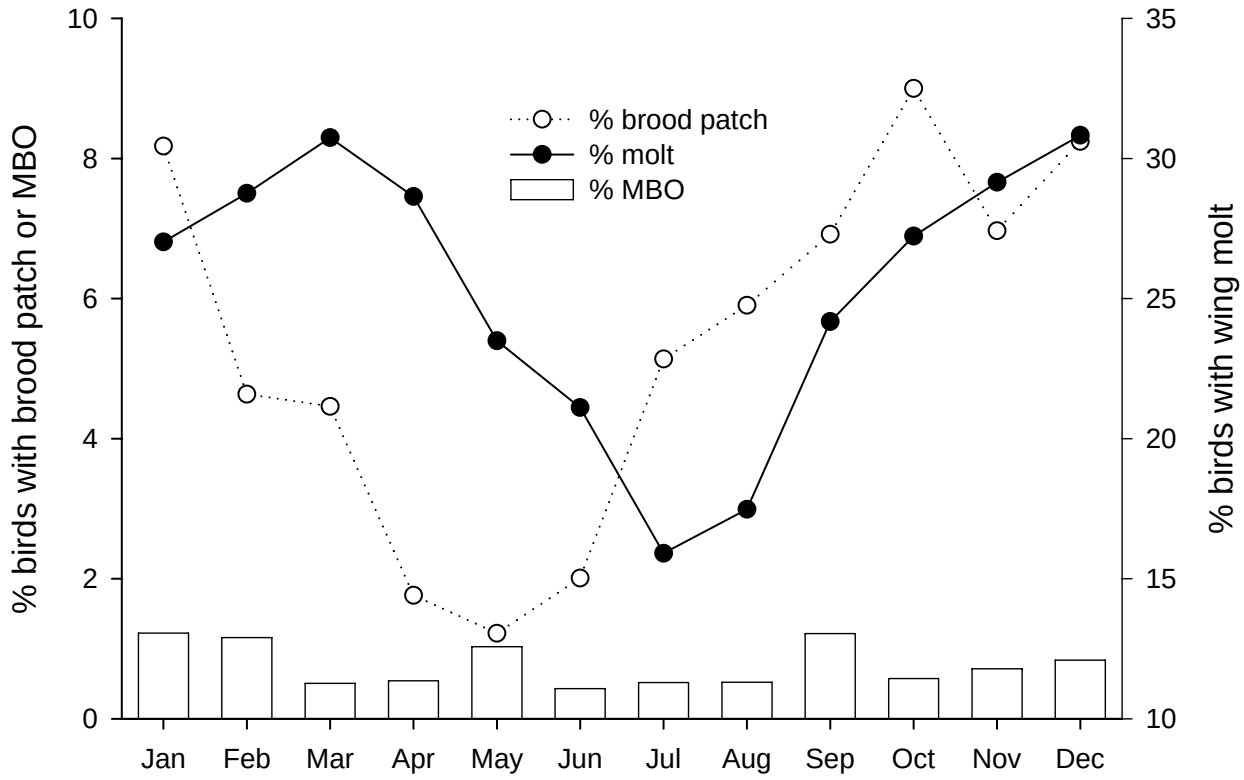


Fig 3.4. The frequency of captures with brood patches, wing molt, and molt–breeding overlap (MBO) across all 87 study species. See Table 3.1 for seasonal patterns of each species.

Table 3.1. The proportion (%) of birds that were breeding (top row for each species) and molting (bottom row for each species) in each month for 31 species near Manaus, Brazil. The color codes indicate intensity (breeding: 0–2%, 2–4%, 4–8%, >8%; molting: 0–8%, 8–16%, 16–32%, >32%). Also shown is the number of birds examined (n). I averaged the monthly population-level overlap (PO) by using the minimum value for proportion of captures either breeding or molting. See Fig. 3.4 for monthly molting and breeding frequency average across all species.

Subfamily or Family	Percent captured with active brood patch (top) and wing molt (bottom)													
Species	Jan	Feb	Mar	Apr	May	Jun	Jul	Aug	Sep	Oct	Nov	Dec	n	PO
Dendrocolaptinae														
Dendrocincla fuliginosa	0	11	6	6	0	0	6	21	14	17	15	6	287	8.1
	19	33	25	7	4	0	2	20	38	41	44	41	386	
Dendrocincla merula	7	4	7	0	3	0	3	3	8	11	17	9	573	6.1
	54	56	40	29	24	18	14	17	42	58	48	78	824	
Certhiasomus stictolaemus	0	0	0	0	0	0	3	13	17	11	20	12	589	6.4
	19	25	22	23	9	15	13	27	46	43	44	33	889	
Glyphorynchus spirurus	16	10	7	3	4	4	3	2	3	4	7	8	2200	4.7
	8	12	32	34	31	33	31	18	13	6	5	4	2771	
Xiphorhynchus pardalotus	3	0	2	0	0	1	5	15	8	9	5	2	1004	4.2
	53	34	24	23	14	11	5	17	46	52	60	60	1300	
Furnariinae														
Automolus infuscatus	6	6	3	0	9	0	6	12	11	7	0	13	514	6.1
	23	33	20	17	16	7	11	31	40	37	40	17	708	
Xenops minutus	0	13	0	0	0	0	8	6	3	11	15	0	286	4.1
	36	38	13	6	0	2	2	7	3	28	41	29	434	
Sclerurinae														
Sclerurus rufigula	13	0	14	13	19	17	3	0	0	0	0	15	275	6.6
	9	0	23	18	28	50	38	30	17	4	6	4	450	
Thamnophilidae														
Thamnophilus murinus	8	17	0	0	0	5	7	18	14	0	8	0	212	5.7
	17	14	50	33	18	28	5	14	24	40	13	53	241	

Table 3.1 Continued.

Thamnomanes ardesiacus	9	3	2	0	0	3	10	7	13	7	3	13	1002	5.7
	65	45	47	49	39	22	14	23	36	44	52	61	1387	
Thamnomanes caesius	5	0	2	0	0	0	10	9	6	7	8	13	804	5.0
	30	36	52	45	35	26	18	22	31	36	39	37	1058	
Myrmotherula axillaris	11	13	3	4	4	3	5	2	4	10	2	4	429	5.4
	34	24	26	15	23	10	14	18	31	32	48	33	549	
Myrmotherula longipennis	13	0	8	2	0	8	12	7	5	5	5	10	582	6.1
	36	17	19	11	10	10	15	30	38	47	53	35	813	
Myrmotherula menetriesii	0	0	0	8	0	6	6	6	5	13	2	0	319	3.8
	61	43	64	20	38	42	27	19	21	25	18	29	432	
Hypocnemis cantator	7	0	3	5	3	13	11	6	7	10	7	6	581	6.5
	29	36	26	37	16	20	12	17	26	26	35	37	799	
Percnostola rufifrons	3	5	13	6	3	3	5	8	10	6	13	9	813	7.0
	46	28	26	49	43	57	48	36	34	33	24	38	1061	
Myrmeciza ferruginea	0	0	31	29	7	6	12	19	31	11	8	31	258	13.8
	33	16	16	30	50	39	29	33	28	25	31	35	334	
Pithys albifrons	10	3	6	1	2	0	1	2	4	4	4	1	2086	3.1
	68	61	63	63	62	59	49	46	59	60	59	57	2636	
Gymnopithys rufigula	5	9	6	6	3	3	4	5	13	13	14	24	1144	8.8
	49	54	56	53	59	61	48	39	49	36	47	49	1548	
Willisornis poecilinota	12	9	9	4	3	2	5	5	6	8	6	8	1950	6.4
	38	40	36	37	36	29	20	8	18	28	31	35	2840	
Formicariidae														
Formicarius colma	23	14	10	9	6	0	0	4	5	6	7	25	388	3.1
	0	0	5	20	38	46	49	49	35	8	2	0	565	

Table 3.1 Continued.

Tyrannidae														
Corythopis torquatus	5	0	0	0	0	10	6	3	7	15	4	0	306	3.0
	43	32	20	10	12	5	3	3	4	13	33	55	538	
Mionectes macconnelli	5	6	13	2	0	0	1	0	0	3	3	6	1191	2.0
	2	14	12	29	18	9	4	1	1	0	1	0	1495	
Myiobius barbatus	5	0	0	0	0	0	4	4	4	4	1	0	654	1.6
	20	15	6	7	10	2	1	8	46	66	59	61	936	
Pipridae														
Lepidothrix serena	10	0	6	3	0	0	1	2	2	7	3	5	619	2.3
	10	25	22	32	8	8	3	0	0	1	1	4	706	
Pipra pipra	7	5	2	0	1	1	3	6	4	9	9	14	1878	2.9
	12	14	30	36	14	8	5	1	1	1	3	10	2248	
Pipra erythrocephala	0	0	0	0	0	0	11	0	15	24	9	33	209	0.0
	13	0	22	17	10	4	0	0	0	0	0	0	239	
Vireonidae														
Hylophilus ochraceiceps	8	0	5	0	0	0	3	10	7	4	8	0	357	2.4
	46	43	43	41	14	8	1	0	3	13	22	38	582	
Polioptilidae														
Microbates collaris	6	0	9	6	12	6	7	1	5	5	9	12	539	6.5
	31	33	37	33	19	18	12	6	12	13	26	30	824	
Turdidae														
Turdus albicollis	18	3	6	6	0	0	2	0	3	6	0	9	714	1.6
	2	22	43	51	46	23	9	2	0	0	0	0	1078	
Thraupidae														
Tachyphonus surinamus	12	16	14	0	0	0	0	0	3	15	10	6	297	4.2
	0	23	43	73	47	38	21	19	6	8	4	8	402	

frequency of molt begins to increase in September, but peaks after breeding (December–March). The proportion of captures with MBO is not correlated with monthly frequencies of brood patches (Pearson's $r = 0.24$, $P = 0.46$; Fig. 3.4), but when the proportion of breeding birds increases, significantly fewer of these have MBO (Pearson's $r = -0.65$, $P = 0.022$). In other words, MBO appears to be present at low frequencies throughout the year, but most breeding birds avoid simultaneously molting and breeding during the peak of breeding.

Correlates of Molt–Breeding Overlap

I will focus subsequent analyses on 31 species with ≥15 observed brood patches. The proportion of these populations either breeding or undergoing wing molt in each month from 1979–2009 indicates substantial variation in the timing and duration of the molting and breeding seasons among species (Table 3.1). Of these 31 species, 20 (65%) have substantially prolonged breeding (≥4% of captures) and molting (≥16% of captures) seasons that each lasted ≥6 months of the year. These prolonged breeding and molting seasons set the stage for MBO to occur at the individual-level. I asked three questions to understand whether patterns at population scales predict MBO frequency.

Does Population-level Overlap of the Molting and Breeding Seasons Predict MBO at the Individual-level?—I averaged the monthly population-level overlap (PO) by using the minimum value for proportion of captures either breeding or molting (Table 3.1). PO positively correlated with the proportion of individuals with MBO ($R^2 = 0.30$, $F_{1,29} = 12.5$, $P = 0.001$; Fig. 3.5).

Does Longer Molt Duration Increase MBO Frequency?—I used molt duration estimates attained by documenting molt extent of individual birds recaptured while progressing through a complete wing molt. Although some estimates of molt duration have lower sample sizes than others, I obtained reasonable molt duration estimates for 27 of the 31 species (average ± SE: 21.2

± 7.5 birds examined per species; Table 3.2). I excluded *Xenops minutus*, *Thamnophilus murinus*, *Pipra erythrocephala*, and *Mionectes macconnelli* because ≤ 2 molting birds were recaptured. For the 27 species analyzed, molt duration positively correlated with the frequency of MBO ($R^2 = 0.69$, $F_{1,25} = 56.9$, $P < 0.001$; Fig. 3.6) and duration of the population's molting season ($R^2 = 0.55$, $F_{1,25} = 31.1$, $P < 0.001$; Fig. 3.7).

Can Birds Adjust the Timing of Molt to Minimize MBO?—Three molt strategies emerged. First were species with short molt duration (MD) relative to their molting season (MS; MD/MS < 0.61), henceforth called *Strategy 1*. These species showed a trend for the greatest variation in initial molt date and a low frequency of MBO (Table 3.2, Fig. 3.8), suggesting they were capable of adjusting the timing of their molt to avoid overlap with breeding. Second were species with MD more similar in length to MS: *Strategy 2*. These species still had MD lasting shorter than the MS (0.61 < MD/MS < 0.84), intermediate variation in molt initiation date, the longest molt duration, and the greatest proportion of birds with MBO (Table 3.2). Species with these first two strategies had a higher frequency of MBO the closer their MD matched the MS length ($R^2 = 0.56$, $F_{1,16} = 20.8$, $P < 0.001$; Fig. 3.8). Third were species with non-overlapping molting and breeding seasons: *Strategy 3*. These species had MD lasting approximately as long as MS (0.84 < MD/MS < 1.16), little variation in molt initiation date, and a low frequency of MBO (Table 3.3, Fig. 3.8) because the molting and breeding seasons were relatively distinct (Table 3.1).

These three life history strategies appear to have a phylogenetic basis. Woodcreepers and antbirds (but also one tanager and one gnateater) typically exhibited the first two strategies, whereas *Strategy 3* species were largely flycatchers, manakins, a vireo, and a thrush, but also two woodcreepers and an antthrush (Table 3.2).

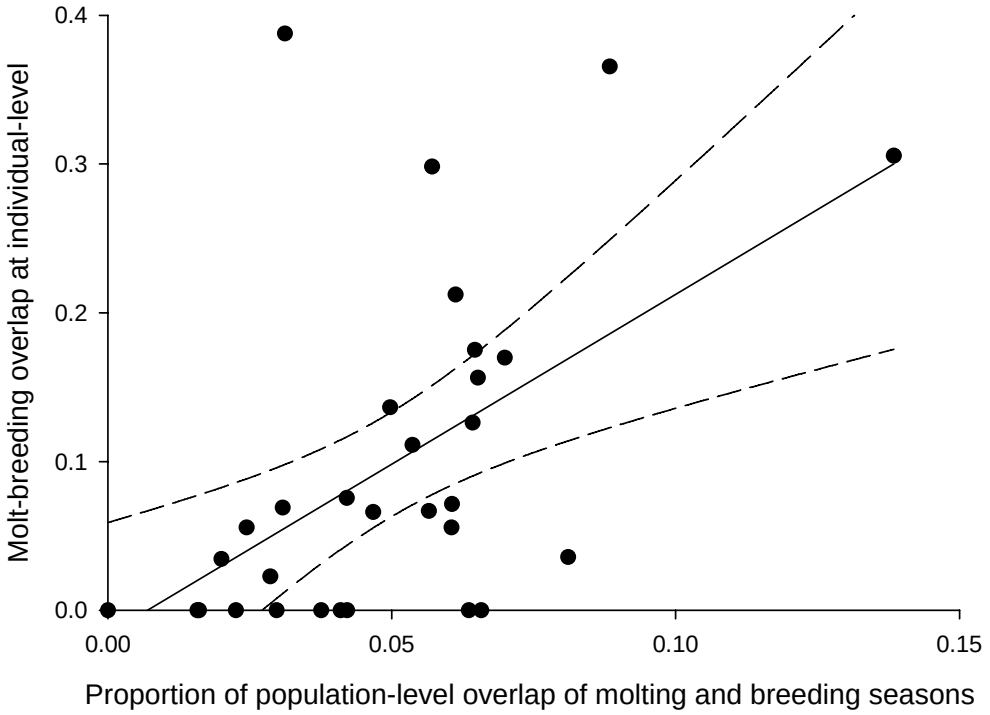


Fig. 3.5. The relationship between molting and breeding overlap at the population- and individual-levels, with regression line and 95% CI, for 31 species near Manaus, Brazil.

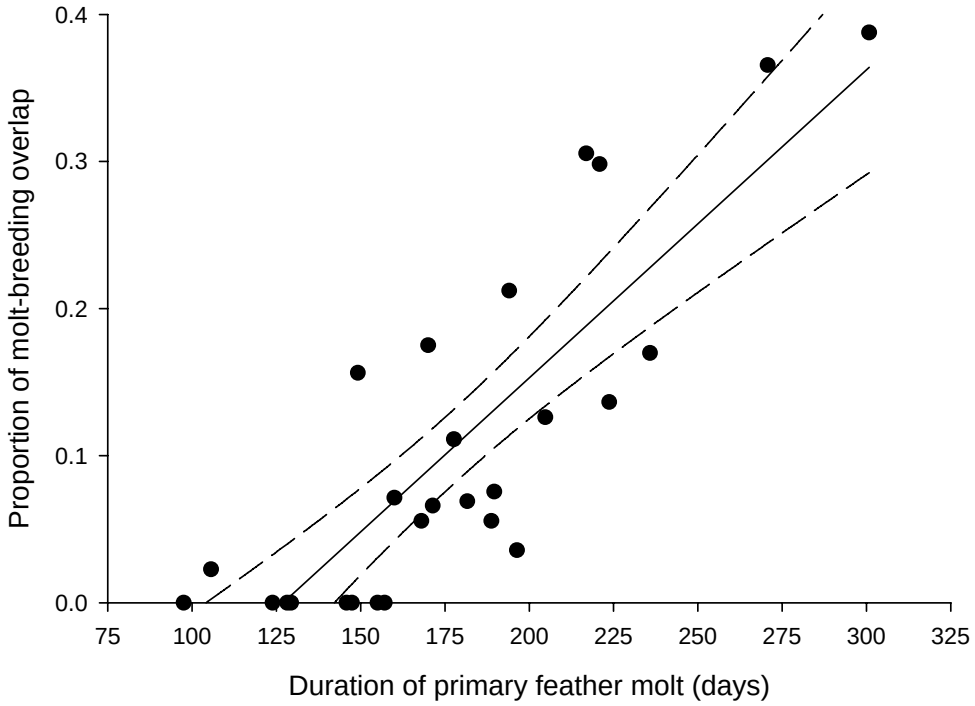


Fig. 3.6. The relationship between the duration of primary feather molt and the proportion of individuals with MBO in 27 species near Manaus, Brazil.

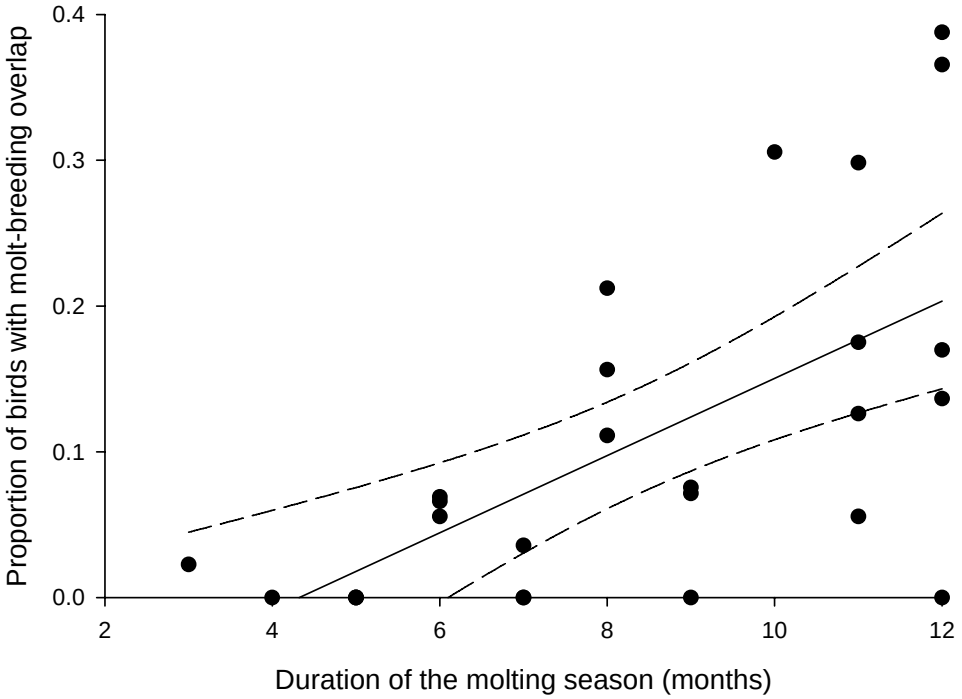


Fig. 3.7. The relationship between the duration of the molting season and the proportion of birds with MBO in 27 species near Manaus, Brazil.

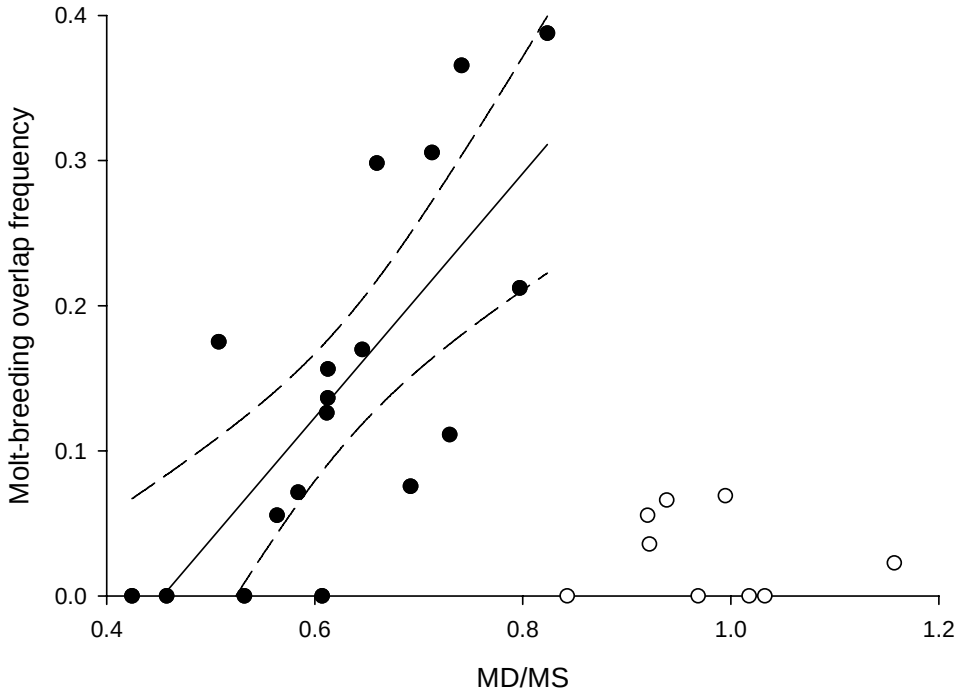


Fig. 3.7. The relationship between molt–breeding overlap frequency and the ratio of molt duration (MD) to molting season length (MS). The regression line and 95% confidence interval only includes species with *Strategies 1* and *2* (filled circles), i.e. excluding species with temporally distinct molting and breeding seasons (*Strategy 3*; open circles; see Table 3.2).

Table 3.2. Three strategies among average molt duration (MD), molting season length (MS), variation in molt initiation date (MI), population-level overlap between molting and breeding seasons (PO), and MBO frequency. Each variable was tested for differences among strategies with a 1-factor ANOVA; letters indicate Tukey-adjusted comparisons of variable means across strategies.

	Strategy 1 MD/MS < 0.61	*Strategy 2* 0.61 < MD/MS < 0.84	*Strategy 3* distinct molting and breeding seasons	$F_{2,24}$	P
MD (days ± SE)	149 ± 13 (A)	217 ± 11 (B)	153 ± 12 (A)	11.0	< 0.001
MS (days ± SE)	287 ± 23 (A)	313 ± 16 (A)	159 ± 12 (B)	15.5	< 0.001
MI (days ± SE)	25 ± 4 (A[a])	22 ± 3 (AB)	15 ± 3 (B[a])	3.3	0.056
PO (% ± SE)	5.6 ± 0.9 (A)	6.6 ± 0.7 (A)	3.3 ± 0.8 (B)	7.3	0.003
MBO (% ± SE)	4.3 ± 2.5	21.3 ± 3.3	2.8 ± 1.0	18.7	< 0.001
Species	*Dendrocincla merula*	*Xiphorhynchus pardalotus*	*Dendrocincla fuliginosa*		
	Certhiasomus stictolaemus	*Thamnomanes ardesiacus*	*Glyphorynchus spirurus*		
	Automolus infuscatus	*Thamnomanes caesius*	*Formicarius colma*		
	Sclerurus rufigularis	*Myrmotherula axillaris*	*Corythopis torquata*		
	Myrmotherula menetriesii	*Myrmotherula longipennis*	*Myiobius barbatus*		
	Hypocnemis cantator	*Percnostola rufifrons*	*Pipra pipra*		
	Tachyphonus surinamus	*Myrmeciza ferruginea*	*Lepidothrix serena*		
		Pithys albifrons	*Hylophilus ochraceiceps*		
		Gymnopithys rufigula	*Turdus albicollis*		
		Willisornis poecilinota			
		Microbates collaris			

[a] tukey-adjusted A–B difference: $P = 0.083$

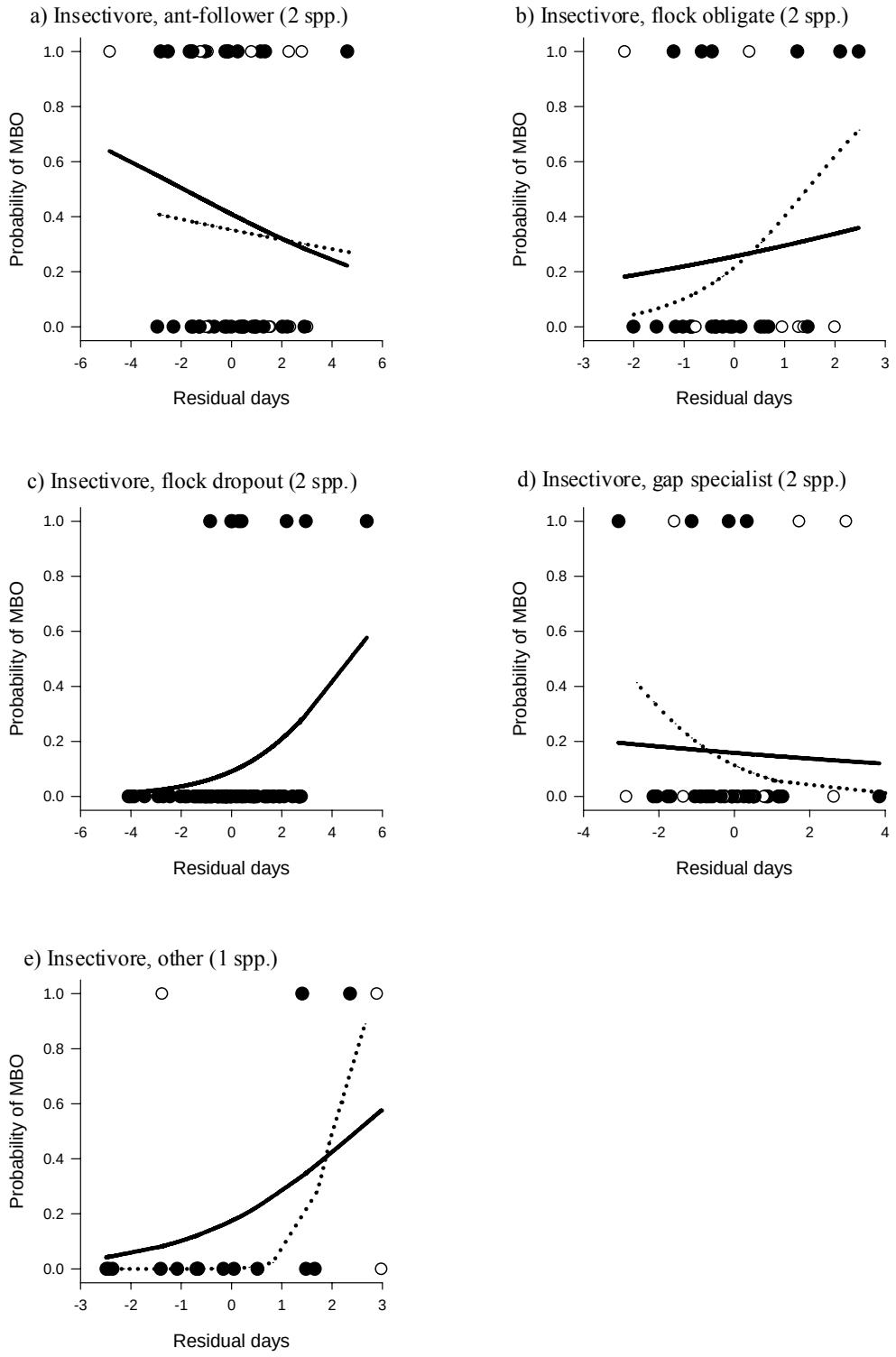


Fig. 3.8. The relationship between feather growth rate (residual of the average number of days for a tail feather to complete molting) and the probability of molt–breeding overlap (MBO) for five guilds representing nine species. Larger residuals represent slower growing feathers. Filled dots represent females and open dots represent known males. Also represented is the probability from logistic regression models for all individuals (solid line) and without males (dotted line).

