

2013

Recovery of understory bird movement in post-pasture Amazonia

Luke L. Powell

Louisiana State University and Agricultural and Mechanical College

Follow this and additional works at: https://digitalcommons.lsu.edu/gradschool_dissertations



Part of the [Environmental Sciences Commons](#)

Recommended Citation

Powell, Luke L., "Recovery of understory bird movement in post-pasture Amazonia" (2013). *LSU Doctoral Dissertations*. 3654.

https://digitalcommons.lsu.edu/gradschool_dissertations/3654

This Dissertation is brought to you for free and open access by the Graduate School at LSU Digital Commons. It has been accepted for inclusion in LSU Doctoral Dissertations by an authorized graduate school editor of LSU Digital Commons. For more information, please contact gradetd@lsu.edu.

RECOVERY OF UNDERSTORY BIRD MOVEMENT IN POST-PASTURE AMAZONIA

A Dissertation

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

in

The School of Renewable Natural Resources

by
Luke L. Powell
B.S., Tufts University, 2003
M.S., University of Maine, Orono, 2008
December 2013

Dedicated to memory of my grandmother, Nina Volkmar Powell (1912–2011). Her appreciation for nature and the outdoors was an inspiration to me and countless others.

ACKNOWLEDGMENTS

Phil Stouffer, my advisor, has been incredibly accommodating throughout this process. Early on, his NSF grant gave me the flexibility to travel back and forth to Brazil and allowed me to spend as much time in the field as I needed. Phil's timely edits and sage advice helped me navigate the waters of graduate and academic life, yet his just-right hands-off approach gave me confidence in that he trusted me to make decisions, but he was always there when I did need guidance. Phil was also trusting enough to let me pursue side projects during the writing of this document, most of which have developed into meaningful manuscripts and have helped make me a more well-rounded ecologist. Thank you Phil for everything.

Many outstanding field technicians contributed to my mist-netting and radio-tracking efforts over the years, including Paul Des Brisay, Elizabeth Condon, Gilberto Fernandez Arellano, Rachelle McLaughlin, and Aída Rodrigues. *Mateiros* Jairo Lopes, Alercio Marajo de Reis (AKA Leo), and Osmaido provided great company and hard work during difficult field conditions. I am grateful for the field contributions of Karl Mokross, Tatiana Straatmann, Marconi Cerqueira and Camila Duarte as well.

Erik Johnson, my academic older brother in the Stouffer lab, patiently walked me through the ins and outs of graduate life at LSU as well as the field life at the BDPFF— *muito obrigado Erikee*. Matt Brooks was also an early inspiration, helping me to adapt to graduate life in Baton Rouge when I moved here in 2009, as was Austin Humphries. Aída Rodrigues exercised saintly patience by allowing me muddle-through Portuguese during fieldwork. Jared Wolfe and Kristin Brzeski were enormously generous in letting me stay at their house in Baton Rouge once I moved to New Orleans; time and time again they fed me well, gave me a place to sleep and gave their friendship, and for that I am eternally grateful. Erik Johnson, Matt Brooks, Falyn Owens,

Emma DeLeon, Karl Mokross, Jared Wolfe, Sinead Borchert, Angelica Hernandez Palma, Kristina Cockle and Christy Bergeon Burns were ideal lab mates – I was lucky to have them as colleagues and friends.

My graduate committee has been accommodating and encouraging throughout this process; thank you Kyle Harms, Stefan Woltmann, Van Remsen, and early on, Mike Chamberlain, who left for a faculty position at UGA. The LSU “Bird Lunch” group has been an outstanding resource for discussing early ideas and fledgling datasets with bright minds in ornithology—thanks to Van and the grad students at the LSU Museum of Natural Sciences for keeping this tradition going. Kristina Cockle, Emma DeLeon, Kyle Harms, James Hines, Catherine Lindell, Karl Mokross, James Nichols Erik Johnson, Mike Murphy, Falyn Owens, J. V. Remsen, G. Bruce Williamson, Jared Wolfe, Stefan Woltmann, and several anonymous reviewers provided constructive reviews as I was developing these chapters. The staff at the School of Renewable Natural Resources office was incredibly helpful through my PhD. Allen Rutherford was very generous with funding to present results from this dissertation at conferences, and Nedra Ghoram, Karen Cambre, Charlotte Moore and Rhonda Shepard provided invaluable administrative support. Michael Lefsky and Scott Saleska provided (unpublished) canopy height models derived from LiDAR imagery.

Bret Elder, James Geaghan and Mike Kaller provided statistics consultations for the borders analysis (Chapter 2). Andres Zurita contributed the modeling effort in the edges chapter (Chapter 4), while James Nichols helped with the proportions of home range/ core area analysis in Chapter 3 and James Hines and James Nichols patiently worked with me to build the models in Chapter 5. I thank Curtis Marantz and Michael Patten for sharing woodcreeper resources.

By following a path as a tropical conservation biologist, my uncle George V. N. Powell provided inspiration; he proved to me that it was possible to live such a life. Bill Glanz, my master's adviser at University of Maine, provided sage support in encouraging me to follow a path to the tropics as I developed as a young biologist.

Generous grants from the following organizations helped me pay field technicians and purchase radio transmitters: the American Ornithologists' Union Research Award, the American Ornithologists' Union Frank M. Chapman Award, the Wilson Ornithological Society's Paul A. Stewart Award, and the American Philosophical Society's Lewis and Clark Fund. Over the longer term, the following funding sources contributed to data I used in this dissertation: National Science Foundation's Long Term Ecological Research grant (Stouffer LTREB 0545491), World Wildlife Fund-U.S., the MacArthur Foundation, the Andrew W. Mellon Foundation, U.S. Agency for International Development, U.S. National Aeronautics and Space Administration, Brazil's Ministry for Science and Technology, the Summit Foundation, Shell Oil, Citibank, Champion International, the Homeland Foundation, and the National Geographic Society. My Master's advisers Bill Glanz and Tom Hodgman prepared me for this PhD, and for a life of doing science; thank you Bill and Tom. Not to be forgotten are the contributions of all the dogs who spent so many hours lying next to me, lowering my blood pressure and stress levels while I was sitting at home writing this document: Gunner, Ja, Tigger, Moses, Willie and Mr. Eli. I conducted this research under LSU Institutional Animal Care and Use Committee approval and under applicable Brazilian permits.

Thank you Hannah Powell for providing loving support over the years. Finally, thank you Mom and Dad for providing unwavering support and for encouraging me to be myself.

TABLE OF CONTENTS

ACKNOWLEDGMENTS	iii
ABSTRACT.....	vii
CHAPTER 1: GENERAL INTRODUCTION	1
LONG-TERM CHANGES IN AMAZONIA	1
BIOLOGICAL DYNAMICS OF FOREST FRAGMENTS PROJECT (BDFFP).....	2
VALUE OF THE MATRIX AND CONTRIBUTION OF SECONDARY GROWTH TO BIOLOGICAL DIVERSITY	7
CONCEPTUAL MODEL: CHANGES IN AVIAN SPACE USE WITH SUCCESSION OF SECONDARY FOREST	9
LITERATURE CITED	11
CHAPTER 2: RECOVERY OF UNDERSTORY BIRD MOVEMENT ACROSS THE INTERFACE OF PRIMARY AND SECONDARY AMAZON RAINFOREST	15
INTRODUCTION	15
METHODS	18
RESULTS	24
DISCUSSION	29
LITERATURE CITED	34
CHAPTER 3: FOREST RECOVERY IN POST-PASTURE AMAZONIA: TESTING A CONCEPTUAL MODEL OF SPACE USE BY INSECTIVOROUS UNDERSTORY BIRDS	39
INTRODUCTION	39
METHODS	42
RESULTS	50
DISCUSSION	54
LITERATURE CITED	61
CHAPTER 4: EDGE ANALYSIS REVEALS CHANGES IN HABITAT SUITABILITY THROUGH FOREST SUCCESSION: A CASE STUDY OF UNDERSTORY BIRDS IN THE BRAZILIAN AMAZON.....	67
INTRODUCTION	67
METHODS	70
RESULTS	74
DISCUSSION	79
LITERATURE CITED	85
CHAPTER 5: STATE-SPACE MODELS REVEAL MOVEMENT OF THREE INSECTIVOROUS UNDERSTORY BIRD SPECIES BETWEEN PRIMARY AND SECONDARY FOREST IN A HETEROGENEOUS AMAZONIAN LANDSCAPE	92
INTRODUCTION	92

METHODS	95
RESULTS	100
DISCUSSION	106
LITERATURE CITED	114
APPENDIX A: GUILD ASSIGNMENTS AND COMPLETE MODEL SELECTION	
RESULTS FROM CHAPTER 2.....	119
APPENDIX B: PERMISSION FROM THE AUK TO REPRINT PREVIOUSLY	
PUBLISHED CHAPTER 2	131
VITA	132

ABSTRACT

I sought to understand how forest fragmentation and secondary growth affect avian movement at the Biological Dynamics of Forest Fragments Project (BDFFP) near Manaus, Brazil. When deforested areas are abandoned, secondary forests regenerate, allowing rainforest animals to gradually recovery their ability to use formerly inhospitable habitat. My colleagues and I captured 2773 understory birds of ten foraging guilds along the edges of primary forest fragments and variable secondary forest. Age of secondary forest along edges was the most important variable driving capture rates on primary/secondary edges. Mean recovery to pre-isolation capture rates was 26 years after abandonment, but terrestrial insectivores took far longer to recover than other guilds, ≥ 54 years. I radio-tracked 73 understory insectivores of three species in variable landscapes to uncover patterns in avian movement in secondary growth—specifically evaluating space use (home range, movement rate, etc.), edge responses and habitat transition probabilities. Space use varied widely as secondary growth recovered, with species showing vastly different spatiotemporal strategies in returning to forest. Woodcreepers *Glyphorhynchus spirurus* and *Xiphorhynchus pardalotus* recovered to primary-forest-level edge responses and transition probabilities after 11–15 and 15–20 years, respectively. En route to recovery, both woodcreepers increased home range sizes and movement rates in young secondary forests. *Formicarius colma*, a common terrestrial insectivore, had a far more rigid strategy, avoiding young secondary forest, then using space in older secondary forest similarly to the way it used space in primary forest. With bird ages pooled, *F. colma* showed a return to no edge response about 28–30 years after land abandonment, with some evidence for an edge response by young birds even 27–31 years post-abandonment. Further, through habitat transition probabilities, I showed that *F. colma* preferred primary forest over 27–31 year-old secondary

forest (the oldest at the BDFFP), indicating that even after 27–31 years, secondary forest had not recovered for movements of this terrestrial insectivore. By quantifying how land-use patterns affect avian movement, connectivity, and community dynamics, we will be generating the understanding necessary to manage heterogeneous landscapes for biodiversity conservation in the 21st century and beyond.

CHAPTER 1: GENERAL INTRODUCTION

LONG-TERM CHANGES IN AMAZONIA

In the Brazilian Amazon alone, an average of 16,000 km² of primary rainforest have been lost each year for the last 20 years (INPE 2010), which has led to the creation of ~20,000 km of new forest edges in the Amazon rainforest each year (D. Skole pers. comm.). The best data available (Greg Asner, pers. comm.) indicate that in the Brazilian Amazon, the area of secondary forest increased from 29,000 to 161,000 km² from 1978–2002 (Neeff et al. 2006). In addition to the immediate effects of deforestation and disturbance, climate change is predicted to drive profound changes to the world's humid tropical forests. Closed-canopy forests are currently found a maximum mean annual temperature of 28°C (Wright et al. 2009), but given the International Panel for Climate Change's (IPCC) intermediate (A1B) scenario for greenhouse gas emissions (Christensen et al. 2007), temperatures in 2100 will exceed 28°C for 75% of the world's tropical forests (Wright et al. 2009). Land with mean annual temperatures greater than 28°C currently support mostly grasslands and deserts (Wright et al. 2009), so in addition to direct anthropogenic change, we may see the “savanna-ization” of much of the world's tropical forest—including the Amazon. Given ongoing deforestation, regrowth of secondary forests, and global climate change, it is clear that we are in the midst of an era of drastic changes to the world's largest rainforest, yet we have few data with which to predict how Neotropical fauna will respond. As climate change alters the distribution of suitable habitat, species are predicted to shift their ranges towards “cool refuges”—defined by Wright et al. (2009) as areas where future temperature regimes match those of the 1960s. Along with parts of southeast Asia, the central and northeastern Amazon contain the humid tropical forests farthest from cool refuges, many of which are more than 1000 km away (Figure 1.1). Most of Amazonia, including my study area

north of Manaus, Brazil, has cool refuges located in the range of 500–1000 km. If we can predict the conditions that allow rainforest species to 1) persist in and 2) move through variable landscape conditions, we will be closer to providing meaningful recommendations to land managers that help maintain biodiversity in the face of rapid anthropogenic change.

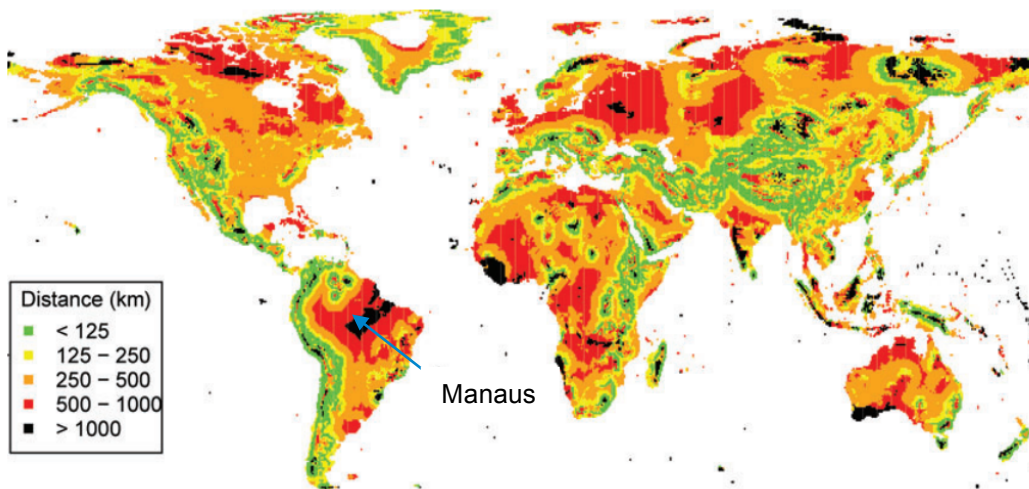


Figure 1.1. Global map of distances to potential cool refuges for mammals, defined as the shortest distance to a destination whose projected 2100 temperature is equal to or cooler than observed 1960s temperatures. Figure from Wright et al. (2009).

BIOLOGICAL DYNAMICS OF FOREST FRAGMENTS PROJECT (BDFFP)

My study site, the BDFFP, is an experimental 800-km² landscape in central Amazonia located 80 km north of Manaus Brazil (project history summarized in Laurance et al. 2002; Figure 1.2).

This project began as Thomas Lovejoy’s experimental attempt to identify the “minimum critical size” of an Amazonian ecosystem (Lovejoy and Oren 1981). Lovejoy and others began studying the uncut continuous forest in the area, knowing that it would soon be cleared by cattle ranchers lured by subsidies from the federal government. BDFFP researchers originally set aside 24 reserves, designed as pockets of old-growth rainforest within a matrix of cattle pastures. In the early 1980s, cattle ranchers began cutting and burning land for cattle pastures, but the subsequent

failure of most cattle ranches allowed for regrowth of much of the pastureland, creating a highly variable inter-fragment matrix. By 1990, eleven of the reserves had been isolated by cattle ranchers (5 of 1 ha, 4 of 10 ha, and 2 of 100 ha), while the remaining 13 remained within continuous forest. Over the 1980s and 1990s, some fragments were re-isolated (slash and burn or slash only) as many as four times (documented in G. Ferraz, unpublished dataset), with 100- to 200-m bands of forest cleared around the fragments (hereafter “border zones”); other fragments were never reisolated. With the realization that many planned reserves, including those of 1000 ha, would probably never be isolated, the project shifted philosophies away from “minimum critical size” (Bierregaard Jr and Gascon 2001) and towards an understanding of edge effects and the dynamics of extinction and colonization of species in 10- and 100-ha fragments.

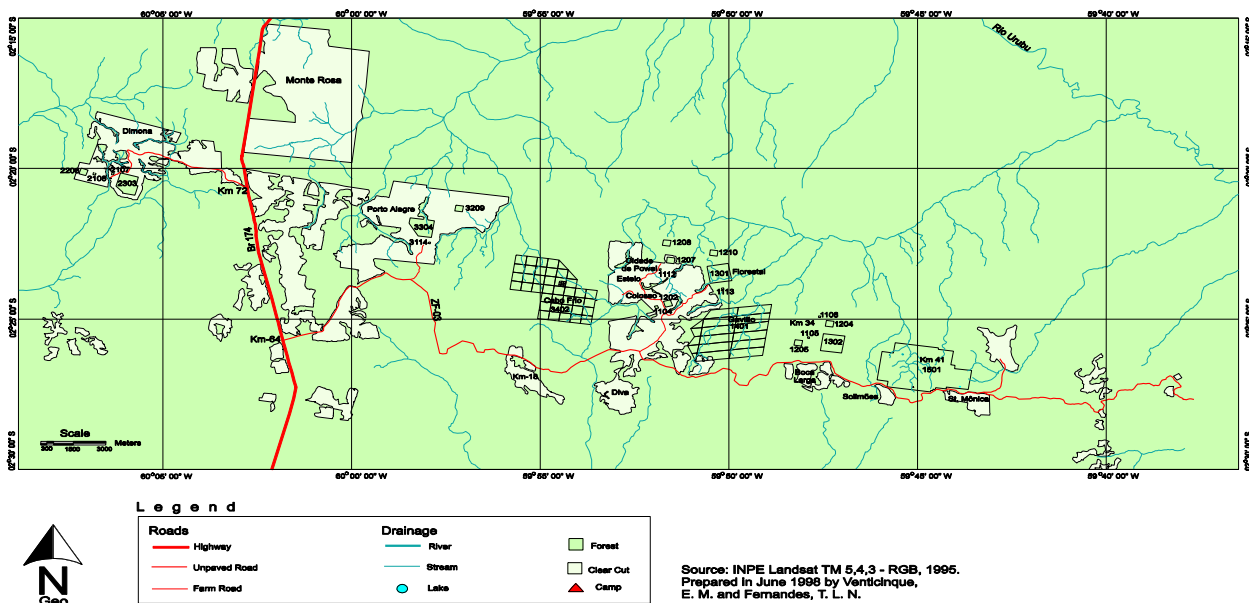


Figure 1.2. Map of the BDFFP north of Manaus, Brazil from 1995. Four-digit numbers represent forest reserves, eleven of which are forest fragments.

After the clearing of rainforest at the BDFFP, unburned pastures became dominated by *Cecropia* trees, whereas burned pastures became dominated by *Vismia* shrubs. Mixed-species flocks reassembled in 10-ha fragments when *Cecropia*-dominated second growth reached 7-9

years-old; obligate ant-following species returned to *Cecropia*-dominated second growth five years after isolation (Stouffer and Bierregaard 1995). By twenty years post-isolation, some guilds (e.g. frugivores, other insectivores, and gap specialists) in 10 and 100 ha fragments had recovered to pre-isolation densities regardless of the second-growth type in the matrix (Stouffer et al. 2006). Recovery in 1 ha fragments has not yet occurred for most major guilds (Stouffer et al. 2006).

The climate at the BDFFP is seasonal, with a distinct dry period lasting from June to October. Peak wet season is January to May and total rainfall is generally between 2000 and 3500 mm per year (Stouffer and Bierregaard 1993; Laurance 2001). The site has little topography, although elevation can range from 50 to 100 m where streams have worn valleys in the forest floor. The predominant vegetative cover is *terra firme* tropical rainforest. Soils are generally nutrient-poor sandy or clay-rich ferrasols, typical of the region. Although published records indicate that the forest canopy is 30–37 m tall with emergent trees reaching 55 m (Gascon and Bierregaard 2001), a LiDAR-based canopy height model from 2007 indicates that mean canopy height is only 23 m tall (unpublished data).

Avian Research at the BDFFP

Researchers at the BDFFP began to compile the avian capture database in 1979 when the project was entirely old-growth tropical rainforest. This mist-netting effort continued through the isolation of forest fragments, with semi-regular sampling performed through 1992. Mist-net sampling resumed in 2000 and 2001, then following a break from 2002–2006, occurred again from 2007–2009. With the arrival of P. C Stouffer to the project in 1991, alternative sampling approaches were undertaken, such as playback, visual surveys, and spot-mapping. As of 1997, 394 species have been documented at the BDFFP (Cohn-Haft et al. 1997) using a combination of

surveying methods; only a few others have been added to the list since then (P. C Stouffer, pers. comm.). Many species are rare at the BDFFP, thus a common approach for analyzing mist-net data has been to pool species into functional guilds to determine the effect of fragmentation (e.g. Stouffer and Bierregaard 1995; Stouffer and Borges 2001; Stouffer et al. 2006). At the onset of the project, very little natural history information was available for most BDFFP species, but recent advances in knowledge of morphology and molt (Johnson 2010) has permitted the analysis of demographic information such as age ratios in fragments vs. continuous forest (Johnson 2011).

The alteration of the landscape at the BDFFP has had quantifiable effects on the avian community. Immediately following the isolation of forest fragments, Lovejoy et al. (1986) and Bierregaard and Lovejoy (1989) documented an influx of birds in fragments, which likely served as temporary refugia after the habitat loss. After this initial influx of individuals, species gradually disappeared from forest fragments because extinction rates exceeded colonization rates (Ferraz et al. 2003); this trend was particularly dramatic in the smaller fragments (Ferraz et al. 2003; Ferraz et al. 2007). Other changes included the disappearance of all three obligate ant-following species (*Pithys albifrons*, *Gymnopithys rufigula*, and *Dendrocincla merula*) and the breakdown of mixed species flocks in 1- and 10-ha fragments within the first two years of isolation (Harper 1987; Bierregaard Jr and Lovejoy 1989). Insectivores— particularly terrestrial insectivores—appear to be the group that is most sensitive to area effects and show the slowest recovery as secondary growth in border zones matures (Stouffer and Bierregaard 1995; Stouffer et al. 2006). Many Amazonian understory insectivores are remarkably specialized primary forest residents, with many having large home ranges (Johnson et al. 2011). Further, birds of the Guianan shield and the BDFFP are believed to have particularly large home ranges relative to

other locations in the Neotropics (Johnson et al. 2011), with poor soils in the region thought to contribute to a lack of productivity (Gentry and Emmons 1987).

Going beyond simple presence/absence, the few studies of individual movement at and near the BDFFP have consistently shown that movement is strongly affected by gaps in habitat (e.g. pasture) and roads (Laurance et al. 2004; Laurance and Gomez 2005). Consistent with other fragmentation studies, forest-dependent insectivores (mixed-species flocks, ant-followers, and terrestrial species) had reduced capture rates across even narrow, unpaved roads, with solitary insectivores particularly vulnerable (Laurance et al. 2004). Capture rates were reduced for most forest guilds within 10–70 m of road margins (Laurance et al. 2004). In a translocation experiment with males of three territorial radio-tagged species (*Formicarius colma*, *Willisornis poecilinotus* and *Thamnomanes caesioides*), Laurance and Gomez (2005) found that paved roads (50–75 m wide) did not impede individuals from returning to their territories, yet a cattle pasture (>250 m wide) did. Translocated adults with territories and mates have extremely strong motivation to return to their original territories (Laurance and Gomez 2005), so although this study showed that those species could physically cross the roads, it remains unknown how roads, edges, pasture, secondary growth, or other barriers affect birds' regular intraterritorial or dispersal movements at the BDFFP.

There has been considerable progress in understanding of the dynamics of changes in the avian community as the landscape at the BDFFP, yet most research has been restricted to changes in presence/absence or mist-net capture rates in fragments vs. continuous forest. We still know little about the contribution of secondary growth to avian diversity, or the effect of secondary growth on individual movement or dispersal.

VALUE OF THE MATRIX AND CONTRIBUTION OF SECONDARY GROWTH TO BIOLOGICAL DIVERSITY

Due in large part to the pervasiveness of island biogeography theory (MacArthur and Wilson 1967), studies of forest fragmentation have tended to effectively, theoretically, or literally consider fragmented landscapes as pockets of primary forest surrounded by seas of inhospitable habitat (Laurance 2008). Although this was an effective early attempt at a deeper understanding of the dynamics of fragmentation, island biogeography theory is limited in that it, ignores the effect of the vegetation in the inter-habitat matrix between forest fragments (Laurance 2008).

Fragmentation in the world's tropical forests is considered the greatest threat to biodiversity in the 21st century (climate change is second; Sala et al. 2000), but large-scale regrowth of deforested areas following deforestation present increasing opportunities for biological conservation outside primary forest. Secondary forests now constitute 4.5 million km² of humid tropical forests worldwide, with enormous amounts of that land in Brazil (Asner et al. 2009). In the most densely-populated rural areas in Amazonia, a full 30% of the original old growth forest has been replaced by secondary forest (Perz and Skole 2003). Secondary growth can likely serve as an effective corridor between primary forest and buffer of primary forest (see Chazdon et al 2009; Lees and Peres 2009), but details remain poorly understood.

Despite this pervasive nature of secondary forests in the tropics, the conservation value of secondary forests for old-growth forest species is still debated (Wright and Muller-Landau 2006a, b), in part because of the lack of empirical studies. For example, many tropical birds can fly across gaps of unsuitable habitat (Laurance and Gomez 2005; Lees and Peres 2009), but despite their mobility, tropical birds do not appear to be as tolerant to secondary growth as other taxa. Of 16 taxonomic groups studied in the Jari forest landscape of northeastern Amazon,

Barlow et al. (2007; Data from Peres, Barlow and Gardner, Jari Project) found that secondary forest contained only 38% of all the primary forest bird species—only grasshoppers and woody vegetation had less. In 9–13-year-old secondary forest at the BDFFP, Stouffer and Borges (2001) found two-, five- and eight-fold reductions in capture rates of ant-followers, terrestrial insectivores, and mixed species flock obligates respectively. Furthermore, Barlow et al. (2007) found that 14–19-year-old secondary forests in the Brazilian Amazon had considerably less conservation value for birds than previously thought; obligate ant-following species, for example, were never detected in secondary forest.

As secondary growth matures, its similarity to old-growth forest increases rapidly (Dent and Wright 2009). Using data from 39 studies, Dunn et al. (2004) concluded that tropical secondary forests may take only 20–40 years to recover species richness of old-growth forest. Unfortunately, older secondary forests are even more poorly studied than young secondary forests (Chazdon et al. 2009), so their conservation value is not well understood. The BDFFP now sits in a matrix of secondary growth that is up to 30-years-old (G. Ferraz, unpublished data), with much of it nearly indistinguishable from primary forest to the naked eye (pers. obs.) so the BDFFP's current landscape presents an opportunity to increase understanding of the usefulness of older secondary growth. Chazdon et al. (2009) stress the need for studies of dispersal and movement in old-growth, second-growth, and matrix habitat—particularly at multiple spatial scales. Given the ongoing fragmentation and conversion of old growth tropical forests to recovering secondary forests (Asner et al. 2009), it is essential that we understand the point at which secondary growth is used as 1) a dispersal corridor and 2) a part of species' home range.

CONCEPTUAL MODEL: CHANGES IN AVIAN SPACE USE WITH SUCCESSION OF SECONDARY FOREST

When anthropogenic cutting and burning removes tropical rainforest leaving barren land, resident understory birds can no longer incorporate the lost forest into their home ranges because suitable habitat is completely absent. As succession occurs and the matrix progresses towards conditions resembling those in mature rainforests, bird species that persist within forest fragments likely show a recovery that parallels the regeneration of the matrix towards conditions found in primary forest. To visualize spatiotemporal dynamics of the recovery process, I constructed a conceptual model predicting space use by insectivorous understory birds during deforestation and subsequent regrowth of secondary forest (Figure 1.3). This progression is undoubtedly species-specific, and probably varies by age, sex, and physiological condition of the individual. Further, species may take different routes to recovery, for example, by circumventing step(s) of the model, such as the expansion of home ranges shown in Figure 1.3d.

This model is based on the literature on my study system (Stouffer and Bierregaard 1995; G Ferraz et al. 2007), my and Stouffer's experience observing and capturing birds at the BDFFP, and the empirical and theoretical literature on metrics of animal space use cited above. The model assumes that space use of territorial insectivorous birds is driven primarily by distribution of resources (i.e. food, mates, nest sites, vegetation structure etc.), that availability of one or more of these resources is low in young secondary forest, and that these resources gradually recover with time since pasture abandonment. Accordingly, the model predicts that space use of understory birds will reflect the distribution of those resources, with birds generally using more space and moving faster when resource density is low (i.e. in young secondary forest); and conversely, using less space and moving slower when resource density is high (i.e. in primary

forest). Here I use both mist net captures along primary/secondary forest borders (Chapter 2, published as Powell et al. 2013) and radio telemetry (Chapter 3: home range and space use; Chapter 4: edge response; Chapter 5: habitat transition probability) to test the predictions summarized in the legend for Figure 1.3.

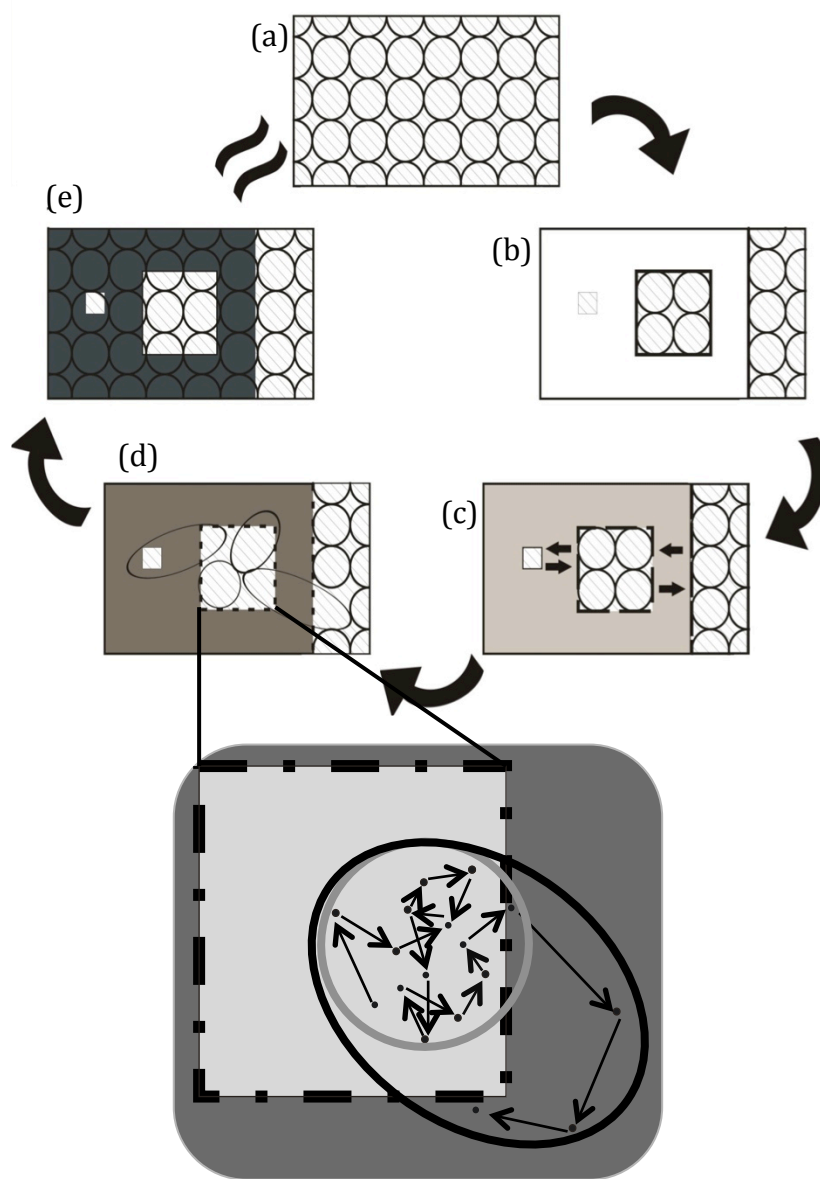


Figure 1.3. Conceptual model illustrating dynamics of avian territories and movement during recovery of secondary forest following deforestation and fragmentation. Circles represent resident bird territories for a hypothetical species ubiquitous in primary forest, diagonally hatched fill represents primary forest and increasingly dark solid shading (white to dark gray)

represents increasingly old secondary forest. Thick black lines representing the edges of primary forest are dashed relative to permeability of the edge. As continuous forest (a) is initially cut (b), birds are entirely excluded from the recently cut area and entirely restricted to forest fragments. At this point, home range boundaries are aligned along the interface and birds are excluded from fragments too small to sustain their home ranges. During early regrowth (c), increased vertical structuring of the young secondary forest permits some movement (e.g. dispersal) across secondary forest—some individuals may occasionally use small fragments. As secondary forest matures and begins to recover resources (d), birds begin to expand their territories into secondary forest and small fragments, showing increased rates of movement across the interface. At the point of recovery (e), bird territory boundaries and cross-interface movements are indistinguishable from those in primary forest, regardless of fragment size. In the close-up of (d) shown below, a higher proportion of the animal's core area (gray ellipse) is within primary forest, whereas the overall home range (black ellipse) contains a higher proportion of secondary forest. Here individual bird movements (thin arrows) show that birds in primary forest move in short, curvy (i.e. high tortuosity) paths; conversely, movements in secondary forest are straighter (i.e. low tortuosity) and longer, so movement rate is relatively high. Further, the close-up depicts that prior to recovery, the distribution of space use within home ranges is heterogeneous about the edge (i.e. there is a quantifiable edge response) and that at any given time, the probability of remaining in primary forest is greater than the probability of remaining in secondary forest (i.e. unequal transition probability between habitats).

LITERATURE CITED

- Asner, G. P., T. Rudel, T. Aide, R. Defries, and R. Emerson. 2009. A contemporary assessment of change in humid tropical forests. *Conservation Biology* 23:1386-1395.
- Barlow, J., T. Gardner, I. Araujo, T. Avila-Pires, A. Bonaldo, J. Costa, M. Esposito, L. Ferreira, J. Hawes, and M. Hernandez. 2007. Quantifying the biodiversity value of tropical primary, secondary, and plantation forests. *Proceedings of the National Academy of Sciences* 104:18555
- Bierregaard Jr, R., and T. Lovejoy. 1989. Effects of forest fragmentation on Amazonian understory bird communities. *Acta Amazonica* 19:215-241.
- Bierregaard Jr, R., and C. Gascon. 2001. The biological dynamics of forest fragments project: overview and history of a long-term conservation project, p. 5–12. *In* R. Bierregaard Jr, C. Gascon, T. E. Lovejoy and R. Mesquita [eds.], *Lessons from Amazonia: The Ecology and Conservation of a Fragmented Forest*. Yale University Press, New Haven.
- Brazilian National Space Research Institute (INPE). 2010. Projecto prodes: Monitoramento da floresta Amazonica Brasileira por satellite. Brasilia: Ministerio da Ciencia e Tecnologia. Online at <http://www.obt.inpe.br/prodes/index.html>.
- Chazdon, R., C. Peres, D. Dent, D. Sheil, A. Lugo, D. Lamb, N. Stork, and S. Miller. 2009. The potential for species conservation in tropical secondary forests. *Conservation Biology* 23:1406-1417.

- Christensen, J., B. Hewitson, A. Busuioc, A. Chen, X. Gao, R. Held, R. Jones, R. Kolli, W. Kwon, and R. Laprise. 2007. Regional climate projections, *Climate Change, 2007: The Physical Science Basis. Contribution of Working group I to the Fourth Assessment Report of the Intergovernmental Panel on Climate Change*. University Press, Cambridge.
- Cohn-Haft, M., A. Whittaker, and P. Stouffer. 1997. A new look at the "species-poor" central Amazon: the avifauna north of Manaus, Brazil. *Ornithological Monographs*:205-235.
- Dent, D., and J. Wright. 2009. The future of tropical species in secondary forests: A quantitative review. *Biological Conservation*.
- Dunn, R. 2004. Recovery of faunal communities during tropical forest regeneration. *Conservation Biology* 18:302-309.
- Ferraz, G., G. J. Russell, P. C. Stouffer, R. O. Bierregaard, S. L. Pimm, and T. E. Lovejoy. 2003. Rates of species loss from Amazonian forest fragments. *Proceedings of the National Academy of Sciences of the United States of America* 100:14069-14073.
- Ferraz, G., J. D. Nichols, J. E. Hines, P. C. Stouffer, R. O. Bierregaard, and T. E. Lovejoy. 2007. A large-scale deforestation experiment: Effects of patch area and isolation on Amazon birds. *Science* 315:238-241.
- Gascon, C., and R. O. Bierregaard, 2001. The Biological Dynamics of Forest Fragments Project. Pages 31–45 *in* *Lessons from Amazonia: The Ecology and Conservation of a Fragmented Forest* (R. O. Bierregaard, Jr., C. Gascon, T. E. Lovejoy, and R. C. G. Mesquita, Eds.). Yale University Press, New Haven, Connecticut.
- Gentry, A. H., and L. H. Emmons., 1987. Geographical variation in fertility, phenology, and composition of the understory of Neotropical forests. *Biotropica* 19:216–227.
- Harper, L. H. 1987. Conservation of Ant following Birds in Central Amazonian Forest Fragments, Ph. D. Dissertation. State University of New York, Albany, NY.
- Johnson, E. I. 2010. Banding guide to the birds of The Biological Dynamics of Forest Fragments Project. School of Renewable Resources, Louisiana State University, Baton Rouge, LA.
- Johnson, E. I. 2011. Fragmentation Sensitivity and its Consequences on Demography and Host–Ectoparasite Dynamics in Amazonian Birds. Ph.D. dissertation, Louisiana State University, Baton Rouge.
- Johnson, E.I., Stouffer, P.C. and Vargas, C.F., 2011. Diversity, biomass, and trophic structure of a central amazonian rainforest bird community. *Revista Brasileira de Ornitologia* 19(1):1–16.
- Laurance, S. G. W., P. C. Stouffer, and W. E. Laurance. 2004. Effects of road clearings on movement patterns of understory rainforest birds in central Amazonia. *Conservation Biology* 18:1099-1109.

- Laurance, S. G. W., and M. S. Gomez. 2005. Clearing width and movements of understory rainforest birds. *Biotropica* 37:149-152.
- Laurance, W. F. 2001. The hyper-diverse flora of the Central Amazon: an overview, p. 47-53. *In* R. Bierregaard Jr, C. Gascon, T. E. Lovejoy and R. Mesquita [eds.], *Lessons from Amazonia: The Ecology and Conservation of a Fragmented Forest*. Yale University Press, New Haven.
- Laurance, W. F. 2008. Theory meets reality: How habitat fragmentation research has transcended island biogeographic theory. *Biological Conservation* 141:1731–1744.
- Laurance, W.F., T. Lovejoy, H. Vasconcelos, E. Bruna, R. Didham, P. Stouffer, C. Gascon, R. Bierregaard, S. Laurance, and E. Sampaio. 2002. Ecosystem decay of Amazonian forest fragments: a 22-year investigation. *Conservation Biology* 16:605-618.
- Lees, A. C., and C. A. Peres. 2009. Conservation value of remnant riparian forest corridors of varying quality for Amazonian birds and mammals. *Conservation Biology* 22(2):439–449.
- Lees, A. C., and C. A. Peres. 2009. Gap-crossing movements predict species occupancy in Amazonian forest fragments. *Oikos* 118:280-290.
- Lovejoy, T. E., and D. C. Oren. 1981. The minimum critical size of ecosystems, p. 7-12. *In* R. L. Burgess and D. M. Sharp [eds.], *Forest Island Dynamics in Man-Dominated Landscapes*. Springer-Verlag, New York.
- Lovejoy, T., R. Bierregaard Jr, A. Rylands, C. Quintela, L. Harper, K. Brown Jr, A. Powell, and G. V. N. Powell. 1986. Edge and other effects of isolation on Amazon forest fragments, p. 257-285. *In* M. E. Soule [ed.], *Conservation Biology: the Science of Scarcity and Diversity*. Sinauer Associates, Inc., Sunderland, MA.
- MacArthur, R., and E. Wilson. 1967. *The Theory of Island Biogeography*. Princeton University Press, Princeton, NJ.
- Neeff, T., R. M. Lucas, J. R. Santos, E. S. Brondizio, and C. C. Freitas. 2006. Area and age of secondary forests in Brazilian Amazonia 1978–2002: An empirical estimate. *Ecosystems* 9:609–623.
- Perz, S., and D. Skole. 2003. Secondary forest expansion in the Brazilian Amazon and the refinement of forest transition theory. *Society and Natural Resources* 16:277-294.
- Sala, O., F. Chapin III, J. Armesto, E. Berlow, J. Bloomfield, R. Dirzo, E. Huber-Sanwald, L. Huenneke, R. Jackson, and A. Kinzig. 2000. Global biodiversity scenarios for the year 2100. *Science* 287:1770.
- Stouffer, P. C., and R. O. Bierregaard 1993. Spatial and temporal abundance patterns of Ruddy Quail-Doves (*Geotrygon montana*) near Manaus, Brazil. *Condor* 95:896-903.

- Stouffer, P. C., and R. O. Bierregaard. 1995. Use of Amazonian forest fragments by understory insectivorous birds. *Ecology* 76:2429-2445.
- Stouffer, P. C., R. O. Bierregaard, C. Strong, and T. E. Lovejoy. 2006. Long-term landscape change and bird abundance in Amazonian rainforest fragments. *Conservation Biology* 20:1212-1223
- Stouffer, P. C., and S. H. Borges. 2001. Conservation recommendations for understory birds in Amazonian forest fragments and second growth areas, p. 248–261. *In* R. Bierregaard Jr, C. Gascon, T. E. Lovejoy and R. Mesquita [eds.], *Lessons from Amazonia: The ecology and conservation of a fragmented forest*. Yale University Press, New Haven.
- Wright, S. J., and H. Muller-Landau. 2006a. The Future of tropical forest species. *Biotropica* 38:287-301.
- Wright, S. J., and H. Muller-Landau. 2006b. The uncertain future of tropical forest species. *Biotropica* 38:443.
- Wright, S. J., H. Muller-Landau, and J. Schipper. 2009. The future of tropical species on a warmer planet. *Conservation Biology* 23:1418-1426.

CHAPTER 2: RECOVERY OF UNDERSTORY BIRD MOVEMENT ACROSS THE INTERFACE OF PRIMARY AND SECONDARY AMAZON RAINFOREST¹

INTRODUCTION

Over the past 20 years, timber harvests and agricultural expansion have removed >328,000 km² of the Brazilian Amazon—an area larger than Poland (Brazilian National Space Research Institute [INPE] 2010). Although deforestation rates have slowed since 2005, the Brazilian Amazon continues to lose 7,000 km² per year (INPE 2010). Further, changes to the Brazil Forest Code may expose an additional 220,000 km² of forest to legal clearing (Sparovek et al. 2010, Nazareno et al. 2012). In contrast to much of the southern Amazon, where clearcuts often produce long-term pasturelands, in eastern and central Amazonia, clearcut areas are typically abandoned within 5 years after conversion to cattle pasture (Fearnside 2005). In the Brazilian Amazon, the area of secondary forest increased from 29,000 to 161,000 km² from 1978 to 2002 alone (Neeff et al. 2006). These vast expanses of secondary forest will inevitably become a necessary element of conservation planning, particularly given that growth of secondary forests from abandoned pastures represents a significant way to offset carbon lost to deforestation in the Amazon (Nepstad et al. 2009, Asner et al. 2010).

Despite the pervasiveness of secondary forests in the tropics, understanding of them is poor and their conservation value is still debated (Brook et al. 2006; Wright and Muller-Landau

¹ This chapter previously appeared as:

Powell, L.L., Stouffer, P.C. and Johnson, E.I., 2013. Recovery of Understory Bird Movement Across the Interface of Primary and Secondary Amazon Rainforest. *The Auk* 130(3):450–468.

It is reprinted by permission of Luke L. Powell and *The Auk*—see the permission letter in Appendix B.

2006a, b), in part because few empirical studies exist. Despite their perceived mobility, tropical birds do not appear to be as tolerant of secondary forest as other taxa. For instance, records of 16 taxonomic groups studied in the Jari forest landscape of the northeastern Amazon showed that in 14- to 19-year-old secondary forest, only grasshoppers had a lower proportion of primary-forest species than birds; only 38% of all the primary-forest bird species were present (data from C. A. Peres, J. Barlow, T. A. Gardner, and the Jari Forest Project database; for further details, see Barlow et al. 2007). In 9- to 13-year-old secondary forest at my study site, the Biological Dynamics of Forest Fragments Project (BDFFP), Stouffer and Borges (2001) found two-, five-, and eightfold reductions in capture rates of ant-followers, terrestrial insectivores, and mixed-species flock obligates respectively. Stratford and Stouffer (1999), also working in young secondary forest at the BDFFP, speculated that the terrestrial insectivores would be the last to recover as secondary forest matures. Using data from 10 studies (7 from the Neotropics), Dunn (2004) concluded that avian richness in tropical secondary forests may take only 20 years to recover to levels seen in primary forest, although contemporary bird distributions at the BDFFP, where some secondary forest is now 30 years old, suggest otherwise. The effects of fragmentation and isolation are now well known at the BDFFP (Laurance et al. 2011); however, few have studied the effect of secondary forest on birds: Stouffer and Borges (2001) and Borges and Stouffer (1999) studied understory birds in young secondary forest, and Sberze et al. (2009) studied the nocturnal bird community. Older secondary forests are even more poorly studied than young secondary forests (Chazdon et al. 2009). Consequently, research in the now more than 30-year-old secondary forests of the BDFFP represents a much-needed opportunity to quantify the conservation value of older secondary forest.

Primary forest in Amazonia is becoming increasingly fragmented because of high levels

of forest loss and subsequent regeneration of secondary forest, with a staggering 53,000 km of forest edges created each year (Numata et al. 2011). This boundary between primary and secondary forest (hereafter “the interface”) may present a barrier to movement, but propensity to cross a barrier likely varies widely among species and foraging guilds. Understanding how animals perceive the permeability of the interface can lead to a quantification of the value of secondary forest as a corridor among primary forest patches. For individuals moving across a fragmented landscape, the interface is the first step toward movement among remnant patches of primary forest; this process is fundamental to understanding source–sink and metapopulation dynamics (Brawn and Robinson 1996), gene flow and genetic structuring (Bates et al. 2004), and species’ persistence in isolated forest fragments (Ferraz et al. 2007).

I formulated a conceptual model to describe the spatiotemporal dynamics of understory bird movement during forest fragmentation and regrowth of secondary forests (Figure 1.3). The overarching assumption of the model is that as secondary forests regrow following clear-cutting and abandonment, the permeability of the interface increases for understory birds, eventually reaching a point of “recovery” at which bird movement across the interface is essentially identical to what was observed pre-isolation (i.e., prior to clear-cutting continuous primary forest). The model proceeds as follows: (1) as continuous forest is initially clearcut, rainforest birds are entirely excluded from the recently cut (and often burned) area and essentially imprisoned within forest fragments. At this point, territory boundaries are aligned along the interface, birds are excluded from fragments too small to sustain their territories (Stouffer and Bierregaard 1995a), and capture rates along the interface are effectively zero. During early regrowth, (2) vertical structure of the young secondary forest permits some movement (i.e., dispersal) across secondary forest—a few individuals may occasionally use small fragments

(Stouffer and Bierregaard 1995a). As secondary forests age and begin to recover resources, (3) birds begin to expand their territories into secondary forest and into small fragments (Borges and Stouffer 1999, Stouffer et al. 2011), showing increased rates of movement across the interface. At the point of recovery, (4) bird territory boundaries and cross-interface movements are indistinguishable from those in primary forest, regardless of fragment size.

Here I used mist-net captures to study the dynamics of recovery of movement along the interface, with particular interest in quantifying how movement (i.e., capture rate) changes as secondary forest matures. Specifically, I sought to answer two questions about the system. (1) What land-use history characteristics affect recovery of movement along the interface? And (2) how long does it take for understory avian guilds to recover to pre-isolation movement across the interface?

METHODS

For this chapter colleagues and I conducted fieldwork from October 1992 to September 2011 at the BDFFP. Forest fragments are embedded in a variable inter-fragment matrix (non-primary-forest areas beyond the border, hereafter “the matrix”), which has included active cattle pasture, zero- to 30-year-old secondary-growth forest, and unpaved forest roads. The 140-km² experimental forest within the BDFFP is embedded within a vast area of primary rainforest to the north, east and west, with increasing anthropogenic influence to the south (for detailed descriptions of the site, see Bierregaard et al. 2001, Laurance et al. 2011 and Chapter 1).

Sampling

Post-isolation mist netting took place in June to October during three time blocks: 1992–1993, 2000–2001, and 2007–2011. I ran mist nets (NEBBA type ATX, 36-mm mesh, 12 × 2 m) along the interface on approximately 1-m-wide trails with the bottom of nets set at ground level.

Post-isolation nets were run in lanes of four consecutive nets, with one lane per side of each of 11 square forest fragments. I assumed that samples in different time blocks were independent given that the generation time of many small tropical birds is <6 years and species turnover within fragments at the BDFFP is high among 6-year intervals (Stouffer et al. 2011). I netted each lane for 1 day at a time, beginning at 0600 hours and continuing until 1400 hours, unless heavy rains forced us to close the nets. Within time blocks, I generally sampled lanes at intervals of ≥ 6 weeks. From 1992–1993, 2000–2001, and 2007–2011, we sampled along the interface of secondary-forest and primary-forest fragments.

Because my site exhibited the typical tropical pattern of high richness but low abundance, I pooled species into guild assignments modified from Stouffer et al. (2006; Appendix A, Table A.1). I defined guilds as follows: non-forest species included any understory species typically absent inside but present outside unbroken forest; edge species frequented edges or tree fall gaps; core frugivores were common and primarily frugivorous; ant-followers foraged only by following insects fleeing from army ant swarms; sallying insectivores were solitary sallying species; bark insectivores were woodcreepers that were solitary and not obligate ant followers; flock dropouts were facultative mixed-species flock participants; flock obligates were obligate mixed-species flock participants; near-ground insectivores foraged in the lowest stratum of the forest, but rarely on the ground; and terrestrial insectivores foraged by walking along the forest floor (Cohn-Haft et al. 1997). I excluded canopy species, raptors, kingfishers, and large ground omnivores, such as tinamous and cracids, because they are rare or cannot be reliably sampled with mist nets. I excluded hummingbirds because previous work at the site showed that matrix and border age have little effect on hummingbird movement (Stouffer and Bierregaard 1995b). Finally, I excluded species never caught in forest fragments (and that were thus unavailable to be

caught along the interface) or that did not fit guild assignments.

My measure of bird movement along the interface was capture rate per 1,000 mist-net hours. I acknowledge that capture rate is an imperfect metric of movement, because structural differences among habitats may affect capture rate (Remsen and Good 1996). Capture rate conveniently normalizes unequal sampling effort among samples. I estimated time to recovery (see below) based on a single pre-isolation capture rate for each guild across fragments (mean [\pm SE] fragment⁻¹ = $2,678 \pm 1,088$ net-hours before isolation). Pre-isolation nets were arranged in 8- or 16-net lanes in reserve (soon to be fragment) interiors as summarized below; more detail is provided in Stouffer and Bierregaard (1995a).

I had to consider the possibility that avian abundance within fragments affected capture rate along the interface. Therefore, I summarized post-isolation capture rates from fragment interiors during each time block and used those values as an index of avian abundance in fragment interiors, which I then included as a variable in my candidate model set. In interiors, post-isolation nets were in single lanes of 8 (in 1-ha fragments) or 16 nets (in 10-ha fragments); these interior nets were run on the same days as the nets along the interface. In 100-ha forest fragments, two or three 16-net lanes were separated by ≥ 200 m. Because 100-ha fragments had >1 interior net lane, I calculated capture rate separately for each interior net lane, and then used those values to represent interior capture rate for the nearest interface net lane.

Because of concerns about the independence of interface net lanes only 70 m apart along 1-ha fragments, I pooled the four net lanes along the interface of each 1-ha fragment, creating a single sample for each 1-ha fragment during each time block. I assumed that net lanes along the sides of 10- and 100-ha fragments, all separated by ≥ 220 m, were spatially independent (sensu Hill and Hamer 2004), so I did not pool those lanes. To ensure that I had a large enough sample

of the oldest secondary forest, I added four four-net samples along the interface of continuous primary forest and 27- to 30-year-old secondary forest in 2011—these were the only locations not sampled prior to isolation. This gave us a total of 91 samples, each with at least 63 net-hours (mean = 282; maximum = 1,175).

Model selection

To normalize residuals and meet the assumptions of parametric statistics, I log-transformed the response variable, capture rate along the interface. During exploratory analyses, I attempted to fit asymptotic models (i.e., models in which the capture rate curve reaches an asymptote when capture rate stabilizes), but these models fit poorly because in most cases I had few data with which to model the tail of the asymptote. In other words, if recovery to pre-isolation occurred at 27 years, asymptotic models probably fit poorly because the oldest secondary forest at the BDFFP was only 30 years old, so there were few data with which to fit the asymptotic part of the curve. I therefore used log-transformed linear models, which appeared to fit the data well on the basis of residual plots. Even so, I focused on the trajectory toward recovery and ignored the exponential path of the curve after it crossed the pre-isolation capture rate.

I used an information-theoretic framework (Burnham and Anderson 2002) to model capture rates as a function of land-use history around forest fragments. I formed *a priori* candidate model sets for each of the 10 avian guilds, representing combinations of land-use history characteristics hypothesized to affect capture rate (Table A.2–A.11); global models for each guild are provided in Table 2.1. Variable definitions are as follows: BorderYrs (age of secondary growth along primary–secondary forest interface), Area (area of primary forest fragment adjacent to the interface), MatrixYrs (age of initial cut of the entire ranch in which

fragments are embedded), BorderBurn (whether secondary forest adjacent to the interface was burned at least once), MatrixBurn (whether the ranch was burned when it was initially cut), CF800 (area of continuous forest [CF = unbroken primary rainforest, excluding forest fragments] within 800 m of the sample location, as estimated using LANDSAT imagery and project records), and InteriorCapRate (guild-specific capture rate in the forest fragment interior). I determined the age of secondary growth through examination of BDFFP monthly reports, interviews with project directors (G. Ferraz, unpubl. data) and LANDSAT imagery. Candidate model sets were based on my knowledge of the species' behavior as well as previous work at the BDFFP on landscape effects on recovery rates of avian guilds within forest fragments (Stouffer et al. 2006, Stouffer and Bierregaard 2007). In selecting candidate models, I included only what I consider to be biologically plausible combinations of variables (Burnham and Anderson 2002). For example, Stouffer and Bierregaard (2007) found that the amount of continuous forest within 700 m of fragments affected recovery of capture rates of frugivores within fragments, so I included that variable in my candidate set of models affecting interface capture rates of frugivores. Preliminary analyses suggested that for three guilds less dependent on large patches of primary forest (i.e., flock dropouts, edge species, and core frugivores), capture rates along the interface were highest when secondary forest was of intermediate age (5–15 years old). For these three guilds, I included two models with a quadratic effect of border age, which would allow the trend in capture rate to be highest (or lowest) at intermediate border age. For several guilds, I included models with interaction terms between BorderYrs and Area as well as BorderYrs and BorderBurn because I suspected that the effects of Area and BorderBurn on capture rates would decrease considerably as secondary forest along the border matured (Table 2.1). BorderBurn and MatrixBurn were the only highly correlated variables (Spearman's $\rho = 0.61$), so I avoided

including those two variables together in the same model. Finally, I had no reason to suspect that fragment size affected capture rates of edge species or non-forest species along the interface, so I did not include this variable in the candidate set for these guilds. For the four samples from 2011 along the interface of secondary forest and primary continuous forest, I took a simplistic approach to area, using 1,000 ha as the area for those samples. I used PROC MIXED in SAS, version 9.2 (SAS Institute, Cary, North Carolina), to calculate Akaike's information criterion corrected for small sample size (AIC_c) for each model in the candidate and considered models, with $\Delta AIC_c < 2$ as those with substantial support (Burnham and Anderson 2002).

Table 2.1 Complete list of all *a priori* candidate sets of models describing capture rates along the primary-secondary forest interface for 10 avian guilds at the Biological Dynamics of Forest Fragments Project, 1991–2011. Checkmarks indicate that the model was included in the candidate set for a given guild. The global model for each guild is a saturated model including all variables and interactive effects listed for the guild.