Does the Molt Rate of Individual Birds Influence Their Probability of Having MBO?—I measured daily growth (rate/length) of non-induced outer tail feathers from birds with brood patches and used logistic regression to test whether individual birds that molted more slowly had an increased probability of MBO. Although there were differences among guilds (Wald's χ^2_4 = 15.5, P = 0.004), more slowly grown feathers did not increase the probability of MBO (Wald's χ^2_1 = 2.4, P = 0.12), although there may have been an interaction between feather growth rate and guild (Wald's χ^2_4 = 7.9, P = 0.096; Fig 3.8). I conducted the analysis a second time using only females and the interaction became nearly significant (Wald's χ^2_4 = 8.8, P = 0.066), indicating guild-specific responses affect the influence of feather growth rates on MBO (Fig. 3.8). Flock obligates (*Thamnomanes* spp.), flock dropouts (*Glyphorynchus spirurus* and *Xiphorhynchus pardalotus*), and other insectivores (*Willisornis poecilinota*) had increasing probabilities of MBO when feather growth rates were slower.

Molt–Breeding Overlap and Fragmentation Sensitivity

I predicted that if frequent MBO was detrimental to living in forest fragments and if birds were physiologically capable of separating the timing of molt and breeding, then birds with brood patches in fragments would be less likely to be molting simultaneously. Ten of the 31 focal species were never seen with MBO and of the remaining 21, none decreased MBO with decreasing fragment size (Table 3.3), including three species with a capacity to vary their molt initiation date (Table 3.2). Three of the 21 species, however, showed a statistical difference (P < 0.05) and one species showed a trend (0.05 < P < 0.10) for a non-linear change in MBO frequency against fragment size (*Pithys albifrons* and *Microbates collaris*, *Thamnophilus murinus* and *Myrmotherula axillaris*; Table 3.3).

Table 3.3. The number of captures with molt–breeding overlap (MBO) and breeding without molt (B) by fragment size for 31 species with ≥15 brood patches. Also shown is the chi-square statistic (χ^2, df ≤ 3) and associated *P*-value to examine differences in the frequency of MBO by fragment size. *P*-values in bold are significant ($P < 0.05$).

Species		1-ha	10-ha	100-ha	forest	χ^2	*P*
Dendrocincla fuliginosa	MBO	0	0	0	1	1.0	0.60
	B	0	4	10	13		
Dendrocincla merula	MBO	0	0	0	2	0.7	0.87
	B	2	5	2	25		
Certhiasomus stictolaemus	MBO	0	0	0	0	-	-
	B	0	1	17	23		
Glyphorynchus spirurus	MBO	1	1	4	1	5.2	0.16
	B	25	21	20	33		
Xiphorhynchus pardalotus	MBO	1	1	2	0	3.8	0.28
	B	6	10	10	23		
Automolus infuscatus	MBO	0	0	0	2	1.4	0.71
	B	1	5	5	15		
Xenops minutus	MBO	0	0	0	0	-	-
	B	1	4	4	7		
Sclerurus rufigularis	MBO	0	0	0	0	-	-
	B	0	0	4	11		
Thamnophilus murinus	MBO	0	1	0	0	6.7	0.073
	B	5	1	5	3		
Thamnomanes ardesiacus	MBO	2	1	3	11	0.3	0.95
	B	7	2	6	25		
Thamnomanes caesius	MBO	1	1	1	3	0.7	0.87
	B	4	7	12	15		
Myrmotherula axillaris	MBO	0	1	1	0	10.4	**0.015**
	B	5	0	3	8		
Myrmotherula longipennis	MBO	0	0	0	7	2.4	0.30
	B	2	2	5	19		
Myrmotherula menetriesii	MBO	0	0	0	0	-	-
	B	2	5	4	5		
Hypocnemis cantator	MBO	2	1	0	4	2.1	0.56
	B	10	3	7	13		
Percnostola rufifrons	MBO	4	1	0	4	1.1	0.78
	B	18	8	3	15		
Myrmeciza ferruginea	MBO	0	2	3	6	0.6	0.73
	B	0	5	4	16		

Table 3.3 Continued.

Pithys albifrons	MBO	0	2	0	17	7.1	**0.029**
	B	0	0	6	24		
Gymnopithys rufigula	MBO	3	5	7	19	1.2	0.77
	B	4	5	15	35		
Willisornis poecilinota	MBO	0	1	4	9	1.5	0.67
	B	3	14	18	62		
Formicarius colma	MBO	0	0	0	2	1.5	0.47
	B	0	8	4	15		
Corythopis torquatus	MBO	0	0	0	0	-	-
	B	1	3	6	7		
Mionectes macconnelli	MBO	0	0	0	1	0.3	0.97
	B	2	1	3	22		
Myiobius barbatus	MBO	0	0	0	0	-	-
	B	0	2	5	9		
Lepidothrix serena	MBO	0	0	0	0	-	-
	B	2	1	4	9		
Pipra pipra	MBO	0	0	0	2	1.4	0.72
	B	7	10	18	51		
Pipra erythrocephala	MBO	0	0	0	0	-	-
	B	2	3	4	7		
Hylophilus ochraceiceps	MBO	0	0	0	1	0.2	0.65
	B	0	0	3	14		
Microbates collaris	MBO	0	2	1	2	11.9	**0.008**
	B	4	0	6	17		
Turdus albicollis	MBO	0	0	0	0	-	-
	B	0	4	2	17		
Tachyphonus surinamus	MBO	0	0	0	0	-	-
	B	1	2	2	14		
TOTAL (21 spp w/ MBO and ≥15 brood patches)	MBO	14	20	26	93	2.3	0.51
	B	112	128	205	542		
TOTAL (all 87 species)	MBO	16	25	33	113	2.2	0.54
	B	141	175	259	710		

Because study species did not appear capable of avoiding MBO when occupying fragments (Table 3.3) and because MBO as a life-history trait may be disadvantageous for living in stressful environments (such as forest fragments compared to interior forest), I predicted that species with more frequent MBO would be more sensitive to fragmentation. I used multiple linear regression to evaluate the effect of three measures of fragmentation sensitivity on the frequency of MBO, not including preisolation relative abundance because it was highly correlated with maximum capture rate decline following isolation (Table 3.4). Across the 31 study species, greater fragmentation sensitivity predicted more frequent MBO ($R^2 = 0.34$, $F_{3,27} = 4.6$, $P = 0.010$). Each of the three measures of fragmentation sensitivity also strongly predicted MBO. First, the greatest decrease in capture rates following isolation increased MBO (Fig. 3.8; $t_{1,27} = 3.2$, $P = 0.004$). Second, the smallest change in capture rates after second growth recovered populations decreased MBO (Fig. 3.9; $t_{1,27} = -2.50$, $P = 0.018$). Third, species with greater transience had decreased MBO frequency (Fig. 3.10; $t_{1,27} = -2.9$, $P = 0.007$).

I also conducted an analysis of fragmentation sensitivity on MBO frequency using taxonomic groupings to evaluate phylogenetic effects of fragmentation sensitivity on MBO. With low sample sizes, these models were not statistically significant, but fragmentation sensitivity explained a high proportion of the variance in MBO within taxa (Furnariidae: $R^2 = 0.58$, $t_{1,6} = 1.8$, $P = 0.29$; Thamnophilidae: $R^2 = 0.26$, $t_{1,11} = 1.8$, $P = 0.41$; Tyrannidae including Pipridae: $R^2 = 0.56$, $t_{1,4} = 0.9$, $P = 0.58$; Figs. 3.11,3.12,3.13). With only three species of 10-primaried oscines and one 9-primaried oscine, I was unable to run a full multiple regression; however, combining these two suborders again indicated a high R^2 despite non-significance for each of the three fragmentation sensitivity measures in simple linear regression models (maximum capture rate decrease: $R^2 = 0.31$, $F_{1,2} = 0.90$, $P = 0.44$; minimum capture rate

decrease: $R^2 = 0.78$, $F_{1,2} = 7.0$, $P = 0.12$; transience: $R^2 = 0.85$, $F_{1,2} = 10.9$, $P = 0.081$; Figs. 3.11,3.12,3.13). In summary, the effects, although not significant probably due to very low sample sizes, suggested that the expected patterns of increasing fragmentation sensitivity corresponded with an increase in MBO frequency.

When in the Molt Cycle Does Breeding Occur?

Among Furnariidae with MBO, brood patches were observed mainly from p1–4 and p9–10, but among Thamnophilidae with MBO, brood patches were observed throughout the molt cycle (Table 3.5).

Table 3.4. Pearson's partial correlation coefficients (*r*) among four measures of fragmentation sensitivity metrics. Bold values represent significant correlations (***: P < 0.001; ** P < 0.01; * P < 0.05).

	Preisolation relative density	Maximum decline	Post-isolation recovery	Transience
Preisolation relative density	1.0	**0.93*** **	**0.42***	0.01
Maximum decline	-	1.0	**0.66*** **	-0.05
Post-isolation recovery	-	-	1.0	**-0.50****
Transience	-	-	-	1.0

DISCUSSION

Breeding and Molting Seasonality at the BDFFP

The breeding season, as measured by brood patches, peaks during the late dry and early wet season at the BDFFP for many species (October–January; Fig. 3.4), similar to other Amazonian bird communities (Verea et al. 2009). Some species, including *Dendrocincla fuliginosa*, *Percnostola rufifrons*, *Myrmeciza ferruginea*, *Gymnopithys rufigula*, and *Microbates collaris*, also have a secondary breeding peak during the wet season (often February–April). A

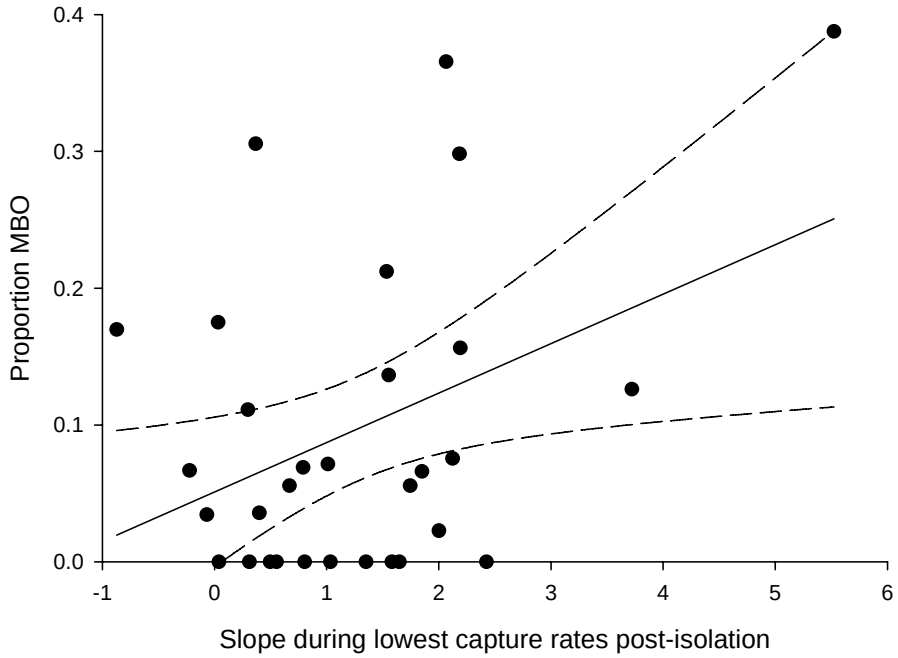


Fig. 3.8. The relationship between molt–breeding overlap (MBO) frequency and the slope across fragment size classes of minimum capture rates during post-isolation for 31 species at the BDFFP near Manaus, Brazil. The regression line and 95% confidence interval was drawn on back-transformed data (see text for statistics on arcsine-transformed MBO).

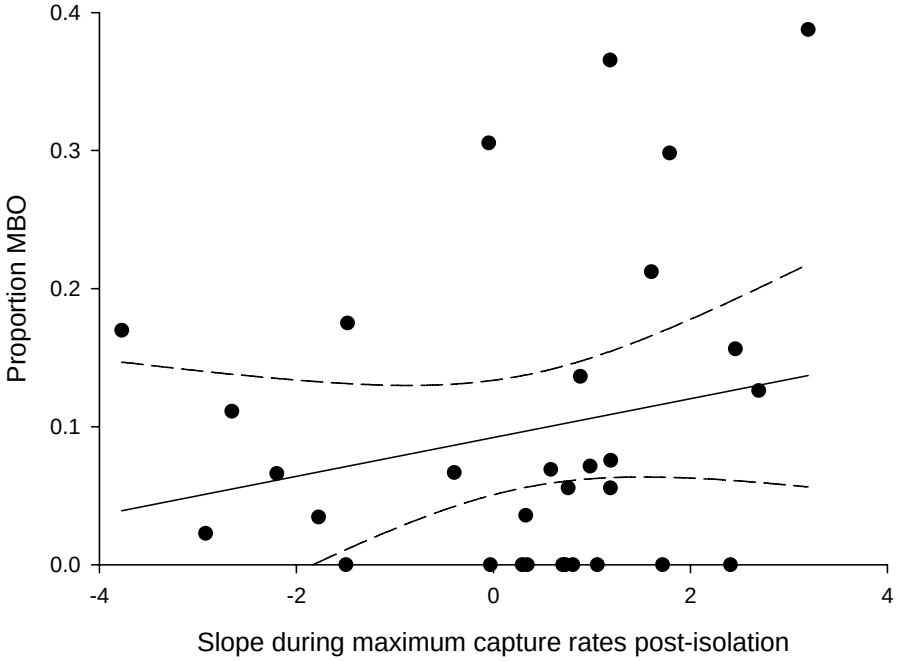


Fig. 3.9. The relationship between molt–breeding overlap (MBO) frequency and the slope across fragment size classes of maximum capture rates during post-isolation for 31 species at the BDFFP near Manaus, Brazil. The regression line and 95% confidence interval was drawn on back-transformed data (see text for statistics on arcsine-transformed MBO).

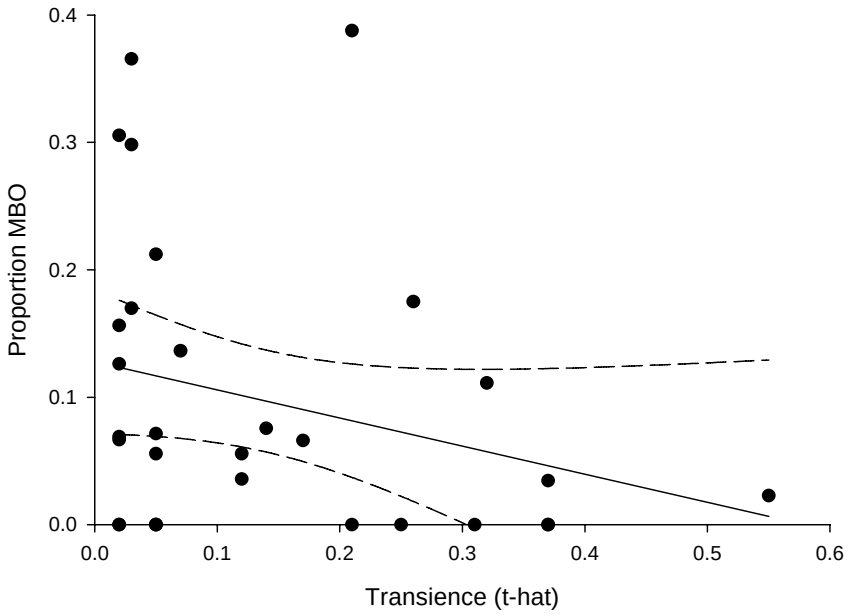


Fig. 3.10. The relationship between molt–breeding overlap (MBO) frequency and transience rates (Chapter 2) for 31 species at the BDFFP near Manaus, Brazil. The regression line and 95% confidence interval was drawn on back-transformed data (see text for statistics on arcsine-transformed MBO frequencies).

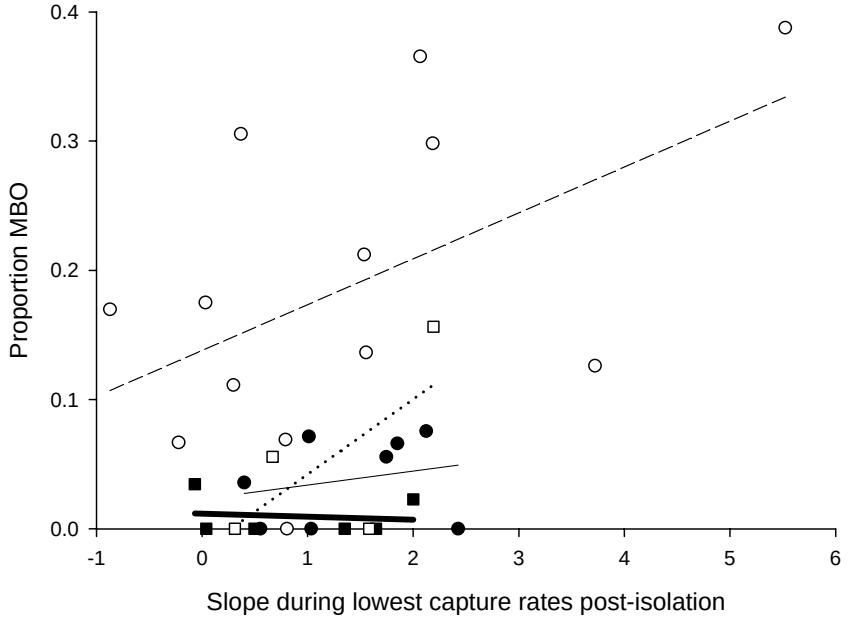


Fig. 3.11. The relationship between molt–breeding overlap (MBO) frequency and the slope across fragment size classes of minimum capture rates during post-isolation by taxonomic groupings. Regression lines were drawn on back-transformed data (see text for statistics on arcsine-transformed MBO). Furnariidae (filled circles, thin solid line); Thamnophilidae (open circles, dashed line); Tyrannidae and Pipridae (filled squares, thick solid line); oscines (open squares, dotted line).

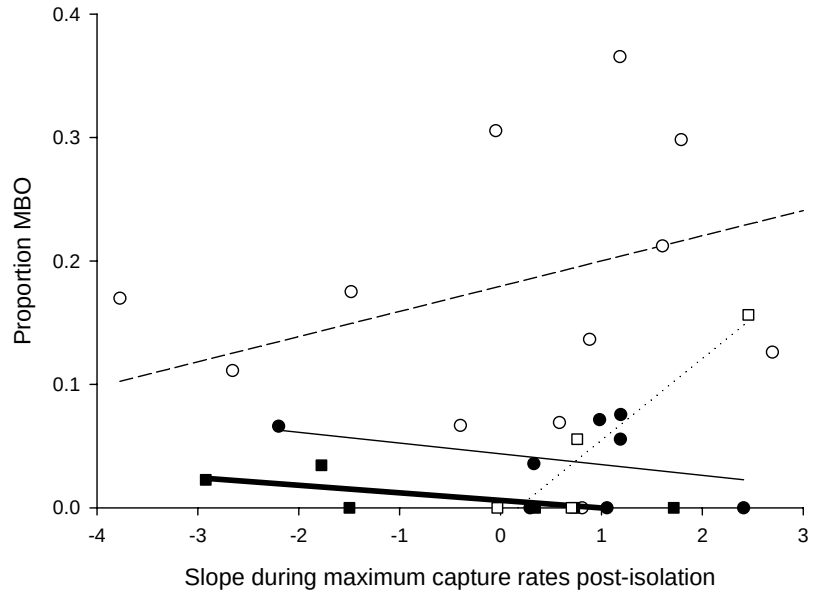


Fig. 3.12. The relationship between molt–breeding overlap (MBO) frequency and the slope across fragment size classes of maximum capture rates during post-isolation by taxonomic groupings. Regression lines were drawn on back-transformed data (see text for statistics on arcsine-transformed MBO). Furnariidae (filled circles, thin solid line); Thamnophilidae (open circles, dashed line); Tyrannidae and Pipridae (filled squares, thick solid line); oscines (open squares, dotted line).

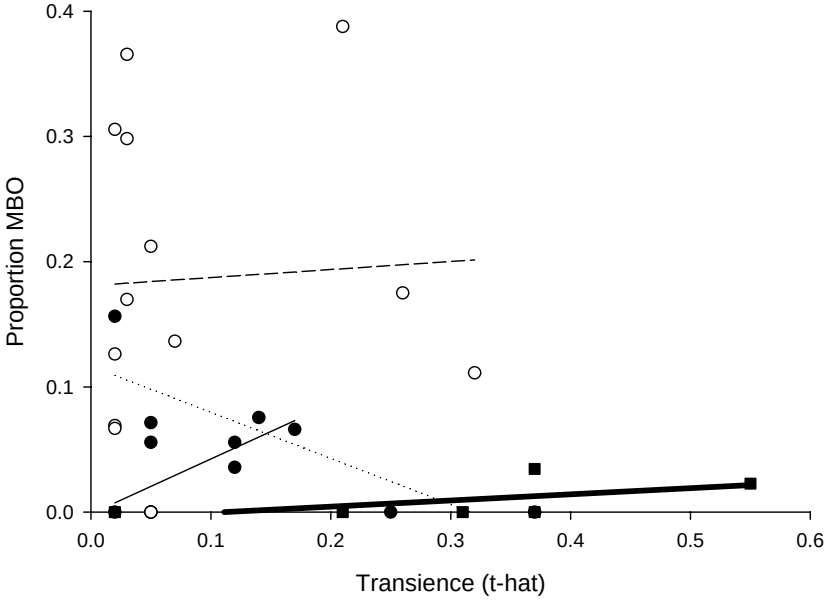


Fig. 3.13. The relationship between molt–breeding overlap (MBO) frequency and the slope across fragment size of maximum capture rates during post-isolation by taxonomic groupings. Regression lines were drawn on back-transformed data (see text for statistics on arcsine-transformed MBO). Furnariidae (filled circles, thin solid line); Thamnophilidae (open circles, dashed line); Tyrannidae and Pipridae (filled squares, thick solid line); oscines (open squares, dotted line).

Table 3.5. The number of birds with brood patches, but stage of primary feather molt (p1–10) by species and family.

Family	Primary feather molt											
Species	p1	p2	p3	p4	p5	p6	p7	p8	p9	p10	Unk	# MBO
Furnariidae	1.5	4.5	1.5	2.5	1.0	0.0	1.0	0.0	3.0	2.0	6.0	23
Philydor erythrocercum			1									1
Automolus infuscatus					1							1
Xenops minutus			0.5	0.5							1	2
Dendrocincla fuliginosa							1					1
Dendrocincla merula									2			2
Glyphorynchus spirurus	0.5	1.5		2							3	7
Dendrocolaptes picumnus		1										1
Dendrocolaptes certhia	1									1		2
Xiphorhynchus pardalotus		2							1	1	1	5
Campylorhamphus procurvoides											1	1
Thamnophilidae	16.0	17.0	17.5	16.0	10.5	13.5	11.0	13.5	12.0	22.0	19.0	171
Frederickena viridis								0.5	0.5	1		2
Thamnophilus murinus			0.5	0.5								1
Thamnomanes ardesiacus	2.5	1.5	2	1.5	1	5.5	2.5	0.5	2	1	1	21
Thamnomanes caesius	1	3.5	1	0.5				1	0.5	2.5		10
Myrmotherula gutturalis	2				2			1		1		6
Myrmotherula axillaris					1					1		2
Myrmotherula longipennis		1	1	1			1	1	2	1	1	9
Myrmotherula guttata				0.5	0.5			1				2
Hypocnemis cantator		0.5	1.5	1	1			3			3	10
Percnostola rufifrons		2		3			0.5		0.5		6	12
Myrmeciza ferruginea	0.5			0.5	1		2	2	1	1	2	10
Pithys albifrons	3	1	4	3.5	2.5	3	3	1	2	2	2	27
Gymnopithys rufigula	5.5	3.5	5	4	1	4	0.5	2	2.5	6	3	37
Willisornis poecilinota	1.5	4	1.5	1		0.5	1.5	0.5	0.5	4	1	16
Hylophylax naevia										1		1
Myrmornis torquata			1	1	0.5	0.5			1.5	0.5		5

Table 3.6. Summary of molt–breeding overlap (MBO) summaries across the tropics (<23˚ latitude) for studies reporting year-round breeding and molting phenologies for >5 species, sorted by increasing distance from equator. Region 1: Western Hemisphere, 2: Africa, 3: Asia, 4: Oceania. Molt assessment 1: wing molt only, 2: wing or body molt. Breeding assessment 1: brood patch, 2: cloacal protuberance, 3: gonad size

Latitude	Region	% MBO[a]	% all captures with MBO	% captures in breeding condition	Molt assessment	Breeding assessment	Source
2˚S	1	12.7	0.7	5.5	1	1	This study
2˚N	3	-[b]	2.0	-[b]	1	1	Yap 2005
5˚S	2	-[b]	4.2	-[b]	2	1,3	Moreau 1936
7˚S	1	0.0	0.0	24.1	1	1	Magalhaes et al. 2007
9–11˚N	1	-[b]	8.1	-[b]	1	1,3	Foster 1975
10˚N	1	-[b]	0.3	-[b]	1	1	Verea et al. 2009
18–22˚S	1	8.3	1.8	21.0	1	1	Marini and Duraes 2001
20–21˚S	1	13.1	3.2	24.7	2	1	Piratelli et al. 2000
19–20˚N	4	-[b]	3.2	-[b]	1	1,2	Ralph and Fancy 1994
22˚S	1	0.0	0.0	4.3	1	1	Mallet-Rodrigues et al. 2005
32˚S–4˚N	2	-[b]	1.5	-[b]	1	1,3	Payne 1969

[a] MBO defined as the proportion of birds in breeding condition simultaneously molting
[b] not reported by author

few species breed most frequently during the wet season (December–April), including *Sclerurus rufigularis*, *Mionectes macconnelli*, and *Turdus albicollis* (Table 3.1). Typical of most passerines, a complete post-nuptial ("pre-basic" *sensu* Humphrey and Parkes 1959, Howell et al. 2003) molt follows breeding in all study species, but may rarely be incomplete, arresting between p4 and p8, in a few individuals of *Glyphorynchus spirurus* and *Pithys albifrons*, but possibly also others (E. I. Johnson, unpublished data).