Candidate model ^a	Flock dropouts	Edge species	Non-forest	Core frugivores	Six remaining guilds ^b
BorderYrs	✓	✓	✓	✓	✓
BorderYrs ²	✓	✓		✓	
Area	✓			✓	✓
Area MatrixYrs	✓			✓	✓
BorderYrs Area	✓			✓	✓
BorderYrs * Area ^c	✓			✓	✓
BorderYrs BorderUnburned	✓	✓	✓		✓
BorderYrs * BorderUnburned	✓	✓	✓		✓
BorderYrs MatrixUnburned	✓	✓	✓		✓
BorderYrs MatrixYrs	✓	✓	✓	✓	✓
BorderYrs MatrixYrs BorderUnburned	✓	✓	✓		✓
BorderYrs MatrixYrs MatrixUnburned	✓	✓	✓		✓
MatrixYrs MatrixUnburned	✓	✓	✓		✓
BorderYrs ² MatrixYrs	✓	✓		✓	
BorderYrs Area CF800				✓	
BorderYrs * Area CF800				✓	
BorderYrs CF800				✓	
Area CF800				✓	
InteriorCapRate	✓	✓	✓	✓	✓
InteriorCapRate BorderYrs	✓	✓	✓	✓	✓
InteriorCapRate BorderYrs Area	✓			✓	✓
NULL	✓	✓	✓	✓	✓

^a BorderYrs = age of secondary growth along primary–secondary forest interface; Area = area of primary forest fragment adjacent to secondary forest; MatrixYrs = age of initial cut of the entire ranch in which fragments are embedded; BorderUnburned = whether secondary forest adjacent to the interface was left unburned; MatrixUnburned = whether the ranch was left unburned when it was initially cut; CF800 = area of continuous forest within 800 m of sample; and InteriorCapRate = guild-specific capture rate in the forest fragment interior.

^b Remaining guilds: obligate ant-followers, sallying insectivores, bark-foraging insectivores, obligate mixed flock species, near-ground insectivores, and terrestrial insectivores.

^c Interactive models also include additive effects.

Time to recovery

I considered “recovery” to be the age of the border at which capture rate reached the pre-isolation capture rate for a guild. I calculated pre-isolation capture rate for each forest fragment and then used those calculations along with the best-fit model for each guild to calculate the time to recovery. To maximize parsimony via exclusion of parameters with little predictive power, I did not include parameters in the model that I used to calculate time to recovery if the parameter \pm SE in the best-fit model overlapped zero. To calculate an estimate of error in the recovery calculation, I used the intersections of the SE curves for interface capture rate and pre-isolation capture rate; this produced asymmetrical SEs. Finally, I was particularly interested in terrestrial insectivores, but capture rates were too low to model species-specific recovery rates, so I used bar graphs to examine species-specific capture rates over time for this guild.

RESULTS

In >25,928 net-hours, I recorded 3,735 captures along the interface, 2,773 of which I assigned to 1 of the 10 avian guilds for which I modeled capture rates.

Model selection

For each of 10 guilds, the best-fit model performed substantially better than a null model (mean ΔAIC_c of null model = 31.7). Residual plots of best-fit models generally showed little skew and normal distributions. BorderYrs was included in the best-fit model of all 10 avian guilds (Table 2.1 and Tables A.2–A.11) and, as expected, the parameter estimate for BorderYrs was positive for all guilds except non-forest species. In other words, increasingly old secondary forest along the interface was associated with higher capture rates of all guilds except non-forest species, which I caught more often along the interface when secondary forest was young. Other land-use-history variables were generally less influential than BorderYrs, in that

BorderUnburned, MatrixYrs, MatrixUnburned, and Area occurred in best-fit models for 3, 2, 2, and 2 guilds, respectively. CF800 had little effect on the capture rate of core frugivores, in that the best-fit model including that variable received essentially no support ($\Delta AIC_c = 17.7$).

InteriorCapRate was included in the best-fit model for core frugivores, ant-followers, and near-ground insectivores but had little effect on other guilds.

Table 2.2. Details of the best-fit models predicting capture rates for each of 10 avian guilds along the primary-secondary forest interface at the Biological Dynamics of Forest Fragments Project, 1991–2011.

Guild	Parameter(s) in best-fit model ^a	$\hat{\beta}$	SE	Number of models ^b
Non-forest species	BorderYrs	−0.11	0.03	11
	BorderUnburned	−1.49	0.42	
	BorderYrs*BorderUnburned	0.09	0.04	
Edge species	BorderYrs	0.08	0.03	13
	BorderUnburned	1.59	0.44	
	BorderYrs*BorderUnburned	−0.11	0.04	
Core frugivores	BorderYrs	0.03	0.01	16
	InteriorCapRate	0.02	0.00	
Ant-followers	BorderYrs	0.12	0.02	16
	InteriorCapRate	0.02	0.01	
Sallying insectivores	BorderYrs	0.10	0.02	16
	MatrixUnburned	−1.15	0.39	
Bark-foragers	BorderYrs	0.07	0.02	16
	MatrixYrs	−0.01	0.00	
Flock dropouts	BorderYrs	0.12	0.02	18
	MatrixUnburned	−0.75	0.38	
Flock obligates	BorderYrs	0.17	0.03	16
	Area	0.50	0.12	
	BorderYrs*Area	−0.02	0.01	
Near-ground insectivores	BorderYrs	0.09	0.02	16
	InteriorCapRate	0.03	0.01	
	Area	−0.13	0.08	
Terrestrial insectivores	BorderYrs	0.06	0.02	16
	BorderUnburned	0.50	0.19	
	MatrixYrs	0.00	0.00	

^a Intercept parameter not shown.

^b Total number of *a priori* models run in the candidate set for the guild, including the null model. See Table 1 footnote for variable definitions. Complete model selection results can be found in Tables S2–S11.

Time to recovery

Mean time to recovery to pre-isolation capture rates across all 10 guilds was 26 years (asymmetric SE = 13 years below and 16 years above estimate). Nine of 10 guilds showed a recovery to pre-isolation capture rates between 13 and 34 years (Figure 2.1); my model projects that terrestrial insectivores will take considerably longer at 54 years (with unburned borders) or 67 years (with burned borders; Figure 2.2).

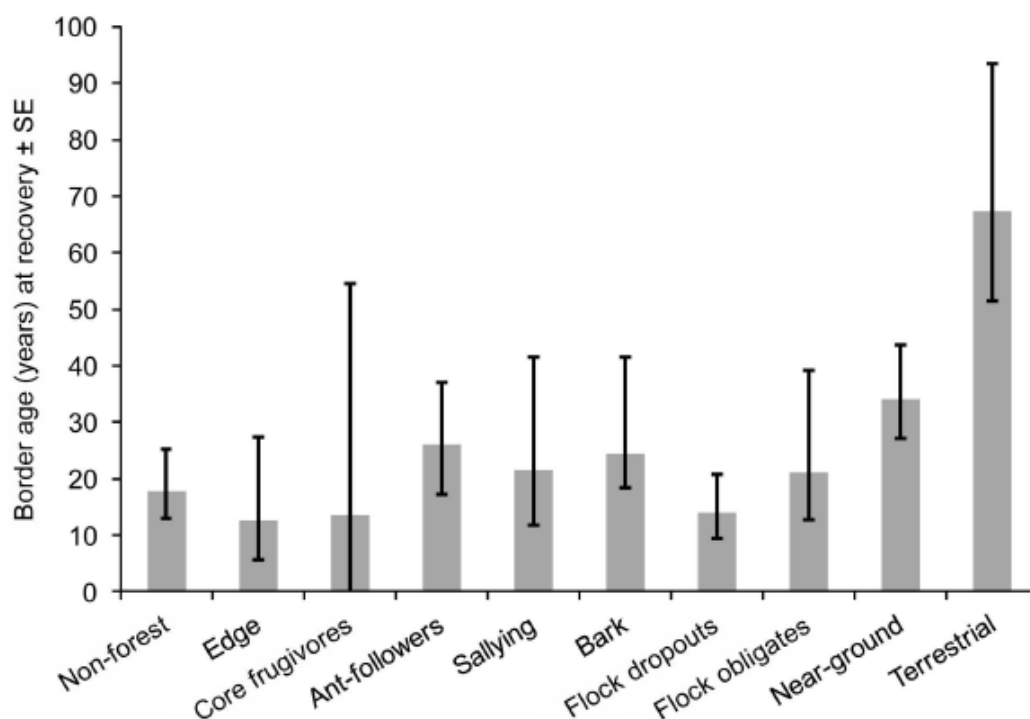


Figure 2.1. Estimated time to recovery of capture rates along primary–secondary forest interface to pre-isolation capture rates. For 9 of 10 guilds, capture rates were low along the interface when borders were young, then recovered to pre-isolation capture rates in time. Conversely, capture rates of non-forest species were high along the interface when borders were young, then took ~19 years to decrease to pre-isolation levels. To simplify visualization of recovery for guilds with best-fit models including variable(s) other than border age, values shown represent estimates for burned border (non-forest, edge, terrestrial), burned matrix (sallying, flock dropouts), 10-ha fragments (flock obligates) or mean capture rate in fragment interiors (core frugivores, ant-followers, near-ground). Guilds to the right of core frugivores are insectivorous.

Area appeared to be an important driver of capture rates of flock obligates along the interface, in that it was included in the best-fit model for the guild and showed an interaction with BorderYrs (Table 2.2). Although Area had a strong effect on capture rates of flock obligates in the early years after abandonment, the interaction term in the best-fit model suggested that Area had little effect in later years; recovery time was similar among 1-, 10-, and 100-ha fragments at 22.2 years (SE = 5.3 years below and 8.3 years above), 20.9 years (8.2 years below and 18.2 years above), and 17.9 years (12.2 years below and 82.3 years above), respectively. Guilds that I suspected to be among the least sensitive to young secondary forest predictably took the least time to recover: edge species (13 years with border burned; 17 years with border unburned), core frugivores (13 years), and flock dropouts (14 years with burned matrix; 21 years with unburned matrix).

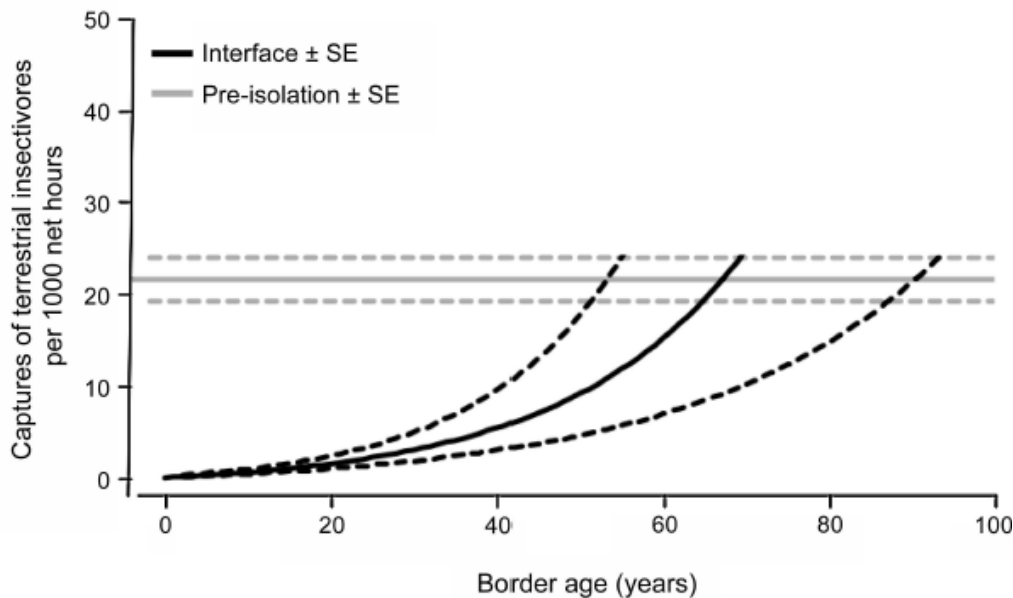


Figure 2.2. Curve for the best-fit model predicting capture rate of terrestrial insectivores along the interface of primary forest and secondary forest at the Biological Dynamics of Forest Fragments Project, 1992–2011. The oldest secondary forest sampled was 30 years old, so beyond 30 years, the curve is a projection. The curve shown represents samples with borders burned at least once. Curve is grayed out above the pre-isolation value because I was only interested in modeling recovery up to the pre-isolation capture rates, not beyond.

Terrestrial insectivores

Of the 12 species of terrestrial insectivores, 6 were never captured along the interface: *Sclerurus caudacutus*, *Myrmornis torquata*, *Grallaria varia*, *Hylopezus macularius*, *Conopophaga aurita*, and *Cyphorhinus arada*. Each of these six species was captured at least once within post-isolation forest fragments, indicating that they were available for capture along the interface but were not caught. I caught 45 individuals from the remaining six terrestrial insectivore species: *S. ruficularis* (6), *S. mexicanus* (5), *Myrmeciza ferruginea* (11), *Formicarius colma* ($n = 19$), *F. analis* (1), and *Corythopsis torquatus* (3). When borders were young (1–3 years), I caught only two terrestrial insectivores in 9,858 net-hours: one *S. ruficularis* and one *F. colma*. Capture rates of the six terrestrial insectivores I captured along the interface increased with increasing border age, but only *S. mexicanus* appeared to reach pre-isolation capture rates by 17 to 30 years (Figure 3.3). *Sclerurus ruficularis* was conspicuously absent when borders were <14 years old—I caught one in 22,576 net-hours.

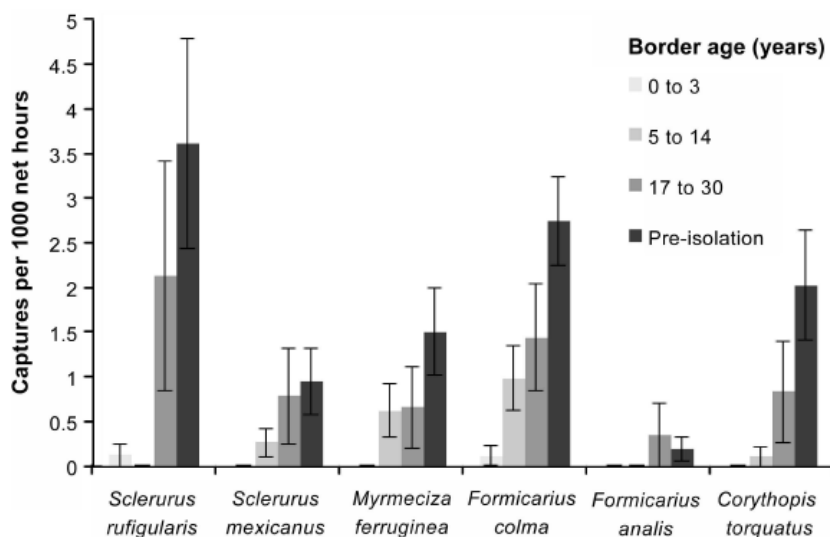


Figure 2.3. Capture rates of six terrestrial insectivore species along the primary–secondary forest interface, grouped by age of the secondary forest along the border. The six other terrestrial insectivore species in the guild (*Sclerurus caudacutus*, *Myrmornis torquata*, *Grallaria varia*, *Hylopezus macularius*, *Conopophaga aurita*, and *Cyphorhinus arada*) were never captured along the interface.

DISCUSSION

Although secondary forest is now an important component of the Amazonian landscape, I have few data with which to determine how secondary forest management and distribution affect animal movements. I found that border age had a pervasive influence on capture rates along the interface and that 9 of 10 guilds showed recovery of pre-isolation capture rates along the interface with borders between 13 and 34 years old—terrestrial insectivores should take ~60 years. Border age was included in the best-fit model for all guilds, with a strong positive effect—except for non-forest species, for which the effect was predictably negative (Table 2.2). The relative importance of other land-use-history characteristics varied, with no other variable appearing in more than three best-fit models. This importance of border age strongly suggests that management along the interface, specifically age since last cut, is the most important factor driving interface permeability. In other words, birds regain the ability to cross the interface primarily because of secondary forest regrowth in that immediate location; fragment size, burn history, and matrix effects are generally less important. Two previous studies at the BDFFP (Stouffer et al. 2006, Stouffer and Bierregaard 2007) also showed pervasive effects of border age, but on capture rates in forest fragment interiors. Border age thus appears to drive not only colonization–extinction dynamics within forest fragments, but also the permeability of the interface along the edges of forest fragments.

For most guilds in my study, the variation in border age encapsulated most of the variation in interface capture rates without the addition of interior capture rate to the best-fit model. This weak effect of interior capture rate suggests that when birds recolonize fragments following isolation (Stouffer et al. 2011), many likely cross the interface once (e.g., during dispersal), then remain to live within forest-fragment interiors. This pattern may be particularly

prevalent with terrestrial insectivores because 6 of 12 species in the guild were captured at least once in forest-fragment interiors but were never captured along the interface. Area, so important in driving capture rates in fragment interiors (Stouffer et al. 2006, Ferraz et al. 2007), was included in the best-fit model for only near-ground insectivores and flock obligates, which suggests that for most guilds, the age of the border drives capture rates along the interface, regardless of fragment size. Given the similarity of recovery times in different fragment sizes for flock obligates and the importance of the interaction term between Area and BorderYrs, area effects may be more important early in recovery, then less important as borders mature; this fits with my conceptual model.

The effect of burning was variable among guilds but clearly had a negative effect on terrestrial insectivores. When burned plots were essentially scorched earth, I did not catch terrestrial insectivores, but the effect appeared to weaken as borders matured, with the recovery time of the guild only marginally different between burned (67 years; SE = 16 years below and 26 years above estimate) and unburned (54 years; SE = 16 years below and 27 years above estimate) treatments. Both floral and avian communities are radically affected by burning following post-clearcut abandonment at the BDFFP (Borges and Stouffer 1999, Mesquita et al. 2001). Over time, the dichotomy between secondary forests dominated by tall, fast-growing *Cecropia* (unburned) and short, dense *Vismia* (burned) decreases considerably, with both becoming more similar to primary forest (Norden et al. 2011). Chronosequences at the BDFFP show that basal area in *Cecropia*-dominated plots was ~3 times that found in *Vismia* plots 5 years after abandonment, but those values converge to 35 m² ha⁻¹ after ~22 years (G. B. Williamson, unpubl. data). Structural convergence toward primary forest-like vegetation probably has a profound effect on decisions made by moving birds.

Recovery of structural complexity over time

Mean recovery to pre-isolation capture rates was 26 years (SE = 13 years below and 16 years above estimate), roughly consistent with Dunn's (2004) estimate of recovery of tropical avian species richness in 20 years. Not surprisingly, edge species and flock dropouts, among the first guilds to colonize young secondary forest, were among the first to recover, ~14 years after cutting and abandoning the border. Stouffer and Bierregaard (2007) estimated that in the interiors of 1- and 10-ha fragments at the BDFFP, flock dropouts recovered 21 years after border abandonment and core frugivores 15 years after. Flock obligates, thought to be among the most sensitive guilds, were surprisingly quick to recover, at ~21 years, consistent with Stouffer and Bierregaard's (2007) estimate of fragment interior recovery for the guild (16 years). As Stratford and Stouffer (1999) envisioned, terrestrial insectivores indeed took the longest to recover (mean 61 years), nearly tripling Dunn's (2004) recovery estimate. Even along the interface with the oldest secondary forest at the BDFFP, individual species of terrestrial insectivores were remarkably consistent in providing no evidence of recovery (Figure 3.3), but I caution that my estimate of recovery for this guild is a projection beyond 30 years—only time will tell precisely how long terrestrial insectivores take to recover. It seems unlikely that the vulnerability within terrestrial insectivores is phylogenetically conserved, because the 12 species are members of seven different families. Curiously, near-ground insectivores (a guild in which the sample is dominated by *Willisornis poecilinotus*) had the second-longest recovery time, 34 years. In the rainforests of Peninsular Malaysia, both Peh et al. (2005) and M. Zakaria Hussin (unpubl. data) have also found that ground-dwelling species are most vulnerable to disturbance, which suggests that the structure of secondary forest near the ground may drive movement rates and/or occupancy, so these forest floor guilds could potentially be used as indicators of the quality of

tropical secondary forests worldwide. Aside from vegetation structure itself, mechanism(s) driving the absence of terrestrial insectivores from secondary forests may include lack of resources (e.g., food, nest sites), light or heat aversion, or elevated predation risk (Wright et al. 1994, Raheem et al. 2009).

The structural complexity of the understory converges with primary forest over time since abandonment (Norden et al. 2011), which likely helps drive the recovery of bird movement. Five years after abandonment, basal area of trees at the BDFFP is dominated by a monoculture of *Vismia* (cut and burned; dominance = 0.90) or *Cecropia* trees (cut only; dominance = 0.79); monogeneric dominance is reduced to 0.35 after 22 years in *Vismia* plots, and to 0.05 after 26 years in *Cecropia* plots (G. B. Williamson, unpubl. data). Further, linear regressions predict that tree species at the BDFFP increase from only 10 species per 500 m² after 5 years (*Cecropia* and *Vismia* plots) to approximately 50 and 117 species after 26 years for *Vismia* and *Cecropia* plots, respectively (Williamson et al. 2013). Thus, at the mean recovery time of 26 years post-abandonment for all avian guilds in the present study, secondary forest trees are 5 to 12 times more diverse than after only 5 years, providing direct benefits to frugivores (e.g., availability of new fruit species) and indirect benefits to insectivores (habitat for new species of arthropods).

Caveats

My study focused on quantifying recovery of avian movement but is not an attempt to document demographic patterns, measures of fitness, or site fidelity. For example, movement rates may recover, but secondary forest or small fragments of primary forest could be occupied by less competitive or young birds that are less productive (Johnson 2011) or in poorer condition (Stratford and Stouffer 2001). I therefore advocate the further development of aging techniques

for tropical birds (Johnson 2010, Johnson et al. 2011) so that underlying demographic patterns can be understood. Further, estimates of survival would certainly be meaningful predictors of recovery, but even long-term capture data sets like that of the BDFFP suffer from sampling issues that make the estimation of survival challenging (Ruiz-Gutiérrez et al. 2012). Ultimately, a complete understanding of the dynamics of secondary forest recovery will depend on researchers' ability to integrate measures of movement, demography, and fitness, building toward a comprehensive model of (meta)population movement and population viability in variable landscapes.

Finally, my study provides a robust framework for studying avian movement along the primary–secondary forest interface, but the landscape context of the BDFFP likely makes my recovery estimates optimistic in relation to heavily fragmented landscapes. The landscape context of the secondary forest has a considerable influence on recovery (Chazdon et al. 2009), with mostly primary forest landscapes recovering faster than degraded landscapes (Dent and Wright 2009). Landscapes under heavy deforestation pressure such as vast tracts of Pará and Rondônia likely present fewer opportunities for bird colonization of forest fragments than more remote, intact areas of Amazonia (INPE 2010). Further, agricultural expansion in fragmented areas results in less clearcut abandonment, more burning, and, thus, less forest succession (Fearnside 2005). The hundreds of square kilometers of unbroken primary rainforest that surround the BDFFP provide opportunities for (re)colonization of forest fragments isolated by dozens to hundreds of meters. My estimates can be interpreted positively, in that 9 of 10 guilds recovered in <34 years. However, without the opportunities for recolonization from large tracts of primary rainforest nearby, recovery times will be much longer (and infinite as species become extinct on the landscape).

Conservation implications

Even with heavy deforestation over the past few decades, most of the Amazon rainforest remains unbroken within vast continuous blocks; 54% of Amazonia is set aside in protected areas (Soares-Filho et al. 2010). Thus, the majority of Amazonian second growth is quite similar to the BDFFP—surrounded by mostly continuous primary forest—so my estimates of recovery time should apply broadly. Amazonia now contains vast areas of secondary forest that are not a substitute for primary forest (Gibson et al. 2011) but could at least serve as corridors among patches of primary forest. I clearly show that secondary growth has value for understory birds: 34-year-old secondary forest is not a barrier to 9 of 10 avian guilds, and by ~60 years, even terrestrial insectivores will likely view the interface as entirely permeable. For a more complete understanding of the conservation value of secondary forest as a corridor, we must combine knowledge of area and isolation with an understanding of how animals move (and disperse) among forest fragments imbedded in a matrix of roads, agricultural land, and variable secondary forest.

LITERATURE CITED

- Asner, G. P., G. V. N. Powell, J. Mascaro, D. E. Knapp, J. K. Clark, J. Jacobson, T. Kennedy-Bowdoin, A. Balaji, G. Paez-Acosta, E. Victoria, and others. 2010. High-resolution forest carbon stocks and emissions in the Amazon. *Proceedings of the National Academy of Sciences USA* 107:16738–16742.
- Barlow, J., T. A. Gardner, I. S. Araujo, T. C. Ávila-Pires, A. B. Bonaldo, J. E. Costa, M. C. Esposito, L. V. Ferreira, J. Hawes, M. I. M. Hernandez, and others. 2007. Quantifying the biodiversity value of tropical primary, secondary, and plantation forests. *Proceedings of the National Academy of Sciences USA* 104:18555–18560.
- Bates, J. M., J. Haffer, and E. Grismer. 2004. Avian mitochondrial DNA sequence divergence across a headwater stream of the Rio Tapajós, a major Amazonian river. *Journal of Ornithology* 145:199–205.
- Bierregaard, R. O., Jr., C. Gascon, T. E. Lovejoy, and R. C. G. Mesquita, Eds. 2001. *Lessons from Amazonia: The Ecology and Conservation of a Fragmented Forest*. Yale University Press, New Haven, Connecticut.

- Borges, S. H., and P. C. Stouffer. 1999. Bird communities in two types of anthropogenic successional vegetation in central Amazonia. *Condor* 101:529–536.
- Brawn, J. D., and S. K. Robinson. 1996. Source–sink population dynamics may complicate the interpretation of long-term census data. *Ecology* 77:3–12.
- Brazilian National Space Research Institute (INPE). 2010. Projeto prodes: Monitoramento da floresta Amazônica Brasileira por satélite. Ministério da Ciência e Tecnologia, Brazil. [Online.] Available at www.obt.inpe.br/prodes/index.html.
- Brook, B. W., C. J. A. Bradshaw, L. P. Koh, and N. S. Sodhi. 2006. Momentum drives the crash: Mass extinction in the tropics. *Biotropica* 38:302–305.
- Burnham, K. P., and D. R. Anderson. 2002. *Model Selection and Multimodel Inference: A Practical Information-Theoretic Approach*, 2nd ed. Springer, New York.
- Chazdon, R. L., C. A. Peres, D. Dent, D. Sheil, A. E. Lugo, D. Lamb, N. E. Stork, and S. Miller. 2009. The potential for species conservation in tropical secondary forests. *Conservation Biology* 23:1406–1417.
- Cohn-Haft, M., A. Whittaker, and P. C. Stouffer. 1997. A new look at the “species-poor” central Amazon: The avifauna north of Manaus, Brazil. Pages 205–235 *in* *Studies in Neotropical Ornithology Honoring Ted Parker* (J. V. Remsen, Jr., Ed.). Ornithological Monographs, no. 48.
- Dent, D. H., and S. J. Wright. 2009. The future of tropical species in secondary forests: A quantitative review. *Biological Conservation* 142:2833–2843.
- Dunn, R. R. 2004. Recovery of faunal communities during tropical forest regeneration. *Conservation Biology* 18:302–309.
- Fearnside, P. M. 2005. Deforestation in Brazilian Amazonia: History, rates, and consequences. *Conservation Biology* 19:680–688.
- Ferraz, G., J. D. Nichols, J. E. Hines, P. C. Stouffer, R. O. Bierregaard, Jr., and T. E. Lovejoy. 2007. A large-scale deforestation experiment: Effects of patch area and isolation on Amazon birds. *Science* 315:238–241.
- Gascon, C., and R. O. Bierregaard, Jr. 2001. The Biological Dynamics of Forest Fragments Project. Pages 31–45 *in* *Lessons from Amazonia: The Ecology and Conservation of a Fragmented Forest* (R. O. Bierregaard, Jr., C. Gascon, T. E. Lovejoy, and R. C. G. Mesquita, Eds.). Yale University Press, New Haven, Connecticut.
- Gibson, L., T. M. Lee, L. P. Koh, B. W. Brook, T. A. Gardner, J. Barlow, C. A. Peres, C. J. A. Bradshaw, W. F. Laurance, T. E. Lovejoy, and N. S. Sodhi. 2011. Primary forests are irreplaceable for sustaining tropical biodiversity. *Nature* 478:378–381.

- Hill, J. K., and K. C. Hamer. 2004. Determining impacts of habitat modification on diversity of tropical forest fauna: The importance of spatial scale. *Journal of Applied Ecology* 41:744–754.
- Johnson, E. I. 2010. Banding guide to the birds of the Biological Dynamics of Forest Fragments Project. School of Renewable Resources, Louisiana State University, Baton Rouge.
- Johnson, E. I. 2011. Fragmentation Sensitivity and its Consequences on Demography and Host–Ectoparasite Dynamics in Amazonian birds. Ph.D. dissertation, Louisiana State University, Baton Rouge.
- Johnson, E. I., J. D. Wolfe, T. B. Ryder, and P. Pyle. 2011. Modifications to a molt-based ageing system proposed by Wolfe et al. (2010). *Journal of Field Ornithology* 82:422–424.
- Laurance, W. F., J. L. C. Camargo, R. C. C. Luizão, S. G. Laurance, S. L. Pimm, E. M. Bruna, P. C. Stouffer, G. B. Williamson, J. Benítez-Malvido, H. L. Vasconcelos, and others. 2011. The fate of Amazonian forest fragments: A 32-year investigation. *Biological Conservation* 144:56–67.
- Nazareno, A. G., J. M. Feres, D. de Carvalho, A. M. Sebbenn, T. E. Lovejoy, and W. F. Laurance. 2012. Serious new threat to Brazilian forests. *Conservation Biology* 26:5–6.
- Neeff, T., R. M. Lucas, J. R. Santos, E. S. Brondizio, and C. C. Freitas. 2006. Area and age of secondary forests in Brazilian Amazonia 1978–2002: An empirical estimate. *Ecosystems* 9:609–623.
- Nepstad, D., B. S. Soares-Filho, F. Merry, A. Lima, P. Moutinho, J. Carter, M. Bowman, A. Cattaneo, H. Rodrigues, S. Schwartzman, and others. 2009. The end of deforestation in the Brazilian Amazon. *Science* 326:1350–1351.
- Norden, N., R. C. G. Mesquita, T. V. Bentos, R. L. Chazdon, and G. B. Williamson. 2011. Contrasting community compensatory trends in alternative successional pathways in central Amazonia. *Oikos* 120:143–151.
- Numata, I., M. A. Cochrane, C. M. Souza, Jr., and M. H. Sales. 2011. Carbon emissions from deforestation and forest fragmentation in the Brazilian Amazon. *Environmental Research Letters* 6:044003.
- Peh, K. S. H., J. de Jong, N. S. Sodhi, S. L. H. Lim, and C. A. M. Yap. 2005. Lowland rainforest avifauna and human disturbance: Persistence of primary forest birds in selectively logged forests and mixed-rural habitats of southern Peninsular Malaysia. *Biological Conservation* 123:489–505.
- Raheem, D. C., F. Naggs, P. James Chimonides, R. C. Preece, and P. Eggleton. 2009. Fragmentation and pre-existing species turnover determine land-snail assemblages of tropical rain forest. *Journal of Biogeography* 36:1923–1938.

- Remsen, J. V., Jr., C. D. Cadena, A. Jaramillo, M. Nores, J. F. Pacheco, J. Pérez-Emán, M. B. Robbins, F. G. Stiles, D. F. Stotz, and K. J. Zimmer. 2013. A classification of the bird species of South America. Version 13 April 2013. American Ornithologists' Union. [Online.] Available at www.museum.lsu.edu/~Remsen/SACCBaseline.html.
- Remsen, J. V., Jr., and D. A. Good. 1996. Misuse of data from mist-net captures to assess relative abundance in bird populations. *Auk* 113:381–398.
- Ruiz-Gutiérrez, V., P. F. Doherty, Jr., E. Santana C., S. C. Martínez, J. Schondube, H. V. Munguía, and E. Iñigo-Elias. 2012. Survival of resident Neotropical birds: Considerations for sampling and analysis based on 20 years of bird-banding efforts in Mexico. *Auk* 129:500–509.
- Sberze, M., M. Cohn-Haft, and G. Ferraz. 2009. Old growth and secondary forest site occupancy by nocturnal birds in a Neotropical landscape. *Animal Conservation* 13:3–11.
- Soares-Filho, B., P. Moutinho, D. Nepstad, A. Anderson, H. Rodrigues, R. Garcia, L. Dietzsch, F. Merry, M. Bowman, L. Hissa, and others. 2010. Role of Brazilian Amazon protected areas in climate change mitigation. *Proceedings of the National Academy of Sciences USA* 107:10821–10826.
- Sparovek, G., G. Berndes, I. L. F. Klug, and A. G. O. P. Barretto. 2010. Brazilian agriculture and environmental legislation: Status and future challenges. *Environmental Science and Technology* 44:6046–6053.
- Stouffer, P. C., and R. O. Bierregaard, Jr. 1993. Spatial and temporal abundance patterns of Ruddy Quail-Doves (*Geotrygon montana*) near Manaus, Brazil. *Condor* 95:896–903.
- Stouffer, P. C., and R. O. Bierregaard, Jr. 1995a. Use of Amazonian forest fragments by understory insectivorous birds. *Ecology* 76:2429–2445.
- Stouffer, P. C., and R. O. Bierregaard, Jr. 1995b. Effects of forest fragmentation on understory hummingbirds in Amazonian Brazil. *Conservation Biology* 9:1085–1094.
- Stouffer, P. C., and R. O. Bierregaard, Jr. 2007. Recovery potential of understory bird communities in Amazonian rainforest fragments. *Revista Brasileira de Ornitologia* 15:219–229.
- Stouffer, P. C., R. O. Bierregaard, Jr., C. Strong, and T. E. Lovejoy. 2006. Long-term landscape change and bird abundance in Amazonian rainforest fragments. *Conservation Biology* 20:1212–1223.
- Stouffer, P. C., and S. H. Borges. 2001. Conservation recommendations for understory birds in Amazonian forest fragments and second growth areas. Pages 248–261 *in* Lessons from Amazonia: The Ecology and Conservation of a Fragmented Forest (R. O. Bierregaard, Jr., C. Gascon, T. E. Lovejoy, and R. C. G. Mesquita, Eds.). Yale University Press, New Haven, Connecticut.

- Stouffer, P. C., E. I. Johnson, R. O. Bierregaard, Jr., and T. E. Lovejoy. 2011. Understory bird communities in Amazonian rainforest fragments: Species turnover through 25 years post-isolation in recovering landscapes. *PloS ONE* 6:e20543.
- Stratford, J. A., and P. C. Stouffer. 1999. Local extinctions of terrestrial insectivorous birds in a fragmented landscape near Manaus, Brazil. *Conservation Biology* 13:1416–1423.
- Stratford, J. A., and P. C. Stouffer. 2001. Reduced feather growth rates of two common birds inhabitig central Amazonian forest fragments. *Conservation Biology* 15:721–728.
- Williamson, G. B., J. B. Longworth, T. V. Bentos, and R. C. G. Mesquita. 2013. Rates of change in tree communities along alternative successional pathways in the Central Amazon. *Plant Ecology and Diversity* 6: in press.
- Wright, S. J., M. E. Gompper, and B. DeLeon. 1994. Are large predators keystone species in Neotropical forests? The evidence from Barro Colorado Island. *Oikos* 71:279–294.
- Wright, S. J., and H. C. Muller-Landau. 2006a. The future of tropical forest species. *Biotropica* 38:287–301.
- Wright, S. J., and H. C. Muller-Landau. 2006b. The uncertain future of tropical forest species. *Biotropica* 38:443–445.

CHAPTER 3: FOREST RECOVERY IN POST-PASTURE AMAZONIA: TESTING A CONCEPTUAL MODEL OF SPACE USE BY INSECTIVOROUS UNDERSTORY BIRDS

INTRODUCTION

Over the last 20 years, the Brazilian Amazon, comprising about 60% of the entire Amazon, has seen a 328,000 km² of rainforest cut and abandoned or converted to anthropogenic land uses, representing an area larger than Poland (INPE 2010). Although deforestation rates in the Brazilian Amazon have slowed since 2005, in large part because of moratoriums on forest clearing for soy (in 2006; Rudorff et al. 2011) and beef (in 2009; Boucher, 2011), it continues to lose 7000 km² per year (INPE 2010). Furthermore, changes made to Brazil's Forest Code in 2012 could expose an additional 220,000 km² of forest to legal clearing (Nazareno et al. 2012; Sparovek et al. 2010). However, not all deforested lands remain as such; in the eastern and central Brazilian Amazon, the typical post-deforestation pattern has been abandonment either immediately, or about five years after conversion to cattle pastures, whereupon the transition from pasture to secondary forest begins (Fearnside 2005). The best data available (Greg Asner, pers. comm.) indicate that in the Brazilian Amazon alone the area of secondary forest increased from 29,000 to 161,000 km² from 1978–2002 (Neeff et al. 2006). These vast expanses of secondary forests in Amazonia present an opportunity for conservation, yet understanding of their value for wildlife is poor and their conservation value is still debated, in part because there are few empirical studies in secondary growth (Wright and Muller-Landau 2006a; Wright and Muller-Landau 2006b; Brook et al. 2006).

Space use by insectivorous understory birds should be a particularly good indicator of intact ecological processes within primary and secondary rainforests because this community is diverse, relatively easy to sample, sensitive to forest fragmentation and often specialized on

high-quality forest (Barlow et al. 2007; Stouffer and Bierregaard 1995; Sekercioglu et al. 2002). Our understanding of details of when and how insectivorous birds return to regenerating secondary forests is in its infancy; however, a recent study from my study site at the Biological Dynamics of Forest Fragments Project (BDFFP) revealed that capture rate (an index of movement rate) of 9 of 10 guilds of understory birds crossing into secondary forest recovered to baseline rates of primary forest within 13 to 34 years after pasture abandonment (Powell et al. 2013, Chapter 2). Terrestrial insectivores—strong-legged, stubby-winged birds that forage by walking along the forest floor—were the last guild to recover, taking an estimated 60 years (Powell et al. 2013). Although capture rates from standardized mist netting can be useful metrics of bird occupancy and abundance in heterogeneous tropical landscapes (Stouffer and Bierregaard 1995; Ferraz et al. 2007), they reveal only part of the story of avian space use during secondary forest maturation. Understanding movement patterns of individual birds is particularly important in heterogeneous landscapes because the accumulation of individuals' movements ultimately drives source-sink and metapopulation dynamics (Brawn and Robinson 1996), gene flow and genetic structuring (Bates et al. 2004), and species' persistence in isolated forest fragments (Ferraz et al. 2007). Detailed studies of individual movement can reveal mechanisms behind the spatiotemporal dynamics of how animals return to recovering landscapes. Specifically, both theoretical and empirical work from temperate ecosystems demonstrate that animals in high-quality habitats rich in resources (e.g. food, cover etc.) have small home ranges and core areas, use areas of high resource availability within home ranges, and move slowly in curvy paths relative to animals able to tolerate lower quality habitats (Fryxell et al. 2008; Caldwell and Nams 2006; Arditi and Dacorogna 1988; Vásquez et al. 2002; Ward and Saltz 1994); however, those patterns in metrics of space use are poorly understood for most organisms, particularly in the

tropics. Alternatively, individuals of a given species may avoid poor quality habitats entirely. When rainforest is cleared and burned, what generally remains is scorched earth with little or no resources for rainforest animals. As animals gradually begin to return as the vegetation recovers after abandonment, the spatial patterns revealed by metrics of space use should reflect the gradual recovery of the vegetation and associated resources, with those patterns of space use eventually being indistinguishable from those of primary forest at the point of rainforest “recovery” from the perspective of animal space use. The better we can develop a mechanistic understanding of spatiotemporal dynamics of how animals return to young secondary forests after timber harvests and abandonment of agricultural lands, the better our ability to manage these lands for biodiversity conservation.

To visualize spatiotemporal dynamics of the recovery process, I constructed a conceptual model predicting space use by insectivorous understory birds during deforestation and subsequent regrowth of secondary forest (Figure 1.3). I predicted that if individuals are incorporating edges into their home ranges they would spend more time in primary forest than secondary forest; thus, core areas should contain more primary forest than home ranges (Figure 1.3e). Finally, I predicted that path tortuosity (i.e. curviness) would be highest in primary forest because a greater concentration of resources should lead to denser, more curvy movement paths and few long, straight paths (e.g. Arditi and Dacorogna 1999, Vásquez et al. 2002).

I used radio-tagged understory birds to test five specific predictions of my conceptual model: 1) home range area is smaller for birds using primary forest than for birds using secondary forest; 2) core area is smaller for birds using primary forest than for birds using secondary forest; 3) for birds whose home range includes edges, the proportion of primary forest in the core area will be greater than the proportion of primary forest in the home range; 4)

movement rate will be lower in primary forest than in secondary forest; and 5) tortuosity will be greater for movement paths in primary forest than in secondary forest. My second objective was to compare the dynamics of space use among three understory insectivores with different natural history strategies: Wedge-billed Woodcreeper (*Glyphorhynchus spirurus*), Chestnut-rumped Woodcreeper (*Xiphorhynchus pardalotus*), and Rufous-capped Anthrush (*Formicarius colma*). Given enough time since abandonment and enough primary forest nearby to insure colonists, I expected all species to eventually display indistinguishable space use in secondary and primary forest (Figure 1.3e), with recovery (i.e. passage through stages depicted in Figure 1.3c and 1.3d) fastest for more secondary-growth tolerant species.

METHODS

For this chapter, my colleagues and I conducted fieldwork from June to October from 1995 to 1997 and 2009 to 2011 at the BDFFP. For more details about the study site, see Chapter 1. Here I categorized secondary forest into four age classes based on availability in the landscapes used by radio-tagged birds. The youngest secondary growth was 8 to 14 years old with an average canopy height of about 6 m. Two intermediate secondary growth categories were 15 to 18 years old (canopy \approx 14 m) and 21 to 24 m tall (canopy \approx 16m). The oldest secondary forest was 27 to 31 years old, and averaged 19 m tall, considerably shorter than primary forest at BDFFP (canopy \approx 23m). Canopy heights were estimated from LiDAR-based canopy height models (Michael Lefsky and Scott Saleska, unpublished data).

Study Species

I selected three common study species that were easy enough for us to capture to obtain a reasonable sample size. The three species varied in their natural histories and abundances in secondary forest.

At 14 g, *G. spirurus* (Wedge-billed Woodcreeper) is the smallest of 13 woodcreeper species at the BDFFP and perhaps the most versatile in habitat use and association with mixed species flocks. The species is abundant at the BDFFP, with primary forest densities of 33 per 100-ha (Johnson et al. 2011), and considerable overlap among home ranges (Gradwohl and Greenberg 1980; Darrah 2013). The species is abundant in the interiors of primary forest, but also common along edges, in 1-ha forest fragments, and in secondary forest (Cohn-Haft et al. 1997; Marantz et al. 2003; Levey 1988; Stratford and Stouffer 2001). *Glyphorhynchus spirurus* forages by “creeping” up tree trunks, rapidly chiseling at the bark with its short, pointed bill, in search of invertebrate prey (Skutch 1969); numerous diet analyses suggest that the species is exclusively insectivorous (Marantz et al. 2003). Individuals can forage in pairs, alone, or with mixed-species flocks led by *Thamnomanes* antshrikes passing through their territories (Jullien and Thiollay 1998). The species is a secondary cavity nester (i.e. it does not excavate its own cavities), both parents attend the nest (Marantz et al. 2003), and it can nest in secondary forest (PCS unpublished data).

The majority of *Xiphorhynchus pardalotus* (Chestnut-rumped Woodcreeper; approx. 38 g) at the BDBFF are core members of mixed-species flocks led by *Thamnomanes* antshrikes (Develey and Stouffer 2001). Although most often found in mixed-species flocks, *X. pardalotus* is not considered an obligate mixed-species participant at the BDFFP; rather, it is known as a “flock dropout” as it also forages individually, in pairs, or occasionally at swarms of army ants (Stouffer et al. 2006; Marantz et al. 2003). Both *X. pardalotus* and *G. spirurus* are capable of leaving primary forest, as both regularly crossed edges created by 20-year-old forested roads at the BDFFP (Laurance et al. 2004). Densities of *X. pardalotus* in primary forest are 18 per 100-ha at the BDFFP (Johnson et al. 2011), with territorial pairs maintaining home ranges with little

overlap; generally there is only one pair per flock (Jullien and Thiollay 1998). The species uses its stiff tail to “creep” up trunks where it forages for invertebrates, using a wide variety of foraging maneuvers including pecking, sallying, probing, gleaning and flaking (LLP, unpublished data). At a time when secondary growth at the BDFFP was considerably younger (i.e. < 17 years old), the species was listed as an exclusively primary forest resident (Cohn-Haft et al. 1997), although others (Marantz et al. 2003; Willis 1977) have reported the species’ use of older secondary growth. The species is a secondary cavity nester with both parents attending the young; nests are not known from secondary forest.

Formicarius colma (Rufous-capped Antthrush; approx. 46 g) is a common understory terrestrial insectivore found mainly in primary forest. The species is not generally known to occupy secondary forest (Cohn-Haft et al. 1997; Krabbe and Schulenberg 2003), and movement by the species was strongly impeded by 20-year-old edges created by forest road clearings at the BDFFP (Laurance et al. 2004). The species does not forage with mixed-species flocks or at army ant swarms; rather, it walks along the forest floor alone or in pairs, where it forages by picking invertebrates from leaf litter, flipping leaves as it goes (Krabbe and Schulenberg 2003). Density of the species in primary forest at the BDFFP is 11 per 100-ha (Johnson et al. 2011) and territorial pairs maintain home ranges with little overlap (Stouffer 2007). Pairs appear to nest in cavities outside the dry season, although it is unclear if the species is a secondary cavity nester (Stouffer et al. 2013; Marantz et al. 2003).

Captures

I captured target species with both passive and target netting techniques and marked captured birds with uniquely numbered aluminum bands. Radio-tagged birds were distributed throughout the experimental forest at the BDFFP, including all three landscapes (“fazendas”:

ranches) and parts of nine forest fragments (Figure 3.1). Passive netting was conducted using a standardized sampling protocol at the BDFFP. In short, I deployed mist nets (NEBBA type ATX, 36-mm mesh, 12 x 2 m) along approximately 1-m-wide trails, with the bottom of each net set at ground level. Nets were set in lanes of four (along the primary/secondary forest edges), eight (in 1-ha forest fragments), or 16 consecutive nets (in 10- or 100-ha forest fragments). I netted each net lane for one day at a time, beginning at 0600 and continuing until 1400 hours, unless heavy rains forced us to close the nets. To supplement the sample of passively caught target species, I target-netted using species-specific playback (Naka et al. 2009). Following each capture, I waited at least 24 hours before collecting relocation data to allow each bird time to adjust to the transmitter and bands. The two woodcreepers cannot be reliably aged in the hand after their skulls ossify early in their first year of life because formative plumage is currently indistinguishable from definitive plumage, so I radio-tagged only “adult” woodcreepers with ossified skulls. I defined “adult” *F. colma* as those captured in definitive basic plumage, meaning they have at least begun their second prebasic molt (*sensu* Johnson et al. 2011, Wolfe et al. 2010). I defined “young” *F. colma* as those individuals captured in juvenal or formative plumage within the first molt cycle (Johnson 2010; E I Johnson et al. 2011; Wolfe et al. 2010). I fitted each bird with a radio transmitter (< 5% of body weight) from Holohil Systems Ltd. (Carp, Ontario; model BD-2) using a 0.8-mm-diameter elastic thread harness (Rappole and Tipton 1991). For perhaps a dozen individuals, I attached a “weak link” harness in 2010 (Dylan Kessler, unpublished manuscript), in which I spliced in a 1-cm long piece of rubber band into the elastic harness; however, *X. pardalotus* were able to break the weak link within a couple of weeks, so I abandoned the weak-link technique and returned to the elastic thread technique.

Radio-tracking

I radio-tracked 23 *G. spirurus*, 23 *X. pardalotus* and 27 *F. colma* (Figure 3.1). My observations confirmed that all species could easily cross their home ranges in 15 minutes, so I used this interval as the minimum time between relocations, thus providing biological independence among locations (Lair 1987). I stratified daylight hours into four equal time blocks, collecting at least five locations within each time block to control for diurnal patterns in bird activity (Otis and White 1999). I tracked individuals as frequently as possible over a period lasting an average of 22.9 (± 2.4 SE) days.

To locate birds, one or two technicians using hand-held Yagi antennas recorded (1) the compass direction of the strongest radio signal from the bird and (2) their receiving location using a hand-held GPS receiver (estimated error < 6 m). In most cases, technicians arranged themselves on the trail network to maximize triangulation precision such that bearings were as close to 90° from each other as feasible (60° when > 2 bearings were taken) and as close to target birds as possible without noticeably affecting behavior. I collected all (2–4) bearings for each location within a 10-minute window, then waited at least 15 minutes before attempting to relocate the bird. I triangulated bearings with Location of a Signal (LOAS) version 4.0.3.3 (BiotasTM n.d.), and excluded locations for which the error ellipse was $> 40\%$ of the home range size. When the trail system permitted (i.e. gridded trails separated by 100 m), I eschewed triangulation and instead simply walked around the bird with the antenna until I could confirm that it was within a 0.25-ha square, and I then recorded its location as the center of that square. Five *F. colma* radio-tracked from 1995–1997 were previously reported in Stouffer et al. (1997) and Stouffer (2007); all other birds were tracked from 2009–2011.

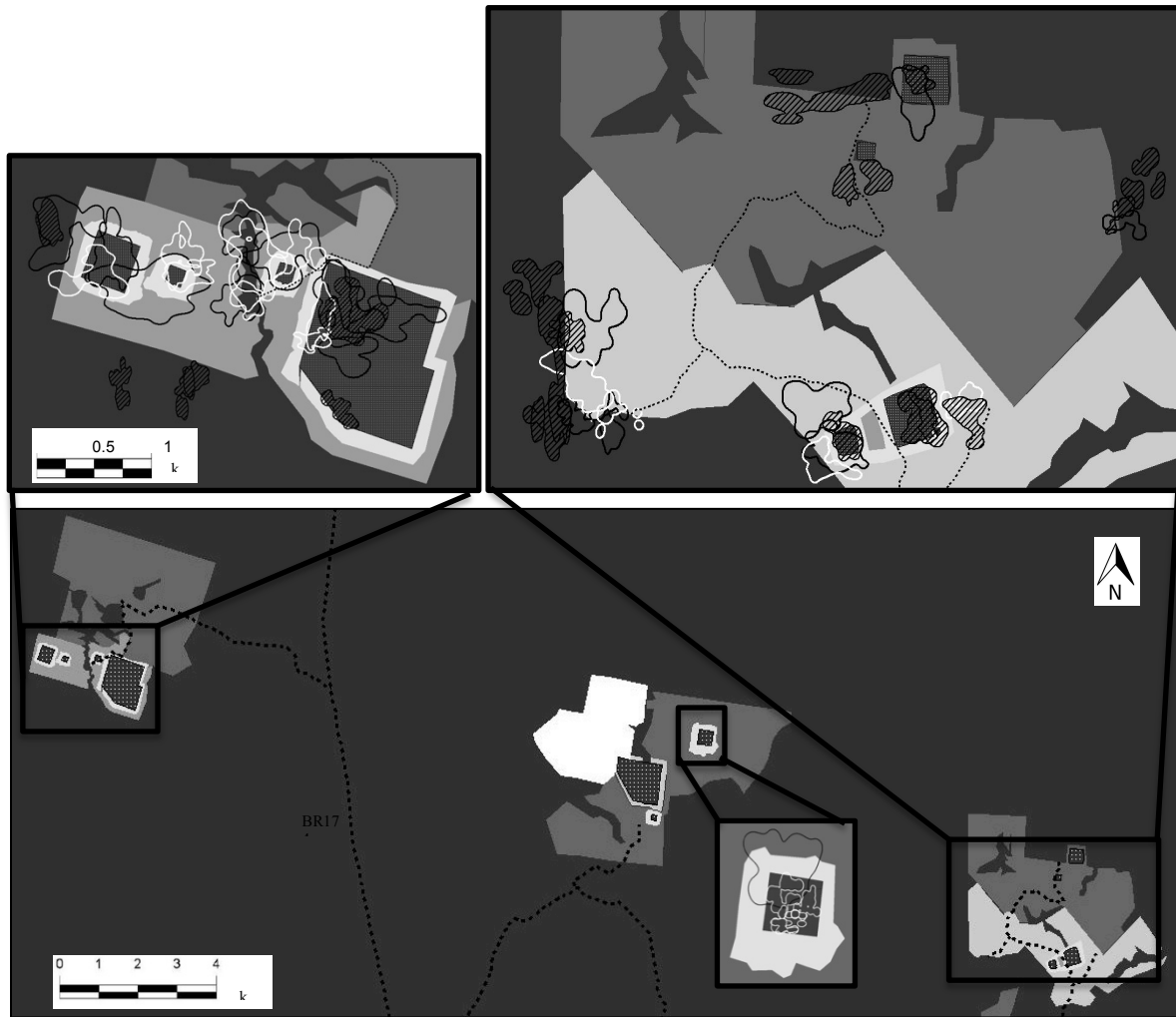


Figure 3.1. Home ranges of radio-tagged *Glyphorhynchus spirurus* (white polygons), *Xiphorhynchus pardalotus* (black polygons) and *Formicarius colma* (hatched polygons) at the Biological Dynamics of Forest Fragments Project. Shade of gray represents forest age, indicating 8–14, 15–18, 21–24, and 27–31 year-old secondary forest, with the darkest gray representing primary forest. Dashed black lines represent roads, and speckled dark gray polygons represent primary forest fragments ($n=11$) and white represents pasture. Insets are identified with thick black outlines; scale bar in top left inset also represents scale in the other two insets. Eighteen additional home ranges located 9 km east in continuous forest (at “KM 41”) are omitted to save space.

Statistical Analyses

Home range and core area. I estimated 95% fixed kernel densities (KDE; referred to hereafter as “home range”) using the ABODE extension for ArcGIS (Laver 2006) using fixed rather than adaptive kernels based on Seaman and Powell’s (1996) recommendation. I used the Gaussian (bivariate normal) kernel form and a least-squares cross-validation for automated

bandwidth selection. Kernels had a grid size setting of “resolution 100”, contouring was performed by volume, and I rescaled home ranges to unit variance. I calculated core areas for each individual using Powell’s (2000) objective and area-independent method (Laver and Kelly 2008) in ABODE for ArcGIS (Laver 2006; ESRI 2009) as follows: rather than arbitrarily using 50% KDE, I used ABODE to calculate the probability of use for each cell of the KDE and defined core range as the area where the probability density was significantly greater than expected by a random distribution; settings were otherwise identical to those used for home range. I excluded home ranges and core areas for individuals for which I had fewer than 15 locations (second lowest = 20 locations; mean = 43 locations/bird). To determine if home range or core area varied among birds primarily using three broad habitat types (i.e. 1-ha forest fragments and secondary forest, 10- and 100- ha fragments, and primary forest), I conducted two two-way ANOVAs with size of home range or core area as the response variable, species and habitat as explanatory variables, and individual as the sampling unit. In each ANOVA, I checked for interaction effects between habitat and species, but they were not significant ($P > 0.3$), so I present results of the additive models. I combined birds in 1-ha fragments with those using secondary forest because all birds that used 1-ha forest fragments also used a considerable amount of secondary forest.

Proportions of home range and core area in primary vs. secondary forest. This analysis required that birds had both primary and secondary forest available to them, so I only used birds captured < 200 m from an interface between primary and secondary forest. I then used GIS to calculate the proportion of each home range and core area located in primary and secondary forest. I calculated a value for $\hat{\theta}$ for each bird, representing the ratio of the proportion of the home range in primary forest to the proportion of the core area in primary forest; I then

calculated $\hat{\pi}$, the proportion of individuals with $\hat{\theta} < 1$. To answer whether a higher proportion of home ranges and core areas were located within primary forest relative to secondary forest, I ran a Z-test on $\hat{\pi}$ values for each species to determine if the observed proportion of $\hat{\theta} > 1$ was greater than expected by chance.