Molt–Breeding Overlap Frequency

Among passerines at the BDFFP since 1982, only 0.7% of all captures were molting and breeding simultaneously, which is arguably low compared to other tropical and subtropical communities (e.g. Foster 1975, Table 3.6), but differences in how MBO frequencies are calculated prohibits direct comparisons. MBO frequency measured by the proportion of birds simultaneously molting and breeding among all captures is often erroneously reported because this metric includes non-breeding season captures and demographic groups that do not typically develop brood patches (like males of some species or subadults). Instead, MBO should be reported as the frequency of birds in breeding condition that are simultaneously molting, as I have done. At 18–22˚S, Marini and Durães (2001) found 8.3% MBO when expressed as the percentage of breeding birds simultaneously molting. This is consistent with Foster's (1975) results: 8.1% MBO at 10˚N and 12.7% at the BDFFP (2˚S). Once outside of Amazonia, MBO frequencies may decrease (as in Foster 1975, Marini and Durães 2001), but geographical patterns are difficult to confidently discern because so few community-level datasets are available, and because MBO frequencies likely depend on the biome, region, and taxonomic composition of the avian community (e.g., Poulin et al. 1992, Mallet-Rodrigues et al. 2005, Magalhães et al. 2007; Table 3.6, Fig. 3.2). Other studies reported only the percentage of all captures with MBO and

did not report the number or proportion of captures in breeding condition, making it impossible to assess the true frequency of MBO (e.g. Ralph and Fancy 1994, Yap 2005, Verea et al. 2009; Table 3.6). Certainly, much study remains to document regional patterns in MBO because of both inconsistencies in reporting appropriate metrics, and inconsistencies in how to define molting and breeding (Table 3.6).

In a seminal paper, Foster (1975) suggested that MBO was frequent in a variety of tropical species from Costa Rica and probably throughout the tropics. Her criteria for breeding included enlarged gonads, but few specimens included data on the presence or absence of a brood patch, which may have created an overestimate of MBO frequency because enlarged gonads can be maintained year-round in many tropical species (Moreau 1936, Miller 1962, Snow and Snow 1964, Davis 1971, but see Wikelski et al. 2003a). Regardless, MBO has since been confirmed in many species throughout the Neotropics (Avery 1985, Piratelli et al. 2000, Marini and Durães 2001, Rohwer et al. 2009, but see Wikelski et al. 2000). MBO among passerines at the BDFFP is especially pervasive (12.7% of all breeding individuals). Of 31 species with ≥15 brood patches, at least one individual was molting and breeding simultaneously in 21 of these species. Of the remaining 56 species (with <15 brood patches), MBO was observed in 21 of these. MBO frequency was greatest in the two ant-followers, *G. rufigula* and *P. albifrons*, with at about 1/3 of all birds with brood patches simultaneously molting remiges.

One reason why such a low proportion of individuals were observed to simultaneously breed and molt (0.7%) at the BDFFP was because so few were in breeding condition (5.5%). This breeding frequency is much lower than several tropical and subtropical year-round studies that report >20% of captures with brood patches (Table 3.6). This reduced breeding frequency at the BDFFP may be typical of central Amazonia, perhaps because not every breeding pair

attempts to breed each year. Alternatively, brood patches may not fully develop in some groups (e.g., ant-followers) as nesting may occur sporadically in response to ephemeral and unpredictable resource availability.

Correlates of Molt–Breeding Overlap

The duration of molt at least partially explained MBO frequency at the BDFFP: species with greater MBO frequency were those with prolonged molts, often taking at least 150 days to complete primary feather replacement (Fig. 3.6). From an energy budget perspective, it may be particularly costly to molt and breed simultaneously if energetic resources are dedicated to a rapid molt. By slowing the rate of molt, daily energetic demands may be reduced and would minimize costs of MBO. A slow molt that decreases the gap in the flight feathers may also reduce predation risk, especially during take off, and may ensure greater feather quality or allow resources to be diverted to increased immunological vigor (Slagsvold and Dale 1996, Hedenström and Sunada 1999).

The length of the molting season and amount of overlap with the breeding season also predicted MBO frequency. In particular, a number of species had overlapping molting and breeding seasons, but those with relatively short molts apparently adjusted the timing of molt initiation and avoid MBO. *G. rufigula* and *P. albifrons* represented the extreme in seasonal strategies, with at least 36% in *G. rufigula* and 46% in *P. albifrons* molting year-round and individuals taking 10–11 months to complete their wing molt. These species may not follow an annual cycle, instead breeding when highly unpredictably local conditions are suitable (i.e., when enough ant swarms in their home range are simultaneously swarming [J. Chaves-Campos, personal communication]). From 2007–2009, I noted two *P. albifrons* that temporarily arrested their molt for 1–3 months and then continued molting later; this pattern was also evident five

times in the BDFFP database before 2007. From 2007–2009, I also noted five cases of individuals that arrested wing molt (as in an incomplete molt, *sensu* Pyle 1997), but I never recaptured these birds to determine whether molt reinitiated. Presumably this arrested molt coincides with a breeding attempt, but many individuals may not be physiologically capable of arresting molt before breeding begins, thus accounting for the high proportion of *P. albifrons* with MBO.

I showed that decreased feather growth rates increased an individual bird's probability of having MBO in 5 of 10 species. To my knowledge, this has not been demonstrated before and provides a unique insight into how individual birds physiologically strategize their molting and breeding schedules. Decreased feather growth rates can be caused by nutritional deficiencies (Grubb 1989), such as those experienced in forest fragments (Stratford and Stouffer 2001). Thus, decreased nutritional condition caused by forest fragmentation may not only be directly detrimental to body condition, but it could also increase the probability of MBO and indirectly decrease the suitability of forest fragments to birds (see below).

MBO occurred nearly throughout the molting cycle in Furnariidae and completely throughout molting cycle in Thamnophilidae. Given that brood patches for a single brood may last up to four weeks and these taxa complete primary molt in about 100–300 days, most birds with a brood patch and with even p1 or p2 molting were probably physiologically prepared to breed. This suggests that the internal mechanisms that regulate molt and breeding may be distinct in these families, especially in Thamnophilidae.

Molt–Breeding Overlap as an Indicator of Fragmentation Sensitivity

Because molting and breeding are each energetically demanding, their overlap may be particularly challenging; thus, incorporating MBO into a species' life history should follow

sufficient and predictable resource availability. Therefore, I predicted that increasing frequency of MBO becomes increasingly disadvantageous for living in seasonal environments. Indeed, MBO was not observed in arid tropical habitats in Venezuela with pronounced seasonality (Poulin et al. 1992). Amazonian rainforest fragments are more seasonal than continuous forest, with greater daily and annual variation in temperature, humidity, wind, and light (Endler 1993, Laurance et al. 2002, Walther 2002). Species did not appear to be capable of adjusting MBO when occupying forest fragments, suggesting that this life history trait was not particularly flexible in the face of changing abiotic (and biotic) conditions at the local level, or that different abiotic conditions in fragments were not strong enough to elicit a change. Either way, my prediction was supported by the data the BDFFP: species with greater MBO typically were more sensitive to fragmentation.

Despite the strong relationship between MBO and fragmentation sensitivity, species with low MBO showed greater variation in fragmentation sensitivity, whereas species with high MBO were nearly always fragmentation sensitive (Figs. 3.8, 3.9, 3.10). Clearly, a variety of other traits are linked to fragmentation sensitivity, such as home range size, body size, and foraging strategy (Henle et al. 2004, Stouffer et al. 2006). In particular, several fragmentation-sensitive species without MBO were obligate mixed-flock species (e.g., *Certhiasomus stictolaemus*, *Xenops minutus*, *Myrmotherula menetriesii*) and their disappearance likely is linked to the collapse of flocks as the nuclear *Thamnomanes* spp. with high MBO disappeared. In a second example, two terrestrial insectivores, *Sclerurus rufigularis* and *Corythopis torquatus*, did not have MBO, but were very sensitive to fragmentation, typical of Amazonian terrestrial insectivores (see Chapter 2 for a discussion on terrestrial insectivore sensitivity).

Notable exceptions of species with high MBO, but low fragmentation sensitivity, were seen in the gap specialists, *Percnostola rufifrons* and *Hypocnemis cantator*. By living in gaps, these species likely experience greater daily and seasonal variability in abiotic conditions than did typical understory species, but their high frequency of MBO does not appear to be disadvantageous to these conditions. Thamnophilidae in particular have prolonged breeding and molting seasons and frequent MBO (see also Ryder and Wolfe 2009, Wolfe et al 2009) so it is unclear if frequent MBO in thamnophilid gap specialists represents phylogenetic stagnation or adaptive specialization. Even within the Thamnophilidae, increasing MBO increases with fragmentation sensitivity, with these gap specialists being notable exceptions. Given that we know so little about resource use and its seasonality in most Amazonian species, more study is needed to understand how these gap specialists interact with the environment – it may be that increased productivity in gaps may actually increase resource predictability, i.e., decrease apparent seasonality and promote MBO.

Evolutionary Considerations of Molt–Breeding Overlap

Taxonomic patterns of MBO frequency among 87 passerine species coupled with an understanding of how MBO increases sensitivity to more seasonal abiotic conditions provides insight into why temperate species typically do not molt and breed simultaneously. It also becomes impossible to avoid the question why some taxa "escaped" the tropics while others did not. Among suboscines with MBO, Funariidae are more widespread and may be more physiologically predisposed to regulate the independence of molting and breeding than Thamnophilidae for example. Thamnophilidae are among the most biogeographically restricted among the families I examined (del Hoyo et al. 1992–2010), at least for those with larger sample sizes, and this may be partially explained by their apparent inability to regulate the independence

of molting and breeding cycles. Families of the Tyrannini (i.e., Tyrannidae, Pipridae, Cotingidae, Tityridae) have the lowest MBO among the suboscines. Although the latter three are largely frugivorous and may be limited to the tropics because of the year-round availability of fruit, the Tyrannidae have done well in temperate environments.

Particularly well-represented in temperate regions of the Western Hemisphere are 9-primaried oscines and several 10-primaried oscine clades. Interestingly, these are the groups that have among the lowest MBO frequency at the BDFFP. Although there is large variation especially within the 10-primaried oscines, the Polioptilidae is largely a tropical family and in this dataset is represented by strictly tropical genera. *Pheugopedius*, *Troglodytes*, and *Turdus* all have temperate congeners (or near congeners) and MBO was not observed in these genera at the BDFFP.

By no means to do I suggest that MBO is the primary mechanism for understanding patterns of global biogeography. Instead, I see it as a trait that encompasses several other life history traits, such as prolonged molt and prolonged breeding. Adapting to temperate environments may require specifically regulating molt or breeding duration or both, thus indirectly decreasing the frequency of MBO. MBO frequency is also not necessarily phylogenetically rigid. Groups with temperate representatives, such as the Troglodytidae, Polioptilidae, and Cardinalidae that have species that breed and molt simultaneously in tropical zones (see also Marini and Durães 2001), but apparently rarely in temperate zones. This may not be surprising as the physiological controls that respond to photosensitivity and especially photorefractoriness can be plastic within groups (Hahn and McDougall-Shackleton 2008).

Although there is still a lot to learn about the physiology allowing MBO to exist and the role of the environment on MBO, this research suggests that it is relevant to understanding

fragmentation sensitivity in central Amazonian birds. Future studies of MBO should report both the proportion of total birds with MBO as well as the proportion with breeding evidence that are simultaneously molting. This will facilitate cross-regional comparisons to understand the frequency, extent, and variation of breeding, molting, and their overlap among tropical birds. Because this trait appears to be useful for understanding life history variation and its role in sensitivity to anthropogenic landscape change in the central Amazon, I suggest that it will provide a new tool for researchers to understand fragmentation sensitivity in birds.

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CHAPTER 4: AVIAN ECTOPARASITE ASSEMBLAGES ON AMAZONIAN BIRDS IN A FRAGMENTED LANDSCAPE

INTRODUCTION

Despite interest in the study of avian ectoparasites over the last half century, the field is still in its infancy because of the limited number of dedicated researchers, including specialized taxonomists of these diverse groups, and the magnitude of host and parasite species involved. Although there are recent advances in describing host–ectoparasite associations in the northern temperate zone (e.g. Gaud and Atyeo 1996, Price et al. 2003, Proctor 2003) and even to some degree in the tropics and southern latitudes (Clayton et al. 1992, Lindell et al. 2002, Price et al. 2003, Stornl et al. 2005), there are large gaps in our understanding of ectoparasite assemblages (but see Clayton and Tompkins 1995, Lindström et al. 2009), especially in the Amazon Basin. No study to my knowledge has simultaneously examined patterns of multiple ectoparasite orders on Neotropical bird hosts. Furthermore, few studies have examined the effects of anthropogenic habitat modification on parasite community organization (Lindell et al. 2002, McCallum and Dobson 2002, Vögeli et al. 2011). In this chapter, I examine variation in ectoparasite assemblages on a variety of bird species in a human-modified Amazonian landscape.

Avian ectoparasites include chewing lice (Insecta, Phthiraptera), mites and ticks (Arachnida, Acari), fleas (Insecta, Siphonaptera), and flies (Insecta, Diptera). Phthiraptera include lice in the suborders Amblycera, Ischnocera, and Rhynchophthirina; the latter are not parasitic on birds. Phthiraptera complete their entire life cycle on the bodies of hosts; they die in a few hours to a few days without their host. They are oviparous and have three larval instars, which generally have similar foraging behaviors as adults. They range in size from < 1 to 10 mm, are dorso-ventrally flattened, and are wingless (Marshall 1981). They do not stray from the

host, but can be transferred between individual hosts by direct contract during social encounters or through phoresy on Hippoboscid flies (horizontal transmission) and during care of young (vertical transmission; Keirans 1975, Clayton and Tompkins 1995, Lee and Clayton 1995, Rózsa et al. 1996).

Mites, ticks, fleas, and parasitic flies typically complete at least one part of their life-cycle away from the host, but there is tremendous variation in their life histories. Some spend much of their time away from the host and will only opportunistically feed on birds (e.g. ticks, fleas) whereas others live in nest materials, such as the mite genera *Dermanyssus* and *Ornithonyssus* (order Mesostigmata; Clayton and Tompkins 1995, Proctor and Owens 2000). Some feather mites (order Astigmata) live in feather quills and eat the pith, but many other feather mites do not destroy feathers and instead live on feather surfaces consuming uropygial oils, fungi, pollen spores, and other debris (Proctor and Owens 2000). Horizontal and vertical transmission in mites can occur much like in lice and include direct contact as well as phoresy on Hippoboscid flies (Hill et al. 1967, Philips and Fain 1991, Proctor 2003, but see Jovani et al. 2001).

Patterns of avian ectoparasite abundance and diversity may be expected to vary across a gradient of habitat quality resulting from habitat fragmentation, but the conclusions from the few studies examining such patterns are conflicting. For example, several studies suggest that endoparasite abundance and prevalence increase with increasing fragmentation and human disturbance in Afrotropical primates (Gillespie and Chapman 2006, Mbora and McPeek 2009). In constrast, Vogeli (2011) found that populations of Dupont's Lark (*Chersophilus duponti*) isolated in fragments showed that diversity of bacteria, viruses, and protozoans decreased as fragement size decreased, which was associated with decreased host density. Avian ectoparasite

loads in southeast Asian fragments did not differ with variation in fragment size (Sodhi 2002), nor did ectoparasite loads differ across a range of fragment sizes in the Afrotropics (Bobo 2007). For the European Blackbird (*Turdus merula*), avian malaria, haematazoa, and ticks (*Ixodes* sp.) were more prevalent in more natural forest and rural habitats than in urban habitats; the absence of parasites may be one factor facilitating colonization of unnatural urban environments in these blackbirds (Gregoire et al. 2002, Geue and Partecke 2008, Evans et al. 2009). Thus, the relationship between fragmentation and parasitism remains unclear with conflicting outcomes and may be situation and taxon dependent.

I examined patterns of ectoparasite load (defined to include prevalence [presence–absence], abundance [number of individual ectoparasites per individual host], and richness [number of ectoparasite species per individual host]) from 23 passerine host species near Manaus, Brazil. I first examined patterns of ectoparasite load across the 23 host species for Astigmata feather mites, haematophagous mites (including Prostigmata, Mesostigmata, and Ixodida), and chewing lice to determine whether there were differences in ectoparasite loads by host taxonomic groupings or body size (Rózsa 1997, Clayton and Walther 2001). I then tested whether ectoparasite communities responded to two habitat types utilized by their hosts, forest edge and interior forest. Complex reciprocal host–parasite relationships, variation in life history strategies of host and parasite taxa, and the lack of consistency from the few previous studies makes it difficult to predict how ectoparasite loads are affected by forest fragmentation (Blanchet et al. 2009). I expected hosts in poor quality habitat could be more susceptible to ectoparasitism by not effectively defending themselves in suboptimal habitats (Quillfeldt et al. 2004). Alternatively, hosts in suboptimal habitat could instead have fewer ectoparasites if reduced habitat quality decreases the quality of hosts, thus hosts would provide fewer resources for

ectoparasites (Tschirren et al. 2007, Bize et al. 2008). Even so, correlates of ectoparasite abundance are challenging to interpret without an experimental approach of understanding the complex interplay between hosts and their ectoparasites; I will further explore the consequences of habitat fragmentation on host–ectoparasite dynamics using an experimental approach in Chapter 5.

METHODS

Bird Sampling and Target Species

I conducted this study during three dry seasons (June–November) from 2007–2009, although in 2009 I only sampled in June and July. Birds were captured with mist-nets set at ground level in 1-, 10-, and 100-ha fragments in 2007 and 2009 and in continuous forest in 2008. Nets were arranged inside and along the borders of fragments (see Chapter 2 for details).

I considered two types of habitat: interior forest and forest edge. Forest interiors were sampled in all three field seasons whereas edges were sampled in 2007 and 2009, thus there should be little, if any, bias due to annual differences in climate or other factors. Biases were further minimized because the timing and intensity of the wet and dry seasons were similar 2006–2008, averaging 2714 (SE ± 22) mm of rainfall per year.

To assign individuals to edge or interior habitat types, I used mist-net capture locations (border nets and interior nets) and information from spot-mapping surveys (Johnson et al. 2011, E. I. Johnson, unpublished data) of color-banded and unbanded birds to categorize their space use in the fragmented landscape. In continuous forest, home range sizes of target species were at least 4 ha (Johnson et al. 2011), thus I considered all captures in and around 1-ha fragments to be occupying edge habitat. In 10-ha fragments, all target species were frequently encountered along fragment edges and neighboring second growth, even if their home range included the fragment

interior (unpublished data), thus I considered 10-ha fragments to also be edge. In 100-ha fragments all species were considered to occupy edge habitat if ever captured or seen (using unique color-band combinations) along fragment edges, but were otherwise considered to occupy interior habitat if never captured at least 100 m from the fragment edge. This distinction between edges and interior forests is supported by stable isotope studies of moisture gradients; by 100 m from the edge within 100-ha fragments the understory microclimate is similar to continuous forest, whereas 1- and 10-ha fragments have signatures similar to surrounding second growth (Kapos 1989, Kapos et al. 1993).

For this analysis, I studied 23 target bird species from seven families and six ecological guilds (Appendix A) and used these same bird groups for an ectoparasite-removal experiment (Chapter 5) based on their high rates of capture and recapture in multiple fragment sizes (Stouffer and Borges 2001, S.G.W. Laurance et al. 2004, Stouffer et al. 2006).

Ectoparasite Quantification and Removal

For feather mites (Astigmata), I quantified ectoparasite load by assessing the intensity of infestation on wing feathers using an Astigmata wing mite index (WMI; McClure 1989, Behnke et al. 1995, Wiles et al. 2000). By holding the spread wing against ambient light, one can see mites on those feathers. I scored each flight feather on a scale from 0–3 (0 = no mites, 1 = 1–10 mites, 2 = 10–100 mites, and 3 = >100 mites. The scores were then antilog-transformed and averaged across feathers.

I used a technique called dust-ruffling to remove ectoparasites (Walther and Clayton 1997) from a subset of captured individuals from 22 bird species, excluding *Pipra erythrocephala* because of low sample size (see also Chapter 5). I dust-ruffled birds by sprinkling pyrethrin powder (Zema, Research Triangle Park, North Carolina) over the body with

special care to avoid contact with the eyes and bill (Walther and Clayton 1997). I then placed birds in a cloth bag for six minutes to let the pyrethrin kill ectoparasites, and subsequently agitated its feathers with my hands and emptied the contents of the bag over white paper to collect ectoparasites. I reused cloth bags, but thoroughly washed them between usages to minimize ectoparasite contamination between hosts. Although dust-ruffling does not remove all ectoparasites from the host, it removes 10-40% of louse load after three minutes of pyrethrin treatment, and the collected abundance is highly corrected ($0.83 < R^2 < 0.94$) with actual abundance (Clayton and Drown 2001). Although I doubled the exposure time to pyrethrin used by Clayton and Drown (2001) to remove additional ectoparasites, this experiment should be interpreted as a conservative assessment of ectoparasite removal.

I counted the total number of Astigmatid feather mites (here after Astigmata), haematophagous mites (including Mesostigmata, Prostigmata, and Ixodida), and Phthirapteran chewing lice (here after lice). In total I removed ectoparasites from 907 hosts, although I focused on 270 samples collected from adults of the same 22 host species that were used for the ectoparasite-removal experiment outlined in Chapter 5. Dust-ruffling rarely removed fleas, so I excluded them from the study (but see Appendix C). To determine whether the WMI accurately predicted load, I linearly regressed ectoparasite load against WMI after natural-log-transforming both variables.

Patterns of Ectoparasite Load and Prevalence

Ectoparasite abundance often follows a negative binomial distribution, so I tested whether my data fit this distribution using the program Quantitative Parasitology 3.0 (Rósza et al. 2000) for Astigmata, haematophagous mites, and lice. For all ectoparasite taxa across all hosts, abundance frequency distributions fit the negative binomial distribution as expected (all *P*

> 0.05). I also used Quantitative Parasitology 3.0 to calculate prevalence (presence–absence), mean abundance, and their bootstrapped 95% confidence interval based on 1000 resamples. Quantitative Parasitology 3.0 also calculates Poulin's (1993) index of discrepancy, which is a measure of the difference between the observed abundance distribution and an equal number of parasites on all hosts and ranges from 0 (equal distribution) and 1 (greatest aggregation). I calculated mean richness of the number of ectoparasite species/individual and 95% confidence intervals for each host species by hand.

I determined if host body size was a good predictor of mean ectoparasite (Astigmata, haematophagous mite, or louse) abundance or richness using general linear models (proc reg, SAS Institute 2003). Average richness across species satisfied parametric statistical assumptions of normality. I log-transformed host body mass as I expected the relationship to be non-linear, as in species–area accumulation curves (Preston 1962, Rozenzweig 1995).

Host Age and Habitat Effects on Ectoparasite Load and Richness

I aged birds as immature (< 1 years old) or adult (> 1 years old) using plumage and molt criteria (E. I. Johnson, unpublished data; see also Chapter 2, Ryder and Durães 2005, Ryder and Wolfe 2009) to determine whether there were differences in WMI by bird age and habitat type using a generalized linear model (proc genmod, SAS Institute 2003) assuming a negative binomial distribution with ectoparasite (Astigmata, haematophagous mite, or louse) abundance as the dependent variable and bird age, habitat type, and their interaction as fixed independent variables.

Because I only counted Astigmata, haematophagous mites, and lice on adult birds, I used similar generalized linear models, but only including habitat type as a fixed predictor variable. I used general linear models (proc reg and proc mixed, SAS Institute 2003) to determine whether

variation in ectoparasite richness (dependent variable) was due to host habitat type (independent variable). I did not assess differences in prevalence by habitat type because Astigmata were nearly always present and haematophagous mite and louse prevalence were not more informative than richness because of few ectoparasite taxa involved with only a maximum of two haematophagous mite taxa and three louse taxa.

RESULTS

I assigned a wing mite index (WMI) to 2888 captured individuals of the 23 target passerine bird species. Although I removed ectoparasites from 907 birds during the study period, here I focus on 270 individuals representing 22 species. Appendix C lists all ectoparasite taxa (identified to the lowest possible taxonomic level) found on each host species.

Accuracy of Wing Mite Index

The WMI significantly predicted Astigmata abundance as determined from dust-ruffling for all taxa combined and for all guilds and taxonomic classifications, and individual host species with > 15 samples (Table 4.1, Fig. 4.1). The WMI was not useful for predicting haematophagous mite or louse abundance (Table 4.1, Fig. 4.1). I therefore used the 2888 individuals with a WMI for the subsequent analysis simultaneously testing bird age and habitat effects on Astigmata abundance. To assess patterns of haematophagous mite and louse abundance, I instead used the smaller set of 270 samples.

Patterns of Ectoparasite Abundance and Richness

Astigmata, haematophagous mite, and louse abundance followed a negative binomial distribution, being heavily right-skewed, whether examining each bird species, pooling by bird family or guild, or pooling across all bird species (Fig. 4.2, Appendix D). Astigmata were more prevalent and abundant than other ectoparasite groups. Among the 270 hosts examined for

Table 4.1. Results of linear regressions testing the effectiveness of the wing mite index to predict Astigmata abundance, haematophagous mite abundance, and louse abundance on eight host species with large samples, and and guild- and family-level classifications, which pool data from all species in each category. Bold values indicate a significant relationship ($P < 0.05$) between wing mite index and ectoparasite abundance. Both wing mite index and ectoparasite load were natural log-transformed to satisfy assumptions of statistical normality.