Movement rate. I mapped movement paths using the “Movement Parameters” tool in Hawth’s tools v. 3.27 for ArcGIS (Beyer 2004) and calculated the distance between consecutive locations. To standardize the movement rate on a temporal scale, I calculated mean movement rate for consecutive locations within three hours (i.e. “movement paths”). I also calculated movement rates at 30-min, 1-hr and 2-hr intervals, but the 3-hr timescale best accentuated differences among habitat types, so I considered that the most biologically meaningful timescale. First, to determine if movement rate varied among three broad habitat types (i.e. 1-ha forest fragments and secondary forest, 10- and 100- ha fragments and primary forest), I placed each bird into a habitat type and performed a two-way ANOVA with movement rate per individual as the response variable and species and habitat as explanatory variables. Second, to determine if movement rate varied among the five forest age classes or species, I ran a two-way ANOVA with $\log(\text{movement rate})$ as the response variable, species, and forest age class as explanatory variables, and individual as a random effect. Here I used movement paths as the sampling unit because most birds used several different forest age classes, so I could not meaningfully assign individuals to a single forest age class. I included individual as a random effect to account for the variability introduced by including multiple movement paths per individual. Interactive effects between species and habitat were not significant in these movement rate ANOVAs ($P > 0.05$), so I present results of additive models.

Tortuosity. To estimate tortuosity of movement paths, I calculated mean fractal dimension in program FRACTAL v. 5.20.0 (Nams 1996). Tortuosity is a measure of curviness of a movement path, in which 1.0 is a straight line and 2.0 represents a path so curvy that given enough time, it will eventually cover a plane. Mean fractal dimension is considered among the most precise and accurate methods for estimating tortuosity (Nams 2006). Tortuosity is sensitive to interval between relocations; thus, I considered only runs of three or more consecutive locations in which the interval between locations was between 14 and 39 minutes—the majority of my observations. To determine if tortuosity varied among the five forest age classes or bird species, I ran a two-way ANOVA with tortuosity (fractal mean, rank-transformed) as the response variable, species, and forest age class as explanatory variables, and individual as a random effect; movement paths were the sampling unit.

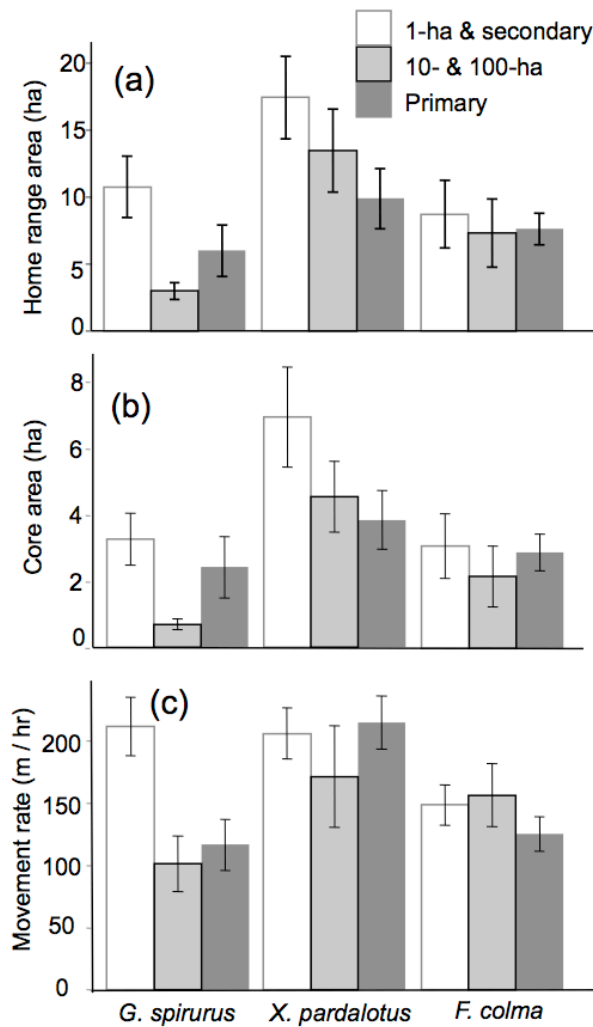
For all ANOVAs I examined Q-Q plots to confirm that assumptions of normality and equality of variance were met, and transformed response variables when needed. I performed all statistical analyses in Program R (R Development Core Team 2012).

RESULTS

Home range and core area

Both habitat ($F_{2,2} = 4.5$, $P = 0.02$) and species ($F_{2,2} = 7.2$, $P = 0.002$) were significant predictors of home range size (Figure 3.2). *Xiphorhynchus pardalotus* had a larger home range than did *G. spirurus* or *F. colma* (Tukey's HSD: $P < 0.05$), and birds using secondary forest or 1-ha fragments had larger home ranges than those using 10- or 100-ha forest fragments or continuous forest (Tukey's HSD: $P < 0.05$; Figure 3.2a). Individual age and sex had no effect on *F. colma* home range size (ANOVA; age: $F_{2,2} = 0.1$, $P = 0.81$; sex: $F_{2,2} = 0.9$, $P = 0.43$).

Likewise, both habitat ($F_{2,2} = 3.6$, $P = 0.03$) and species ($F_{2,2} = 7.7$, $P = 0.001$) were significant predictors of core area. *Xiphorhynchus pardalotus* had a larger core area than did *G. spirurus* or *F. colma* (Tukey's HSD: $P < 0.05$; Figure 3.2b). Individuals using secondary forest and 1-ha fragments had larger core areas than those using 10- or 100-ha forest fragments. Core area in continuous forest was intermediate to, but not statistically different from, the other two habitats (Tukey's HSD: $P > 0.05$). Bird age and sex had no effect on core area of *F. colma* (ANOVA; age: $F_{2,2} = 0.1$, $P = 0.72$; sex: $F_{2,2} = 0.7$, $P = 0.51$).



3.2. Home range (95% kernel density estimate), core area and movement rate (on a three-hr timescale) of radio-tagged *Glyphorhynchus spirurus*, *Xiphorhynchus pardalotus* and *Formicarius colma* as grouped by the main habitat used by the individual. Error bars represent 1 SE.

Proportions of home range / core area in primary vs. secondary forest

For all three species, when individuals had home ranges that included both primary and secondary forest, the proportion of core area in primary forest was greater than proportion of home range in primary forest (mean proportions: *G. spirurus* core = 0.68, home range = 0.57, $n = 18$; $Z = 4.08$, $P < 0.01$; *X. pardalotus* core = 0.56, home range = 0.48, $Z = 3.50$, $P < 0.01$, $n = 13$; *F. colma* core = 0.76, home range = 0.73, $Z = 3.46$, $n = 18$, $P < 0.01$).

Movement rate

Both habitat ($F_{2,2} = 4.6$, $P = 0.01$) and species ($F_{2,2} = 5.0$, $P = 0.01$) were significant predictors of movement rate on the three-hour timescale (Figure 3.2c). *Xiphorhynchus pardalotus* moved faster than did *G. spirurus* or *F. colma* (Tukey's HSD: $P < 0.05$), and individuals using primarily secondary forest and 1-ha fragments moved faster than those using primarily 10- or 100-ha forest fragments or continuous forest (Tukey's HSD: $P < 0.05$). For *F. colma*, age did not affect movement rate, nor did sex (ANOVA; age: $F_{2,2} = 1.2$, $P = 0.30$; sex: $F_{2,2} = 0.0$, $P = 0.84$).

When examining movement paths with individual bird as a random effect, I found that both forest age class ($\chi^2 = 11.1$, $P = 0.02$) and species ($\chi^2 = 18.2$, $P < 0.001$) were significant predictors of movement rate (Figure 3.3). Only one pairwise comparison of among-forest age classes was significant: movement rate was greater in 21–24 year-old forest than in primary forest (Tukey's HSD: $P < 0.05$). As in the individual-based analysis of movement, *X. pardalotus* moved faster than *G. spirurus* or *F. colma* (Tukey's HSD: $P < 0.05$). Sex had no effect on path-based movement rate of *F. colma* ($\chi^2 = 0.18$, $P = 0.67$). Age of *F. colma* had a significant effect on path-based movement rate ($\chi^2 = 7.34$, $P = 0.007$); young birds moved more slowly (132 ± 9.9 m / hr) than adults (157 ± 8.8 m / hr).

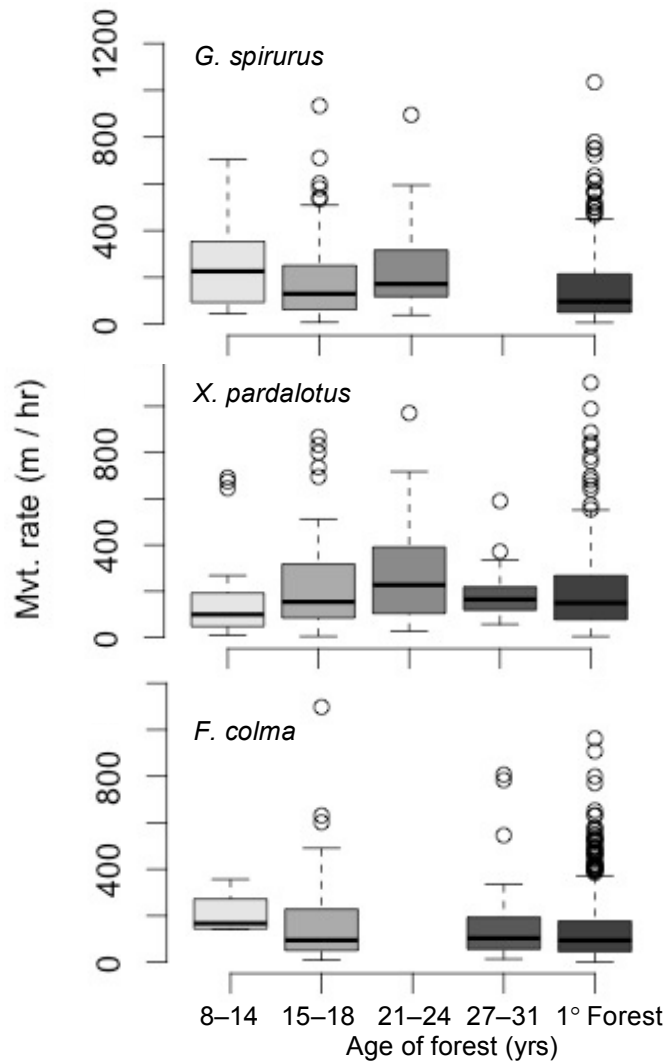


Figure 3.3. Box and whisker plots of the movement rate (three-hr timescale) of radio-tagged *Glyphorhynchus spirurus*, *Xiphorhynchus pardalotus* and *Formicarius colma* as grouped by forest age class—here each movement represents one sample unit. Dark horizontal lines represent means, box min and max represent 25th and 75th percentiles, respectively, whiskers represent max and min values, and circles represent outliers (defined as > 1.5 times the box length away from the box).

Tortuosity

Neither forest age class ($F = 1.3$, $P = 0.26$) nor species ($F = 2.1$, $P = 0.13$) were significant predictors of path tortuosity (Figure 3.4). Pairwise comparisons showed no differences among species or habitats ($P > 0.05$). Bird age and sex had no effect on path tortuosity in *F. colma* (ANOVA; age: $F = 1.5$, $P = 0.24$; sex: $F = 0.1$, $P = 0.76$).

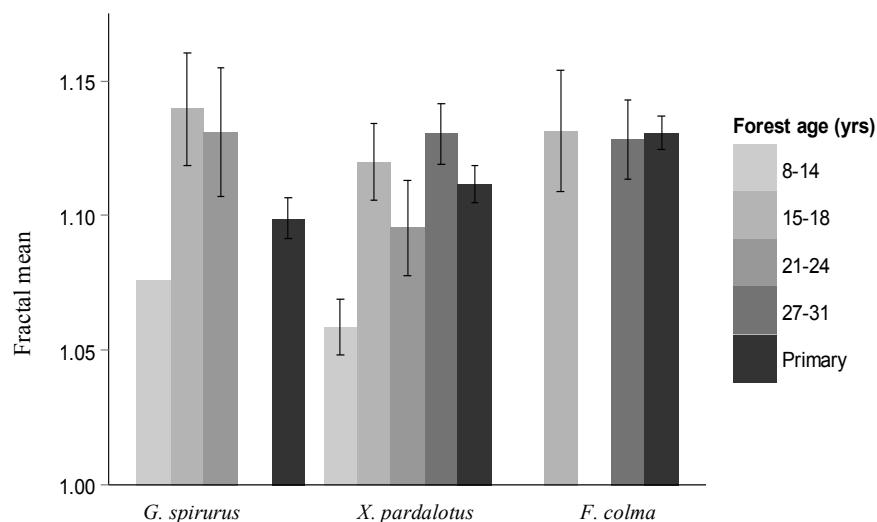


Figure 3.4. Mean fractal dimension (\pm SE; i.e. tortuosity) of movements by radio-tagged *Glyphorhynchus spirurus*, *Xiphorhynchus pardalotus* and *Formicarius colma* as grouped by forest age class—here each movement represents one sample unit. Missing bars indicate no data and missing error bar is due to $n = 1$.

DISCUSSION

I found some support for four of five predictions outlined in my conceptual model of the dynamics of space use by Amazonian birds (Figure 1.3; Table 3.1). In general, birds using secondary forest had larger home ranges, larger core areas, and faster movement rates than those in primary forest. Although the two woodcreepers provided evidence to support all but the tortuosity prediction, *F. colma* only provided support for the prediction of a larger proportion of primary forest in core area relative to home range. Contrary to my predictions, movement paths

appeared no less tortuous in secondary forest relative to primary forest. The two woodcreepers did show some evidence of less tortuous movements across 8–14 year-old secondary forest, (Figure 3.4), but sample size was too small for broad conclusions. I cannot exclude the possibility that collecting very precise location data on smaller spatiotemporal scales (e.g. Simpfendorfer et al. 2012) may reveal a correlation between tortuosity and habitat. This lack of effect for my tortuosity prediction may be an artifact of the temporal scale of sampling. In several cases, I observed radio-tagged birds flying hundreds of meters across secondary forest in a few minutes or less into patches of primary forest. Many of these rapid secondary forest-crossing movements would not have been included in the tortuosity analysis (or the movement rate analysis), because fractal mean requires at least three consecutive locations, and I gathered bird locations at a minimum of every 15 minutes.

Table 3.1. Space use metrics, prediction with respect to primary/secondary forest use, and support for prediction by radiotelemetry data from understory Amazonian birds: *Glyphorhynchus spirurus*, *Xiphorhynchus pardalotus*, and *Formicarius colma*. Y = supported; N = no support, (Y) = partial support.

<i>Space use metric</i>	<i>Prediction</i>	<i>Support for prediction</i>		
		<i>G. spirurus</i>	<i>X. pardalotus</i>	<i>F. colma</i>
home range area:	primary < secondary forest	Y	Y	N
core area:	primary < secondary forest	(Y)	Y	N
% primary in core area vs. home range:	% primary in core area > % primary in home range	Y	Y	Y
movement rate				
(individual-based)	primary < secondary forest	Y	N	N
(path-based)	primary < secondary forest	(Y)	(Y)	N
tortuosity (i.e. path curviness)	primary > secondary forest	N	N	N

Glyphorhynchus spirurus appeared to be the most flexible of the three species at tolerating primary forest fragmentation as it adjusted its home range size, core area, and movement rate in secondary forests. This result was expected because of the species' known use of edges, secondary forests, and flexible use of mixed-species flocks (see methods: study species; Stouffer and Bierregaard 1995; Cohn-Haft et al. 1997; Stouffer et al. 2006). Individuals using secondary forest had home ranges nearly twice as large as those in continuous primary forest (Figure 3.2a), and moved nearly twice as fast as those in continuous primary forest (Figure 3.2c). The ability to expand home range size and to increase movement rates over those in primary forest may have allowed the species to persist in young secondary forest, where resources (i.e. food, mates, cover from predators) are presumably less common. In the Atlantic rainforest of southeastern Brazil, frugivorous Swallow-tailed Manakins (*Chiroxiphia caudata*) were similarly flexible in fragmented landscapes, showing larger mean step lengths, greater maximal daily movements, and larger home ranges relative to individuals that used only primary forest (Hansbauer et al. 2008). Because so few rainforest species' individual movements are well known, it is unclear whether *G. spirurus* and *C. caudata* are exceptional, or whether this spatiotemporal plasticity with respect to fragmentation and secondary forest recovery is a typical pattern for more tolerant, opportunistic species.

Curiously, I found the smallest home ranges and core areas of *G. spirurus* in 10- and 100-ha primary forest fragments, i.e., roughly half the size of those in continuous primary forest and one third the size of those secondary forest (Figure 3.2a, 3.2b). I suspect that reduced densities or absence of other woodcreepers in small fragments might explain this pattern. There are 12 other species at the BDFFP; aside from *X. pardalotus*, all other woodcreepers at the BDFFP have home ranges larger than 10-ha, effectively excluding them from small, isolated fragments

(Stouffer and Bierregaard 1995; Johnson 2011; L.L. Powell and P. C Stouffer unpublished telemetry data). In continuous forests throughout the Neotropics, including in continuous primary forest at the BDFFP, *G. spirurus* often has considerable territorial overlap with conspecifics (Gradwohl and Greenberg 1980; Darrah 2013, P. C Stouffer, unpublished data); however, in forest fragments at the BDPFF (esp. 10-ha fragments) *G. spirurus* had relatively small home ranges that they rarely left, with little overlap between adjacent territory holders (L. L. Powell pers. obs.). I speculate that *G. spirurus* in small fragments were released from competition from other exclusively insectivorous small woodcreepers (e.g. *Sittasomus griseicapillus*, *Certhiasomus stictolaemus*, *Deconychura longicauda*; Marantz 2004), and thus decreased their home range size as they were able to fill a larger niche and exploit resources that would normally be monopolized by other woodcreepers with larger home range sizes and less tolerance for secondary forest. To test this prediction, I envision a competition experiment in which other woodcreepers are removed from medium-size (20- to 50-ha) forest fragments. I predict that the remaining *G. spirurus* would reduce their home range size and movement rate, and defend more exclusive territories than before the removal.

Xiphorhynchus pardalotus showed intermediate flexibility in space use and had significantly larger home ranges and core areas than the other species. Because most radio-tracked individuals regularly associated with a single mixed-species flock, space use by this species is inevitably tied to the space use by the resident flock. Typically, mixed-species flocks in primary forest in the Guiana Shield have home ranges of about 10 ha (Develey and Stouffer 2001; Jullien and Thiollay 1998), and accordingly my radio-tagged *X. pardalotus* had a mean home range size of 9.9 ha in continuous primary forest ($n = 7$). In contrast, the six *X. pardalotus* that used mostly secondary forest had home ranges of 17.4 ha. Generally, *X. pardalotus* does

temporarily “drop out” of mixed species foraging flocks at the BDFFP, and obligate mixed species flock species avoid secondary forest younger than about 15 years-old (Cohn-Haft et al. 1997; Stouffer and Bierregaard 1995), recovering to primary-forest levels of movement about 21 years after land abandonment (Powell et al. 2013). Flock dropouts (i.e. *X. pardalotus*, *G. spirurus* and *Myrmotherula axillaris*) took only 14 years to recover after abandonment at the BDFFP, suggesting that flock dropouts like *X. pardalotus* in secondary growth landscapes can temporarily drop out of a resident flock, forage in intermediate-age secondary growth (i.e. 14–21 years old), then return to the flock, thereby increasing home range size relative to individuals in continuous forest alone. It remains unclear why *X. pardalotus* in 21–24 year-old secondary forest (but not in other forest age classes) moved faster than in primary forest, but I speculate it relates to the return of mixed-species flock obligates to this forest age class.

Formicarius colma appeared to be the least plastic species of the three; it showed no evidence of adjusting its home range size, core area, or movement rates in secondary forest as the other species did (Table 3.1). The species showed a fundamentally different response to second growth development than the other species, essentially skipping step “d” in my conceptual model (Figure 1.3d) and proceeding directly from step “c” to step “e” (Figure 1.3c, 1.3e). *Formicarius colma* was practically absent from secondary forest younger than about 27–31 years (Powell et al 2013), but when it did enter that oldest secondary forest, it used space indistinguishably from the way it used space in primary forest. As with the other species, *F. colma* did have a higher proportion of core area in primary forest relative to home range, which suggests that individuals occupying the interface of primary and secondary forest concentrate their movements in primary forest. The pattern observed in *F. colma* matches that of another Neotropical terrestrial insectivore, *Sclerurus scansor*. While other more flexible species adjusted home range size and

movement rates in fragmented Atlantic rainforest, *S. scansor* did not (Hansbauer et al. 2008). Tropical terrestrial insectivores may represent the rainforest guild most sensitive to fragmentation (Canaday and Rivadeneyra 2001; Peh et al. 2005; Stratford and Stouffer 2013; Powell et al. 2013). Powell et al. (2013) projected that terrestrial insectivores, including *F. colma*, captured at the primary/secondary forest interface at the BDFFP will not recover to pre-isolation capture rates until about 60 years after pasture abandonment, nearly 30 years later than the next closest guild. Even in 17–30 year old secondary forest, capture rates of terrestrial insectivores along the primary/secondary interface were still only 50% of those in primary forest (Powell et al. 2013). Although *F. colma* is indeed sensitive relative to my other two focal species, I selected *F. colma* because it was the most sensitive species that was common enough to obtain a reasonable sample, so there are almost certainly other species that are more sensitive indicators of recovery to primary forest conditions (Stouffer et al. 2011). Six of the twelve terrestrial insectivores in Powell et al. (2013), for example, were never caught along edges, even 27–31 years after land abandonment (i.e. *Sclerurus caudacutus*, *Myrmornis torquata*, *Grallaria varia*, *Hylopezus macularius*, *Conopophaga aurita*, *Cyphorhinus arada*). In my study, I had so few locations of *F. colma* in 21–24 year-old secondary forest that I was unable to calculate movement rates or tortuosity, so it is certainly possible that 27–31 year-old secondary forest is not entirely recovered—at least from the perspective of *F. colma*—and almost certainly from the perspective of other sensitive terrestrial insectivores. The mechanism behind why *F. colma*, *S. scansor* and other terrestrial insectivores show such an apparently inflexible spatial response to recovering secondary growth remains unclear, but may be a key piece of why this guild is particularly sensitive to forest disturbance.

Space use is simply one way to describe the suitability of a given habitat to an animal. By understanding the spatiotemporal dynamics of the species that are tolerant (e.g. *G. spirurus*) and intolerant (e.g. *F. colma*) of forest fragmentation and young secondary forest, I can work towards managing landscapes appropriately as they continue to change. Metrics of fitness such as survival and nest success can provide a more direct understanding of species' requirements and how they respond to perturbations in the environment, but those measures of fitness are often difficult to quantify, so less direct measures such as patterns of space use are critical. Even at the BDFFP, the largest and longest-running study of rainforest fragmentation in the world, where there are now more than 60,000 captures of understory birds, long-term studies of avian survival remain challenging because banding protocols were not designed to address survival—a common problem for long-term study sites (Ruiz-Gutiérrez et al. 2012). In the smallest forest fragments, where population processes are particularly of interest to conservation biologists, there are few individuals and many transients, further complicating survival analyses (Stouffer and Bierregaard 1995; Johnson 2011). Nest success is also very difficult to quantify at the BDFFP and elsewhere in the tropics because most species are uncommon to rare and do not have a short interval in which they breed and nests are difficult to find (Stouffer et al. 2013). By following radio-tagged individuals, I provide a more mechanistic view of how rainforest birds respond to forest fragmentation and the recovery of secondary forest than studies of capture rate and survival alone; I also provide an alternative to difficult-to-quantify components of survival. Analyses of movement patterns can be interpreted as an indirect measure of fitness—the consequence of animals moving adaptively to maximize fitness. As the area of deforested land and secondary forest in tropical rainforests continues to increase in the 21st century, understanding how animals move through a spatiotemporally complex mosaic of habitats will be

critical to biodiversity conservation. Quantifying the value of marginal (and economically inconsequential) habitats such as secondary forest will be essential as land managers attempt to maintain species persistence and landscape connectivity in increasingly heterogeneous landscapes that were formerly unbroken primary rainforest.

LITERATURE CITED

- Arditi, R. and Dacorogna, B., 1988. Optimal foraging on arbitrary food distributions and the definition of habitat patches. *American Naturalist* 131(6):837–846.
- Barlow, J. , Mestre, L. a. M., Gardner, T. a. and Peres, C., 2007. The value of primary, secondary and plantation forests for Amazonian birds. *Biological Conservation* 136(2):212–231.
- Bates, J.M., Haffer, J. and Grismer, E., 2004. Avian mitochondrial DNA sequence divergence across a headwater stream of the Rio Tapajos, a major Amazonian river. *Journal of Ornithology* 145(3):199–205.
- Beyer, H.L., 2004. Hawth's Analysis Tools for ArcGIS. Available at <http://www.spatialecology.com/htools>.
- Bierregaard Jr., R.O. , Gascon, C., Lovejoy, T. E. and Mesquita, R. 2001. *Lessons from Amazonia: the Ecology and Conservation of a Fragmented Forest*, Ann Arbor, MI: Yale Univ Press.
- Biotas (TM); Ecological Software Solutions LLC., 2004. *Location of a Signal (LOAS)*. Version 4.0.3.3.
- Boucher, D.H., 2011. Brazil's success in reducing deforestation. UCS Tropical Forest and Climate Briefing #8. Cambridge, MA: Union of Concerned Scientists. Online at www.ucsusa.org/assets/documents/global_warming/Brazil-s-Success-in-Reducing-Deforestation.pdf.
- Brawn, J.D. and Robinson, S.K., 1996. Source-sink population dynamics may complicate the interpretation of long-term census data. *Ecology* 77(1):3–12.
- Brazilian National Space Research Institute (INPE), 2010. *Projecto prodes: Monitoramento da floresta Amazônica Brasileira por satélite*. Brasilia: Ministerio da Ciencia e Tecnologia. Online at <http://www.obt.inpe.br/prodes/index.html>.
- Brook, B.W., Bradshaw, C. J. A., Koh, L. P. and Sodhi, N. S., 2006. Momentum drives the crash: mass extinction in the tropics. *Biotropica* 38(3):302–305.

- Caldwell, I.R. and Nams, V.O., 2006. A compass without a map: Tortuosity and orientation of eastern painted turtles (*Chrysemys picta picta*) released in unfamiliar territory. *Canadian Journal of Zoology* 1137:1129–1137.
- Canaday, C. and Rivadeneyra, J., 2001. Initial effects of a petroleum operation on Amazonian birds: Terrestrial insectivores retreat. *Biodiversity and Conservation* 10:567–595.
- Cohn-Haft, M., Whittaker, A. and Stouffer, P.C., 1997. A new look at the “species-poor” central Amazon: the avifauna north of Manaus, Brazil. *Ornithological Monographs*, 48:205–235.
- Darrah, A., 2013. Ecology and Flock-following Behavior of the Wedge-billed Woodcreeper in Eastern Ecuador, PhD Dissertation, University of Arkansas. University of Arkansas.
- Develey, P.F. and Stouffer, P.C., 2001. Effects of roads on movements by understory birds in mixed-species flocks in central Amazonian Brazil. *Conservation Biology* 15(5):1416–1422.
- ESRI, 2009. ArcGIS Desktop: 9.3. Redlands, CA: Environmental Systems Research Institute.
- Fearnside, P.M., 2005. Deforestation in Brazilian Amazonia: history, rates, and consequences. *Conservation Biology* 19(3):680–688.
- Ferraz, G., Nichols, J. D., Hines, J. E., Stouffer, P. C., Bierregaard Jr., R. O. & Lovejoy, T. E., 2007. A large-scale deforestation experiment: Effects of patch area and isolation on Amazon birds. *Science* 315(5809):238–241.
- Fryxell, J.M., Hazell, M., Börger, L., Dalziel, B. D., Haydon, D. T., Morales, J. M., McIntosh, T. & Rosatte, R. C., 2008. Multiple movement modes by large herbivores at multiple spatiotemporal scales. *Proceedings of the National Academy of Sciences* 105(49):19114–19119.
- Gascon, C. and Bierregaard Jr, R.O., 2001. The Biological Dynamics of Forest Fragments Project. In R. O. Bierregaard Jr et al., eds. *Lessons from Amazonia: The Ecology and Conservation of a Fragmented Forest*. New Haven: Yale University Press: 31–45.
- Gradwohl, J. and Greenberg, R., 1980. The formation of antwren flocks on Barro Colorado Island, Panama *The Auk*:385–395.
- Hansbauer, M.M., Storch, I., Pimentel, R. G. and Metzger, J. P., 2008. Comparative range use by three Atlantic Forest understory bird species in relation to forest fragmentation. *Journal of Tropical Ecology* 24:291–299.
- Howell, S.N.G., Corben, C., Pyle, P., and Rogers, D. I., 2003. The first basic problem: a review of molt and plumage homologies. *The Condor* 105(4):635–653.
- Johnson, E.I., 2010. Banding guide to the birds of The Biological Dynamics of Forest Fragments Project.

- Johnson, E.I., 2011. Fragmentation sensitivity and its consequences on demography and host-ectoparasite dynamics in Amazonian birds, PhD Dissertation, Louisiana State University. Baton Rouge, LA: Louisiana State University.
- Johnson, E.I., Wolfe, J. D., Ryder, B. T., and Pyle, P., 2011. Modifications to a molt-based ageing system proposed by Wolfe et al.(2010). *Journal of Field Ornithology* 82(4):422–424.
- Johnson, E.I., Stouffer, P.C. and Vargas, C.F., 2011. Diversity, biomass, and trophic structure of a central amazonian rainforest bird community. *Revista Brasileira De Ornithologia* 19(1):1–16.
- Jullien, M. and Thiollay, J.-M., 1998. Multi-species territoriality and dynamic of neotropical forest understorey bird flocks. *Journal of Animal Ecology* 67(2):227–252.
- Krabbe, N. and Schulenberg, T.S., 2003. Family Formicariidae (ground-antbirds). In *Handbook of the Birds of the World Volume 8. Broadbills to Tapaculos*. Lynx Edicions Barcelona, Spain: 682–731.
- Lair, H., 1987. Estimating the location of the focal center in red squirrel home ranges. *Ecology* 68(4):1091–1101.
- Laurance, S.G.W., Stouffer, P.C. and Laurance, W.F., 2004. Effects of road clearings on movement patterns of understory rainforest birds in central Amazonia. *Conservation Biology* 18(4):1099–1109.
- Laurance, W.F. et al., 2011. The fate of Amazonian forest fragments: A 32-year investigation. *Biological Conservation* 144(1):56–67.
- Laver, P., 2006. ABODE version 5: Kernel home range estimation from ArcGIS, using VBA and Objects. <http://filebox.vt.edu/users/plaver/abode/download.html>. Downloaded March 3, 2008.
- Laver, P.N. and Kelly, M.J., 2008. A critical review of home range studies. *Journal of Wildlife Management* 72(1):290–298.
- Levey, D.J., 1988. Tropical Wet Forest Treefall Gaps and Distributions of Understory Birds and Plants. *Ecology* 69(4):1076–1089.
- Marantz, C.A., Aleixo, A., Bevier, R., L. & Patten, M. A., 2003. Family Dendrocolaptidae (Woodcreepers). In J. A. del Hoyo, A. Elliott, and D. A. Christie, eds. *Handbook of the Birds of the World. Volume 8. Broadbills to Tapaculos*. Lynx Edicions. Barcelona, Spain.: 358–447.
- Naka, L.N., Stouffer, P. C., Cohn-Haft, M., Marantz, C. A., Whittaker, A., and Bierregaard Jr., R.O., 2009. Birds of the terra firme forests north of Manaus: Guianan area of endemism: four CD-set of audio recordings., INPA.

- Nams, V.O., 2006. Improving accuracy and precision in estimating fractal dimension of animal movement paths. *Acta Biotheoretica* 54(1):1–11.
- Nams, V.O., 1996. The VFractal: a new estimator for fractal dimension of animal movement paths. *Landscape Ecology* 11(5):289–297.
- Nazareno, A.G., Feres, J. M., de Carvalho, D., Sebbenn, A. M., Lovejoy, T. E., and Laurance, W. F., 2012. Serious new threat to Brazilian forests. *Conservation Biology* 26(1):5–6.
- Neeff, T., Lucas, R. M., Santos, J. R., Brondizio, E. S. and Freitas, C. C., 2006. Area and age of secondary forests in Brazilian Amazonia 1978–2002: an empirical estimate. *Ecosystems* 9(4):609–623.
- Otis, D.L. and White, G.C., 1999. Autocorrelation of location estimates and the analysis of radiotracking data. *Journal of Wildlife Management* 63(3):1039–1044.
- Peh, K.S.H., Jong, J., Sodhi, N. S., Lim, S. L. H. and Yap, C. A. M., 2005. Lowland rainforest avifauna and human disturbance: persistence of primary forest birds in selectively logged forests and mixed-rural habitats of southern Peninsular Malaysia. *Biological Conservation* 123(4):489–505.
- Powell, L.L., Stouffer, P.C. and Johnson, E.I., 2013. Recovery of understory bird movement across the interface of primary and secondary Amazon rainforest. *The Auk* 130(3):450–468.
- Powell, R.A., 2000. Animal home ranges and territories and home range estimators. In L. Boitani and T. Fuller, eds. *Research techniques in animal ecology: controversies and consequences*. New York, NY: Columbia University Press: 65–110.
- R Development Core Team, 2012. R Version 2.14.1: A Language and Environment for Statistical Computing. R Foundation for Statistical Computing, Vienna, Austria. <http://www.R-project.org>.
- Rappole, J.H. and Tipton, A.R., 1991. New harness design for attachment of radio transmitters to small passerines. *Journal of Field Ornithology* 62(3):335–337.
- Rudorff, B.F.T., Adami, M., Aguiar, D. A., Moreira, M. A., Mello, M. P., Fabiani, L., Amaral, D. F. and Pires, B. M., 2011. The soy moratorium in the Amazon biome monitored by remote sensing images. *Remote Sensing* 3(1):185–202.
- Ruiz-Gutiérrez, V., Doherty Jr, P. F., Santana C., E., Martínez, S. C., Schondube, J., Munguía, H. V and Iñigo-Elias, E 2012. Survival of resident Neotropical birds: Considerations for sampling and analysis based on 20 years of bird-banding efforts in Mexico. *The Auk* 129(3):500–509.
- Seaman, D.E. and Powell, R.A., 1996. An evaluation of the accuracy of kernel density estimators for home range analysis. *Ecology* 77(7):2075–2085.

- Sekercioglu, C.H., Ehrlich, P. R., Daily, G. C., Aygen, D., Goehring, D. & Sandí, R. F., 2002. Disappearance of insectivorous birds from tropical forest fragments. *Proceedings of the National Academy of Sciences* 99(1):263–267.
- Simpfendorfer, C.A., Olsen, E. M., Heupel, M. R. & Moland, E., 2012. Three-dimensional kernel utilization distributions improve estimates of space use in aquatic animals. *Canadian Journal of Fisheries and Aquatic Sciences* 69(3):565–572.
- Skutch, A.F., 1969. Life histories of Central American birds. III. Families Cotingidae, Pipridae, Formicariidae, Furnariidae, Dendrocolaptidae, and Picidae. *Pacific Coast Avifauna* 35.
- Sparovek, G., Berndes, I., Klug, I.C.F., Barreto, A.G.O.P. 2010. Brazilian agriculture and environmental legislation: status and future challenges. *Environmental Science and Technology* 44(16):6046–6053.
- Stouffer, P.C., 2007. Density, territory size, and long-term spatial dynamics of a guild of terrestrial insectivorous birds near Manaus, Brazil. *Auk* 124(1):291–306.
- Stouffer, P.C., 1997. Interspecific aggression in Formicarius antthrushes? The view from central Amazonian Brazil. *Auk* 114(4):780–785.
- Stouffer, P.C., Bierregaard Jr., R. O., Strong, C. & Lovejoy, T. E., 2006. Long-term landscape change and bird abundance in Amazonian rainforest fragments. *Conservation Biology* 20(4):1212–1223.
- Stouffer, P.C., Johnson, E. I., Bierregaard Jr., R. O. & Lovejoy, T. E., 2011. Understory bird communities in Amazonian rainforest fragments: species turnover through 25 years post-isolation in recovering landscapes. *PloS one* 6(6), p.e20543.
- Stouffer, P.C. and Bierregaard Jr., R.O., 1995. Use of Amazonian forest fragments by understory insectivorous birds. *Ecology* 76(8):2429–2445.
- Stouffer, P.C. and Bierregaard Jr., R.O., 1993. Spatial and temporal abundance patterns of Ruddy Quail-doves (*Geotrygon montana*) near Manaus, Brazil. *Condor* 95(4):896–903.
- Stouffer, P.C., Johnson, E.I. and Bierregaard, R.O., 2013. Breeding seasonality in Central Amazonian rainforest birds. *The Auk* 130(3):529–540.
- Stratford, J.A. and Stouffer, P.C., 2013. Microhabitat associations of terrestrial insectivorous birds in Amazonian rainforest and second-growth forests. *Journal of Field Ornithology* 84:1–12.
- Stratford, J.A. and Stouffer, P.C., 2001. Reduced feather growth rates of two common birds inhabiting central Amazonian forest fragments. *Conservation Biology* 15(3):721–728.

- Vásquez, R.A., Ebensperger, L.A. and Bozinovic, F., 2002. The influence of habitat on travel speed, intermittent locomotion, and vigilance in a diurnal rodent. *Behavioral Ecology* 13(2):182–187.
- Ward, D. and Saltz, D., 1994. Foraging at different spatial scales: Dorcas gazelles foraging for lilies in the Negev Desert. *Ecology* 75:48–58.
- Willis, E.O., 1977. Lista preliminar das aves da parte noroeste e áreas vizinhas da Reserva Ducke, Amazonas, Brasil. *Revista Brasileira de Biologia* 37(3):585–601.
- Wolfe, J.D., Ryder, T.B. and Pyle, P., 2010. Using molt cycles to categorize the age of tropical birds: an integrative new system. *Journal of Field Ornithology* 81(2):186–194.
- Wright, S.J. and Muller-Landau, H.C., 2006a. The future of tropical forest species. *Biotropica* 38(3):287–301.
- Wright, S.J. and Muller-Landau, H.C., 2006b. The uncertain future of tropical forest species. *Biotropica* 38(4):443–445.

CHAPTER 4: EDGE ANALYSIS REVEALS CHANGES IN HABITAT SUITABILITY THROUGH FOREST SUCCESSION: A CASE STUDY OF UNDERSTORY BIRDS IN THE BRAZILIAN AMAZON

INTRODUCTION

Habitat loss leads to fragmentation and isolation of remnant habitat, and generally a more heterogeneous landscape rich in edges between different habitat types. In the Brazilian Amazon alone, an average of 16,000 km² of primary rainforest have been lost each year for the last 20 years (INPE 2010), which has led to the creation of ~20,000 km of new forest edges in the Amazon Rainforest each year (D. Skole pers. comm.). Edge effects are currently recognized as one of the principal mechanisms behind the response of species and communities to fragmentation (Ries et al. 2004; Banks-Leite et al. 2010). In the Amazon rainforest although both yearly deforestation rates and the number of new large-scale clearings have decreased (INPE 2010), the number of new small (< 50 ha) forest clearings has remained consistent (Rosa et al. 2012); thus there is now an enormous and ever growing matrix of roadways (Brandão and Souza 2006) and small deforested patches, and an associated network of forest edges much greater than would be created by an equivalent area of large clearings.

Edge responses vary enormously depending on the two habitats juxtaposed, yet the majority of studies of edge effects are binary, measuring edge effects simply based on the juxtaposition of habitat and non-habitat, an oversimplification that is not representative of the majority of edges (Kapos 1989; Laurance 2004; Ewers and Didham 2006a; Ries and Sisk 2010; Zurita et al. 2012; Peyras et al. 2013). The mechanisms driving ecological alterations along edges are diverse, including desiccation stress to vegetation, wind shear, wind turbulence, alterations of light levels and ground temperature; these changes produce an alteration on the temporal and spatial distribution of resources available for animals and ecological interactions

(Ries et al. 2004). Negative edge responses to the boundary between habitats have been well documented in tropical fauna, including beetles (Didham et al. 1998), ants (Carvalho and Vasconcelos 1999), butterflies (Brown and Hutchings 1997), and understory rainforest birds (Laurance et al. 2004). Resident insectivorous birds of the rainforest understory are especially edge-averse; even more so than their temperate and frugivorous counterparts, making them sensitive to deleterious effects of forest fragmentation relative to other foraging guilds (Lindell et al. 2007; Newbold et al. 2013).

There are several likely reasons for the edge sensitivity of resident tropical insectivores, including high food choice specialization (Rosenberg 1990; Marra and Remsen 1997), differences in insect community composition between edge and interior (Didham et al. 1998), the relative abundance of fruit and nectar favored by frugivores and nectarivores along edges due to increased light (Stiles 1975; Levey 1988; Rodewald and Brittingham 2004), and the relative habitat flexibility of migrant species (i.e. non-residents). In their review of avian edge responses, Lindell et al. (2007) found that Neotropical birds avoided edges more than their temperate counterparts (50% vs. 13%), and that those tropical edge avoiders were more likely to be insectivorous than not. At my study site, BDFFP north of Manaus, Brazil, Susan Laurance (2004) found that five of eight foraging guilds of understory insectivorous birds had lower capture rates within 70 m of forest road edges, including all 14 species of terrestrial insectivore.

In addition to the creation of new edges, timber management along with the abandonment of agricultural areas creates a complex landscape including patches of primary forest, agricultural areas and secondary forest in different stages of regeneration. Precise estimates of the amount of secondary forest in Amazonia remain elusive (Greg Asner, pers. comm.), but the best available data indicate that in the Brazilian Amazon alone, the area of secondary forest

increased from 29,000 to 161,000 km² from 1978–2002 (Neeff et al. 2006)—about the size of Florida. Together, edges and secondary growth age have powerful effects on species composition and abundance. For example, Powell et al. (2013), working at the BDFFP, showed sharp reductions in capture rates for forest species captured along the edges of habitat and non-habitat; yet after abandonment of deforested areas, nine of ten foraging guilds recovered to pre-isolation capture rates in 13 to 34 years. Terrestrial insectivores were the most edge-averse guild, with return to pre-isolation capture rates predicted to be about 60 years post-abandonment (Powell et al. 2013). It is increasingly clear that: 1) edges are not static in time; 2) edges influence communities within forest fragments; and 3) edges and secondary forest composition influences the community at the landscape scale (Porensky 2011).

As we continue to lose primary tropical forests and the remaining patches become increasingly fragmented by variable inter-fragment matrix habitats (including vast areas of secondary forest), it is increasingly important to understand how animals respond to those edges across space and time. Because edges are essentially the first barrier for a dispersing animal to cross if it is to move among forest fragments, many hard edges on the landscape scale can reduce functional connectivity among forest fragments (Banks-Leite et al. 2010; Porensky 2011; Zurita et al. 2012), thus reducing gene flow (Bates et al. 2004), altering metapopulation dynamics (Brawn and Robinson 1996), and generally creating small, isolated populations with higher extinction risk (Laurance 2000). Specifically, few studies have tracked edge responses of tropical birds continuously over space (i.e. inside and outside edges; but see Zurita et al. 2012), while none has also tracked the dynamics of avian edge responses across ages of secondary forest. Further, most studies of edge effects do not consider distance as a continuous factor or focus only on the interior side of the edge (Ewers and Didham 2006).

Here I present what I believe is the most realistic and practically applicable approach for studying the spatiotemporal effect of edges on Amazonian birds with respect to secondary growth (Ewers and Didham 2006; Zurita et al. 2012). My main objectives were twofold: 1) to quantify and compare the edge responses of three common understory insectivore species with different patterns of space use among primary forest and three age classes of secondary forest; and 2) to estimate the time after land abandonment when edges no longer influence space use (i.e. “recovery” of secondary forest in terms of edge response). Given known differences in natural histories and tolerance of secondary forest among my three study species (see Methods: Study species), I predicted that edge avoidance would gradually decrease with age of secondary growth adjacent to primary forest, and that *Formicarius colma*, a terrestrial insectivore, would need the oldest secondary forest to show no edge response, whereas *Glyphorhynchus spirurus*, the most flexible and edge-tolerant of my target species, would be the quickest to recover.

METHODS

Study area

I conducted fieldwork from June to October of 2009, 2010, and 2011 at the BDFFP, approximately 80 km north of Manaus, Amazonas, Brazil (2°30’S, 60°W). For detailed descriptions of the site, see Bierregaard and Gascon 2001; Laurance et al. 2011, and Chapter 1. After isolation, edge effects penetrated 10 to 300 m into primary forest at the BDFFP (Laurance et al. 2002); but this distance can extend 2-3 km with frequent fire disturbance (Cochrane and Laurance 2002; Briant et al. 2010).

For this chapter, I divided second growth available to radio-tagged birds into three age classes. The youngest secondary growth was 8 to 14 years old with an average canopy height of about 6 m. Intermediate secondary growth, 15 to 24 years old, averaged a 17-m-tall canopy.

The oldest secondary forest was 27 to 31 years old, and averaged 19 m tall, considerably shorter than primary forest at BDFFP, which averaged about 23 m tall in areas available to radio-tagged birds. Canopy heights were estimated from LiDAR-based canopy height models within home ranges of radio-tagged birds. Tree mortality near edges (Laurance et al. 2002) may have contributed to differences in canopy heights between these estimates and those widely cited for the BDFFP (30–37 m in continuous forest; Gascon et al. 2001).

Study Species

See Chapter 3 for details on study species.

Captures and Radiotracking

I captured target species with both passive and target netting techniques and marked captured birds with uniquely numbered aluminum bands (more detail on captures and radiotracking in Chapter 3). I Radio-tagged birds throughout the BDFFP, including parts of nine forest fragments on all three *fazendas* (Figure 3.1).

Data analysis

In this chapter I categorized secondary forest into three age classes based on availability in the landscapes used by radio-tagged birds. Similar to the analysis of Zurita et al (2012), I estimated the activity/density of each species in secondary forest along distance belts in relation to primary forest (distance to the edge of primary forest). Distance belts were: 0–20, 21–50, 51–100, 101–150, 151–200, 201–500, 501–1000, > 1000 m. The activity/density represents the number of telemetry records per distance belt, as corrected by the amount of available habitat within a buffer around the capture location, where diameter of the buffer was equal to the diameter of the mean home range for the species (Hausbauer 2008, Zurita et al 2012; home

ranges from Chapter 3.). For example, if young secondary forest represents only 20% of the total habitat cover inside the buffer, I weighted the activity of each species in this habitat by 0.2.

To evaluate the response of species to different edges (primary forest and three categories of secondary forest), I used the approach of Ewers and Didham (2006) and Zurita et al. (2012). This methodology provides a continuous approach to analyze the response of species through the primary-secondary forest interface. I used a series of theoretical models to quantify whether three species showed edge avoidance, edge preference or no response to edges. I first performed non-linear regression models (mean, lineal, power, sigmoid and unimodal) representing theoretical “complete” (sampling distances include all the area of the edge response) and “incomplete” (edge effects extent beyond sampling distances in one or both habitats) edge responses using the activity/density of each species as the dependent variable and the distance (grouped on distance belts) to the primary-secondary forest edge as the independent variable. I denoted distances inside primary forest as positive values on the x-axis whereas distances inside secondary forest were negative (zero is the edge). I then used Akaike’s Information Criterion with a correction for small sample size (AIC_c) to compare among the five regression models. The models included the complete range of edge responses (a detailed description of equations and the procedure can be found on Ewers and Didham 2006 and Zurita et al. 2012):

- 1) Mean: the species shows similar activity/density in both habitats (primary and secondary) and no edge response.
- 2 & 3) Lineal and power: in both cases the species shows preference for one habitat over the other; however, in the case of lineal function the response is incomplete in both habitats and in the case of power function the response is complete in one habitat and incomplete in the other.

- 4) Sigmoid: the species prefers one habitat over another (a complete edge response). This function is characterized by Y_{\min} and Y_{\max} , representing the activity/density of the species beyond the edge response on non-preferred and preferred habitat, respectively.
- 5) Unimodal: the species prefers edge, with higher abundance on the ecotone between habitats relative to both primary and secondary forest interior. When the unimodal function showed the best fit to the data, I performed two additional power regressions on each side of the ecotone to estimate activity/density in each habitat beyond the edge response.

As a measure of edge effects on species activity I estimated the magnitude of the edge effect, which represents the difference (expressed as a percentage) on species activity in both habitats beyond edge effect. To estimate the magnitude of the edge effect, I calculated the percent difference between the lower and upper asymptote of the sigmoid function (Y_{\min} and Y_{\max}) or the lower and upper asymptote of the power functions (in the case of an unimodal response). To quantify suitability of my three age classes of secondary forest relative to primary forest, I divided activity/density on primary forest beyond edge effect (Y_{\max}) by activity/density on secondary forest beyond edge effect (Y_{\min}), where a coefficient of one (or higher) indicates similar (or higher) suitability of secondary forest and primary forest and a coefficient lower than one indicates higher suitability of primary forest. I explored three theoretical functions to the relation between the primary/secondary forest suitability and forest age: lineal, exponential, or sigmoid increase. Because the number of independent secondary forest ages (3) was too small to perform a regression analysis, I only performed non-parametric correlations and a visual

exploration of the area covered by the three potential functions; the intersection between this area and the line of $y = 1$ is the age when the suitability of both forest types became similar.

RESULTS

In this analysis, I included 17 *G. spirurus*, 18 *X. pardalotus* and 19 *F. colma*, which included 644 locations from *G. spirurus*, 695 locations for *X. pardalotus*, and 800 locations for *F. colma*. The 19 *F. colma* included 7 young, 11 adults, and 1 of unknown age; 13 were males, 3 were females, and 3 were not sexed. The woodcreepers were all considered adults having formative or definitive basic plumage with ossified skulls.

Glyphorhynchus spirurus showed a strong unimodal positive edge response in young secondary forest. Activity levels were highest within 100 m of the primary forest side of the edge

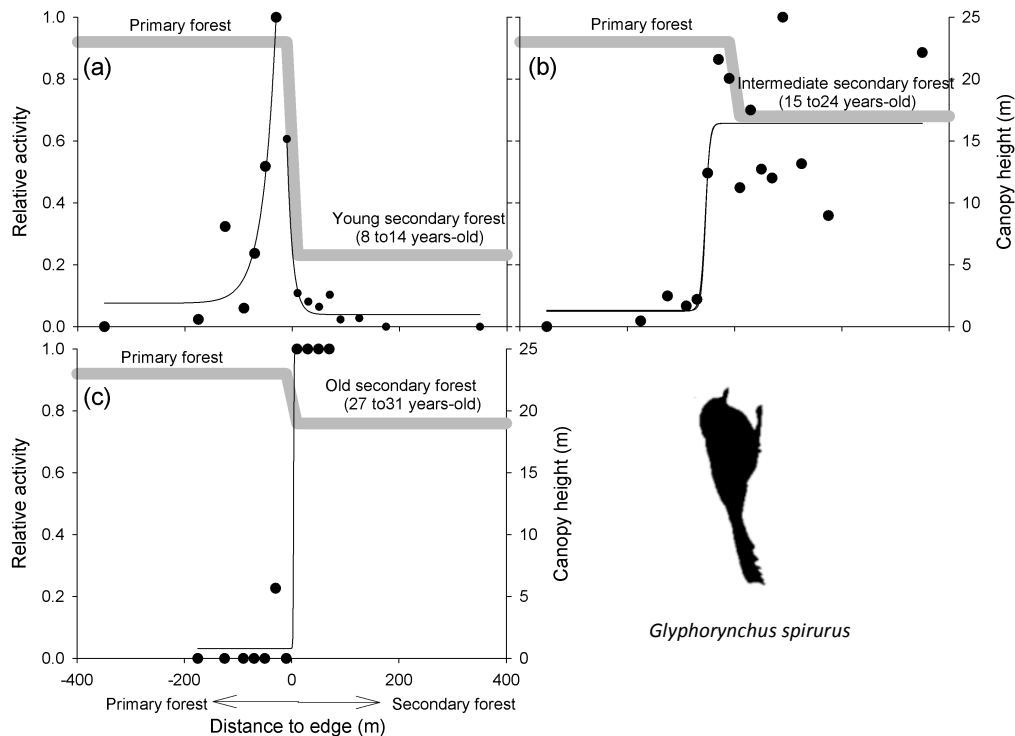


Figure 4.1. Response of radio-tagged *Glyphorhynchus spirurus* to edges between primary forest and a) young (6–14 years old), b) intermediate (15–24 years old), and c) old (27–30 years old) secondary forest in the Brazilian Amazon. Gray line represents relative canopy height, with primary forest = 23m.

(Figure 4.1a). Intermediate and old secondary forest had increasingly higher activity levels than primary forest for *G. spirurus*, as represented by the sigmoidal response curves (Figure 4.1b and 4.1c).

Xiphorhynchus pardalotus also showed a strong sigmoidal edge response to young secondary forest with activity levels dropping off sharply 100 m into secondary forest (Figure 4.2a). The species showed no response to intermediate secondary forest edges (Figure 4.2b). *Xiphorhynchus pardalotus* showed a strong unimodal positive response at edges of primary forest and old secondary forest with activity concentrated precisely along the edge (Figure 4.2c).

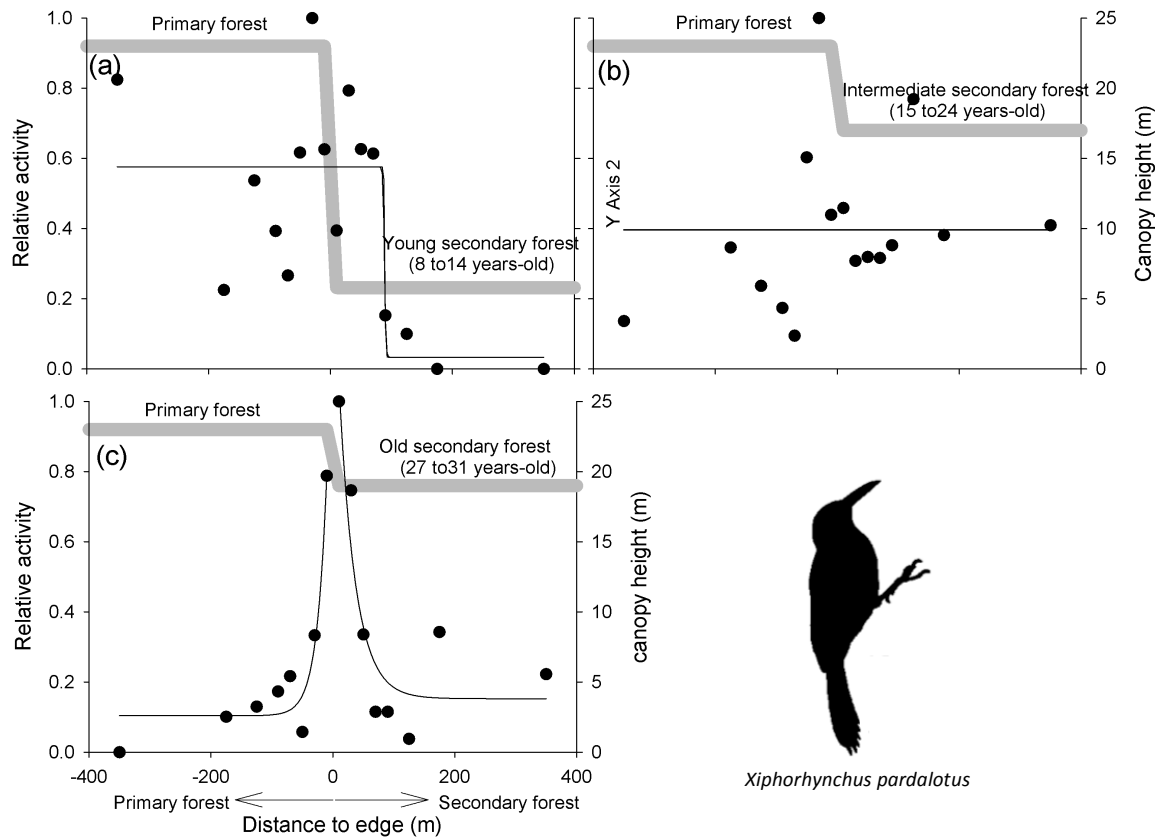


Figure 4.2. Response of radio-tagged *Xiphorhynchus pardalotus* to edges between primary forest and a) young (6–14 years old), b) intermediate (15–24 years old) and c) old (27–30 years old) secondary forest in the Brazilian Amazon. Gray line represents relative canopy height, with primary forest = 23m tall.

When I pooled bird ages, *F. colma* showed a strong unimodal edge response when primary forest abutted young secondary growth, with activity concentrated about 50 m inside the primary forest (Figure 4.3a). In intermediate secondary forest, *F. colma* showed a sigmoidal response, with most activity clustered > 100 m inside the primary forest (Figure 4.3b). With age classes pooled, the species showed no edge response between primary and old secondary forest—both habitats were equally suitable (Figure 4.3c).