Guild		Astigmata			haematophagous mites			lice		
Species	n	$F_{1,n-2}$	*P*	R^2	$F_{1,n-2}$	*P*	R^2	$F_{1,n-2}$	*P*	R^2
Frugivore (5 spp.)	66	**45.2**	**<0.001**	**0.42**	<0.1	0.985	<0.01	2.0	0.159	0.03
Pipra pipra	47	**10.2**	**0.003**	**0.18**	1.8	0.193	0.04	0.1	0.731	<0.01
Ant-follower (3 spp.)	47	**32.9**	**<0.001**	**0.43**	0.3	0.602	0.01	2.5	0.120	0.05
Pithys albifrons	27	**9.6**	**0.005**	**0.28**	0.3	0.643	0.01	0.2	0.671	0.01
Gymnopithys rufigula	18	**49.5**	**<0.001**	**0.77**	<0.1	0.891	<0.01	2.7	0.119	0.15
Flock obligate (6 spp.)	34	**22.3**	**<0.001**	**0.41**	<0.1	0.898	<0.01	<0.1	0.902	<0.01
Thamnomanes spp.	21	**4.5**	**0.047**	**0.19**	0.6	0.446	0.03	<0.1	0.960	<0.01
Flock dropout (4 spp.)	61	**21.0**	**<0.001**	**0.26**	<0.1	0.871	<0.01	0.2	0.686	<0.01
Glyphorynchus spirurus	32	**6.9**	**0.014**	**0.19**	0.3	0.609	0.01	<0.1	0.921	<0.01
Xiphorhynchus pardalotus	17	**5.2**	**0.038**	**0.26**	0.2	0.654	0.01	0.2	0.893	<0.01
Gap specialist (*Percnostola*)	34	**31.9**	**<0.001**	**0.50**	<0.1	0.999	<0.01	<0.1	0.958	<0.01
Other insectivore (3 spp.)	28	**60.9**	**<0.001**	**0.70**	<0.1	0.996	<0.01	0.5	0.480	0.02
Willisornis poecilinota	19	**16.6**	**<0.001**	**0.49**	0.5	0.830	<0.01	0.7	0.409	0.04
Furnariidae (5 spp.)	56	**15.2**	**<0.001**	**0.22**	0.9	0.341	0.02	2.6	0.110	0.05
Thamnophilidae (10 spp.)	138	**121.7**	**<0.001**	**0.47**	<0.1	0.908	<0.01	0.8	0.389	0.01
Tyrannidae + *Schiffornis* (3 spp.)	7	**25.9**	**0.004**	**0.84**	<0.1	0.961	<0.01	0.2	0.649	0.04
Pipridae (2 spp.)	56	**12.2**	**0.001**	**0.18**	1.7	0.194	0.03	0.2	0.679	<0.01
10-primaried oscines (2 spp.)	13	**40.2**	**<0.001**	**0.79**	3.5	0.090	0.24	0.1	0.753	0.01
ALL TAXA	270	**251.0**	**<0.001**	**0.48**	0.6	0.433	<0.01	1.1	0.291	<0.01

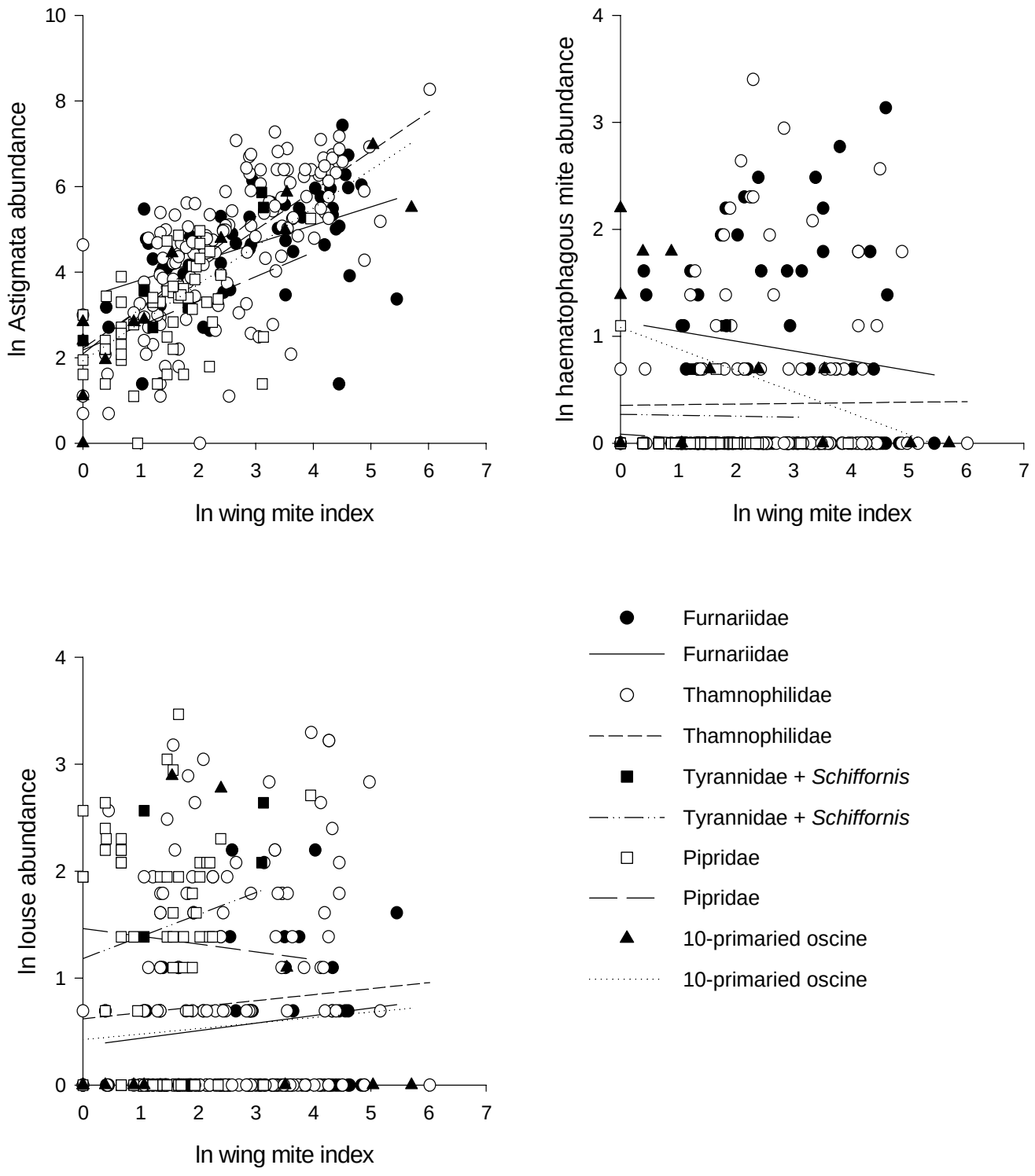

Fig. 4.1. Ability of wing mite index to predict Astimata, haematophagous mite, and louse load. Best fit regression lines are provided for each family.

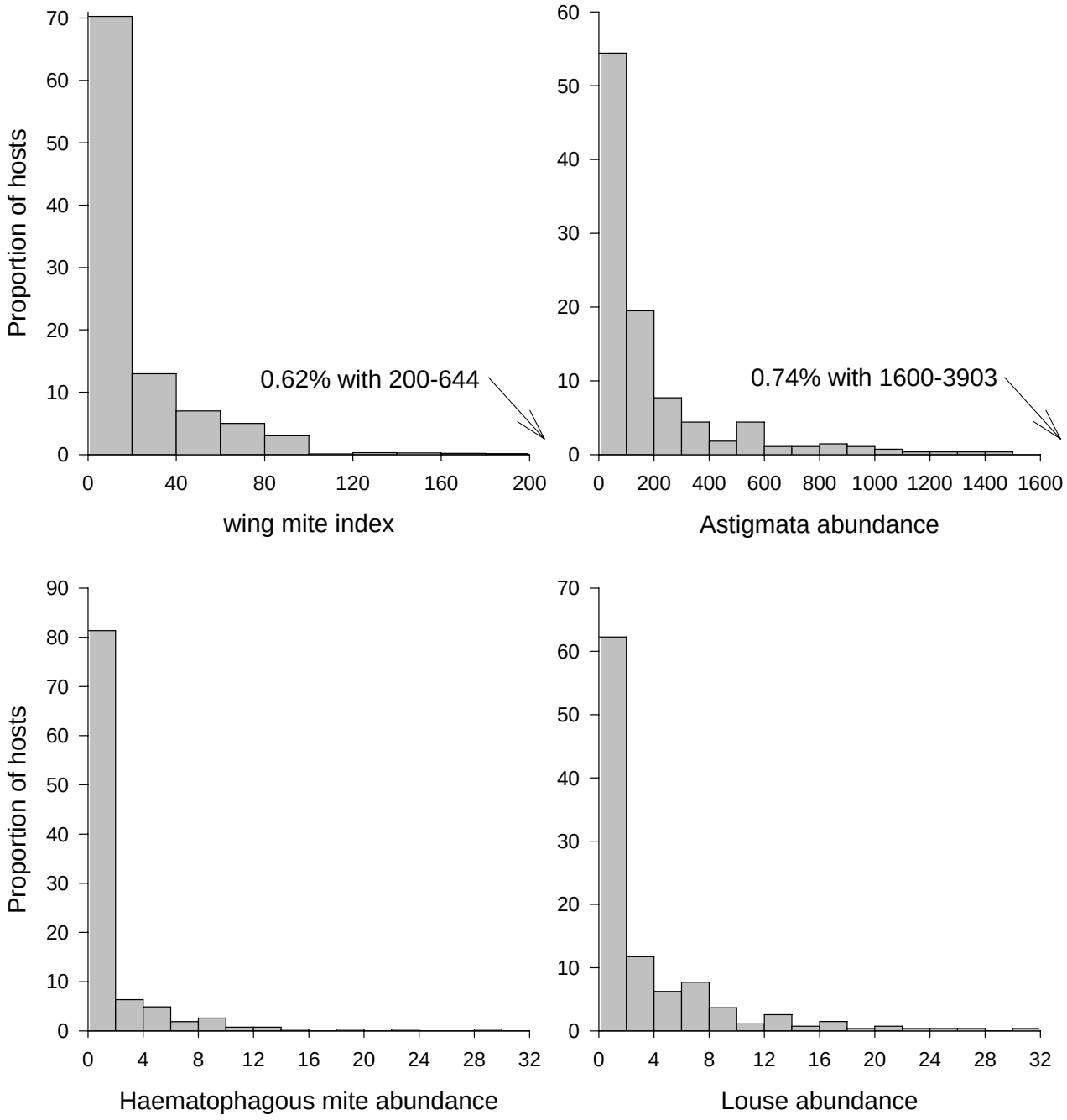

Fig. 4.2. Frequency distributions of wing mite index, Astigmata abundance, haematophagous mite abundance, and louse abundance on all 23 (wing mite index) or 22 (Astigmata, haematophagous mite, and louse load) host species.

Table 4.2. Summary of the wing mite index (WMI) for 23 host species by sample size (n), prevalence, mean and median intensity, mean abundance, and their 95% confidence intervals (CI).

Species	n	prevalence (± 95% CI)	mean WMI (± 95% CI)	index of discrepancy
Certhiasomus stictolaemus	38	100.0 (91.2–100.0)	15.0 (10.0–24.4)	0.57
Dendrocincla fuliginosa	43	100.0 (91.3–100.0)	45.9 (36.7–54.9)	0.38
Dendrocincla merula	48	97.9 (88.9–99.9)	14.4 (10.0–20.7)	0.58
Glyphorynchus spirurus	307	99.3 (97.6–99.9)	37.7 (33.4–42.5)	0.54
Xiphorhynchus pardalotus	98	100.0 (96.2–100.0)	45.9 (36.5–61.7)	0.56
Thamnomanes ardesiacus	129	99.2 (95.9–100.0)	32.2 (26.4–43.3)	0.53
Thamnomanes caesius	111	99.1 (95.2–100.0)	25.9 (21.5–36.4)	0.52
Epinecrophylla gutturalis	75	65.3 (54.0–75.5)	5.2 (2.6–10.6)	0.87
Myrmotherula axillaris	71	98.6 (92.5–99.9)	11.7 (9.0–16.3)	0.54
Myrmotherula longipennis	68	100.0 (94.5–100.0)	20.5 (16.7–24.5)	0.44
Myrmotherula menetriesii	39	97.4 (86.4–99.9)	9.5 (6.8–13.1)	0.52
Pithys albifrons	354	98.3 (96.4–99.3)	14.8 (13.1–16.6)	0.54
Gymnopithys rufigula	137	98.5 (94.7–99.7)	19.9 (16.7–23.3)	0.52
Percnostola rufifrons	108	99.1 (95.1–100.0)	47.3 (38.2–62.3)	0.54
Willisornis poecilinota	166	95.8 (91.4–98.0)	47.7 (37.3–64.3)	0.66
Mionectes macconnelli	177	93.2 (88.5–96.1)	9.8 (7.9–11.9)	0.61
Myiobius barbatus	69	98.6 (92.3–99.9)	13.4 (10.2–18.0)	0.55
Schiffornis turdinus	33	84.8 (68.4–93.8)	5.0 (2.7–9.3)	0.69
Lepidothrix serena	125	95.2 (89.7–97.9)	4.2 (3.5–5.2)	0.54
Pipra pipra	463	95.9 (93.7–97.5)	6.0 (5.3–6.7)	0.54
Pipra erythrocephala	101	90.1 (82.8–94.7)	4.6 (3.8–5.8)	0.52
Turdus albicollis	84	100.0 (95.5–100.0)	45.7 (36.9–60.2)	0.50
Microbates collaris	44	61.4 (46.4–75.3)	4.3 (1.3–15.2)	0.87
All 23 species	2888	95.9 (95.1–96.6)	21.1	0.66

Table 4.3. Summary of Astigmata prevalence, mean abundance, mean richness, and sample size (n) for eight host taxa (two *Thamnomanes* spp. pooled) with at least 15 samples evaluated.

Species	n	prevalence (± 95% CI)	mean abundance (± 95% CI)	mean richness (± 95% CI)	index of discrepancy
Pipra pipra	48	97.9 (88.9–99.9)	37.1 (26.6–54.9)	3.1 (2.7–3.5)	0.57
Pithys albifrons	29	100.0 (88.5–100.0)	120.9 (76.1–188.5)	6.7 (6.0–7.4)	0.55
Gymnopithys rufigula	18	100.0 (80.0-100.0)	255.9 (132.5–523.4)	5.9 (5.1–6.8)	0.62
Thamnomanes spp.	21	100.0 (84.1–100.0)	293.4 (183.4–436.2)	7.1 (6.4–7.8)	0.50
Glyphorynchus spirurus	32	100.0 (89.5–100.0)	152.2 (111.8–223.8)	4.4 (3.9–4.9)	0.49
Xiphorhynchus pardalotus	17	100.0 (80.4–100.0)	183.7 (117.2–271.4)	5.9 (5.0–6.9)	0.44
Percnostola rufifrons	34	100.0 (90.2–100.0)	487.2 (338.9–899.7)	5.6 (5.1–6.2)	0.55
Willisornis poecilinota	18	100.0 (81.5–100.0)	286.8 (148.1–549.6)	5.4 (4.3–6.5)	0.61
All 22 study species	270	98.9 (96.8–99.7)	195.0 (160.9–245.0)	5.1 (4.8–5.4)	0.67

Table 4.4. Summary of haematophagous mite prevalence, mean abundance, mean richness, and sample size (n) for eight host taxa (two *Thamnomanes* spp. pooled) with at least 15 samples evaluated.

Species	n	prevalence (± 95% CI)	mean abundance (± 95% CI)	mean richness (± 95% CI)	index of discrepancy
Pipra pipra	48	4.3 (0.1–14.9)	0.1 (0.0–0.2)	0.1 (0.0–0.2)	0.94
Pithys albifrons	29	11.1 (0.3–29.2)	0.4 (0.0–1.3)	0.3 (0.1–0.4)	0.91
Gymnopithys rufigula	18	27.8 (11.7–52.9)	0.8 (0.2–2.6)	0.3 (0.1–0.5)	0.81
Thamnomanes spp.	21	28.6 (13.3–50.6)	1.8 (0.6–4.8)	0.4 (0.1–0.6)	0.81
Glyphorynchus spirurus	32	81.3 (64.2–91.5)	4.3 (2.9–6.4)	1.0 (0.8–1.2)	0.53
Xiphorhynchus pardalotus	17	23.5 (8.5–48.9)	0.9 (0.2–2.5)	0.4 (0.1–0.8)	0.81
Percnostola rufifrons	34	11.8 (4.1–27.6)	0.2 (0.0–0.3)	0.2 (0.1–0.4)	0.87
Willisornis poecilinota	18	83.3 (58.6–95.3)	5.3 (3.0–10.3)	0.8 (0.6–1.1)	0.57
All 22 study species	270	30.2 (25.0–36.0)	1.3 (1.0–1.8)	0.4 (0.3–0.5)	0.85

Table 4.5. Summary of louse prevalence, mean abundance, mean richness, and sample size (n) for eight host taxa (two *Thamnomanes* spp. pooled) with at least 15 samples evaluated.

Species	n	prevalence (± 95% CI)	mean abundance (± 95% CI)	mean richness (± 95% CI)	aggregation index (index of discrepancy)
Pipra pipra	48	79.2 (65.7–88.9)	5.5 (4.1–7.5)	1.4 (1.1–1.7)	0.52
Pithys albifrons	29	55.2 (36.0–72.8)	2.4 (1.4–3.8)	0.6 (0.4–0.9)	0.67
Gymnopithys rufigula	18	82.4 (58.4–95.0)	3.9 (2.2–8.1)	0.9 (0.6–1.2)	0.56
Thamnomanes spp.	21	22.7 (9.4–45.3)	1.3 (0.3–3.7)	0.2 (0.1–0.4)	0.85
Glyphorynchus spirurus	32	21.9 (10.5–39.0)	0.3 (0.1–0.6)	0.2 (0.1–0.4)	0.81
Xiphorhynchus pardalotus	17	64.7 (40.6–83.4)	1.8 (0.9–3.3)	0.7 (0.4–0.9)	0.61
Percnostola rufifrons	34	55.9 (38.1–72.4)	4.4 (2.5–7.2)	0.6 (0.4–0.9)	0.70
Willisornis poecilinota	18	44.4 (23.7–67.0)	2.4 (0.9–6.3)	0.4 (0.2–0.6)	0.74
All 22 study species	270	50.5 (44.5–56.6)	2.9 (2.4–3.5)	0.7 (0.6–0.8)	0.74

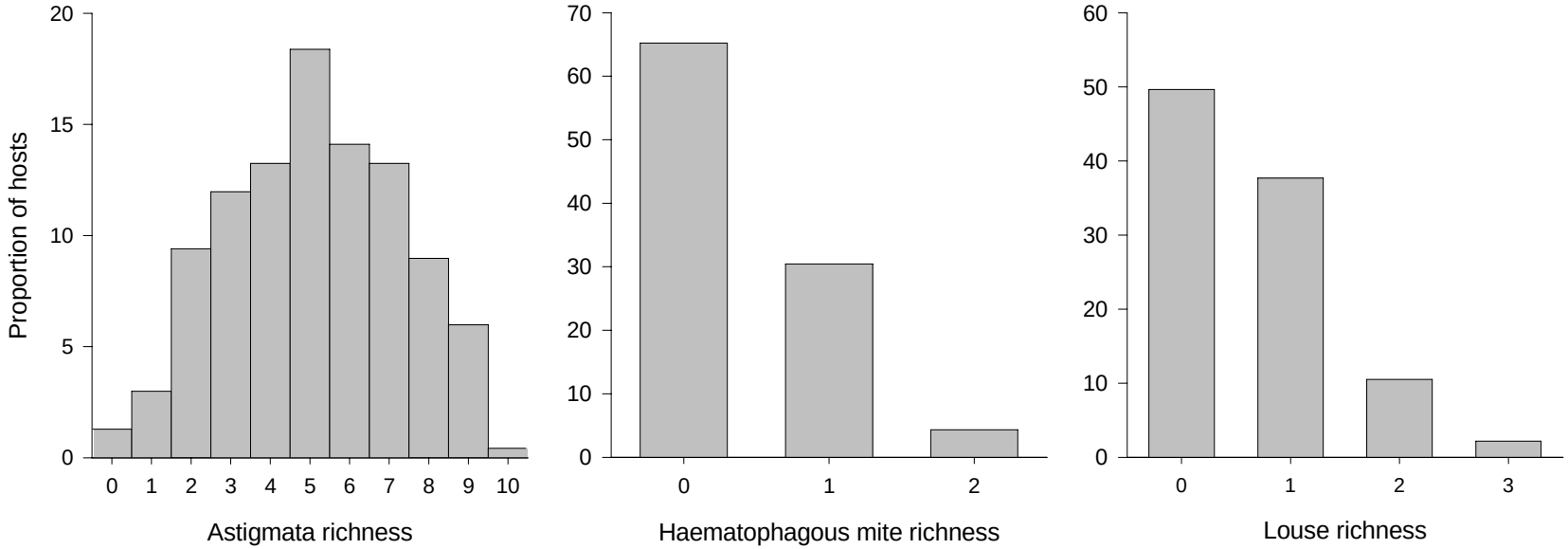

Fig. 4.3. Frequency distributions of Astigmata, haematophagous mite, and louse richness across all 22 host species.

ectoparasites, 267 (98.9%) were infested with Astigmata, while 50.2% had lice, 35.6% had haematophagous mites, and 4.8% had fleas. I found one *Percnostola rufifrons* hosting 3903 individual Astigmata, whereas the maximum number of lice on a single host was 31 (on *Pipra pipra*) and the maximum number of haematophagous mites was 29 (on *Willisornis poecilinota*). Nearly 3% of hosts had more than 1000 Astigmata and 65% of hosts had more than 31. Only 3% of hosts had more lice than Astigmata, and only 1.1% of hosts had more haematophagous mites than Astigmata.

Patterns of Astigmata richness approximated a normal distribution with a maximum of 10 on a single species and 10 on a single host with a median, mode, and mean of five taxa per individual host (Fig. 4.3). Only a single *Pithys albifrons* had 10 Astigmata taxa and several other thamnophilids including *Thamnomanes ardesiacus*, *T. caesius*, *Myrmotherula longipennis*, *Myrmotherula menetriesii*, *P. albifrons*, *G. rufigula*, and *W. poecilinota* had up to nine Astigmata taxa. Maximum haematophagous mite richness was two and maximum louse richness was three (Fig. 4.3). Only *P. pipra* had three species of lice coexisting on the same host, whereas all 21 other host species had either one or two.

Across the 23 study species, body size significantly predicted average wing mite index ($F_{1,22} = 12.0$, $P = 0.002$, $R^2 = 0.36$; Fig. 4.4). I visually examined the mean residuals by host taxonomic families and guilds to determine whether these groups were more or less heavily infested with wing mites for a given body size than expected, defined as the average across all host species (Table 4.6); sample sizes for each group were small, so I did not construct a statistical test. Only the manakins (Pipridae) had confidence intervals that did not overlap zero suggesting a lower than expected wing mite index for their body size (Table 4.6). All guilds had 95% confidence intervals that overlapped zero (Table 4.6). Therefore, there was little evidence

to suggest that the wing mite index was driven by host taxonomy or guild *per se*, except perhaps for manakins, but that instead a combination of body size and other unknown factors drive wing mite abundance.

Host body size did not predict average Astigmata abundance ($F_{1,6} = 1.9$, $P = 0.22$, $R^2 = 0.24$), haematophagous mite abundance ($F_{1,6} = 1.1$, $P = 0.33$, $R^2 = 0.16$) or louse abundance ($F_{1,6} < 0.1$, $P = 0.92$, $R^2 < 0.01$) across the eight host species with > 15 samples. Including five more species with between 5 and 15 samples, however, changed the result with increasing host body size predicting increased average Astigmata abundance ($F_{1,11} = 14.6$, $P = 0.003$, $R^2 = 0.57$, slope = 5.3 ± 0.3 Astigmata/log host mass [g]). Host body size also nearly significantly positively predicted louse abundance ($F_{1,11} = 3.5$, $P = 0.087$, $R^2 = 0.24$, slope = 0.5 ± 0.6 lice/ log host mass [g]), but did not predict haematophagous mite abundance ($F_{1,11} = 0.1$, $P = 0.72$, $R^2 = 0.01$) after including the additional five host species.

Host body size did not predict Astigmata richness ($F_{1,6} = 2.6$, $P = 0.16$, $R^2 = 0.30$), haematophagous mite richness ($F_{1,6} = 0.6$, $P = 0.46$, $R^2 = 0.09$), or louse richness ($F_{1,6} < 0.1$, $P =$

Table 4.6. Average wing mite index residual from the best fit line (see Fig. 4.3) and 95% confidence intervals (CI) for each of seven host families.

Family or Guild	Wing mite index residual	95% CI
Furnariidae (5 spp.)	4.6	-17.2 – 26.5
Thamnophilidae (10 spp.)	1.7	-4.6 – 8.0
Tyrannidae + *Schiffornis* (3 spp.)	-7.0	-33.9 – 19.9
Pipridae (3 spp.)	-9.2	-10.9 – -7.3
10-primaried oscines (2 spp.)	3.6	-22.0 – 25.6
Frugivore (6 spp.)	-6.9	-21.3 – 7.4
Ant-follower (3 spp.)	14.0	-33.4 – 5.4
Flock obligate (6 spp.)	2.9	-3.2 – 8.9
Flock dropout (4 spp.)	10.0	-4.1 – 24.1
Gap specialist (1 spp.)	12.5	NA
Other insectivore (3 spp.)	4.6	-26.4 – 35.5

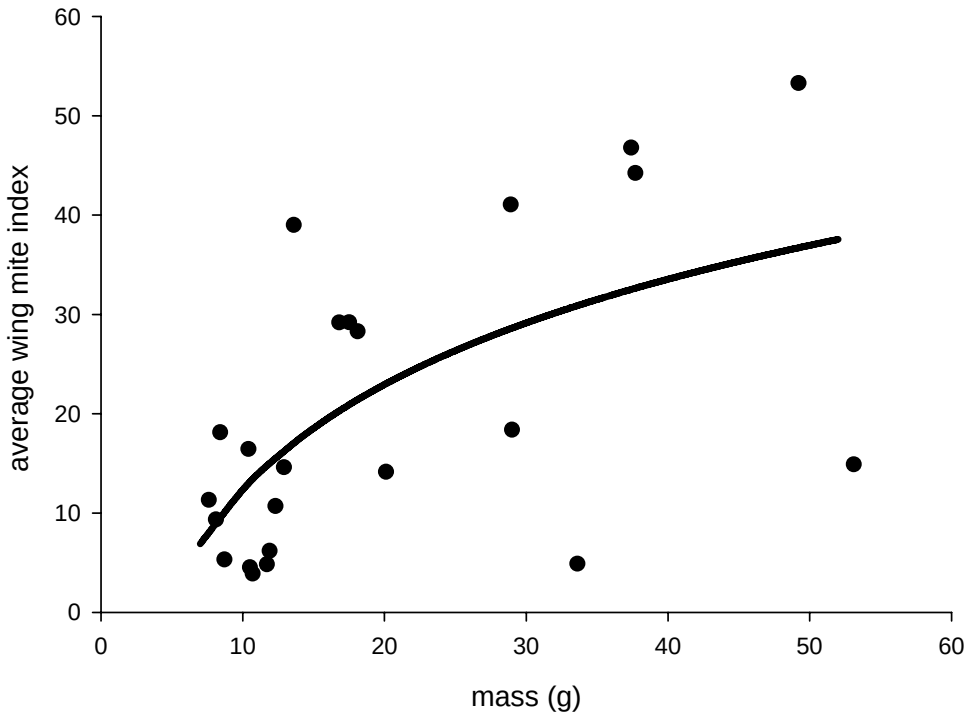

Fig. 4.4. The relationship between body size (mass) and average wing mite index by host species with the best fit regression line.

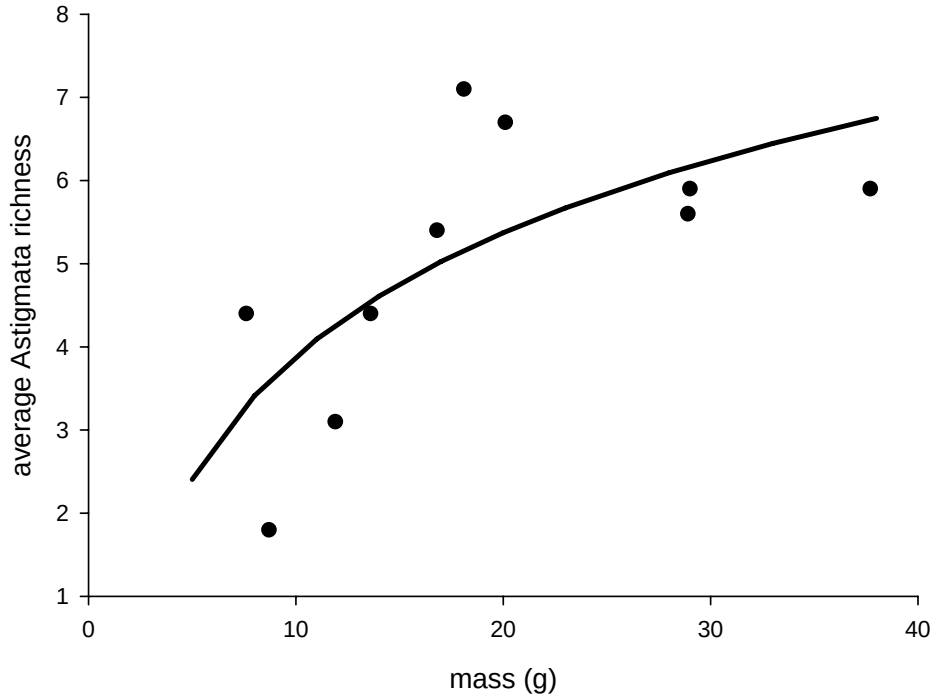

Fig. 4.5. The relationship between body size (mass) and average Astigmata richness by host species with the best fit regression line.

0.97, $R^2 < 0.01$) for the eight host species with > 15 samples. Including two more host species with between 5 and 15 samples, however, changed the result with increasing host body size predicting increased average Astigmata richness ($F_{1,8} = 7.3$, $P = 0.027$, $R^2 = 0.48$, Fig. 4.5), but not haematophagous mite richness ($F_{1,8} < 0.1$, $P = 0.99$, $R^2 < 0.01$) or louse richness ($F_{1,8} = 0.8$, $P = 0.40$, $R^2 = 0.09$).

Host Age and Habitat Effects on Ectoparasite Load and Richness

I assessed the difference in WMI (a proxy for Astigmata load; Fig. 4.1), by bird age, habitat type, and their interaction using a generalized linear model assuming a negative binomial distribution. Differences in WMI by age or habitat were not consistently observed, but when they did appear, immatures always had larger WMI than adults and forest edges had larger WMI than interior forest with one exception. For 11 host species with aging criteria, five had significant differences by age and two had nearly significantly differences (Fig. 4.6, Appendix D). Two host species had significantly higher WMI along edges, one had nearly significantly higher WMI along edges, and one had higher WMI in interior forest (Fig. 4.6, Appendix D). One species had a significant interaction with interior forest adults having greater WMI than other treatments (Fig. 4.6, Appendix D). Two species had a nearly significant interaction; in both species immatures in interior forest had greater WMI than other treatments (Fig. 4.6, Appendix D).

For the subset of 270 adults from which I removed ectoparasites, there were few occasions of Astigmata load differing by habitat type (Table 4.7). *P. albifrons* had significantly more Astigmata along edges (interior: $e^{4.4 \pm 0.2}$, edges: $e^{5.4 \pm 0.4}$) and *Glyphorynchus spirurus* had nearly significantly more along edges (interior: $e^{4.7 \pm 0.2}$, edges: $e^{5.4 \pm 0.2}$). Similarly, I detected a few cases of haematophagous mite loads differing by habitat type among adult hosts; only *W.*

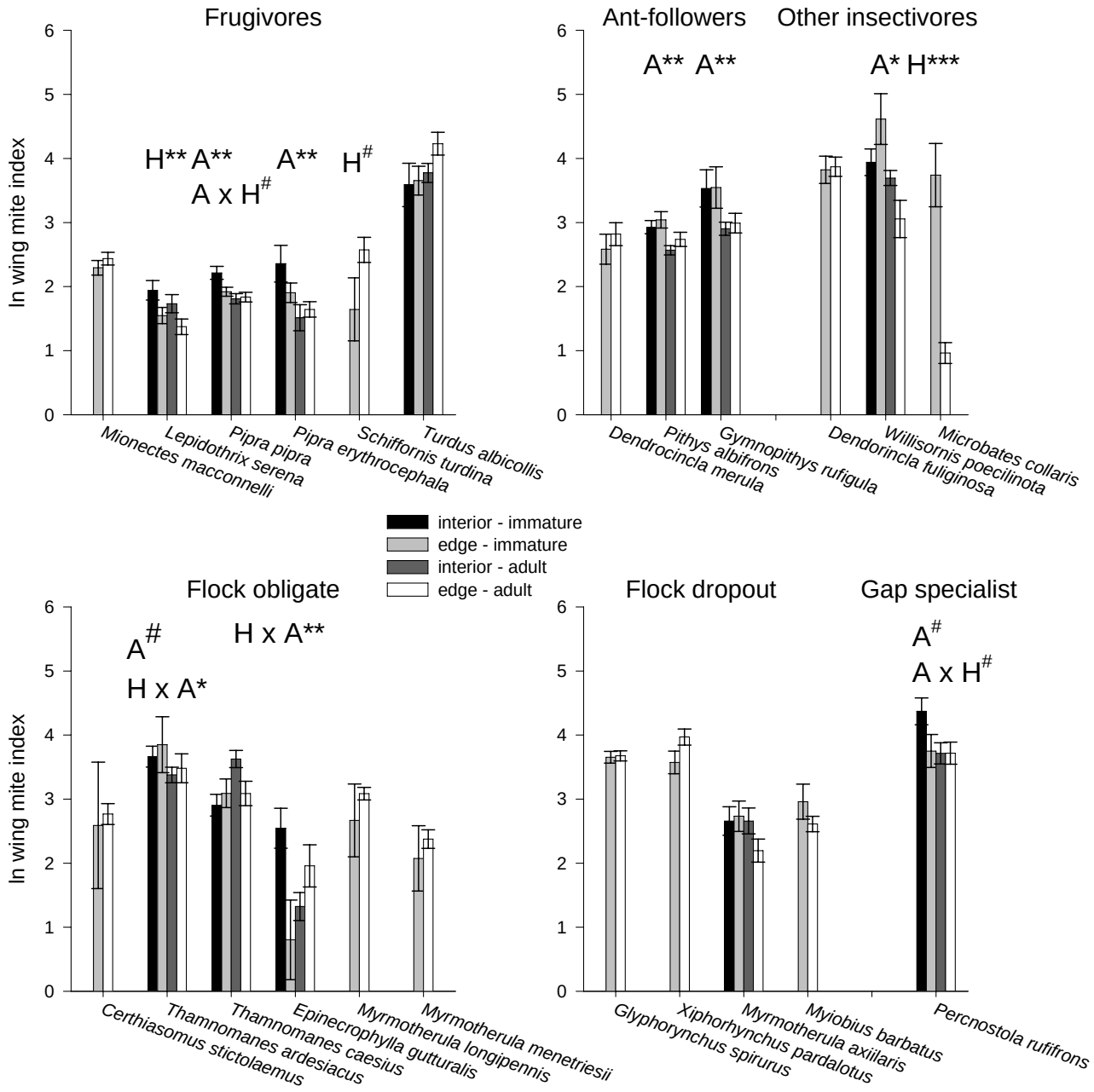

Fig. 4.6. The wing mite index for 23 species of understory birds across seven families, sorted by guild, separated by habitat type (H: forest interior and fragment edge) and bird age (A: immature and adult when known). *** $P < 0.001$; ** $P < 0.01$; * $P < 0.05$; # $0.05 < P < 0.10$ for each host species (see Appendix D for test statistics and exact P-values).

Table 4.7. Sample size, test statistics, and *P*-values from three generalized linear models testing the effects of habitat type on Astigmata, haematophagous mite, and louse abundance. ND = sample size too small or prevalence too low to construct statistical test.

		Astigmata		Haematophagous mites		Lice	
Species	n	$F_{1,n-2}$	*P*	$F_{1,n-2}$	*P*	$F_{1,n-2}$	*P*
Glyphrynchus spirurus	30	3.6	0.057	0.2	0.66	3.2	0.075
Xiphorhynchus pardalotus	17	0.2	0.70	1.1	0.31	2.2	0.14
Thamnomanes spp.	20	0.9	0.35	3.6	0.059	<0.1	0.90
Myrmotherula axillaris	9	<0.1	0.84	ND	ND	2.3	0.13
Gymnopithys rufigula	19	2.3	0.13	0.6	0.44	0.6	0.44
Pithys albifrons	29	**6.3**	**0.012**	0.3	0.57	<0.1	0.84
Percnostola rufifrons	33	0.1	0.74	0.1	0.79	<0.1	0.99
Willisornis poecilinota	19	0.1	0.71	**6.4**	**0.011**	3.3	0.069
Pipra pipra	48	0.1	0.79	ND	ND	1.9	0.17
Lepidothrix serena	9	<0.1	0.99	ND	ND	1.2	0.27
Turdus albicollis	6	2.3	0.13	0.0	1.00	0.2	0.69

poecilinota had significantly more haematophagous mites along edges (interior: $e^{1.2 \pm 0.4}$, edge: $e^{2.5 \pm 0.2}$) whereas *Thamnomanes* spp. had nearly significantly more haematophagous mites along edges (*Thamnomanes* spp. interior: $e^{-0.1 \pm 1.1}$, edge: $e^{1.6 \pm 0.4}$). There were no instances of louse loads significantly differing by habitat type among adult hosts, but two species had nearly significantly more lice along edges (*G. spirurus* interior: $e^{-2.0 \pm 0.8}$, edge: $e^{-0.5 \pm 0.4}$; *W. poecilinota* interior: $e^{0.1 \pm 0.5}$, edge: $e^{1.9 \pm 0.9}$).

There were no instances of Astigmata, haematophagous mite, or louse richness significantly differing among habitat types (Table 4.8). Astigmata richness was nearly significantly higher in *G. rufigula* interior: $e^{6.5 \pm 0.5}$, edge: $e^{5.0 \pm 0.6}$). Haematophagous mite richness was nearly significantly higher along edges in one case (*W. poecilinota* interior: $e^{0.8 \pm 0.1}$, edge: $e^{1.3 \pm 0.2}$), but nearly significantly lower along edges (*P. rufifrons* interior: $e^{0.4 \pm 0.1}$, edge: $e^{0.1 \pm 0.1}$). In one case, louse richness was nearly significantly higher along edges (other insectivore interior: $e^{0.2 \pm 0.1}$, edge: $e^{0.7 \pm 0.2}$).

Table 4.8. Sample size, test statistics, and *P*-values from three generalized linear models testing the effects of habitat type (forest interior and fragment edge) on Astigmata, haematophagous mite, and louse richness. ND = not determined.

Guild or Clade		Astigmata		Haematophagous mites		Lice	
Species	n	$F_{1,n-2}$	*P*	$F_{1,n-2}$	*P*	$F_{1,n-2}$	*P*
Frugivore (5 spp.)	67	ND	ND	0.7	0.41	0.4	0.53
Pipra pipra	48	0.1	0.72	0.1	0.72	1.5	0.23
Ant-follower (3 spp.)	50	1.4	0.24	<0.0	0.95	0.4	0.53
Gymnopithys rufigula	19	4.2	0.056	0.2	0.66	0.5	0.50
Pithys albifrons	29	0.1	0.78	0.6	0.46	<0.1	0.98
Flock obligate (6 spp.)	32	1.1	0.31	0.1	0.72	0.1	0.83
Thamnomanes spp.	20	0.4	0.55	0.1	0.83	0.8	0.40
Flock dropout (4 spp.)	59	0.3	0.57	<0.1	0.86	0.5	0.47
Glyphrynchus spirurus	30	0.1	0.80	2.3	0.14	1.6	0.14
Xiphorhynchus pardalotus	17	<0.1	0.88	1.1	0.31	2.6	0.13
Gap specialist (*P. rufifrons*)	33	2.1	0.16	3.2	0.085	0.2	0.63
Other insectivore (3 spp.)	27	ND	ND	0.2	0.63	4.2	0.052
Willisornis poecilinota	19	2.0	0.18	3.5	0.081	2.3	0.15
Furnariidae (5 spp.)	53	<0.1	0.99	<0.1	0.90	<0.1	0.98
Thamnophilidae (10 spp.)	139	0.6	0.43	0.1	0.79	2.5	0.12
Pipridae (2 spp.)	57	ND	ND	0.7	0.42	0.8	0.38
Tyrannidae + *Schiffornis* (3 spp.)	7	ND	ND	0.5	0.51	0.5	0.51
10-primaried oscines (2 spp.)	12	ND	ND	0.0	1.00	0.7	0.42

DISCUSSION

A subset of central Amazonian passerines about 80 km north of Manaus, Brazil were infested by a variety of ectoparasites, including mites (Astigmata and haematophagous mites), ticks (Ixodida), lice (Phthiraptera), and fleas (Siphonaptera; Appendix C). The wing mite index was a strong predictor of Astigmata abundance (Fig. 4.1), as in previous studies (McClune 1989, Behnke et al. 1995) although several Astigmata taxa do not occupy remiges (Proctor and Owens 2000, Proctor 2003). Proctophyllodidae were among the most common wing feather mites and

typically outnumbered all other Astigmata combined (E. I. Johnson, unpublished data and personal observation). Generally, Astigmata were less abundant on Pipridae than Furnariidae and Thamnophilidae, even after controlling for body size. Pipridae, however, had among the highest louse abundances and *Pipra pipra* was the only species with individuals simultaneously hosting three louse genera. Hosts with three louse taxa always included two Amblyceran (*Myrsidea* sp. and *Rincinus* sp.) and one Ischnoceran genus (Appendix C).

There was great variation in the mean prevalence and abundance of ectoparasites among host species both within and between families (Tables 4.2–4.5). Prevalence of wing mites assessed through the wing mite index (WMI) was generally very high across all taxa (>90% in 20 of 23 hosts and all with >60%) compared to a similar survey from Portugal (>90% in 4 of 21 hosts and 11 hosts with <60%; Behnke et al. 1995). Because there are few studies examining ectoparasites from multiple host species from the same region, it is difficult to know if differences between birds in Manaus and Portugal reflect a true latitudinal gradient, phylogenetic differences, or seasonal differences, all of which can affect wing feather mite loads (Clayton et al. 1992, Salkeld et al. 2008, Haribal et al. 2011).

Host body size ranged from 7.6 to 53.1 g and was a good predictor among species for mean WMI, mean Astigmata abundance, and mean Astigmata richness (Figs. 4.4 and 4.5) as was shown in other studies (Rózsa 1997. Morand et al. 2002). However, mean Astigmata richness qualitatively leveled off, with an average of about six Astigmata morphotaxa on hosts above 15 g. This suggests that birds between 15 and 50 g provide a limited set of microhabitats (e.g. head, wing, back, etc) and that these have all been colonized by ectoparasites specialized to one or more regions (Dubinin 1951 as cited in Proctor 2003, Choe and Kim 1988). Birds less than 15 g, however, appear to host fewer species; perhaps because each body region is smaller, ectoparasite

population sizes would be smaller and increase their risk of extinction, thus decreasing richness (MacArthur and Wilson 1967)

Mean haematophagous mite or louse abundance and richness, however, did not vary with body mass across host species. In contrast, Clayton and Walther (2001) found that mean louse abundance increased with host body size, but included both passerines and non-passerines with a greater range of host body size (up to 383 g) than in my study that only included passerines with a maximum body size of 53 g. Variation in mean louse and haematophagous mite richness was also low in my study, with a maximum of three louse taxa and two haematophagous mite taxa on a single host. In addition to low diversity, the various haematophagous mite taxa (including Mesostigmata, Prostigmata, and Ixodida) had low prevalence, probably because they spend a considerable time away from the host (e.g. Prostigmata; O'Conner 1982, Proctor and Owens 2000) or were not always removed through dust-ruffling (e.g. Ixodida). Therefore, it is not suprising that low variation in host body mass did not significantly predict variation in louse or haematophagous mite richness or abundance. Adding additional host species might change this result.

Ectoparasite Loads by Host Age

Immature hosts often had a higher wing mite index (WMI), suggesting that they had more Astigmata feather mites (Fig. 4.6). Greater ectoparasite loads in immatures has been repeatedly observed in other studies, although a second peak can occur later in life as hosts reach their maximum life expectancy (Potti and Merino 1995, Møller and De Lope 2002). Although this pattern might be expected for true parasites, most Astigmata are assumed to be commensial or even mutualistic because they clean rather than consume feathers (Figuerola 2000, Jovani and Blanco 2000, Blanco and Tella 2001, Pap et al. 2005, Brown et al. 2006, Chapter 5). These

differences in Astigmata loads between host age classes may be a consequence of vertical transmission, where adult ectoparasite loads are reduced as ectoparasites colonize host offspring. The persistence of ectoparasite populations may depend on these rare of opportunities for dispersal and colonization because an individual host is essentially a small island. Furthermore, nestlings and fledglings have high metabolic output (Drent and Daan, 1980, Dunn 1980) and are a potentially attractive resource for ectoparasites, even for Astigmata that rely on feather debris. Reduced preening skills by immatures may also increase the debris load on feathers, thus making immatures more attractive to Astigmata. These Astigmata populations may decrease as the host becomes more efficient in preening and removing food sources that Astigmata would otherwise be consuming.

Ectoparasite Differences by Habitat

On 28 of 30 tests of host ectoparasite abundance comparisons and 20 of 23 WMI comparisons by habitat type, there were no differences in mean abundance between forest interiors and fragment edges (Fig. 4.6, Table 4.7, Appendix D), and none of 49 tests indicated a difference in ectoparasite richness between habitat types (Table 4.8). Only in *Pithys albifrons* were Astigmata loads greater along edges and in *Willisornis poecilinota* were haematophagous mite loads greater along edges. *Myiobius barbatus* and *Microbates collaris* had larger WMI along edges, but *Lepidothrix serena* had larger WMI in interior forest. These five statistically significantly differences out of 53 total comparisons is close to the Type I error rate of detecting false positives 5% of the time. Only four of the five differences indicated more ectoparasites along edges. I have little confidence that these differences are biologically relevant as they do not consistently appear in other hosts and do not always differ in the same direction.

To summarize, there was little evidence that host habitat quality influenced ectoparasite loads in this central Amazonian fragmented landscape. Similar studies in southeast Asia and tropical Africa also found no difference in ectoparasite loads between fragments and continuous forest, despite decreased host density in small fragments (Sodhi 2002, Bobo 2007). Consistency among these studies suggests that it was not failure to detect differences, but that this may be an emerging pattern in host–ectoparasite relationships., and there are several possible explanations. First, the habitat for the ectoparasite may be the host itself, which is a consistent theme in avian host–parasite studies (Clayton et al. 1992). One might argue that human-modified landscapes may alter this otherwise predictable natural balance and reduce the ability for hosts to regulate ectoparasites in reduced-resource habitats. A second explanation may therefore posit that similar ectoparasite loads across habitats could instead reflect a balance between reduced ectoparasite maintenance offset by reduced transmission rates due to lower bird densities. Animal density is often inversely proportional to parasite abundance and prevalence (e.g. Püttker et al. 2008, Mbora and McPeek 2009). Mist-netting is subject to bias for estimating bird density, but may be a good proxy for understanding transmission rates of parasites and diseases as it measures a combination of bird density and bird movement rates (Remsen 1994). Many of the host species I studied had lower capture rates in small fragments (Chapter 2, see also Stouffer et al. 2006, Ferraz et al. 2007). Third, it may be that after 7–24 years of second growth regeneration, that hosts are not affected by this change in habitat. I would argue that this third conclusion lacks empirical support, since bird populations remain affected by fragmentation (Chapter 2). I will further explore these questions in the next chapter where I summarize results of an ectoparasite-removal experiment, and suggest that the first and second hypotheses have merit depending on the species involved.

Opportunities for Further Study

To date, I am only confident of louse identifications to genus and mite identification to family (J. Weckstein and M. Valim, personal communication; Appendix C); many of these likely represent new taxa to science since the central Amazon region and these host taxa have been poorly studied and sampled (Gaud and Atyeo 1996, Price et al. 2003, Proctor 2003, 2007). We are only just beginning to understand ectoparasite assemblages on many tropical host species (Clayton et al. 1992) and new ectoparasite species and genera are still being described on Furnariidae, Thamnophilidae, and Pipridae (Price and Clayton 1996, Hernandes et al. 2007, Cicchino and Valim 2008, Mironov et al. 2008, Sychra et al. 2010). I therefore encourage avian ectoparasite taxonomists to examine these specimens to determine species-level identifications. Given the extent of this collection, with 907 samples from 23 host species, additional community-level studies could be conducted once more detailed information about the taxa is understood. Specimens are stored in ethanol at the Entomology Collection of the Instituto Nacional de Pesquisas da Amazônia (INPA) in Manaus, Amazonas, Brazil and are available for further study.

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CHAPTER 5: AN ECTOPARASITE-REMOVAL EXPERIMENT TO QUANTIFY THE EFFECTS OF ECTOPARASITES ON AMAZONIAN BIRDS IN A FRAGMENTED LANDSCAPE

INTRODUCTION

To what degree are ectoparasites detrimental on birds? There are strong theoretical arguments for the evolutionary optimization of host–parasite relationships, where pressures exerted by parasites elicit evolved host defenses (Van Valen 1973). Such reciprocal host–parasite dynamics makes it difficult to quantify parasite pressure since it is not necessarily correlated with parasite density (Lee and Clayton 1995, Sheldon and Verhulst 1996, Clayton et al. 1999, Blanchet et al. 2009). High parasite pressure may lead to low parasite density because of host investment in defense, which could take away from other daily needs of the host, such as foraging and mate acquisition, ultimately decreasing host fitness (Cotgreave and Clayton 1994, Moyer et al. 2002, Owen et al. 2010).

Human-modified landscapes present novel challenges to birds defending themselves against parasites (Loye and Carroll 1995, Tripet et al. 2002). Ectoparasite maintenance may suffer as the host faces challenges to fulfill other requirements, such as nutrition, predator detection, mate acquisition, and territory defense in isolated habitat patches, whereas transmission rates may differ due to changes in social interactions among individual hosts. Shifts in host–parasite relationships may therefore be part of the process that drives avian population declines and extinctions in fragmented landscapes. Ectoparasite virulence may be greater in the humid tropics (Møller 1998, Møller et al. 2009), which could increase the risk of tropical birds to ectoparasite pressures in rainforest fragments compared to temperate regions. In this chapter, I summarize an ectoparasite-removal experiment designed to quantify the effects of ectoparasites on host condition in a human-modified Amazonian landscape.

Most lice are presumed to be harmful to birds because they feed on skin, freshly emerged feathers, non-living keratin of feather barbules, and blood (Marshall 1981). Louse abundance is often proportional to its negative impact on the host (Booth et al. 1993, Møller et al. 1996, Whiteman and Parker 2004, but see Schmid-Hempel and Koella 1994, Clayton and Tompkins 1995). Lice have been shown to have negative consequences on host flight performance (Barbosa et al. 2002), metabolism (Booth et al. 1993), body condition (Møller et al. 1996, Whiteman and Parker 2004, Møller and Rózsa 2005), mate selection (Hamilton and Zuk 1982, Clayton 1990, Kose et al. 1999), and survival (Clayton et al. 1999). Haematophagous lice also transmit diseases and endoparasites (Seegar et al. 1976, Holmstad 2008).

Mites, ticks, fleas, and parasitic flies typically complete at least one part of their life-cycle away from the host, with great variation in life histories. Some spend much of their time apart from the host and will only opportunistically feed on birds (e.g. ticks) while others live in nest materials, such as the fowl mites *Dermanyssus* spp. and *Ornithonyssus* spp. and hen fleas (Møller 1990, Clayton and Tompkins 1995). Some flies, such as *Philornis* spp., live on their hosts subcutaneously as larvae, especially on bird nestlings (Dudaniec and Kleindorfer 2006). These flies, fowl mites, and fleas have been the focus of many controlled experiments with nestlings because it is relatively easy to manipulate their load and nestling density while tracking nutritional outcomes like nestling growth rates through time. These ectoparasites can reduce nesting success, cause nest abandonment, and decrease the condition of the nest's parents (e.g. Richner et al. 1993, Saino et al. 1998, Fitze et al. 2004, Moreno et al. 2009, Norris et al. 2010). Many mites, ticks, and fleas can also be vectors for other diseases and endoparasites because they forage on multiple hosts in their life-time (Phillips 1990, Proctor 2003).

Feather mites (Astigmata) spend much of their lives associated with bird feathers. Some live in feather quills and eat the pith (syringicoles), which has the potential to weaken feathers, but syringicoles are generally considered mildly parasitic at most (Proctor and Owens 2000). Accumulating evidence suggests that mites that live on the surface of feathers (plumicoles) are commensalists or even mutualistic with birds (Figuerola 2000, Jovani and Blanco 2000, Blanco and Tella 2001, Pap et al. 2005, Brown et al. 2006, but see Thompson et al. 1997, Harper 1999). The diet of these feather mites usually consists largely of fungal spores, pollen, algae, or feather-degrading bacteria (Dubinin 1951, Proctor 2003).

Ectoparasite virulence is typically related to their dependence on a single host, such that the more time an ectoparasite spends apart from the host, the more virulent (i.e. the more resources they take from the host) they become when occupying the host (Clayton and Tompkins 1995). Experiments investigating the consequences of ectoparasite virulence on birds have have generally been restricted to captive-held animals (e.g. Rózsa 1993, Clayton and Tompkins 1995) or confined to the nesting period (e.g. Møller 1990, Heeb et al. 1998, Buechler et al. 2002, Fitze et al. 2004, Moreno et al. 2009). The only experimental study that examined the effects of ectoparasites on uncaged non-breeding adult birds found that Rock Pigeons (*Columba livia*) increased their metabolic efficiency when lice were removed (Booth et al. 1993), suggesting that there are indeed consequences of ectoparasites on free-living wild adult birds.

Over the last 20 years, there has been a surge of experimental studies testing the consequences of ectoparasite virulence on their avian hosts (Møller et al. 2009), but a significant gap remains. In particular, studying interactive effects of host habitat quality, especially in human-modified landscapes, has largely been neglected. Birds experience a number of novel pressures resulting from habitat fragmentation and experience decreased fecundity and fitness,

altered populations dynamics, and local extinction (Fahrig 2003, Stratford and Robinson 2005, Stouffer et al. 2006, Tewksbury et al. 2006, Ferraz et al. 2007, Feeley and Terborg 2008, Chapter 2). Changes in host–parasite dynamics may be one mechanism driving these changes. Creative approaches are needed to conduct controlled experiments testing the effects of parasites on free-living birds in altered landscapes.

I designed an ectoparasite-removal experiment to address this issue and study the effects of forest fragmentation on host–ectoparasite dynamics near Manaus, Brazil. Ectoparasites can be effectively removed from birds by sprinkling pyrethrin powder throughout the plumage, known as dust-ruffling (Walther and Clayton 1997). Tracking effects on free-living birds, however, is not as straightforward because birds are difficult to re-sample in a controlled time span. I dealt with these issues by passively mist-netting birds, visiting sites multiple times to recapture them, and using ptilochronology, which provides a permanent record of host condition based on the rate of feather growth (Grubb 1989). Wing and tail feathers, when molting, show alternating lighter and darker bars perpendicular to the rachis, with each light–dark combination representing 24 hours of feather growth (Michener and Michener 1938, Grubb 1989). Birds in better condition are expected to grow feathers faster, and this information is permanently stored in the feather, which in small passerines should complete growth in about one month (Rohwer et al. 2009). Ptilochronology has proven reliable for assessing nutritional condition in a variety of diet-manipulated laboratory experiments (Grubb 1991, White and Kennedy 1992, Jenkins et al. 2001, but see Murphy and King 1991, Murphy 1992) as well as field experiments (Grubb and Cimprich 1990, White et al. 1991, Grubb and Yosef 1994, Carbonell and Telleria 1999, Stratford and Stouffer 2001, Brown et al. 2002, Johnson et al. in review, but see Kern and Cowie 2002).

Ptilochronology has not been used, to my knowledge, to assess the effects of ectoparasites, which can reduce nutritional condition (Coop and Holmes 1996, Quillfeldt et al. 2004). I predicted that because ectoparasites utilize nutrients from their hosts, they have the potential to decrease feather growth rates, analogous to reducing the quality or quantity of the host's diet (Grubb 1989). I also tested the interactive effects of habitat quality, as hosts may respond differently to ectoparasite removal in high and low quality habitats. Finally, I examined how ectoparasite richness and abundance affected feather growth rates with the expectation that haematophagous ectoparasites (some lice and some mites) would be more deleterious to feather growth rates than feather mites (Astigmata).

METHODS

Field Methods

I conducted this ectoparasite-removal study concordant with the other field work described in previous chapters. To summarize, I worked during the dry season (June–November) with mist-nets in and around 1-, 10-, and 100-ha fragments as well as continuous forest. I consider two habitat types: edge and interior forest (see Chapter 4). Edges were sampled in 2007 and 2009 whereas interior forest was sampled during the dry seasons from 2007 through 2009 (see Chapter 2). Each of 11 fragments and two 100-ha continuous forest plots were sampled passively with mist-nets six times within a dry season in 2007 (fragments) or 2008 (continuous forest) and two other 100-ha continuous forest plots were visited twice in 2008. In June and July 2009, I sampled a subset of fragments from each size class both passively and using playback to recapture color-marked study birds.