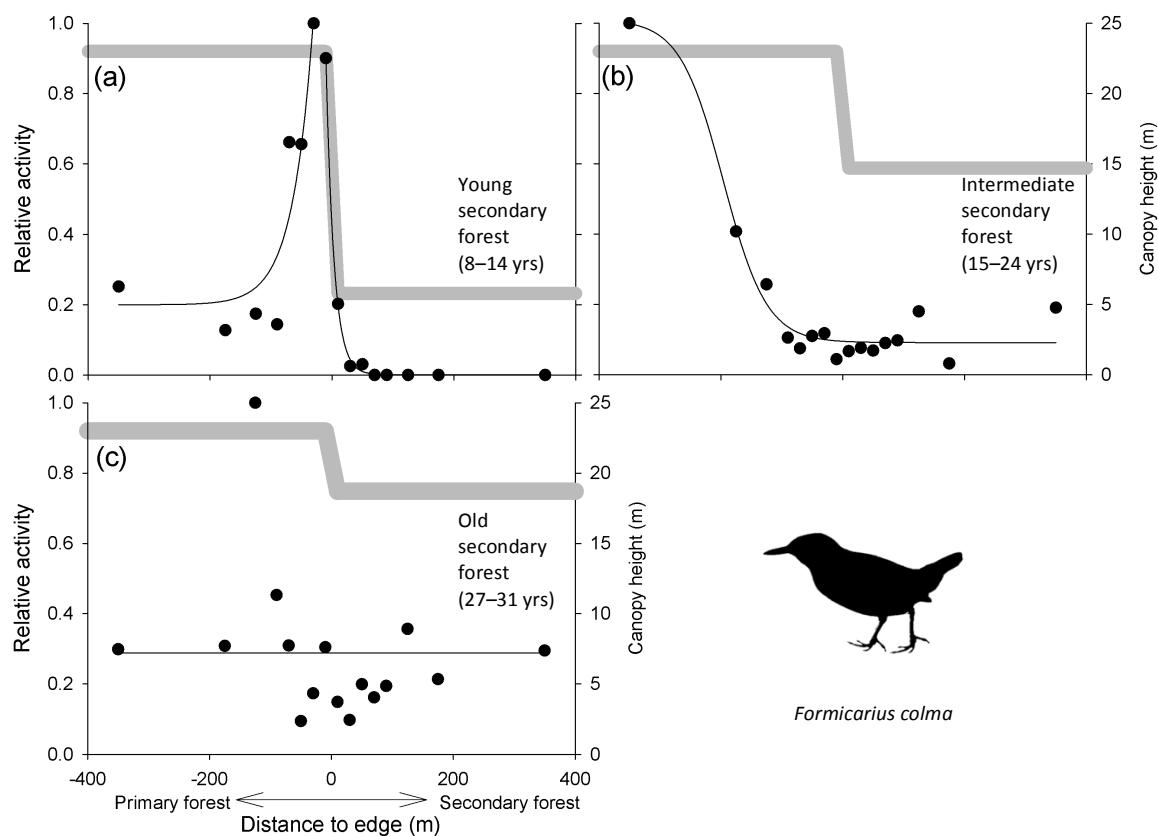


Figure 4.3. Response of radio-tagged *Formicarius colma* to edges between primary forest and a) young (6–14 years old), b) intermediate (15–24 years old) and c) old (27–30 years old) secondary forest in the Brazilian Amazon. Gray line represents relative canopy height, with primary forest = 23m.

Separating *F. colma* by age revealed considerably different edge responses than the pooled dataset. In young secondary forest, young birds showed a unimodal response, clustering

their activity about 50 m inside primary forest, whereas adult birds showed a linear trend with activity increasing with distance inside primary forest (Figure 4.4a). In intermediate secondary forest, both young and adult birds showed a sigmoidal response with higher activity levels within primary forest; adults avoided intermediate secondary forest completely whereas young birds penetrated into intermediate secondary forest more frequently (Figure 4.4b). When primary forest formed an edge with old secondary forest, adult *F. colma* showed no edge response—both habitats were equally suitable; however, young birds showed a linear response, with activity increasing with distance inside primary forest (Figure 4.4c).

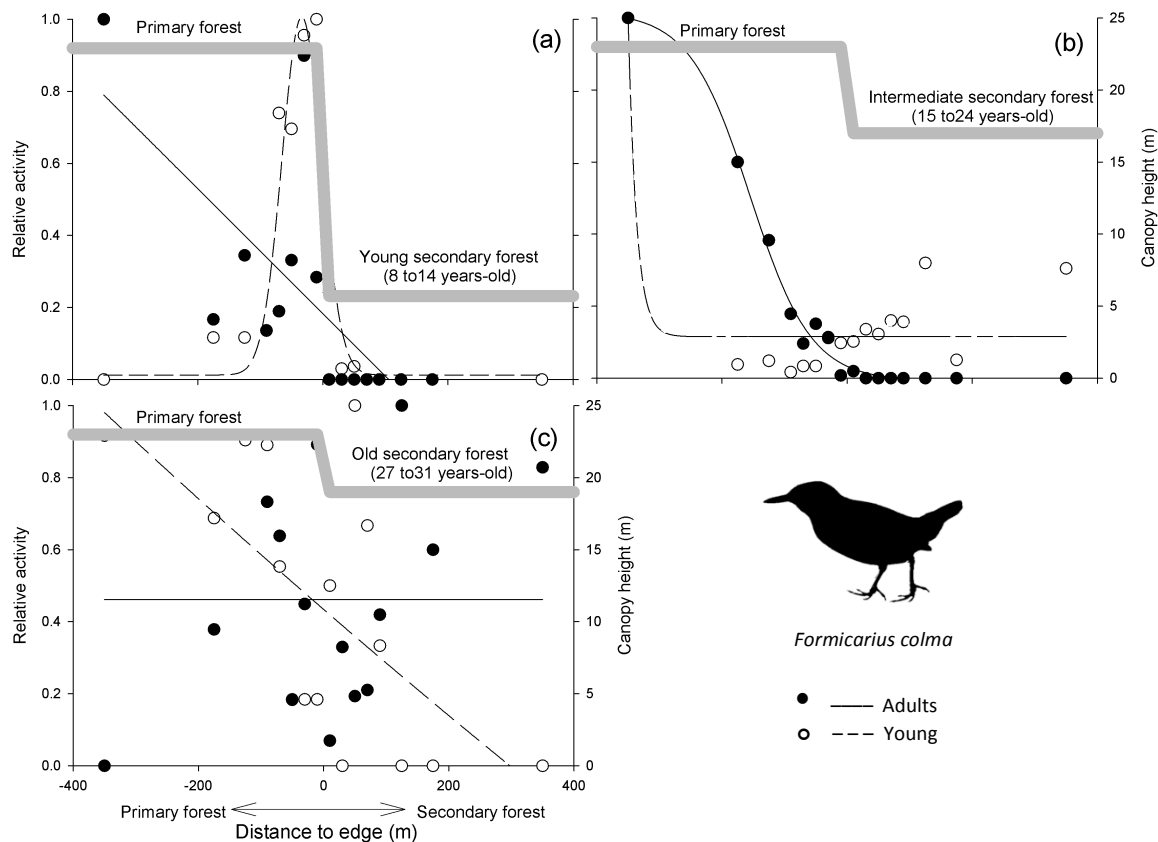


Figure 4.4. Response of radio-tagged juvenile and adult *Formicarius colma* to edges between primary forest and a) young (6–14 years old), b) intermediate (15–24 years old) and c) old (27–30 years old) secondary forest in the Brazilian Amazon. Filled circles and solid lines represent adults; open circles and dashed lines represent juveniles.

When I plotted the relative suitability of secondary forest along with age of secondary forest, I predictably found that for all target species, suitability increased with age of secondary growth (Figure 4.5). Competing models showed little variation in estimates of recovery to suitability of primary forest. As predicted, *G. spirurus* was the first species to show equal suitability of primary and secondary forest (after 11–14 years), whereas *X. pardalotus* took second longest (15–20 years), and *F. colma* the longest (28–30 years; Figure 4.5).

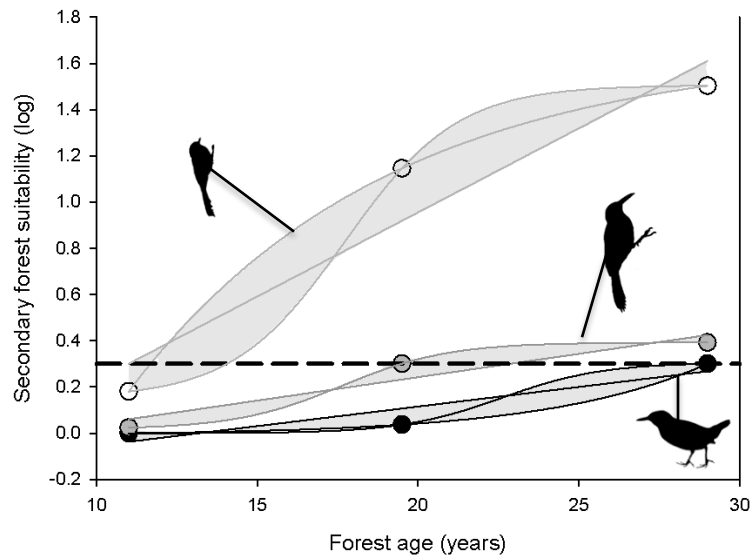


Figure 4.5. Relationship between the relative suitability of primary and secondary forest (secondary forest suitability / primary forest suitability) for three species of understory insectivores at the Biological Dynamics of Fragments Project near Manaus, Brazil. Open circles represent *Glyphorhynchus spirurus*, filled grey circles is *Xiphorhynchus pardalotus* and black circles represent *Formicarius colma*; lines connecting circles represent linear, exponential and sigmoidal regressions for each species. For each species, the point of intersection between regression lines and the dashed line (representing primary forest) is the age when the suitability of primary and secondary forest is equivalent. For *X. pardalotus*, only two regression lines are visible because linear and exponential functions overlap.

DISCUSSION

All three understory rainforest species showed a strong *positive* edge response to at least one age class of secondary growth. For forest birds, edge effects are generally thought to be negative (*sensu* Gates and Gysel 1978, but see Zurita et al. 2012), and the BDFFP is no exception (Laurance et al. 2002), so the strong positive effect was somewhat surprising. *Glyphorhynchus spirurus* and *F. colma* concentrated their activity just inside primary forest—about 50 m inside the edge with young secondary forest. Young secondary forest is noticeably different from primary forest, with a canopy only about 6 m tall (compared to 23 m) and a relatively sparse, dry understory. *Xiphorhynchus pardalotus* did not show a unimodal positive response to young secondary forest, but rather, activity was equally high in primary forest and along the edge, and then dropped off sharply at about 100 m into the secondary growth. I suspect differences between these two woodcreepers can be explained by their foraging strategies and willingness to leave mixed-species flocks. *Xiphorhynchus pardalotus* typically forages with mixed-species flocks (Cohn-Haft et al. 1997; Thiollay and Jullien 1998), so although there may be few foraging opportunities for the species in young secondary forest, it may venture out past the edge along with mixed-species flocks. Mixed species flocks show some evidence for elevated activity along edges at the BDFFP (K. Mokross unpublished data), so *X. pardalotus* may simply join other flock members along edges to reap the benefits of increased vigilance in searching for predators such as *Micrastur* forest falcons; Thiollay and Jullien 1998).

Young *F. colma* showed a peak of activity about 50 m inside young secondary forest edges, whereas adults simply show a linear trend with activity increasing with increasing distance inside primary forest. This suggests that the positive edge response for pooled adult and young *F. colma* (Figure 4.4a) was driven by young birds rather than by adults. Adult *F. colma*

occupy year-round territories that they defend against conspecifics (Stouffer 1997, 2007), so adult territory holders likely push young birds into marginal habitats (i.e. edges alongside young secondary forest), as Johnson et al. (2011) found in small fragments at the BDFFP. Young secondary forest appears to offer few resources for terrestrial insectivores such as *F. colma*, as the understory is relatively devoid of vegetation, dry, bright, and has a vegetation structure generally unsuitable for terrestrial insectivores (Stratford and Stouffer 2013). When primary forest abuts pasture, desiccation, high tree mortality and other edge-associated effects may extend up to 300 m into primary forest at the BDFFP (Laurance et al. 2002), so it seems likely that when primary forest abuts young secondary forest, these edge effects would extend at least 50 m into primary forest (the center of activity of young *F. colma* (Lovejoy et al. 1986; Burke and Nol 1998). Because it is difficult/impossible to determine the age of woodcreepers, it was not possible to determine whether the effect of woodcreepers concentrating activity near edges was driven by young birds pushed towards the edges by dominant adults, as it likely was with *F. colma*. I believe that this phenomenon is less likely to be occurring in woodcreepers than with *F. colma*, as it seems unlikely that the woodcreepers themselves can distinguish between formative- and definitive-plumaged individuals, making it less likely that they would show aggression towards obviously juvenile-plumaged subordinate.

All three target species showed a fundamentally different pattern of activity along the edges of intermediate secondary forest compared to young secondary forest. *Glyphorhynchus spirurus* showed a sharp sigmoidal response along intermediate secondary forest edges, with considerably higher activity levels in the secondary forest. This suggests that *G. spirurus* prefers secondary growth at the intermediate stage to primary forest. One possible explanation is that the absence of most other woodcreeper species from secondary forest (Cohn-Haft et al. 1997, L.L.

Powell pers. obs.), which may allow *G. spirurus* to exploit foraging niches that are not available in relatively species-rich primary forest (i.e. release from competition; Chapter 3).

Xiphorhynchus pardalotus showed no edge response to intermediate secondary forest, suggesting that “recovery” of secondary forest occurs for the species by 15–24 years after abandonment. *Formicarius colma* showed a more gradual negative response to intermediate secondary forest; activity levels were highest at 200 m into primary forest, suggesting that those negative edge effects extend a considerable distance in to the primary forest. Young birds were more likely to venture out into secondary growth than adults. The most likely mechanism to explain this pattern is that rather than restricting *F. colma* to within forest fragments as appears to occur with pasture and young secondary forest edges, the vegetation structure and resources in intermediate secondary forest may allow young birds to wander away from edges of primary forest. Stratford and Stouffer (2012) found that at the BDFFP, terrestrial insectivores were associated with thinner leaf litter (perhaps in part because dead *Cecropia* leaves are too large for small birds to flip) and more large trees, and fewer small trees than expected; those conditions are not likely to arise until secondary forest reaches intermediate age.

Responses of all target species to old secondary forest edges were fundamentally different from responses to younger secondary forest. *Glyphorhynchus spirurus* showed even greater elevation of activity in old secondary forests than in intermediate secondary forests, suggesting that old secondary forests are optimal for this species relative to the other three habitats I studied; however, I include the caveat that I had few observations of *G. spirurus* in old secondary forest, so my estimates of relative activity are imprecise. *Xiphorhynchus pardalotus* showed a strong unimodal positive edge response when the oldest secondary forest abutted primary forest, perhaps due to the species’ participation in mixed-species flocks, which often

show increased activity levels along edges (Karl Mokross, pers. comm.). *Formicarius colma* also showed no response to edges along the oldest secondary growth when I pooled age classes; however, whereas adults showed no edge response, young birds showed a linear trend in which the highest activity levels were in primary forest and tapered to zero after about 300 m into old secondary forest. This suggests that even 30 years after abandonment of deforested areas, resources are still suboptimal for young *F. colma* far from primary forest. If young *F. colma* rarely venture past 300 m past edges, then forest fragments isolated by more than 300 m may be subjected to deleterious effects of isolation, even when the matrix is 27–31 year-old secondary forest (e.g. Stouffer et al. 2011).

My three study species had substantially different patterns of use along edges as secondary growth matured, despite the fact that all are considered understory rainforest species. As I predicted, *G. spirurus* was the first to recover activity levels in secondary forest, followed by *X. pardalotus* and finally *F. colma*. *Glyphorhynchus spirurus* showed a quick recovery to primary forest activity levels along edges at about 11–14 years after abandonment, then showed elevated activity in intermediate and old secondary forest. *Xiphorhynchus pardalotus* showed low activity levels in young secondary forest edges, then equal activity levels along intermediate-age edges, suggesting recovery at about 15–20 years after abandonment. In Powell et al.’s (2013) analysis of capture rates of the guild “mixed-species flock dropouts” (*G. spirurus*, *X. pardalotus* and *Myrmotherula axillaris*) along edges of primary forest and secondary growth from 1991–2011 at the BDFFP, recovery to capture rates in primary forest took 10–21 years after abandonment, matching well with the species-level telemetry estimates of recovery time presented here. *Formicarius colma* activity was concentrated just inside primary forest when young secondary forest abutted it, then concentrated well within primary forest adjacent to

intermediate secondary forest. Adult *F. colma* showed no response to old secondary forest edges, whereas young had a linear negative response to even the oldest secondary forest. For *F. colma* I estimated a return to no edge response about 28–30 years after abandonment, considerably less than previous estimates of recovery time (45–88 years; Powell et al. 2013) for capture rates of terrestrial insectivores at the BDFFP (12 species including *F. colma*). Though *F. colma* was the last to recover in my analysis, the species actually may be among the less sensitive terrestrial insectivores at the BDFFP; six species in Powell et al. (2013) were never captured along the edge with secondary forest of any age.

In the only other study using the same statistical approach I used here, Zurita et al. (2012) analyzed the edge responses of three Atlantic Rainforest birds in Brazil: *Pyriglena leucoptera* (Thamnophilidae; arboreal understory insectivore), *Chiroxiphia caudata* (Pipridae; arboreal frugivore), and *Sclerurus scansor* (Furnariidae; terrestrial insectivore). *Pyriglena leucoptera* showed no edge response between primary forest and young secondary forest, *C. caudata* showed a linear effect, with elevated activity in primary forest. *Sclerurus scansor*, a congener of three species included by Powell et al. in their terrestrial insectivore guild, showed a unimodal response to edges between old (~80) and young (~20–50) secondary forest that was nearly identical to that of *F. colma* in this study, with the peak of activity concentrated about 30-m inside the edge of primary forest (forest ages from M. Hansbauer, pers. comm.). Further research can determine if other terrestrial insectivores show a similar pattern of concentrated activity just inside the edge of primary forest.

This study adds to a growing number of studies concluding that terrestrial insectivores of tropical rainforests are among the first guilds to disappear when forests are fragmented, and among the last to recover after secondary growth is abandoned (Stratford and Stouffer 1999,

2012; Canaday and Rivadeneyra 2001; Peh et al. 2005; Stouffer et al. 2011; Powell et al. 2013, Mohamed Zakaria Hussin, unpublished data from peninsular Malaysia). A similar pattern was found in the forests of Ontario, Canada as well, where terrestrial leaf-flipping Ovenbirds (Parulidae; *Seiurus aurocapilla*) selected nest sites more than 250 m from forest edges, and large forest fragments contained 10 to 36 times more invertebrate biomass in the leaf litter than smaller fragments dominated by edge effects (Burke and Nol 1998). Further, leaf litter depth and invertebrate biomass were greater in Ovenbird territories (which were far from edges) than random locations. The authors suggest that the negative edge response by Ovenbirds was driven by declines in arthropods in leaf litter, which are particularly susceptible to desiccation (Southwood 1966), which occurs along edges of primary forest fragments (Lovejoy et al. 1986). Although Didham et al. (1998) found considerable changes in the beetle community at the BDFFP, including the loss of 14% of the most abundant beetle from the even centers of 100-ha forest fragments, the edge effect on other invertebrates consumed by terrestrial insectivores is poorly understood.

Regardless of the mechanism, in showing that *G. spirurus* and *F. colma* congregate along the primary forest side of young secondary growth edges, this study provides a fundamentally different description of the predicted edge response described in the conceptual model of edge effects by Ries and Sisk (2004). Ries and Sisk's (2004) predict that when resources are supplementary (i.e. not divided), and one habitat is of higher quality than the other (i.e. primary forest vs. young secondary forest), the edge response will be gradual and transitional, with higher activity levels in the higher quality habitat. For both *F. colma* and *G. spirurus* however, I found a unimodal response to young secondary forest edges, with activity concentrated just inside primary forest. For *F. colma*, this effect can probably be attributed to subordinate young

individuals congregating inside forest fragments along edges. Ries and Sisk's (2004) model likely holds for more mobile animals, such as migratory Ovenbirds, which are able to disperse over edges, across poor habitat and into more suitable habitats. Less mobile organisms such as terrestrial insectivores of tropical rainforests, with relatively poor flying ability (Moore et al. 2008; Claramunt et al. 2012), may actually be imprisoned within forest fragments for years after they are isolated. Further development of Ries and Sisk's (2004) model of edge effects should incorporate mobility of the study organism—particularly whether the species is able to cross the matrix of lower-quality habitat.

Given that once vast, homogeneous blocks of tropical rainforest are rapidly becoming perforated by new edges, it is essential that we understand the dynamics of how sensitive species respond to those variable landscapes. Particularly sensitive species and guilds (e.g. terrestrial insectivores) are especially useful as indicators of habitat and landscape quality as landscape change takes place. For rainforest birds, crossing the primary forest edge is the first step towards maintaining connectivity and gene flow across the landscape (Stevens and Coulon 2012), so larger models of functional connectivity can be parameterized by smaller models of species response to edges, such as this one (e.g. Castellón and Sieving 2007). By building models predicting the functional connectivity of sensitive species/guilds in heterogeneous landscapes, we will be in a stronger position to manage for biodiversity conservation in changing landscapes.

LITERATURE CITED

- Banks-Leite, C., R. M. Ewers, and J.-P. Metzger. 2010. Edge effects as the principal cause of area effects on birds in fragmented secondary forest. *Oikos* 119:918–926.
- Bates, J. M., J. Haffer, and E. Grismer. 2004. Avian mitochondrial DNA sequence divergence across a headwater stream of the Rio Tapajos, a major Amazonian river. *Journal of Ornithology* 145:199–205.

- Bierregaard Jr., R. O., C. Gascon, T. E. Lovejoy, and R. Mesquita. 2001. *Lessons from Amazonia: the Ecology and Conservation of a Fragmented Forest*. Yale Univ Press, Ann Arbor, MI.
- Bierregaard Jr., R. O., and C. Gascon. 2001. The Biological Dynamics of Forest Fragments Project: Overview and history of a long-term conservation project. Pages 5–12 in R. O. Bierregaard Jr., C. Gascon, T. E. Lovejoy, and R. Mesquita, editors. *Lessons from Amazonia: The Ecology and Conservation of a Fragmented Forest*. Yale University Press, Ann Arbor, MI.
- Brandão Jr, A. O., and C. M. Souza Jr. 2006. Mapping unofficial roads with Landsat images: a new tool to improve the monitoring of the Brazilian Amazon rainforest. *International Journal of Remote Sensing* 27:177–189.
- Brawn, J. D., and S. K. Robinson. 1996. Source-sink population dynamics may complicate the interpretation of long-term census data. *Ecology* 77:3–12.
- Brazilian National Space Research Institute (INPE). 2010. Projecto prodes: Monitoramento da floresta Amazonica Brasileira por satellite. Brasília: Ministerio da Ciencia e Tecnologia. Online at <http://www.obt.inpe.br/prodes/index.html>.
- Briant, G., V. Gond, and S. G. W. Laurance. 2010. Habitat fragmentation and the desiccation of forest canopies: A case study from eastern Amazonia. *Biological Conservation* 143:2763–2769.
- Burke, D. M., and E. Nol. 1998. Influence of food abundance, nest-site habitat, and forest fragmentation on breeding Ovenbirds. *The Auk* 115:96–104.
- Canaday, C., and J. Rivadeneyra. 2001. Initial effects of a petroleum operation on Amazonian birds: Terrestrial insectivores retreat. *Biodiversity and Conservation* 10:567–595.
- Castellón, T. D., and K. E. Sieving. 2007. Patch network criteria for dispersal-limited endemic birds of South American temperate rain forest. *Ecological Applications* 17:2152–2163.
- Claramunt, S., E. P. Derryberry, J. V Remsen, and R. T. Brumfield. 2012. High dispersal ability inhibits speciation in a continental radiation of passerine birds. *Proceedings of the Royal Society B-Biological Sciences* 279:1567–74.
- Cochrane, M. A., and W. F. Laurance. 2002. Fire as a large-scale edge effect in Amazonian forests. *Journal of Tropical Ecology* 18:311–325.
- Cohn-Haft, M., A. Whittaker, and P. C. Stouffer. 1997. A new look at the “species-poor” central Amazon: the avifauna north of Manaus, Brazil. *Ornithological Monographs* 48:205–235.
- Develey, P. F., and P. C. Stouffer. 2001. Effects of roads on movements by understory birds in mixed-species flocks in central Amazonian Brazil. *Conservation Biology* 15:1416–1422.

- Didham, R. K., P. M. Hammond, J. H. Lawton, P. Eggleton, and N. E. Stork. 1998. Beetle species responses to tropical forest fragmentation. *Ecological Monographs* 68:295–323.
- Ewers, R. M., and R. K. Didham. 2006. Continuous response functions for quantifying the strength of edge effects. *Journal of Applied Ecology* 43:527–536.
- Gascon, C., R. O. Bierregaard Jr., T. E. Lovejoy, and R. Mesquita. 2001. *Lessons from Amazonia: the Ecology and Conservation of a Fragmented Forest*. Yale University Press.
- Gates, J. E., and L. W. Gysel. 1978. Avian nest dispersion and fledging success in field-forest ecotones. *Ecology* 59:871–883.
- Gradwohl, J., and R. Greenberg. 1980. The formation of antwren flocks on Barro Colorado Island, Panama. *The Auk*:385–395.
- Howell, S. N. G., C. Corben, P. Pyle, and D. I. Rogers. 2003. The first basic problem: a review of molt and plumage homologies. *The Condor* 105:635–653.
- Johnson, E. I. 2010. Banding guide to the birds of The Biological Dynamics of Forest Fragments Project. School of Renewable Resources, Louisiana State University, Baton Rouge, LA.
- Johnson, E. I. 2011. Fragmentation Sensitivity and its Consequences on Demography and Host-Ectoparasite Dynamics in Amazonian Birds. Louisiana State University, Baton Rouge, LA.
- Johnson, E. I., P. C. Stouffer, and C. F. Vargas. 2011a. Diversity, biomass, and trophic structure of a central amazonian rainforest bird community. *Revista Brasileira De Ornitologia* 19:1–16.
- Johnson, E. I., J. D. Wolfe, T. Brandt Ryder, and P. Pyle. 2011b. Modifications to a molt-based ageing system proposed by Wolfe et al.(2010). *Journal of Field Ornithology* 82:422–424.
- Kapos, V. 1989. Effects of isolation on the water status of forest patches in the Brazilian Amazon. *Journal of Tropical Ecology* 5:173–185.
- Krabbe, N., and T. S. Schulenberg. 2003. Family Formicariidae (ground-antbirds). Pages 682–731 *Handbook of the Birds of the World Volume 8. Broadbills to Tapaculos*. Lynx Edicions Barcelona, Spain.
- Lair, H. 1987. Estimating the location of the focal center in red squirrel home ranges. *Ecology* 68:1091–1101.
- Laurance, S. G. W. 2004. Responses of understory rain forest birds to road edges in central Amazonia. *Ecological Applications* 14:1344–1357.