Captured target birds were marked with an alpha-numeric aluminum band issued by The Brazilian National Center for Bird Conservation (CEMAVE). About half of the individuals were

randomly assigned to the ectoparasite-removed group, with the other half serving as a control group. Birds in the ectoparasite-removed group were dust-ruffled with pyrethrin powder (Zema, Research Triangle Park, North Carolina) by sprinkling the powder over the body with special care to avoid contact with the eyes and bill (Walther and Clayton 1997). Although dust-ruffling does not remove all ectoparasites from the host, it removes 10-40% of louse load after three minutes of pyrethrin treatment, and the collected load is highly correlated ($0.83 < R^2 < 0.94$) with actual load (Clayton and Drown 2001), although more ectoparasites are collected up to 30 minutes after treatment (Walther and Clayton 1997). I let the powder sit on birds for six minutes and then agitated feathers with my hands over white paper to collect the ectoparasites. Although I doubled the exposure time to pyrethrin to remove additional ectoparasites, this experiment should be interpreted as a conservative assessment of ectoparasite removal. I expected additional weakened or killed ectoparasites to continue to fall off of dusted hosts after release. Same day recaptures were assessed for change in wing mite loads. Observations from these birds suggest the treatment was effective, as it was common for wing mites to have disappeared in recaptured dusted birds (E. I. Johnson, unpublished data). Ectoparasites were stored in 90% ethanol and birds were subsequently released. I counted abundance and richness of each ectoparasite group (Astigmata, haematophagous mites, and lice) in the lab (Chapter 4). Ectoparasite samples have been deposited in the Invertebrate Collection at Instituto Nacional de Pesquisas da Amazônica in Manaus, Brazil.

To measure changes in body condition with ptilochronology, I removed an outer right rectrix (R6) to stimulate an induced feather to grow from the same follicle. I followed the methodology outlined by Grubb (1989), using fine pins to mark each bar on index cards, measuring at least six growth bars on each feather, and using those bars to calculate growth rate.

The difference in feather growth rates between the initial and induced R6 serves as an indicator of changing body condition. To correct for differences in absolute size (feather length and rate is positively correlated with body size; Johnson et al. in press and E. I. Johnson, unpublished data), I used the relative change in growth by measuring the difference in growth rate between the initial and induced feather and dividing by the initial feather growth rate. Thus, more positive values indicate increased feather growth rate and negative values indicate decreased feather growth rate.

I evaluated the repeatability of measurements in *Pipra pipra* R6s, which are among the smallest feathers and have the narrowest growth bars in my study sample. Repeatability was very high and not statistically different when six, seven, eight, or nine bars were measured (E. I. Johnson, ubpublished data). Thus I was confident that a single measure using at least six growth bars provided an accurate measure of feather growth rates.

I only considered birds with non-juvenal rectrices for the study. Juvenile rectrices were relatively long and grew relatively fast for a given body size. This is problematic because the subsequent induced feather was always a shorter, slower-growing adult-like feather. Thus differences in growth rates were driven by age-related changes in feather morphology rather than the experiment. I therefore excluded immatures of species with partial pre-formative molts (*sensu* Howell et al. 2003; see also Chapter 2), like many Thamnophilidae, all Pipridae, *Turdus*, and *Microbates*, because they retained juvenal rectrices throughout their first year of life. Species in my study with complete pre-formative molts, like Dendrocolaptinae, Tyrannidae, and *Schiffornis*, could be used if captured in first formative plumage or older. Non-juveniles of these species were easily discerned from juveniles by plumage pattern, plumage texture, and fully ossified skulls (Pyle 1997).

Analyses

Testing the Assumption that Experimental Birds All Started Similar in Condition.—I used an ANCOVA (proc mixed, SAS Institute 2003) to test whether initial feather growth rates were different between habitat types for the subset of birds used for the ectoparasite-removal experiment, i.e., those that were later recaptured. I used initial feather growth rate as the dependent variable, habitat type (interior forest and forest edge) as a categorical independent variable and initial feather length as a covariate to control for longer feathers growing faster due to differences in body size *per se* and not necessarily body condition. This covariate also allowed me to pool data by family or ecological guild.

Ectoparasite-removal and Feather Growth Change.—My goal of this ectoparasite-removal experiment was to understand the interactive effects of ectoparasites and habitat quality on the body condition of 22 bird species from seven families (see Chapter 4). I assessed the interactive effects of ectoparasite removal and habitat type (edge and interior forest) using a two-factor ANOVA (proc mixed, SAS Institute 2003) with relative change of feather growth rate as a continuous response variable. Although 12 of 22 study species had sufficient samples to analyze at the species-level, using relative feather growth rates allowed me to also pool all species across higher-level host taxonomy and guild to include bird species with low sample size. It would have been more statistically appropriate to control for study site as a random variable, but few to no individuals were captured in the smallest fragments and even 100-ha fragments and continuous forest plots had low samples, preventing use of these statistical models.

An underlying assumption of the experiment is that all birds, regardless of ectoparasite-removal treatment or habitat type, had the same initial mean and variance of ectoparasite load

and diversity, which I showed in Chapter 4 to be largely met for ectoparasite abundance and richness.

Effects of Ectoparasite Community Structure on Feather Growth.—I modeled whether the abundance or richness of ectoparasite taxa that I removed contributed to changes in feather growth rates and whether their effects were habitat-dependent. Using feather growth rate change as a continuous dependent variable, I constructed general linear models (proc mixed, SAS Institute 2003) using natural log-transformed ectoparasite abundance or untransformed ectoparasite richness as covariates (each of three ectoparasite groups was a covariate) with habitat type as a fixed categorical independent variable. Following Sokal and Rohlf (1981), I first ran a fully-parameterized ANCOVA with nine parameters, including an interaction between each ectoparasite group and habitat type. These interactions test whether the regression slopes differ by habitat type. If interactions were not significant ($P > 0.05$), I then ran a reduced-parameter model, eliminating one to all interaction terms to test the whether the slope of each covariate was significantly different than zero.

Ectoparasite Reaccumulation Rates.—Reaccumulation rates between forest edges and interior forest may differ because of differences in host density influencing transmission rates and differences in habitat quality affecting hosts' abilities to regulate ectoparasite loads. I evaluated the effects of habitat type on reaccumulation rates of wing feather mites using a 2 x 2 factorial design mixed model ANCOVA (proc mixed, SAS Institute 2003). I examine whether the WMI upon recapture was different between habitat types (interior forest and forest edge) and between birds recaptured < 40 days after initially captured and birds captured ≥ 40 days. I chose 40 days since this approximates the time to completely regrow a feather and approximately corresponds to the maximum length of time between site visits. I used the WMI from the initial

capture as a covariate to control for individual bird's abilities to regulate ectoparasite load. This also allowed me construct analyses not only at the host species-level, but also grouping across host species by family or ecological guild.

RESULTS

Are There Initial Differences in Body Condition by Habitat Type?

I first tested whether the initial feather growth rates differed by habitat type because my experimental design utilized changes in feather growth rates as an indicator of changing body condition. There were few examples where initial feather growth rates differed between interior and edge forest habitats (Table 5.1). *Glyphorynchus spirurus* was a notable exception, with faster initial feather growth rates along edges (Fig. 5.1) both for the subset of recaptured experimental birds and when all initial feathers were used (Table 5.1). Flock dropouts and Furnariidae also had significantly faster feather growth along edges, but this was largely due the large contribution of *G. spirurus* samples to these groups. *Willisornis poecilinota* also had faster feather growth rates along edges, but only in the subset of birds used for the experiment (Fig. 5.1); including all initial feathers indicated a non-significant difference (Table 5.1).

Does Removing Ectoparasites Benefit Body Condition?

There was considerable variation in how host species, clades, and guilds responded to ectoparasite removal (Table 5.2, Fig 5.2). First, 5 of 11 species, three of six guilds, and three of five clades showed no change in feather growth rates by habitat type or ectoparasite-removal. Second, *Thamnomanes* spp. had increased feather growth rates along fragment edges irrespective of ectoparasite-removal. Third, *Lepidothrix serena*, frugivores as a group, and *Myrmotherula axillaris* experienced nearly significantly slower feather growth rates in the ectoparasite-removed group. This pattern was significant for all Pipridae combined. Fourth, *Pithys albifrons* increased

Table 5.1. Results from an ANCOVA testing differences in initial feather growth rates by habitat type (interior forest and forest edge), controlled for feather length because longer feathers grow faster (all $P < 0.01$, not shown). Significant differences ($P < 0.05$) are in bold. These tests only include the subset of birds that I recaptured and thus were used for the ectoparasite-removal experiment. When differences were significant, I also tested the entire set of initial feathers, which included birds not recaptured, to see if differences in initial feather growth rates in experimental birds were anomalous. Also shown is the average initial daily feather growth rate and SE; for groups of species, this measure is meaningless, thus not shown.

Guild or Family		Habitat type		Initial Feather Growth Rate (mm/day)	
Species	n	$F_{1,n-3}$	*P*	Mean	SE
Frugivore (5 spp.)	85	0.8	0.36		
Lepidothrix serena	16	0.2	0.68	1.45	0.02
Pipra pipra	46	0.3	0.60	1.53	0.02
Turdus albicollis	13	<0.1	0.99	3.37	0.07
Ant-follower (3 spp.)	104	1.5	0.23		
Pithys albifrons	60	0.1	0.75	1.57	0.01
Gymnopithys rufigula	37	1.0	0.34	1.89	0.02
Flock obligate (6 spp.)	52	1.0	0.33		
Thamnomanes spp.	29	2.9	0.10		
Flock dropout (4 spp.)[A]	130	**7.7**	**0.001**		
Glyphorynchus spirurus[B]	94	**4.7**	**0.034**	1.92	0.01
Xiphorhynchus pardalotus	16	0.6	0.47	2.33	0.06
Myrmotherula axillaris	13	0.9	0.36	1.45	0.02
Gap specialist (*Percnostola*)	26	<0.1	0.86	1.87	0.02
Other insectivore (3 spp.)	53	2.9	0.098		
Willisornis poecilinota[C]	37	**4.5**	**0.043**	1.65	0.01
Furnariidae (5 spp.)	131	**9.7**	**0.002**		
Thamnophilidae (10 spp.)	218	2.1	0.15		
Pipridae (3 spp.)	63	0.4	0.52		
Tyrannidae + *Schiffornis* (3 spp.)	17	<0.1	0.86		
10-primaried oscines (2 spp.)	24	<0.1	0.98		

[A]Using all initial feathers: $F_{1,191} = 10.8$, $P = 0.001$
[B]Using all initial feathers: $F_{1,115} = 5.1$, $P = 0.026$
[C]Using all initial feathers: $F_{1,66} = 2.4$, $P = 0.123$

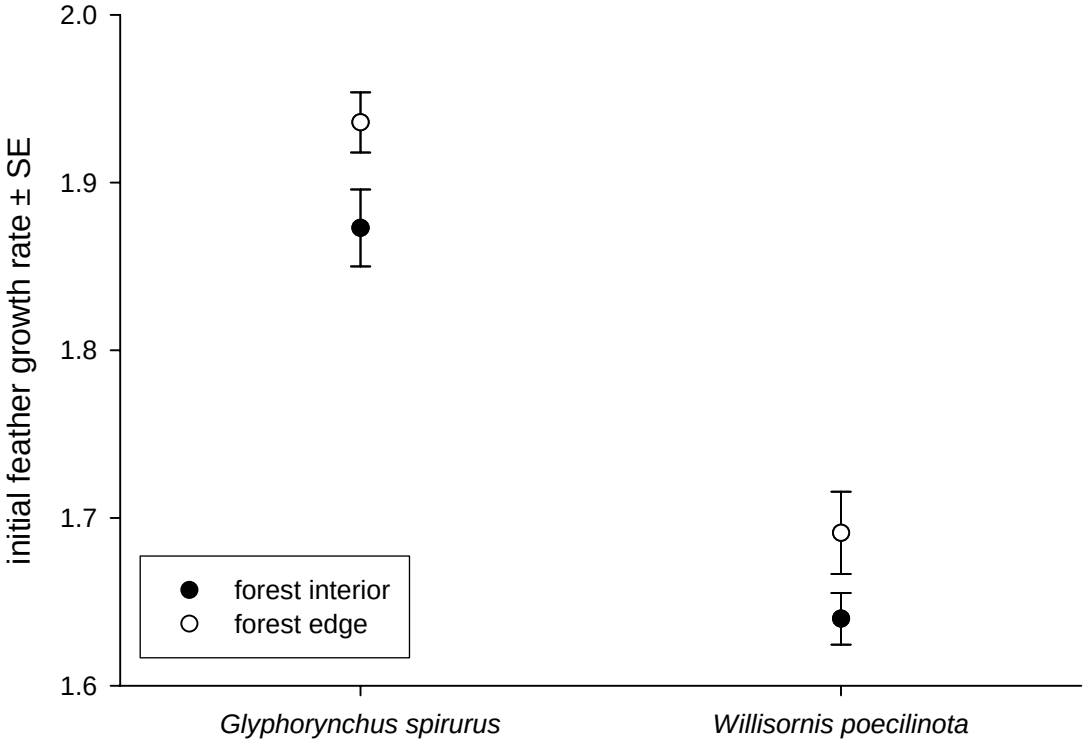


Fig. 5.1. Differences in initial feather growth rates (mm/day) by habitat type in *Glyphorynchus spirurus* and *Willisornis poecilinota* in the subset of recaptured birds used for the ectoparasite-removal experiment. See Table 5.1 for statistical tests.

Table 5.2. Results of the ectoparasite-removal experiment, testing the effects of ectoparasite-removal, habitat type (interior forest and forest edge), and their interaction on changes in feather growth rates. Significant differences ($P < 0.05$) are in bold.

Guild or Family Species	n	Ectoparasite removal		Habitat type		Interaction	
		$F_{1,n-4}$	*P*	$F_{1,n-4}$	*P*	$F_{1,n-4}$	*P*
Frugivore (5 spp.)	85	3.4	0.070	0.1	0.77	0.5	0.48
Lepidothrix serena	16	3.9	0.073	<0.1	0.89	0.3	0.62
Pipra pipra	46	1.4	0.25	0.3	0.58	<0.1	0.95
Turdus albicollis	13	<0.1	0.97	1.4	0.27	2.6	0.14
Ant-follower (3 spp.)	104	**4.1**	**0.047**	0.1	0.74	0.1	0.80
Pithys albifrons	60	3.9	0.055	2.2	0.15	1.0	0.31
Gymnopithys rufigula	37	1.0	0.33	2.1	0.16	0.1	0.72
Flock obligate (6 spp.)	52	<0.1	0.85	2.5	0.12	0.9	0.36
Thamnomanes spp.	29	<0.1	0.90	**4.6**	**0.041**	0.3	0.59
Flock dropout (4 spp.)	130	0.1	0.76	<0.1	0.91	<0.1	0.87
Glyphorynchus spirurus	94	0.8	0.39	<0.1	0.95	0.1	0.81
Xiphorhynchus pardalotus	16	<0.1	0.99	0.3	0.59	<0.1	0.88
Myrmotherula axillaris	13	4.1	0.074	0.2	0.64	<0.1	0.96
Gap specialist (*Percnostola*)	26	0.4	0.51	0.3	0.57	**5.2**	**0.033**
Other insectivore (3 spp.)	53	0.1	0.82	0.6	0.43	2.4	0.13
Willisornis poecilinota	37	<0.1	0.93	2.0	0.17	**10.3**	**0.003**
Furnariidae (5 spp.)	131	0.9	0.35	1.9	0.18	<0.1	0.91
Thamnophilidae (10 spp.)	218	0.3	0.62	<0.1	0.85	**5.7**	**0.018**
Pipridae (3 spp.)	63	**4.1**	**0.047**	0.3	0.62	<0.1	0.83
Tyrannidae + *Schiffornis* (3 spp.)	17	0.4	0.53	0.9	0.35	0.3	0.57
10-primaried oscines (2 spp.)	24	0.1	0.83	0.1	0.75	2.5	0.13

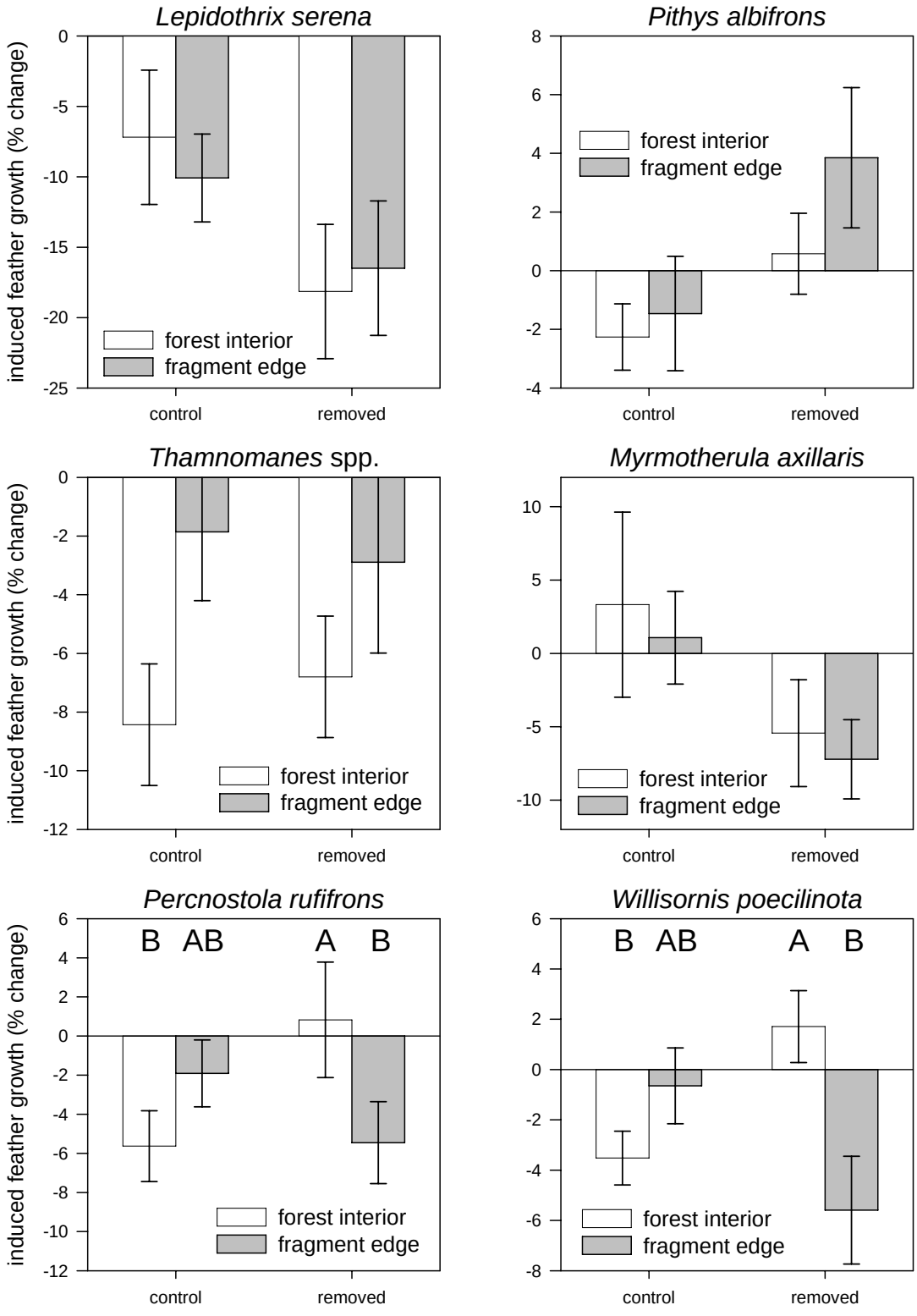
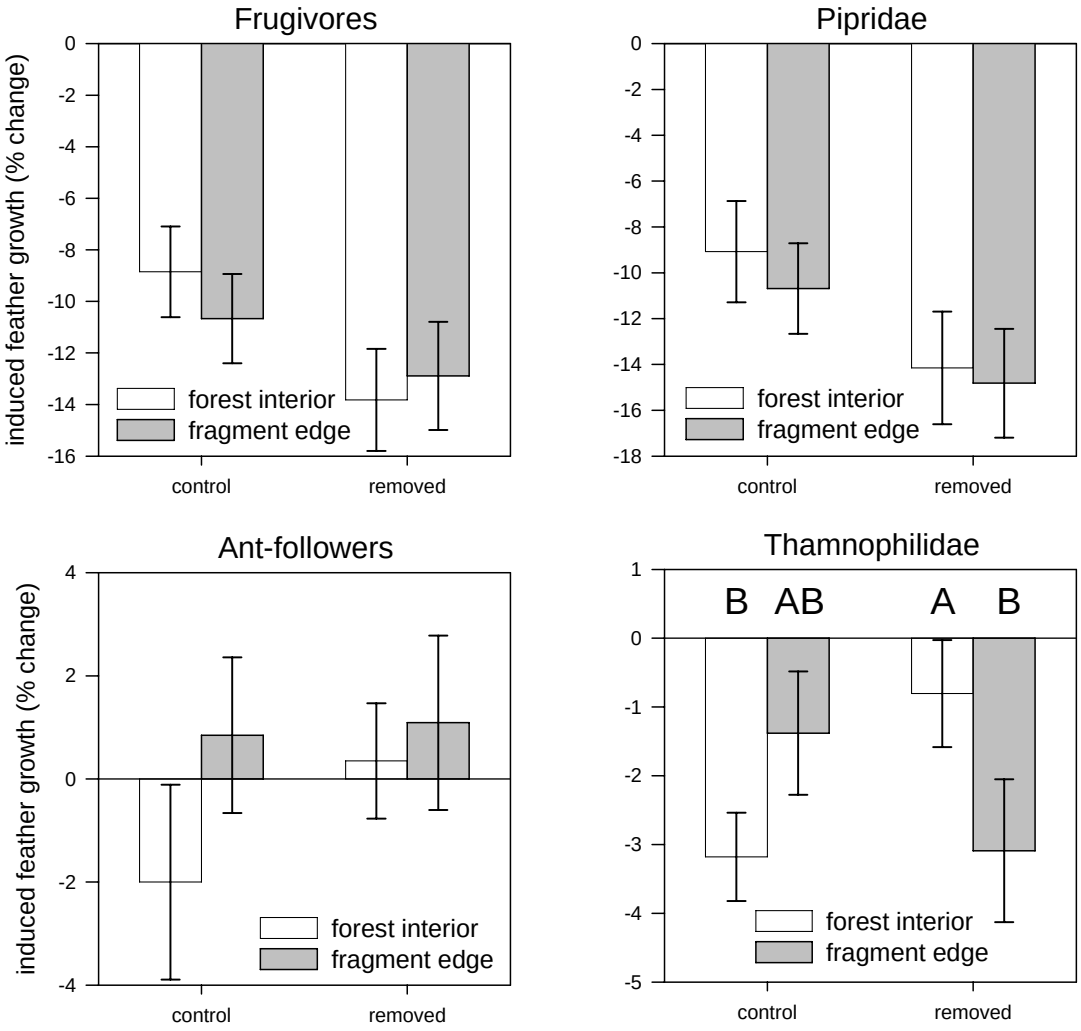


Fig. 5.2. Changes in feather growth rates by habitat type (interior forest and fragment edge) and ectoparasite-removal treatment for six host species, two host families (next page) and two host guilds (next page).

Fig. 5.2 Continued.



feather growth rates after ectoparasite-removal compared to the control group irrespective of habitat type. Fifth, *W. poecilinota*, *Percnostola rufifrons*, and all thamnophilids combined had a significant interaction between habitat type and ectoparasite removal. Birds occupying interior forest increased feather growth rates after ectoparasite removal, as predicted, but birds living along edges did not. Pairwise comparisons also revealed that the control group occupying edges had similar feather growth rates to the other three treatments (Fig 5.2).

Are Changes in Body Condition Caused by Ectoparasite Community Composition?

I examined variation in removed ectoparasite abundance and richness to determine whether these variables corresponded with changes in feather growth rates. Removed Astigmata, haematophagous mite, and louse abundances were rarely associated with changes in feather growth rates (Table 5.3). There were a few expections, however, with frugivores, *Pipra pipra*, and flock obligates responding to the number of lice or Astigmata removed (Table 5.3, Fig. 5.3). Greater numbers of Astigmata removed from frugivores corresponded with faster feather regrowth rates, but only along forest edges. Greater numbers of lice removed from frugivores, however, corresponded with faster regrowth rates in interior forest. This interaction did not appear in *P. pipra*, with greater numbers of removed lice corresponding to faster regrowth rates, regardless of habitat, as also occurred in flock obligates (Fig. 5.3).

The richness of removed ectoparasites more often corresponded with changes in feather growth rates than abundance of removed ectoparasites, and more often showed an interaction with habitat type (Table 5.4). In *Gymnopithys rufigula* and ant-followers, removing greater louse richness corresponded with faster feather growth rates in interior forest, but decreasing growth rates along forest edges (Fig. 5.4). The opposite pattern was observed for Astigmata (significant in ant-followers and nearly significantly across all Thamnophilidae; Table 5.4) and haematophagous mites (in ant-followers only), where removing greater ectoparasite richness corresponded with slower feather growth rates in interior forest and faster feather growth rates along edges (Fig. 5.4). Regardless of habitat type, removing greater louse richness corresponded with increased feather growth rates across all Thamnophilidae, whereas removing greater Astigmata richness corresponded with decreasing feather growth rates in only *W. poecilinota* (Fig. 5.4).

Table 5.3. Statistical results from ANCOVAs testing the effects of habitat type (not shown; see Table 5.2) and three ectoparasite groups, and interactions between ectoparasite abundance and habitat type on feather growth rates for birds treated with pyrethrin. Bold indicates statistical significance ($P < 0.05$). Missing F-statistics and *P*-values indicate variables not included in model. Tyrannidae + *Schiffornis* and 10-primaried oscines not tested because of low sample sizes.

Guild or Family		Lice		Astigmata		Haematophagous mites		Lice × habitat		Astigmata × habitat		Haemat. mites × habitat	
Species	den df	$F_{1, df}$	*P*	$F_{1,df}$	*P*	$F_{1,df}$	*P*	$F_{1,df}$	*P*	$F_{1,df}$	*P*	$F_{1,df}$	*P*
Frugivore (5 spp.)	25	0.5	0.49	1.5	0.24	3.6	0.070	**6.8**	**0.016**	**7.7**	**0.010**		
Pipra pipra	14	**6.0**	**0.028**	3.1	0.099	1.4	0.26						
Ant-followers (3 spp.)	32	0.1	0.77	1.2	0.29	0.2	0.64						
Pithys albifrons	18	0.1	0.71	1.4	0.26	0.1	0.81						
Gymnopithys rufigula	9	0.1	0.80	0.3	0.60	0.4	0.57						
Flock obligate (5 spp.)	16	**6.1**	**0.025**	2.4	0.14	<0.1	0.89						
Thamnomanes spp.	7	0.2	0.64	0.4	0.57	<0.1	0.86						
Flock dropout (4 spp.)	35	<0.1	0.98	<0.1	0.84	2.4	0.13						
Glyphorynchus spirurus	24	0.1	0.82	<0.1	0.88	0.3	0.58						
Gap specialist (*P. rufifrons*)	5	0.3	0.59	0.1	0.76								
Other insectivore (3 spp.)	10	0.1	0.83	0.3	0.58	0.1	0.82						
Willisornis poecilinota	7	<0.1	0.94	3.1	0.12	<0.1	0.95						
Dendrocolaptinae	34	0.1	0.77	0.2	0.70	2.8	0.11						
Thamnophilidae	78	2.0	0.16	0.4	0.51	<0.1	0.90						
Pipridae	19	3.0	0.10	0.5	0.51	<0.1	0.88						

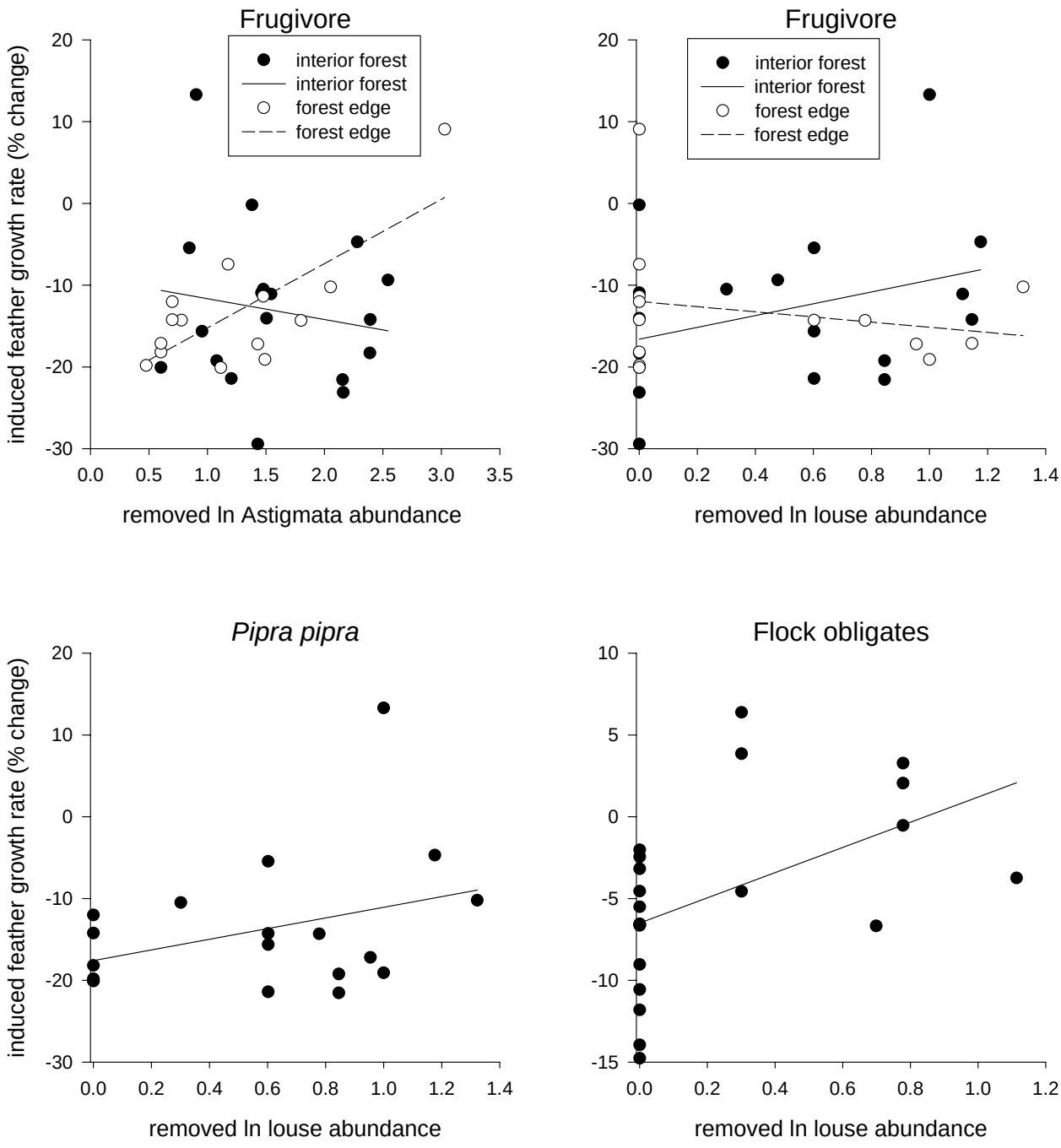


Fig. 5.3. Changes in feather growth rates as a result of the number of Astigmata removed from frugivores or lice removed from frugivores, flock obligates, and *Pipra pipra*.

Table 5.4. Statistical results from ANCOVAs testing the effects of habitat type (not shown; see Table 5.2) and richness of three ectoparasite groups, and interactions between ectoparasite richness and habitat type on feather growth rates for birds treated with pyrethrin. Bold indicates statistical significance ($P < 0.05$). Missing F-statistics and *P*-values indicate variable not included in model. Tyrannidae + *Schiffornis* and 10-primaried oscines not tested because of low sample sizes.

Guild or Family		Lice		Astigmata		Haematophagous mites		Lice × habitat		Astigmata × habitat		Haemat. mites × habitat	
Species	den df	$F_{1, df}$	*P*	$F_{1,df}$	*P*	$F_{1,df}$	*P*	$F_{1,df}$	*P*	$F_{1,df}$	*P*	$F_{1,df}$	*P*
Frugivore (5 spp.)	13	0.7	0.41	2.5	0.14	<0.1	0.84						
Pipra pipra	13	0.7	0.41	2.5	0.14	<0.1	0.84						
Ant-followers (3 spp.)	31	0.1	0.77	<0.1	0.87	<0.1	0.91	**4.3**	**0.046**				
Pithys albifrons	18	0.1	0.75	0.3	0.59	<0.1	0.91						
Gymnopithys rufigula	6	<0.1	0.85	2.5	0.17	4.7	0.073	**37.8**	**0.001**	**10.9**	**0.016**	**8.9**	**0.025**
Flock obligate (5 spp.)	14	**8.7**	**0.011**	1.3	0.27	2.9	0.11						
Thamnomanes spp.	7	0.5	0.51	2.1	0.19	2.7	0.15						
Flock dropout (4 spp.)	34	0.4	0.53	3.6	0.067	<0.1	0.96						
Glyphorynchus spirurus	24	0.2	0.69	4.0	0.057	3.9	0.059						
Gap specialist (*P. rufifrons*)	5	<0.1	0.87	0.1	0.81	.	.						
Other insectivore (3 spp.)	8	0.2	0.69	**20.0**	**0.002**	0.9	0.38						
Willisornis poecilinota	8	0.2	0.69	**20.0**	**0.002**	0.9	0.38						
Dendrocolaptinae	28	0.7	0.41	2.4	0.13	1.0	0.34						
Thamnophilidae	78	**4.2**	**0.044**	<0.1	0.97	0.2	0.63			3.9	0.051		
Pipridae	13	0.7	0.41	2.5	0.14	<0.1	0.84						

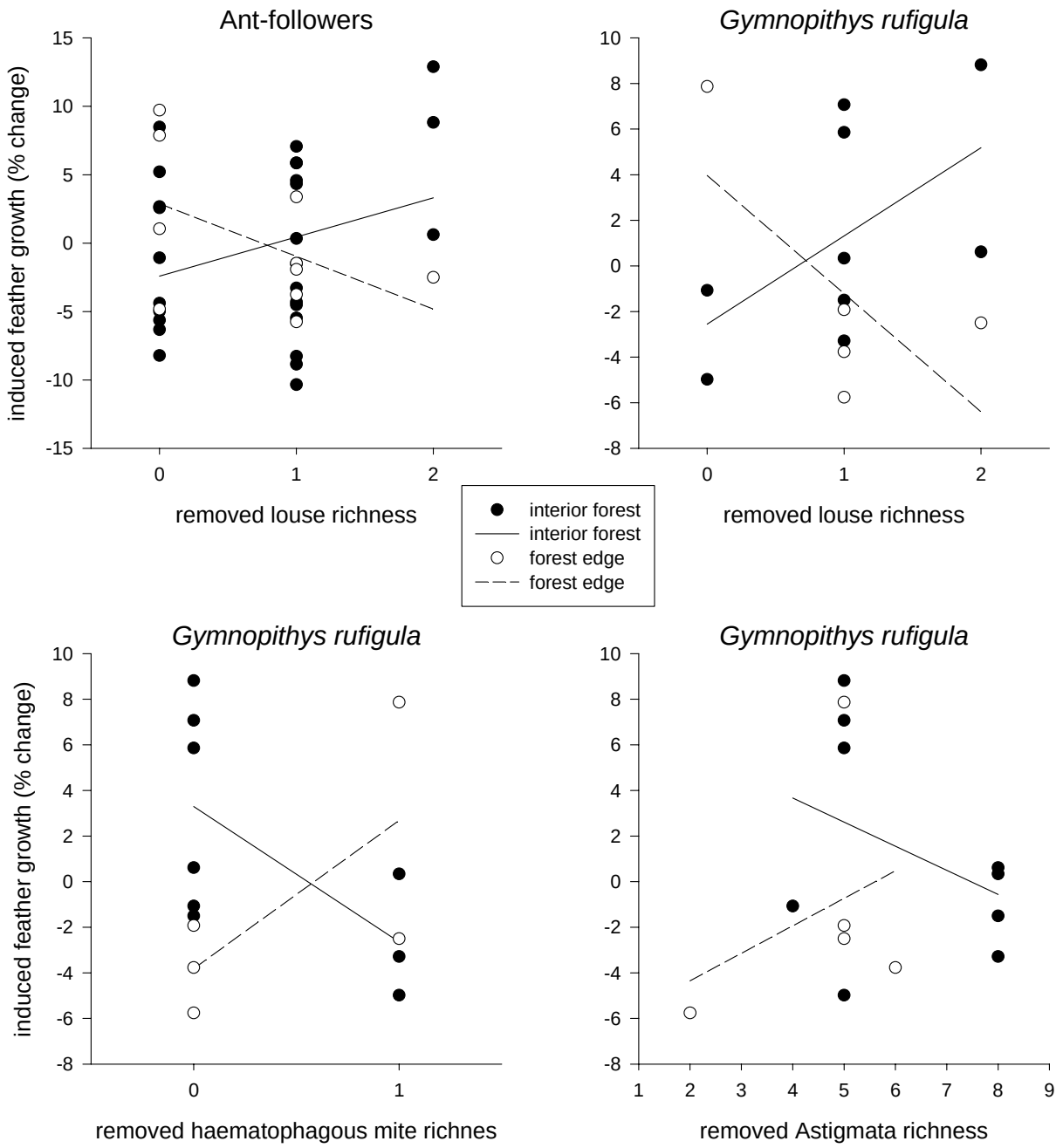
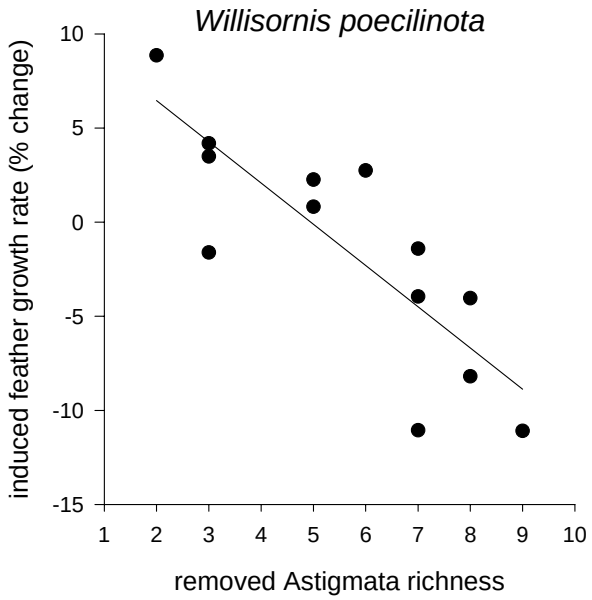
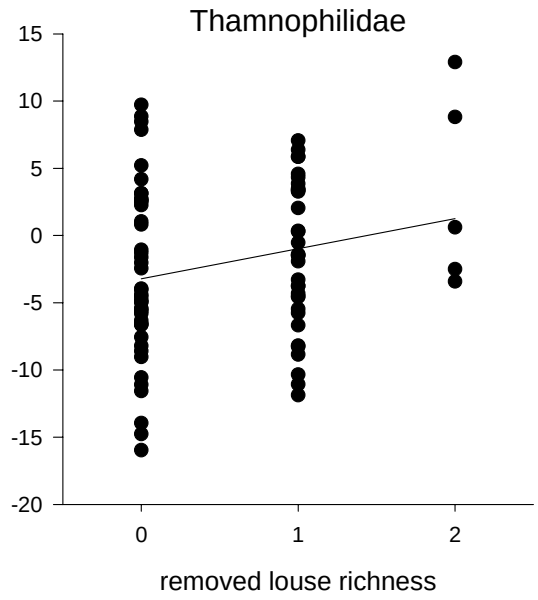


Fig. 5.4. Changes in feather growth rates as a result of the richness of Astigmata or lice removed for two host species, one host guild, and one host family (see also next page). Best-fit linear regression lines are illustrated by habitat type for interactions or for habitats pooled without interactions.

Fig. 5.4 Continued.





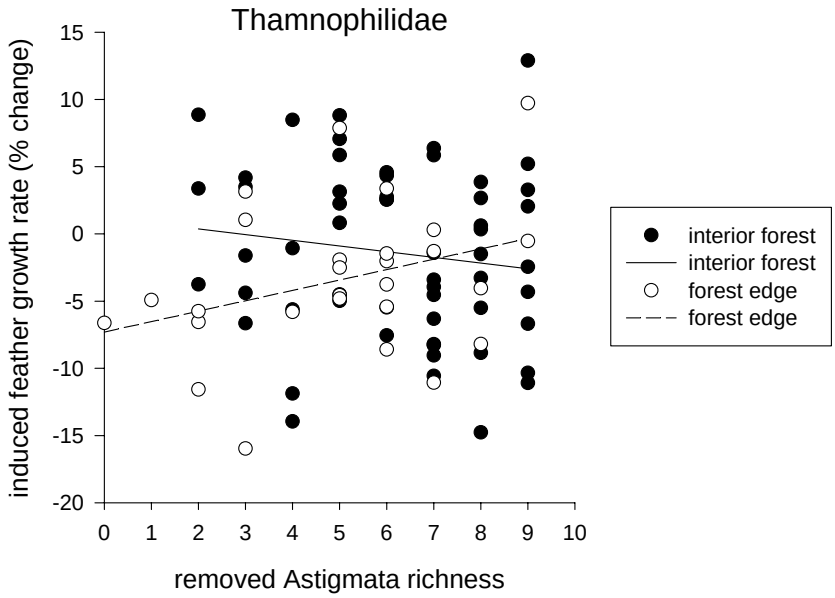


Table 5.5. Results from an ANCOVA testing the effects of habitat type (interior forest and forest edge), time interval between initial and recapture (< 40 and ≥ 40 days), and their interaction on the wing mite index upon recapture for birds treated with pyrethrin. I used initial wing mite index ($WMI_{initial}$) as a covariate to correct for differences in initial wing mite loads. Statistically significant differences ($P < 0.05$) are in bold. Tyrannidae + *Schiffornis* and 10-primaried oscines not tested because of low sample sizes.

Guild		Habitat type		Time interv.		Habitat × time		$WMI_{initial}$	
Species	n	$F_{1,n-5}$	P	$F_{1,n-5}$	P	$F_{1,n-5}$	P	$F_{1,n-5}$	P
Frugivore (5 spp.)	37	0.1	0.76	3.7	0.063	0.2	0.64	1.4	0.25
Pipra pipra	21	0.1	0.78	<0.1	0.91	3.3	0.089	3.1	0.097
Ant-followers (3 spp.)	47	0.9	0.36	2.3	0.13	0.3	0.61	1.4	0.24
Pithys albifrons	29	3.9	0.059	0.1	0.78	0.2	0.63	5.9	0.024
Gymnopithys rufigula	15	0.1	0.75	1.7	0.22	0.6	0.45	<0.1	0.97
Flock obligate (5 spp.)	26	0.9	0.37	3.4	0.079	0.1	0.71	18.9	<0.001
Thamnomanes spp.	14	0.8	0.38	2.6	0.14	<0.1	0.85	5.5	0.043
Flock dropout (4 spp.)	53	3.1	0.086	1.5	0.23	0.1	0.78	8.2	0.006
Glyphorynchus spirurus	36	2.2	0.15	2.2	0.15	0.1	0.79	3.0	0.092
Gap specialist (*P. rufifrons*)	10	0.5	0.52	5.6	0.064	0.8	0.42	0.1	0.79
Other insectivore (3 spp.)	25	1.3	0.26	0.5	0.50	3.0	0.11	21.3	<0.001
Willisornis poecilinota	19	0.8	0.38	0.4	0.54	1.9	0.19	7.4	0.017
Dendrocolaptinae	49	2.4	0.13	1.9	0.18	<0.1	0.88	5.2	0.028
Thamnophilidae	107	1.3	0.26	**8.6**	**0.004**	**4.4**	**0.038**	18.6	<0.001
Pipridae	29	0.8	0.37	<0.1	0.95	3.1	0.090	4.1	0.054

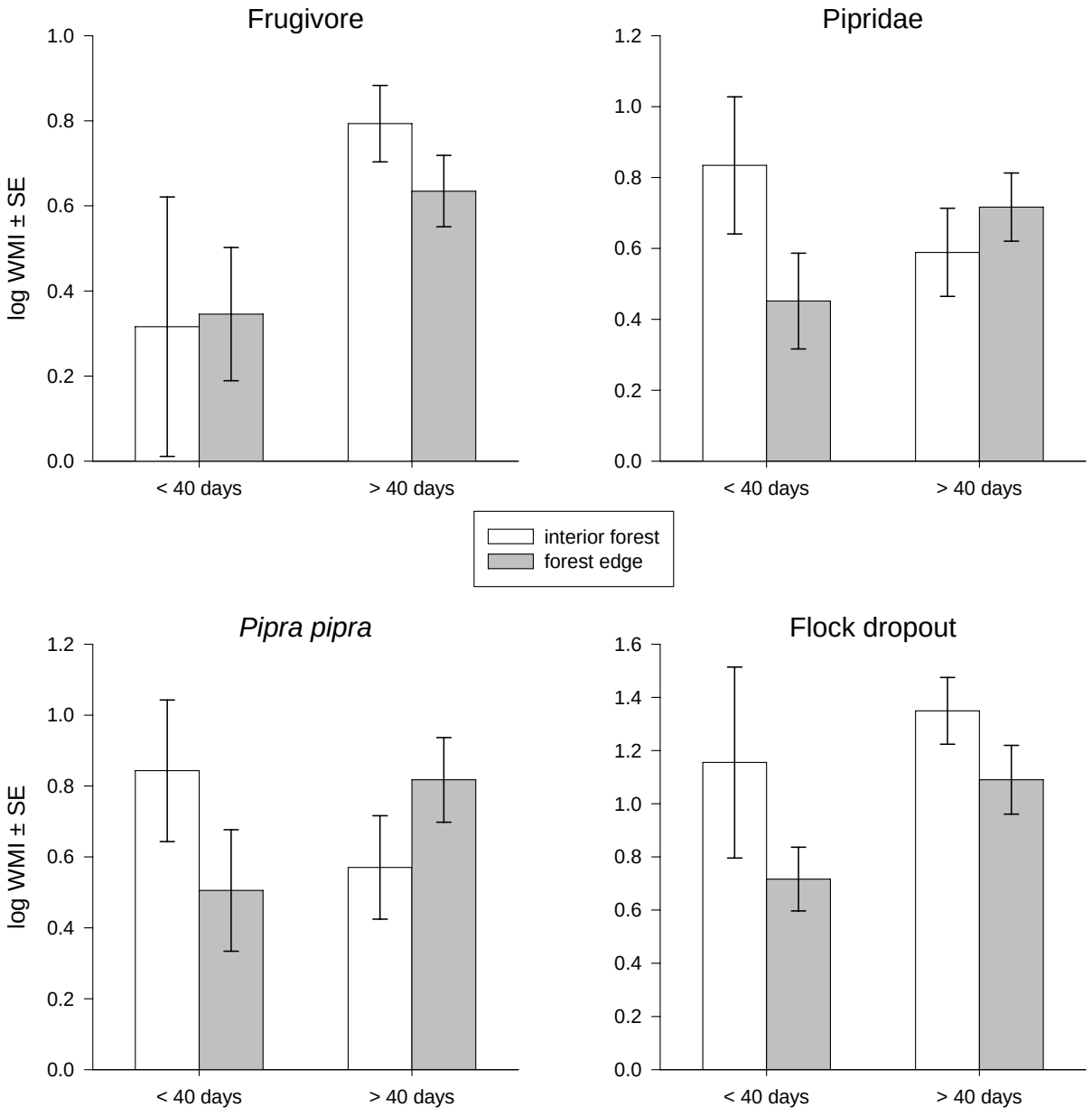
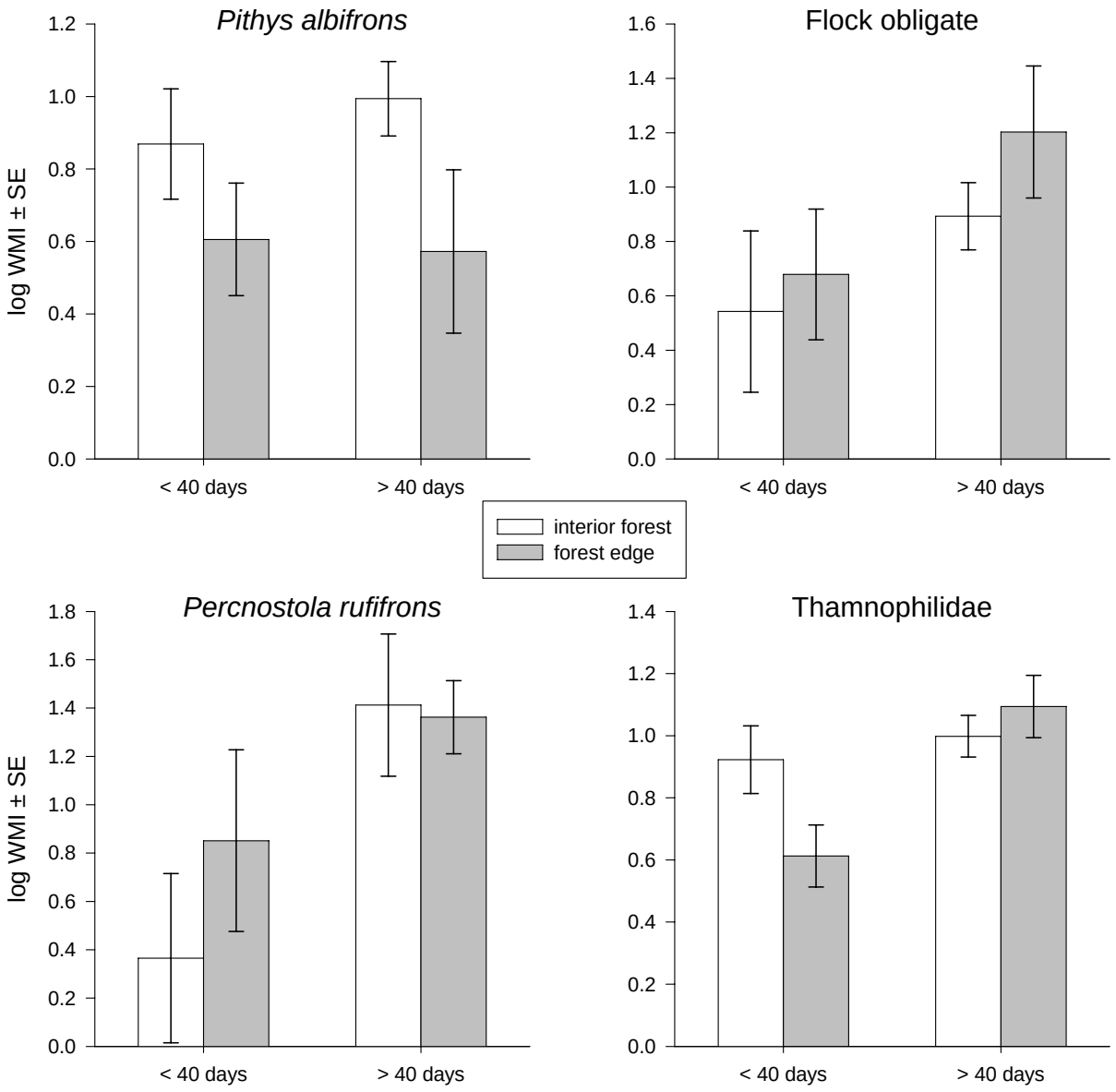


Fig 5.5. Wing mite index (WMI) upon recapture when recaptured < 40 and ≥ 40 days after the initial capture by habitat type (interior forest and forest edge).

Fig. 5.5 Continued.



Reaccumulation Rates of Wing Feather Mites

I examined ectoparasite reaccumulation rates of ectoparasite-removed birds by examining their WMI upon recapture. I contrasted birds recaptured < 40 days later against those recaptured > 40 days later between interior forest and forest edge, correcting for the WMI during initial capture. The only significant difference in WMI among treatments was observed when data from all Thamnophilids were pooled (Table 5.5). For birds recaptured < 40 days after the initial capture, WMI was lower along edges than interior forest (Fig. 5.5). After > 40 days between the initial and recapture, WMI had not changed in interior forest, but increased to interior forest levels along edges.

I detected nearly significant effects in seven taxa (species or families) or guilds, although a consistent pattern did not emerge (Table 5.5, Fig. 5.5). In frugivores, flock obligates, and the gap specialist *P. rufifrons* the WMI index was lower < 40 days between the initial and recapture than ≥ 40 days. In *P. albifrons* and flock dropouts, WMI was higher in interior forest than along edges, regardless of the amount of time between captures. In *P. pipra* and Pipridae, WMI decreased with increasing time since recapture in interior forest, but increased with increasing time since capture along forest edges.

DISCUSSION

Interior rainforest birds are subject to a number of pressures in a fragmented landscape, where fragments often sustain lower population densities and birds experience reduced condition and fitness (Stratford and Stouffer 2001, Stouffer et al. 2006, Feeley and Terborgh 2008, Ruiz-Gutierrez et al. 2008, Sodhi et al. 2008). This, along with a hostile second growth matrix decreasing the ability to disperse, increases their risk of extinction (Ferraz et al. 2007). This ectoparasite-removal experiment revealed that host–ectoparasite dynamics can be altered in

fragmented landscapes, although there was considerable variation in responses among host taxa and host ecological guilds.

Antbirds Respond to Ectoparasite Removal

Thamnophilidae as a group were particularly responsive to ectoparasite-removal. In general, the birds used for the ectoparasite-removal experiment started with similar condition (Table 5.1) and ectoparasite loads (Table 4.7) between interior forest and forest edge habitat types. Only *Willisornis poecilinota* started in slightly better condition along edges, but the difference was barely significant and became non-significant when all initial feather growth rates were used. Releasing Thamnophilidae from ectoparasites improved their body condition in interior forest, indicated by a 2.3% increase in feather growth rates, while birds along edges did not significantly change their body condition and even appeared to slightly decrease in condition (Fig. 5.2). A similar pattern was observed in *W. poecilinota* and *Percnostola rufifrons* with a 5.2% and 6.3% increase in feather growth rates, respectively, in interior forest.

Louse richness, and to a lesser degree louse abundance, had a negative influence on thamnophilid body condition. Feather growth rates improved by 3.8% when two louse species were removed compared to none (Fig. 5.4). Louse abundance did not influence body condition (Table 5.3) except in flock obligates (Fig. 5.3), which included five species of antbirds and one woodcreeper (Appendix A).

In contrast to lice, Astigmata benefited thamnophilid hosts, at least in interior forest, consistent with accumulating evidence of their mutalistic relationship with birds (Figuerola 2000, Jovani and Blanco 2000, Blanco and Tella 2001, Pap et al. 2005, Brown et al. 2006). Removing ten taxa of Astigmata decreased feather growth rates by 2.4% compared to removing two taxa, but only in interior forest (Fig. 5.4). The effect in *W. poecilinota* was especially strong and

consistent between habitat types, with about a 15% decrease in feather growth rate when nine Astigmata taxa were removed compared to two (Fig. 5.4). Along edges, however, removing Astigmata had the opposite effect with thamnophilid feather growth rates increasing 7.1% when nine Astigmata taxa were removed compared to none (Fig. 5.4). Therefore, habitat quality appeared to have influenced how hosts responded to feather mites, as they were beneficial to hosts in interior forests, but switched to being harmful along edges. A similar interaction was observed in ant-followers and *Gymnopithys rufigula* in particular (Fig. 5.4). This switch in how hosts respond to Astigmata may at least partially explain whey ectoparasite removal did not benefit Thamnophilidae along edges.

There were a variety of other responses to the ectoparasite-removal experiment among some thamnophilids and guilds predominated by thamnophilids, although these become difficult to reconcile with the pattern seen in Thamnophilidae as a whole. First, ant-followers (which also included three samples from the woodcreeper *Dendrocincla merula*) had lowest body condition in the interior forest control group (Fig. 5.2). Although it appears that ectoparasite-removal improved body condition regardless of habitat, as in the ant-follower *Pithys albifrons* (Table 5.2), the control group along edges also had comparably good feather growth rates compared to the ectoparasite-removal group. Is this related to the how Astigmata, haematophagous mite, and louse richness interacts with habitat quality to affect body condition? Or was this an artifact of low sample size?

Second, *Thamnomanes* spp. had faster regrowth rates along edges compared to interior forest, regardless of ectoparasite removal. There were no differences in ectoparasite loads (Chapter 4) or ectoparasite reaccumulation rates between habitat types (Table 5.5, Fig. 5.5), suggesting that this was indeed habitat-related. Stratford and Stouffer (2001) found that small

fragments (i.e. edge in my experiment) decreased feather growth rates in two not particularly fragmentation-sensitive species, *Pipra pipra* and *Glyphorynchus spirurus*, so it was surprising to see the opposite trends in this experiment in *Thamnomanes*, fragmentation-sensitive mixed-species flock leaders (Develey and Stouffer 2001, Stouffer et al. 2006, Chapter 2). Possibly birds along edges could be non-breeders, thus giving them the capacity to dedicate energetic resources to feather growth compared to interior forest birds, which may have bred during the experiment.

Manakins Respond to Ectoparasite Removal

Unlike Thamnophilidae, Pipridae did not improve condition when treated with pyrethrin powder and instead decreased feather growth rates by 3.5%. Despite the overall decrease in Pipridae feather growth rates in the ectoparasite-removed group, the results of the ectoparasite-removal experiment on Pipridae had some interesting parallels to what was observed in Thamnophilidae. Lice, for example, also negatively affected Pipridae. The more lice that were removed, the greater the benefit to feather growth rates (Fig. 5.3). Frugivore body condition, which had samples dominated by the manakins *P. pipra* and *Lepidothrix serena*, had a habitat-dependent reaction to Astigmata and louse removal similar to Thamnophilidae. Removing more Astigmata decreased body condition in interior forest, but increased body condition along edges. Removing more lice decreased body condition in interior forest, but decreased body condition along edges (Fig. 5.3).

It is unclear why Pipridae feather growth rates decreased after pyrethrin treatment. Interestingly, *Myrmotherula axillaris*, another small-bodied species, showed a nearly significant (despite a small sample size) decrease in feather growth rate of about 8%. It may be that the pyrethrin treatment had a negative effect on these small-bodied species, despite its potential for

removing harmful lice. It is possible that inhaling or ingesting powder may have caused some long-term harm, although pyrethrin, the active ingredient, attacks the nervous system of invertebrates, and is not the likely culprit (Jackson 1985, Clayton and Tompkins 1995). It is not likely that removing mutualistic Astigmata was responsible for this decline in host body condition because the relationship between Astigmata removal and condition was not significant. Pipridae also had relatively low Astigmata loads for their body size and among the highest louse loads. Whatever the cause of this decline, it is curious that it was particularly evident in small-bodied species.

Other Host Responses to Ectoparasite Removal

Dendrocolaptinae, Tyrannidae + *Schiffornis*, and 10-primaried oscine feather growth rates did not respond to ectoparasite-removal (Tables 5.2–5.4). Part of this may be explained by rapid reaccumulation rates (Table 5.5), but may also include a combination of additional factors. First, *G. spirurus*, for example, was often infested with a nearly subcutaneous orange parasite, possibly a trombiculid chigger. These were apparently not removed effectively after dust-ruffling and may have negated any possible benefits of ectoparasite removal. Second, Dendrocolaptinae were infested with feather-chewing Ischnoceran lice, whereas Thamphilidae and Pipridae were predominately infested with haematophageous Amblyceran lice (Appendix C). Ischnoceran are considered to be more mildly parasitic than Amblyceran because of different food preferences (Møller and Rózsa 2005), thus Dendrocolaptinae may not have shown a response in body condition when their Ischnoceran were removed. Third, Tyrannidae and 10-primaried oscines had relatively low sample sizes, thus it is difficult to conclude whether the ectoparasite-removal experiment did not have an effect or whether sample sizes were too low to detect an effect.

Direct and Indirect Effects of Ectoparasites

Astigmata are a diverse group of organisms, with over 2500 taxa known to associate with birds, but this could easily be an order of magnitude too low since nearly all bird species (apparently excluding penguins) have at least one feather mite taxon (Proctor and Owens 2000, Proctor 2003). All of the species I examined had at least three taxa of Astigmata living on them (Appendix C), although we do not yet know how host specific these taxa are. Because some Astigmata are specialized on uropygial oils, it is believed that at least some have high host specificity (O'Conner 1982). Among at least Thamnophilidae and frugivores, Astigmata appeared to benefit their hosts because as a greater richness or abundance was removed, body condition accordingly decreased. This idea that Astigmata are mutualistic has been proposed elsewhere through correlative approaches (Figuerola 2000, Jovani and Blanco 2000, Blanco and Tella 2001, Pap et al. 2005, Brown et al. 2006), but this idea is much more robustly supported through the experimental approach I developed here. Astigmata are known to consume uropygial oils (O'Conner 1982, Phillips 1990, Blanco et al. 2001, Proctor 2003), which degrade and must be removed and reapplied, but also other debris like pollen, fungal spores, algae, and feather-degrading bacteria (Dubinin 1951 as cited in Proctor 2003).

It was unexpected that Astigmata were beneficial to host feather growth rates in interior forests, but had an opposite effect along forest edges, at least in Thamnophilidae and frugivores. This suggests that feather mites maintain a delicate balance with their hosts that can be disrupted in suboptimal habitat. Feather mites can irritate the skin and cause birds to react by shedding feathers (Proctor 2003) and perhaps the stress of living in a suboptimal environment causes hosts to negatively react to the presence of Astigmata. It is possible that Astigmata become more aggressive to hosts because of increased light intensity along edges. Mites actively avoid bright

light associated with increased ambient temperatures (Wiles et al. 2000) and may have move closer to the skin of the bird, causing increased irritation. Astigmata can also degrade plumage coloration (Figuerola et al. 2003), which may be more important along bright edges, probably not because of sexual or social signaling, but for maintaining feather structure.

Louse removal improved host body condition, at least in frugivores (mostly Pipridae) and Thamnophilidae occupying interior forest. Lice consume feathers and blood and irritate the skin, which directly reduces nutritional condition of their hosts (DeVaney 1976, Booth et al. 1993). Haematophagous Amblycera also impose indirect effects on bird hosts because wounds on hosts can become infected and these lice can transmit endoparasites (Seegar et al. 1976, Holmstad et al. 2008). What is not clear is why host body condition did not decrease with louse removal along forest edges in frugivores and Thamnophilidae (Figs. 5.3, 5.4). One might instead expect that louse removal in suboptimal habitat to be even more beneficial to their host. It is possible other factors were involved or that this pattern was driven by one or two outliers.

Ectoparasite-removal may also have indirect effects on hosts that slow feather growth rates. Feather growth rates, at least in some species, influence the probability of molting and breeding simultaneously, called molt-breeding overlap (Chapter 4). For example, a 5.2% decrease in *W. poecilinota* feather growth rate increases its probability molt-breeding overlap by 33%. Frequent molt-breeding overlap is associated with fragmentation sensitivity, thus ectoparasites not only directly decrease body condition, but may also indirectly increase sensitivity to fragmentation by reducing feather growth rates.

Host–Ectoparasite Dynamics in Fragmented Landscapes

This study illustrates the importance of experimental approaches to understand host–ectoparasite dynamics, especially in human-modified landscapes (Blanchet et al. 2009). A

correlative approach examining ectoparasite load and host body condition between interior forest and forest edge would have concluded that ectoparasites have no affect on their hosts in this fragmented landscape (Chapter 4). Instead, I showed that ectoparasite-removal was generally more advantageous to birds in interior forest than along edges. Feather growth rates provide an approximately one-month record of body condition after ectoparasite removal. After this period wing mite loads appear to have rebounded to pre-removal loads, suggesting that the body condition record captured by ptilochronology reveals the temporal window in which experimental ectoparasite-removal acts. Ectoparasite maintenance is largely controlled through preening (Clayton et al. 2005), but there are also immune responses that buffer hosts against ectoparasite infestations (Sheldon and Verhulst 1996, Saino et al. 1998, Tschirren and Richner 2006, Owen et al. 2010), which may not immediately respond to ectoparasite removal. Hosts in interior forest may be capable of a faster immunological response to ectoparasite removal than birds along forest edges, thus shifting resources to improving feather growth quickly and effectively.

While the field of host–ectoparasite dynamics has made significant progress in recent decades, we need additional studies on the effects of habitat quality on free-living birds before generalizations about the effects of fragmentation on these complex relationships can be made. This study has revealed that host-parasite dynamics can be affected by habitat quality, although not always in predictable ways. Given results from this study, it is possible that ectoparasites, and perhaps especially lice, contribute to population declines in reduced-quality forest fragments through increased pressure on host condition, although the magnitude of their effects is almost certainly host-, ectoparasite-, landscape-, and region-dependent.

Tropical birds may experience higher ectoparasite virulence (Møller 1998, Møller et al. 2009), thus affects of fragmentation on host–ectoparasite dynamics may be particularly strong. Consistencies in the ectoparasite-removal experiment here were seen among closely-related taxa (i.e. within families) rather than across families in the same ecological guild: thus the effects of phylogeny must be considered when making temperate-tropical comparisons (Felsenstein 1985). Creative approaches to the study of host–parasite dynamics in natural and unnatural systems will surely reveal additional interesting and unexpected patterns.

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APPENDIX A: FOCAL STUDY SPECIES, THEIR ECOLOGICAL GUILD (MODIFIED FROM STOUFFER ET AL. 2006), AND CHAPTERS WHERE THEY ARE USED FOR ANALYSES

			Chapter			
Family	Species	Guild	2	3	4	5
Furnariidae	*Sclerurus rufigularis*	Other insectivore		X		
	Automolus infuscatus	Flock obligate		X		
	Xenops minutus	Flock obligate		X		
	Certhiasomus stictolaemus	Flock obligate		X	X	X
	Dendrocincla fuliginosa	Other insectivore		X	X	X
	Dendrocincla merula	Ant-follower		X	X	X
	Glyphorynchus spirurus	Flock dropout	X	X	X	X
	Xiphorhynchus pardalotus	Flock dropout	X	X	X	X
Thamnophlidae	*Frederickena viridis*	Other insectivore	X			
	Thamnophilus murinus	Other insectivore		X		
	Thamnomanes ardesiacus	Flock obligate	X	X	X	X
	Thamnomanes caesius	Flock obligate	X	X	X	X
	Epinecrophylla gutturalis	Flock obligate	X		X	X
	Myrmotherula axillaris	Flock dropout	X	X	X	X
	Myrmotherula longipennis	Flock obligate	X	X	X	X
	Myrmotherula menetriesii	Flock obligate	X	X	X	X
	Pithys albifrons	Ant-follower	X	X	X	X
	Gymnopithys rufigula	Ant-follower	X	X	X	X
	Percnostola rufifrons	Gap specialist	X	X	X	X
	Schistocichla leucostigma	Other insectivore	X			
	Myrmeciza ferruginea	Other insectivore	X	X		
	Myrmeciza atrothorax	Other insectivore	X			
	Hypocnemis cantator	Gap specialist	X	X		
	Willisornis poecilinota	Other insectivore	X	X	X	X
Formicariidae	*Formicarius colma*	Other insectivore	X	X		
Grallariidae	*Grallaria varia*	Other insectivore	X			
	Myrmothera campanisona	Other insectivore	X			
Tyrannidae	*Corythopis torquatus*	Other insectivore		X		
	Mionectes macconnelli	Frugivore		X	X	X
	Myiobius barbatus	Flock dropout		X	X	X
Tityridae	*Schiffornis turdinus*	Frugivore			X	X
Pipridae	*Lepidothrix serena*	Frugivore	X	X	X	X
	Pipra pipra	Frugivore	X	X	X	X
	Pipra erythrocephala	Frugivore	X	X	X	X
Vireonidae	*Hylophilus ochraceiceps*	Flock obligate		X		
Polioptilidae	*Microbates collaris*	Other insectivore		X	X	X
Turdidae	*Turdus albicollis*	Frugivore	X	X	X	X
Thraupidae	*Tachyphonus surinamus*	Frugivore		X		

APPENDIX B. MOLT–BREEDING OVERLAP FREQUENCIES FOR 87 PASSERIFORMES

The number of individuals examined for molt and brood patches (n), the number of birds with brood patches (bp) and primary wing molt, the number of birds with brood patches, but not molting, and the proportion of individuals with molt–breeding overlap (% MBO) across passerines by taxonomic groupings for 87 passerine species at the BDFFP near Manaus, Brazil.

Suborder Family Subfamily Species	n	# bp with molt	# bp w/out molt	% MBO
TOTAL	26850	187	1285	12.7
Suboscines	**24056**	**178**	**1153**	**13.3**
Furnariidae	6467	22	383	5.7
Dendrocolaptinae	4719	17	286	5.6
Certhiasomus stictolaemus	557	0	41	0.0
Dendrocincla fuliginosa	276	1	27	3.6
Dendrocincla merula	529	2	34	5.6
Deconychura longicauda	120	0	4	0.0
Sittasomus griseicapillus	53	0	2	0.0
Glyphorynchus spirurus	2008	7	99	6.6
Hylexetastes perotti	66	0	10	0.0
Dendrocolaptes picumnus	16	1	4	20.0
Dendrocolaptes certhia	97	2	10	16.7
Xiphorhynchus pardalotus	939	4	49	7.5
Campylorhamphus procurvoides	58	0	6	0.0
Furnariinae	1288	4	77	4.9
Philydor erythrocercus	124	1	13	7.1
Philydor pyrrhodes	38	0	2	0.0
Automolus infuscatus	457	2	26	7.1
Automolus ochrolaemus	130	0	9	0.0
Automolus rubiginosus	144	1	8	11.1
Xenops minutus	271	0	16	0.0
Synallaxis rutilans	124	0	3	0.0
Sclerurinae	460	1	20	4.8
Sclerurus rufigularis	261	0	15	0.0
Sclerurus mexicanus	87	0	3	0.0
Sclerurus caudacutus	112	1	2	33.3
Thamnophilidae	10343	142	475	23.0
Frederickena viridis	82	2	4	33.3
Cymbilaimus lineatus	19	0	2	0.0
Thamnophilus murinus	194	1	14	6.7
Thamnomanes ardesiacus	887	17	40	29.8
Thamnomanes caesius	720	6	38	13.6
Epinecrophylla gutturalis	515	3	7	30.0
Myrmotherula axillaris	406	2	16	11.1

Myrmotherula longipennis	534	7	26	21.2
Myrmotherula menetriesii	292	0	16	0.0
Myrmotherula guttata	191	2	8	20.0
Hypocnemis cantator	541	7	33	17.5
Percnostola rufifrons	762	9	44	17.0
Schistocichla leucostigma	140	0	6	0.0
Myrmeciza atrothorax	9	1	0	100.0
Myrmeciza ferruginea	235	11	25	30.6
Pithys albifrons	1801	19	30	38.8
Gymnopithys rufigula	947	34	59	36.6
Willisornis poecilinota	1799	14	97	12.6
Hylophylax naevia	81	1	3	25.0
Myrmornis torquata	160	5	5	50.0
Cercomacra tyrannina	28	1	2	33.3
Formicariidae	421	2	28	6.7
Formicarius analis	47	0	1	0.0
Formicarius colma	374	2	27	6.9
Grallariidae	70	1	9	10.0
Hylopezus macularius	40	1	7	12.5
Myrmothera campanisona	5	0	1	0.0
Grallaria varia	25	0	1	0.0
Conopophagidae	134	4	8	33.3
Conopophaga aurita	134	4	8	33.3
Tyrannidae	3261	4	104	3.7
Corythopis torquatus	295	0	17	0.0
Mionectes macconnelli	1168	1	28	3.4
Hemitriccus zosterops	19	0	5	0.0
Rhynchocyclus olivaceus	101	1	3	25.0
Tolmomyias assimilis	24	0	4	0.0
Tolmomyias poliocephalus	19	0	3	0.0
Platyrinchus saturatus	355	0	8	0.0
Platyrinchus coronatus	344	1	12	7.7
Platyrinchus platyrynchos	31	1	0	100.0
Myiobius barbatus	639	0	16	0.0
Terenotriccus erythrurus	172	0	2	0.0
Rhytipterna simplex	25	0	2	0.0
Ramphotrigon ruficauda	16	0	1	0.0
Attila spadiceus	53	0	3	0.0
Pipridae	2778	2	132	1.5
Corapipo gutturalis	170	0	14	0.0
Lepidothryx serena	590	0	16	0.0
Pipra pipra	1813	2	86	2.3
Pipra erythrocephala	205	0	16	0.0
Cotingidae	21	1	1	50.0
Lipaugus vociferans	21	1	1	50.0
Tityridae	582	0	13	0.0

Schiffornis turdina	573	0	12	0.0
Laniocera hypopyrra	9	0	1	0.0
10-primaried oscines	**2084**	**8**	**93**	**7.9**
Vireonidae	344	1	18	5.3
Hylophilus muscicapinus	6	0	1	0.0
Hylophilus ochraceiceps	338	1	17	5.6
Troglodytidae	545	2	24	7.7
Pheugopedius coraya	101	0	6	0.0
Troglodytes aedon	23	0	3	0.0
Microcerculus bambla	192	1	3	25.0
Cyphorhinus arada	229	1	12	7.7
Polioptilidae	503	5	28	15.2
Microbates collaris	491	5	27	15.6
Ramphocaenus melanurus	12	0	1	0.0
Turdidae	692	0	23	0.0
Turdus albicollis	692	0	23	0.0
9-primaried oscines	**710**	**1**	**39**	**2.5**
Thraupidae	525	0	29	0.0
Tachyphonus cristatus	18	0	1	0.0
Tachyphonus surinamus	283	0	19	0.0
Lanio fulvus	21	0	2	0.0
Ramphocelus carbo	203	0	7	0.0
Incertae sedis	24	0	1	0.0
Coereba flaveola	24	0	1	0.0
Emberizidae	32	0	4	0.0
Volatinia jacarina	5	0	2	0.0
Oryzoborus angolensis	27	0	2	0.0
Cardinalidae	129	1	5	16.7
Cyanocompsa cyanoides	127	1	4	20.0
Caryothraustes canadensis	2	0	1	0.0

APPENDIX C. ECTOPARASITE TAXA FOUND ON EACH OF 22 HOST SPECIES NEAR MANAUS, BRAZIL

Host species	Ectoparasite	Family: Genus
Certhiasomus stictolaemus	Astigmata	Proctophyllodidae
		Unknown
Dendrocincla fuliginosa	Astigmata	Proctophyllodidae
		Unknown
	Ischnocera	Philopteridae: *Rallicola* sp.
Dendrocincla merula	Astigmata	Proctophyllodidae
		Unknown
	Prostigmata	Trombiculiidae
Glyphorynchus spirurus	Astigmata	Proctophyllodidae
		Unknown
	Mesostigmata	Rhinonyssidae
	Prostigmata	Trombiculiidae
	Ixodida	Ixodidae
	Ischnocera	Philopteridae: *Rallicola* sp.
	Siphonaptera	Unknown
Xiphorhynchus pardalotus	Astigmata	Proctophyllodidae
		Unknown
	Mesostigmata	Rhinonyssidae
	Prostigmata	Trombiculiidae
	Ixodida	Ixodidae
	Ischnocera	Philopteridae: *Rallicola* sp.
Thamnomanes ardesiacus	Astigmata	Proctophyllodidae (4 spp.)
		Psoroptoididae
		Trouessartiidae
		Xolalgidae (2 spp.)
		Unknown (2 spp.)
	Prostigmata	Trombiculiidae
	Ixodida	Ixodidae
	Ischnocera	Philopteridae: *Formicaphagus* sp.
	Amblycera	Rincidae: *Rincinus* sp.
Thamnomanes caesius	Astigmata	Proctophyllodidae (4 spp.)
		Psoroptoididae
		Trouessartiidae
		Xolalgidae (2 spp.)
		Unknown
	Mesostigmata	Rhinonyssidae

Thamnomanes caesius	Prostigmata	Trombiculiidae
	Ischnocera	Philopteridae: *Formicaphagus* sp.
	Amblycera	Menoponidae: *Myrsidea* sp.
Epinecrophylla gutturalis	Astigmata	Proctophyllodidae (3 spp.)
		Psoroptoididae
		Unknown
	Prostigmata	Trombiculiidae
	Ixodida	Argasidae
	Amblycera	Menoponidae: *Myrsidea* sp.
Myrmotherula axillaris	Astigmata	Proctophyllodidae (4 spp.)
		Psoroptoididae
		Trouessartiidae
		Xolalgidae
		Unknown
	Amblycera	Rincidae: *Rincinus* sp.
Myrmotherula longipennis	Astigmata	Proctophyllodidae (4 spp.)
		Psoroptoididae
		Trouessartiidae
		Xolalgidae
		Unknown
	Prostigmata	Trombiculiidae
	Amblycera	Rincidae: *Rincinus* sp.
Myrmotherula menetriesii	Astigmata	Proctophyllodidae (4 spp.)
		Psoroptoididae
		Trouessartiidae
		Xolalgidae
		Unknown
	Mesostigmata	Rhinonyssidae
	Ixodida	Ixodidae
	Amblycera	Rincidae: *Rincinus* sp.
Pithys albifrons	Astigmata	Proctophyllodidae (5 spp.)
		Psoroptoididae
		Trouessartiidae
		Xolalgidae (2 spp.)
		Unknown
	Mesostigmata	Rhinonyssidae
	Prostigmata	Trombiculiidae
	Ixodida	Argasidae
	Amblycera	Rincidae: *Rincinus* sp.
		Menoponidae: *Myrsidea* sp.
	Siphonaptera	Unknown

Gymnopithys rufigula	Astigmata	Proctophyllodidae (4 spp.)
		Psoroptoididae
		Trouessartiidae
		Xolalgidae
		Unknown
	Prostigmata	Trombiculiidae
	Ischnocera	Philopteridae: *Formicaphagus* sp.
	Amblycera	Rincidae: *Rincinus* sp.
		Menoponidae: *Myrsidea* sp.
	Siphonaptera	Unknown
Percnostola rufifrons	Astigmata	Proctophyllodidae (4 spp.)
		Psoroptoididae
		Trouessartiidae
		Xolalgidae (2 spp.)
		Unknown
	Prostigmata	Trombiculiidae
		Unknown
	Ixodida	Ixodidae
		Argasidae
	Ischnocera	Philopteridae: *Formicaphagus* sp.
	Amblycera	Menoponidae: *Myrsidea* sp.
	Siphonaptera	Unknown
Willisornis poecilinota	Astigmata	Proctophyllodidae (4 spp.)
		Psoroptoididae
		Trouessartiidae
		Xolalgidae (2 spp.)
		Unknown (2 spp.)
	Mesostigmata	Rhinonyssidae
	Prostigmata	Trombiculiidae
	Amblycera	Rincidae: *Rincinus* sp.
		Menoponidae: *Myrsidea* sp.
	Siphonaptera	Unknown
Myiobius barbatus	Astigmata	Unknown
	Amblycera	Menoponidae: *Myrsidea* sp.
Mionectes macconnelli	Astigmata	Unknown
	Amblycera	Menoponidae: *Myrsidea* sp.
Schiffornis turdina	Astigmata	Proctophyllodidae
		Unknown
	Prostigmata	Trombiculiidae
Lepidothrix serena	Astigmata	Proctophyllodidae (4 spp.)

Lepidothrix serena		Psoroptoididae
		Trouessartiidae
		Unknown
	Ixodida	Argasidae
	Ischnocera	Philopteridae: *Philopterus* sp.
	Amblycera	Rincidae: *Rincinus* sp.
		Menoponidae: *Myrsidea* sp.
Pipra pipra	Astigmata	Proctophyllodidae (4 spp.)
		Psoroptoididae
		Trouessartiidae
		Unknown
	Mesostigmata	Unknown
	Ischnocera	Philopteridae: *Philopterus* sp.
	Amblycera	Rincidae: *Rincinus* sp.
		Menoponidae: *Myrsidea* sp.
	Siphonaptera	Unknown
Microbates collaris	Astigmata	Unknown
	Prostigmata	Trombiculiidae
Turdus albicollis	Astigmata	Proctophyllodidae
		Unknown
	Amblycera	Menoponidae: *Myrsidea* sp.
	Siphonaptera	Unknown

APPENDIX D. EFFECTS OF HABITAT TYPE AND BIRD AGE ON WING MITE INDEX FOR 23 HOST SPECIES

Results of a generalized linear model testing the effects of habitat type (interior forest and fragment edges), bird age (immature and adult), and their interaction on wing mite index for 23 host species. Significant differences are in bold. See Fig. 4.6 for effect sizes.

		Habitat type		Bird age		Interaction	
Species	n	$F_{1,n-4}$	*P*	$F_{1,n-4}$	*P*	$F_{1,n-4}$	*P*
*Certhiasomus stictolaemus**	37	<0.1	0.863	–	–	–	–
*Dendrocincla fuliginosa**	42	0.7	0.420	–	–	–	–
*Dendrocincla merula**	48	0.6	0.429	–	–	–	–
*Glyphrynchus spirurus**	306	0.4	0.553	–	–	–	–
*Xiphorhynchus pardalotus**	96	<0.1	0.968	–	–	–	–
Thamnomanes caesius	105	0.9	0.339	3.8	0.053	**3.9**	**0.049**
Thamnomanes ardesiacus	126	0.3	0.578	1.6	0.201	<0.1	0.878
Epinecrophylla gutturalis	73	1.8	0.185	<0.1	0.932	**7.0**	**0.008**
Myrmotherula axillaris	70	1.2	0.280	1.4	0.246	2.1	0.151
Myrmotherula longipennis	66	0.2	0.627	0.1	0.827	<0.1	0.871
Myrmotherula menetriesii	36	1.8	0.180	1.7	0.191	1.0	0.309
Gymnopithys rufigula	137	0.1	0.832	**7.0**	**0.008**	<0.1	0.877
Pithys albifrons	340	1.8	0.175	**9.9**	**0.002**	0.1	0.794
Percnostola rufigula	106	1.2	0.265	3.0	0.083	3.5	0.062
Willisornis poecilinota	163	1.8	0.181	**5.4**	**0.020**	0.7	0.408
*Myiobius barbatus**	68	**5.5**	**0.019**	–	–	–	–
*Mionectes macconnelli**	177	0.9	0.323	–	–	–	–
Pipra pipra	410	2.7	0.103	**8.8**	**0.003**	3.8	0.051
Pipra erythrocephala	86	0.7	0.417	**7.5**	**0.006**	2.1	0.145
Lepidothrix serena	117	**7.6**	**0.006**	2.0	0.158	<0.1	0.898
*Schiffornis turdinus**	32	3.5	0.061	–	–	–	–
Turdus albicollis	84	1.2	0.275	2.5	0.117	0.7	0.40
*Microbates collaris**	44	**35.8**	**<0.001**	–	–	–	–

* $F_{1,n-2}$

VITA

Erik Ivan Kimberg Johnson was born in Boston, Massachusetts, in August 1979 to Ivan Schubert Carlyle Johnson and Barbara Delia von Randow Johnson. He grew up in Upper St. Clair, Pennsylvania, and graduated from Dickinson College in 2001 where he majored in biology and environmental studies. After college, he worked various jobs, including as a camera salesman and wildlife technician. He then moved to Baton Rouge, Louisiana, and received his Master of Science at Louisiana State University in May 2006. Also in 2006, he married Ceci Marie Scholl Johnson and moved to Lafayette, Louisiana, where they currently reside. He will receive his doctorate in wildlife and fisheries sciences from Louisiana State University in May 2011.