- Laurance, S. G. W., P. C. Stouffer, and W. F. Laurance. 2004. Effects of road clearings on movement patterns of understory rainforest birds in central Amazonia. *Conservation Biology* 18:1099–1109.
- Laurance, W. F. 2000. Do edge effects occur over large spatial scales? *Trends in ecology and evolution* 15:134–135.
- Laurance, W. F., J. L. C. Camargo, R. C. C. Luizão, S. G. Laurance, S. L. Pimm, E. M. Bruna, P. C. Stouffer, G. Bruce Williamson, J. Benítez-Malvido, and H. L. Vasconcelos. 2011. The fate of Amazonian forest fragments: A 32-year investigation. *Biological Conservation* 144:56–67.
- Laurance, W. F., T. E. Lovejoy, H. L. Vasconcelos, E. M. Bruna, R. K. Didham, P. C. Stouffer, C. Gascon, R. O. Bierregaard Jr., S. G. Laurance, and E. Sampaio. 2002. Ecosystem decay of Amazonian forest fragments: A 22-year investigation. *Conservation Biology* 16:605–618.
- Levey, D. J. 1988. Tropical Wet Forest Treefall Gaps and Distributions of Understory Birds and Plants. *Ecology* 69:1076–1089.
- Lindell, C. a., S. K. Riffell, S. a. Kaiser, A. L. Battin, M. L. Smith, and T. D. Sisk. 2007. Edge Responses of Tropical and Temperate Birds. *The Wilson Journal of Ornithology* 119:205–220.
- Lovejoy, T. E., R. O. Bierregaard Jr, A. B. Rylands, C. E. Quintela, L. H. Harper, K. S. Brown Jr, A. H. Powell, and G. V. N. Powell. 1986. Edge and other effects of isolation on Amazon forest fragments. Pages 257–285 in M. E. Soule, editor. *Conservation Biology: the Science of Scarcity and Diversity*. Sinauer Associates, Inc., Sunderland, MA.
- Marantz, C. A., A. Aleixo, L. Bevier, R., and M. A. Patten. 2003. Family Dendrocolaptidae (Woodcreepers). Pages 358–447 in J. A. del Hoyo, A. Elliott, and D. A. Christie, editors. *Handbook of the Birds of the World. Volume 8. Broadbills to Tapaculos*. Lynx Edicions. Barcelona, Spain.
- Marra, P. P., and J. V Remsen Jr. 1997. Insights into the maintenance of high species diversity in the Neotropics: habitat selection and foraging behavior in understory birds of tropical and temperate forests. *Ornithological Monographs* 48:445–483.
- Moore, R. P., W. D. Robinson, I. J. Lovette, and T. R. Robinson. 2008. Experimental evidence for extreme dispersal limitation in tropical forest birds. *Ecology Letters* 11:960–968.
- Neeff, T., R. M. Lucas, J. R. Santos, E. S. Brondizio, and C. C. Freitas. 2006. Area and age of secondary forests in Brazilian Amazonia 1978–2002: an empirical estimate. *Ecosystems* 9:609–623.

- Newbold, T., J. P. W. Scharlemann, S. H. M. Butchart, Ç. H. Sekercioglu, R. Alkemade, H. Booth, and D. W. Purves. 2013. Ecological traits affect the response of tropical forest bird species to land-use intensity. *Proceedings of the Royal Society B-Biological Sciences* 280:1–8.
- Otis, D. L., and G. C. White. 1999. Autocorrelation of location estimates and the analysis of radiotracking data. *Journal of Wildlife Management* 63:1039–1044.
- Peh, K. S. H., J. Jong, N. S. Sodhi, S. L. H. Lim, and C. A. M. Yap. 2005. Lowland rainforest avifauna and human disturbance: persistence of primary forest birds in selectively logged forests and mixed-rural habitats of southern Peninsular Malaysia. *Biological Conservation* 123:489–505.
- Peyras, M., N. I. Vespa, M. I. Bellocq, and G. A. Zurita. 2013. Quantifying edge effects: the role of habitat contrast and species specialization. *Journal of Insect Conservation* 17:807–820.
- Porensky, L. M. 2011. When edges meet: interacting edge effects in an African savanna. *Journal of Ecology* 99:923–934. Wiley Online Library.
- Powell, L. L., P. C. Stouffer, and E. I. Johnson. 2013. Recovery of understory avian movement across the interface of primary and secondary Amazon rainforest. *The Auk* 130(3):459–468.
- Rappole, J. H., and A. R. Tipton. 1991. New harness design for attachment of radio transmitters to small passerines. *Journal of Field Ornithology* 62:335–337.
- Ries, L., R. J. Fletcher Jr, J. Battin, and T. D. Sisk. 2004. Ecological responses to habitat edges: mechanisms, models, and variability explained. *Annual Review of Ecology, Evolution, and Systematics* 35:491–522.
- Ries, L., and T. D. Sisk. 2004. A predictive model of edge effects. *Ecology* 85:2917–2926.
- Ries, L., and T. D. Sisk. 2010. What is an edge species? The implications of sensitivity to habitat edges. *Oikos* 119:1636–1642.
- Rodewald, P. G., and M. C. Brittingham. 2004. Stopover habitats of landbirds during fall: use of edge-dominated and early-successional forests. *The Auk* 121:1040.
- Rosa, I. M. D., C. Souza, and R. M. Ewers. 2012. Changes in size of deforested patches in the Brazilian Amazon. *Conservation Biology* 26:932–937.
- Rosenberg, K. V. 1990. Dead-leaf foraging specialization in tropical forest birds: measuring resource availability and use. *Studies in Avian Biology* 13:360–368.
- Skutch, A. F. 1969. Life histories of Central American birds. III. Families Cotingidae, Pipridae, Formiariidae, Furnariidae, Dendrocolaptidae, and Picidae. *Pacific Coast Avifauna* 35.

- Southwood, T. R. E. 1966. Ecological Methods. Methuen and Co. Ltd., London.
- Stevens, V. M., and A. Coulon. 2012. Landscape effects on spatial dynamics: the natterjack toad as a case study. *Dispersal Ecology and Evolution*:280. Oxford University Press.
- Stiles, F. G. 1975. Ecology, flowering phenology, and hummingbird pollination of some Costa Rican *Heliconia* species. *Ecology* 56:285–301.
- Stouffer, P. C. 1997. Interspecific aggression in *Formicarius* antthrushes? The view from central Amazonian Brazil. *Auk* 114:780–785.
- Stouffer, P. C. 2007. Density, territory size, and long-term spatial dynamics of a guild of terrestrial insectivorous birds near Manaus, Brazil. *Auk* 124:291–306.
- Stouffer, P. C., R. O. Bierregaard Jr., C. Strong, and T. E. Lovejoy. 2006. Long-term landscape change and bird abundance in Amazonian rainforest fragments. *Conservation Biology* 20:1212–1223.
- Stouffer, P. C., and R. O. Bierregaard Jr. 1993. Spatial and temporal abundance patterns of Ruddy Quail-doves (*Geotrygon montana*) near Manaus, Brazil. *Condor* 95:896–903.
- Stouffer, P. C., E. I. Johnson, R. O. Bierregaard Jr., and T. E. Lovejoy. 2011. Understory bird communities in Amazonian rainforest fragments: species turnover through 25 years post-isolation in recovering landscapes. *PloS one* 6:e20543.
- Stouffer, P. C., E. I. Johnson, and R. O. Bierregaard. 2013. Breeding seasonality in Central Amazonian rainforest birds. *The Auk* 130(3):529–540.
- Stratford, J. A., and P. C. Stouffer. 1999. Local extinctions of terrestrial insectivorous birds in a fragmented landscape near Manaus, Brazil. *Conservation Biology* 13:1416–1423.
- Stratford, J. A., and P. C. Stouffer. 2001. Reduced feather growth rates of two common birds inhabiting central Amazonian forest fragments. *Conservation Biology* 15:721–728.
- Stratford, J. A., and P. C. Stouffer. 2013. Microhabitat associations of terrestrial insectivorous birds in Amazonian rainforest and second-growth forests. *Journal of Field Ornithology* 84:1–12.
- Thiollay, J., and M. Jullien. 1998. Flocking behaviour of foraging birds in a neotropical rain forest and the antipredator defence hypothesis. *Ibis* 140:382–394.
- Willis, E. O. 1977. Lista preliminar das aves da parte noroeste e áreas vizinhas da Reserva Ducke, Amazonas, Brasil. *Revista Brasileira de Biologia* 37:585–601.
- Wolfe, J. D., T. B. Ryder, and P. Pyle. 2010. Using molt cycles to categorize the age of tropical birds: an integrative new system. *Journal of Field Ornithology* 81:186–194.

Zurita, G., G. Pe'er, M. I. Bellocq, and M. M. Hansbauer. 2012. Edge effects and their influence on habitat suitability calculations: a continuous approach applied to birds of the Atlantic forest. *Journal of Applied Ecology* 49:503–512.

CHAPTER 5: STATE-SPACE MODELS REVEAL MOVEMENT OF THREE INSECTIVOROUS UNDERSTORY BIRD SPECIES BETWEEN PRIMARY AND SECONDARY FOREST IN A HETEROGENEOUS AMAZONIAN LANDSCAPE

INTRODUCTION

Quantifying the quality of habitat for wildlife is an exceedingly challenging task. Given current rates of anthropogenic habitat change, particularly in tropical rainforests, it is critical that we identify techniques that can estimate the quality of human modified habitats for disturbance-sensitive species. For example, each year $\sim 20,000 \text{ km}^2$ of new forest edges (i.e. boundaries between primary forest and other habitats) are created in the Amazon Rainforest (D. Skole, pers. comm.) and in the Brazilian Amazon, the area of secondary forest increased from 29,000 to 161,000 km^2 from 1978–2002 (Neeff et al. 2006), yet value of edge and secondary forest habitat to rainforest animals remains poorly quantified. Although widely used, current techniques to measure habitat quality are not without difficulties. For example, estimates of species abundance are often used to infer habitat quality, but abundance can be a misleading indicator of habitat quality because animals can congregate in lower quality habitat if dominant individuals push subordinates into suboptimal habitat (Fretwell 1972, Van Horne 1983).

Understory birds are considered excellent study organisms in tropical rainforests because they are diverse, relatively easy to capture, and vary enormously in sensitivity to disturbance (Stouffer and Bierregaard . 1995; Sekercioglu et al. 2002); however, habitat quality remains challenging to quantify. For example, nest success studies are difficult to undertake in the tropics as predation is high, nest success is low (Brawn et al. 2011), and breeding seasons are not necessarily confined to a short time window (Stouffer et al. 2013). Further, long-term survival estimates, which can provide perhaps the most direct indices of habitat quality, are challenging to measure in the tropics because precisely quantifying variation in survival across habitats can require an extraordinary amount of data collected at sampling intervals conducive to existing

survival models (Ruiz-Gutiérrez et al. 2012). Further, long-term bird banding projects were not necessarily designed to estimate survival. Theoretical studies predict that animals will distribute themselves with respect to resources and conspecifics such that fitness differences between habitats could be negligible (Fretwell 1972, Nichols and Kendall 1995); therefore, alternative measures of habitat quality are needed when fitness estimates are not informative nor feasible.

The ideal free distribution predicts that animals will distribute themselves in the highest quality habitat available, where quality is defined in terms of the fitness of individuals in that habitat (Fretwell and Lucas 1969). It follows that given a choice, individuals will move to and remain in high rather than low quality habitat. Thus the probability of moving between habitats should be a function of the quality of those habitats, with a relatively high probability of moving from low to high quality habitat; and conversely, a relatively high probability of remaining in high quality habitat (Fretwell and Lucas 1969; Fretwell 1972; Nichols and Kendall 1995). Multi-state capture-recapture models have been used for >2 decades by wildlife ecologists to estimate survival and transition probabilities for animals occupying habitats of varying quality—generally by capturing and marking many animals and resighting or recapturing them later (Hestbeck et al. 1991; Brownie et al. 1993). Transition probabilities are estimates of the probability that an animal will transition from one state (e.g. habitat) to another. Although it has been known for years that such models could be adapted to accommodate data from animals with transmitters (Nichols 1996), to date there have very been few studies exploiting the existing statistical framework for radio-tagged animals (but see Martin et al. 2006).

It is somewhat surprising that so few telemetry data have been analyzed using state-space models because researchers using that approach can make simplifying assumptions such that survival and detectability (i.e. “recapture” probability) need not be estimated. Detection

probability for animals with transmitters frequently approaches 1, so detectability can be fixed to 1, thus simplifying models considerably (Nichols 1996). Further, in the likely case that individual survival equals 1 during the short temporal window constrained by transmitter life, survival probability can also be fixed at 1, further simplifying the models, and thus restricting inference to estimation of transition probabilities, $\widehat{\psi}$, reflecting movement between habitat states, ultimately an index of habitat quality.

Here I simplify existing multi-state capture-recapture models to quantify the ability of radio-tagged Amazonian birds to move among habitats. Quantifying the point at which quality of secondary forest approaches that of secondary forest for animal movement (i.e. when transition probability in secondary forest is no different from that of primary forest) is a critical conservation issue because secondary forest and other human-altered habitats are being created at a furious pace, producing landscapes that are a heterogeneous mix of habitats, yet understanding of the quality of those habitats for wildlife is still poorly known and much debated (Brook et al. 2006; Wright and Muller-Landau 2006a, 2006b). Amazonia now contains vast areas of secondary forest, which is thought to be useful as a corridor between patches of primary forest (Lees and Peres 2008), but the age at which secondary forest has matured enough to serve as an effective corridor (i.e. as a conduit for animals transitioning between primary and secondary forest) remains unquantified for most rainforest taxa.

Here I use multi-state capture-recapture models to quantify movement of three radio-tagged understory bird species among habitats of differing quality. My primary objective is to use a gradient of secondary growth age classes to determine the age at which transition probabilities for birds moving to and from secondary forest is approximately equal to those for moving to and from primary forest (i.e. “recovery”). In other words, I sought to quantify the age

of recovery of secondary forest, which I defined as the lack of a difference in habitat quality as reflected by similar transition probabilities from primary to secondary forest and vice versa.

METHODS

Study Site

I conducted fieldwork from June to October 2009–2011 at the BDFFP (see Chapter 1 for more details on the study site). Although originally designed to evaluate the effects of area and isolation on wildlife (Bierregaard et al. 2001), abandonment of clearcut areas at the BDFFP beginning in the early 1980s has created the opportunity to study the dynamics of secondary forest recovery (e.g. Stouffer and Bierregaard 2007; Sberze et al. 2009; Powell et al. 2013). Due to the temporal pattern of clear-cutting, secondary forest available to radio-tagged birds (see below) was generally distributed into four age classes—the youngest secondary forest (hereafter “SF₁”) was 8–14 years old with an average canopy height of about 6 m. I defined SF₂ as 15–18 years old with a canopy of ~14-m, whereas SF₃ was 21–24 years old with a ~16-m canopy. The oldest secondary forest at the BDFFP (SF₄) was 27–31-years-old, with a ~19-m canopy, considerably shorter than primary forest at BDFFP, which averaged about 23m. SF₄, all near the fragments at “Cidade Powell”, was never burned; practically all other secondary forest classes were burned periodically since initial isolation (Bierregaard and Gascon 2001). Canopy heights listed here are from areas used by radio-tagged birds and were estimated from a LiDAR canopy height model from 2007 (Michael Lefsky and Scott Saleska, unpublished data).

Study Species

I selected the same three study species as in Chapters 3 and 4: *G. spirurus*, *X. pardalotus* and *F. colma*; see Chapter 3 Methods for natural histories of study species. Each was common

and catchable enough for us to obtain a reasonable sample size, and varied in their natural histories and abundance in secondary forest.

Captures

I captured focal species with both passive and targeted netting techniques. More detail on bird capture and aging can be found in Chapter 3. Here I analyzed data from 19 *G. spirurus*, 18 *X. pardalotus* and 19 *F. colma*. The 19 *F. colma* included 7 young, 11 adults, and 1 bird of unknown age; 13 were males, 3 were females, and 3 were not sexed. A map of the home ranges of the birds analyzed here can be found in Figure 3.1; here I excluded birds captured greater than 200 m from the interface of primary and secondary forest.

Radio-tracking

I tracked each individual as frequently as possible over a period lasting an average of 23.6 (+/- 3.0 SE) days beginning 24 hours after release with a transmitter. For the analysis in this chapter, I recorded 700 locations of *G. spirurus* (mean = 37 ± 2.4 SE per individual), 717 of *X. pardalotus* (40 ± 3.0 SE) and 814 of *F. colma* (43 ± 3.2 SE). For more detail on capture and radio tracking, refer to Chapter 3.

Data analysis

My analysis focused on modeling the transition probability, $\widehat{\psi}^{rr}$, associated with an individual remaining in a given habitat (i.e. making a transition from habitat r to habitat r). Restated, this is the probability that given a bird was found in a given physical state (i.e. habitat) at time t , it would be found in that same state at time $t + 1$. Its complement, $1 - \psi^{rr}$, reflects movement away from state r . I initially developed models with 5 states, primary forest and 4 age classes of secondary forest. However, resulting data were too sparse to support this model. Thus, I subsequently defined two states: primary forest (STATE = 1) and secondary forest (STATE =

2). If at any time individuals were located within the secondary forest state, I specified one of four secondary forest age classes (SF₁–SF₄ as defined above). I used multistate models in program MARK (White and Burnham 1999) with detectability fixed to 1.0 as suggested by Nichols (1996), and survival fixed to 1.0. Only one bird died during the study: a *G. spirurus* that was depredated by a raptor; I only included the data on that individual from the days prior to the depredation. Given the generally high survival and the fact that all birds were easily located (i.e. detected) using radiotelemetry, mortality did not confound detection or state, so my model simplifications seemed appropriate.

To gain insight on differences in $\widehat{\psi}^{rr}$ for birds using different age classes of secondary growth, I initially assigned individuals to one of four secondary forest age class groups, with groups based on the age class of secondary forest that was most available to the individual based on the configuration of the landscape. This “most available” habitat for each bird was also the secondary forest age to which most secondary forest movements of that bird pertained. To help reduce the potential influence of variation in habitat availability on variation in $\widehat{\psi}^{rr}$ I moved five birds to new groups such that for all forest age class groups the 95% confidence interval of the proportion of available primary forest on the landscape relative to the secondary forest age class corresponding to that group overlapped 0.50 (Figure 5.1). In other words, for each forest age class group, the availability of primary and secondary forest age class corresponding to that group was approximately equal; the exception was *F. colma* group 3 ($n = 3$), for which my estimate of $\widehat{\psi}^{rr}$ should be interpreted cautiously due to the greater availability of primary habitat and the poor precision of the estimate (see Discussion). I defined available habitat as that contained in a circle originating at the individual’s capture location with an area equal to the

average home range size for that species (see Chapter 3 for home range sizes). I then performed statistical analyses using these groups as categorical variables.

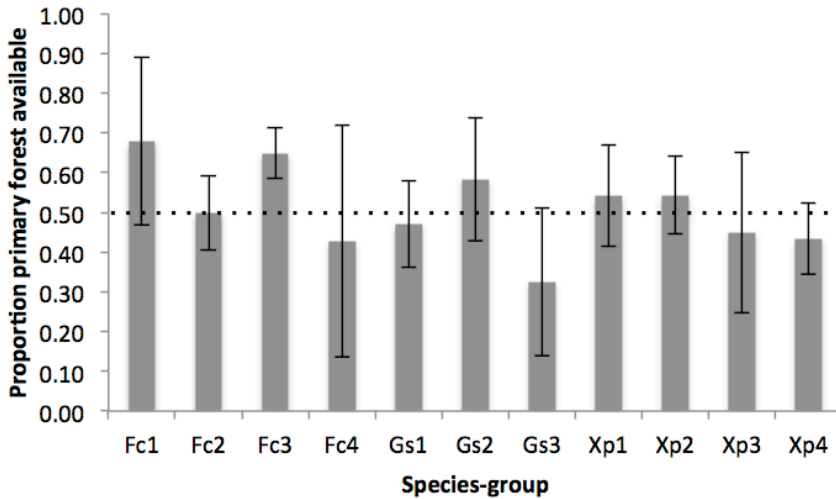


Figure 5.1. Proportion of primary forest available for each species and each group, relative to the proportion of secondary forest available in the secondary forest age class corresponding to that group. Abbreviations on the x-axis correspond to the first letter of the species and genus and the group number (e.g. “Fc1” = *Formicarius colma* in secondary forest age class group 1), and the dotted line shows $y = 0.5$.

To determine the environmental variables affecting, $\widehat{\psi}^{rr}$, I compiled *a priori* candidate models in a model selection framework (Burnham and Anderson 2002) separately for each species, including models with various combinations of five variables that I believed to be biologically meaningful relative to movement probabilities, as based on the literature and my field observations of the species (Tables 5.1–5.3). Candidate sets included 11 models for the two woodcreepers and 14 for *F. colma* (including null models); the latter set was larger because I was able to include the effect of bird age for that species. Support for models including the variable STATE would indicate that the probability that a bird remained in the secondary forest state differed from the probability that the bird remained in primary forest state (i.e., $\widehat{\psi}^{11} \neq \widehat{\psi}^{22}$, regardless of secondary forest age). I had *a priori* information that the three species move

differently in primary and secondary forest (e.g. Powell et al. 2013), so I included STATE in all models except the null. In other words, transition probabilities would not vary by SF if they did not also vary by STATE. Further, to determine how $\widehat{\psi}'''$ varied as secondary forest matured, I included models (labeled SF) in which $\widehat{\psi}'''$ differed for the four secondary forest age class groups (SF₁–SF₄). I was also interested in whether transition probabilities increased or decreased in ordinal fashion with age of secondary growth (Powell et al. 2013); thus, I included a variable in the candidate set (TREND) that treated secondary forest classes as ordinal categories. From my field observations, I knew that bird movement varies widely by time of day, thus I included a variable for time of day (TIMEofDAY) and a quadratic version of the variable (TIMEofDAY²) that allowed movement to vary with time in quadratic fashion; for example, most transitions may take place at the beginning and the end of the day for animals that are most active near dawn and dusk. Here TIMEofDAY referred to 48 15-min sampling occasions throughout the day (0600h–1800h) where a given bird could have ≤ 1 observation per occasion. Finally, as only *F. colma* was possible to age, I included a binary variable for bird age (“BIRD_AGE”: young or adult; see above) in the candidate set of models for this species. I caught only three females, and previous analyses of edge effects using some of the same dataset revealed no sex effects in *F. colma*, (Chapter 4); thus I elected to assume no differences in transition probability by sex.

To quantify the relative fit of competing models, I compared AIC_c values (Akaike’s Information Criterion for small sample sizes; Burnham and Anderson 2002) among models and computed AIC_c model weights, w_i . I based conclusions on parameter estimates that were model-averaged from the entire candidate set; figures also depict model-averaged parameter estimates.

There is no available goodness-of-fit test that is ideal for my models; thus to determine if models fit the data, I used an *ad-hoc* procedure. For the most complex model (greatest number of parameters) in each model set (species), I plotted residuals from the observed and expected numbers of capture histories. I then computed a Pearson chi-square test based on the observed and expected values for numbers of capture histories, pooling adjacent histories with expected value < 2 until the expected value of the sum was > 2 . I then re-ordered the histories randomly and computed another chi-square using the same pooling algorithm. The chi-square statistic was recomputed 4,000 times to evaluate lack of fit.

RESULTS

Results of my limited evaluation of model fit provided no indication of lack of fit for the most highly parameterized models for each species. Specifically, results of the iterated Pearson chi-square test gave no indication of lack-of-model-fit, regardless of the order of the capture-histories ($P > 0.99$ for 96% of ‘shuffles’, $\min(P) = 0.25$). Most residuals were near 0 and none was > 3 .

Model selection results for *G. spirurus* indicated state-specificity (STATE) and strong effects of BIRD_AGE, SF and TIMEofDAY on $\widehat{\psi}^{rr}$, as all three variables were included in the three top models ($\sum w_i = 0.93$; Table 5.1). There was reasonable evidence of a quadratic effect of time, as TIMEofDAY^2 was included in the best-fit model, and model-averaged parameter estimates showed a non-linear effect of TIMEofDAY on transition probabilities (Figure 5.2). The top model included variation associated with STATE as well as an interaction between SF and TIMEofDAY^2 . Thus, in primary growth, *G. spirurus* was most likely to remain in the same state at midday, whereas in secondary growth, the species was most likely to remain in the same state in the morning. For birds in the SF_1 group, $\widehat{\psi}^{11}$ was higher than $\widehat{\psi}^{22}$ throughout the day

(Figure 5.2a); whereas this pattern reversed for SF₂ birds: $\widehat{\psi}^{22}$ was higher than $\widehat{\psi}^{11}$ throughout the day (Figure 5.2b). The pattern reversed again for SF₃ birds, as $\widehat{\psi}^{11}$ was greater than $\widehat{\psi}^{22}$ for most of the day (Figure 5.3). *Glyphorynchus spirurus* models including TREND in $\widehat{\psi}^{rr}$ among SF classes received effectively no support, which was not surprising, as $\widehat{\psi}^{22}$ did not increase steadily with increasingly mature SF (Figure 5.3).

Table 5.1. Candidate model set describing transition probabilities of radio-tagged *Glyphorynchus spirurus* occupying primary and secondary forest at the Biological Dynamics of Forest Fragments Project.

Model ^a	Deviance	K^b	ΔAIC_c^c	w_i
SF * STATE * TIMEofDAY ²	348	10	0.0	0.57
SF * STATE * TIMEofDAY	354	8	1.4	0.28
SF * STATE + TIMEofDAY	358	7	3.9	0.08
STATE * SF	362	6	5.7	0.03
SF * STATE + TIMEofDAY ²	358	8	5.9	0.03
STATE * TREND + TIMEofDAY ²	401	8	48.4	0.00
STATE * TREND	412	4	51.1	0.00
STATE * TIMEofDAY ²	416	6	59.1	0.00
STATE + TIMEofDAY ²	424	4	62.8	0.00
STATE	431	2	66.4	0.00
NULL	455	1	87.9	0.00

^a SF: secondary forest age class; STATE: primary vs. secondary forest; TIMEofDAY: time of day; TREND: linear trend among secondary forest age classes.

^b K : no. of parameters; AIC_c : AIC adjusted for small sample size; ΔAIC_c : difference in AIC_c relative to the most parsimonious value; w_i : Akaike weight.

^c AIC_c value of the best-fit model = 369.

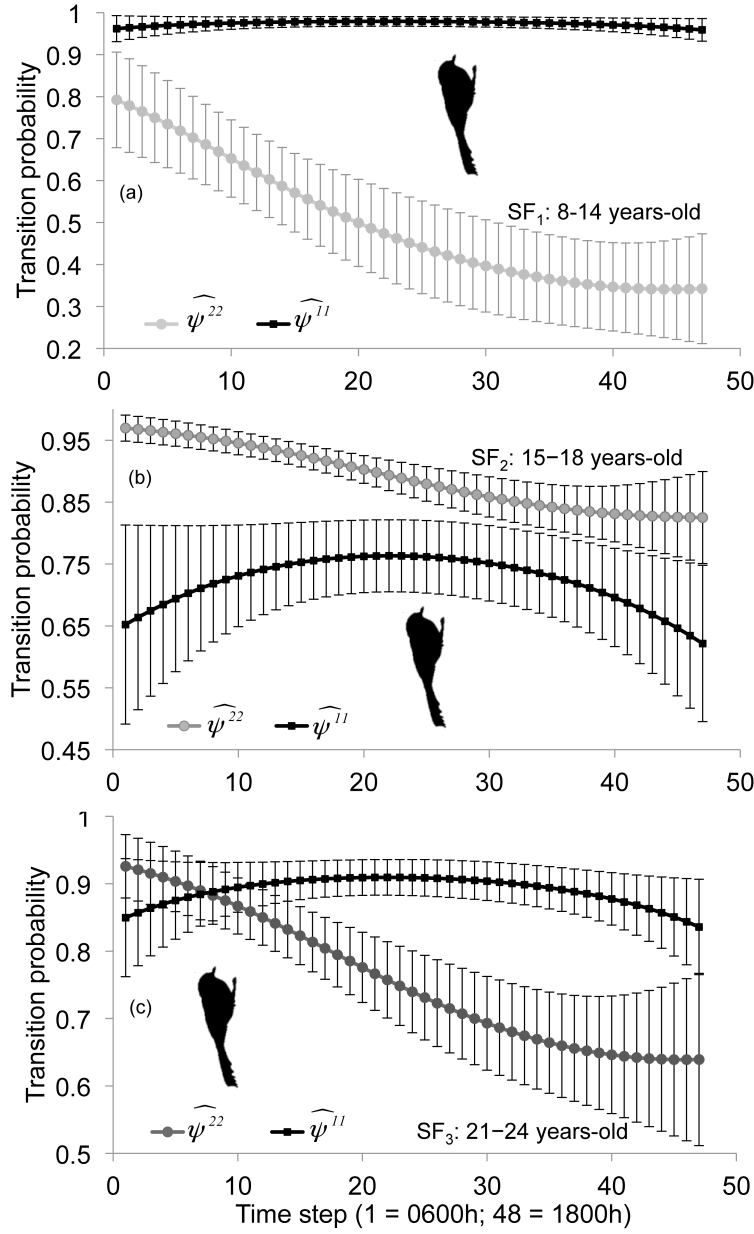


Figure 5.2. Model-averaged estimates of transition probabilities ($\widehat{\psi}^{rr} \pm \text{SE}$) over the course of the day for radio-tagged *Glyphorhynchus spirurus* occupying primary forest and secondary forest of three different age classes (SF₁:SF₃). $\widehat{\psi}^{11}$: probability that a bird occupying primary forest at a given time step will also occupy primary forest in the following time step; $\widehat{\psi}^{22}$: probability of remaining in secondary forest from one time step to the next.

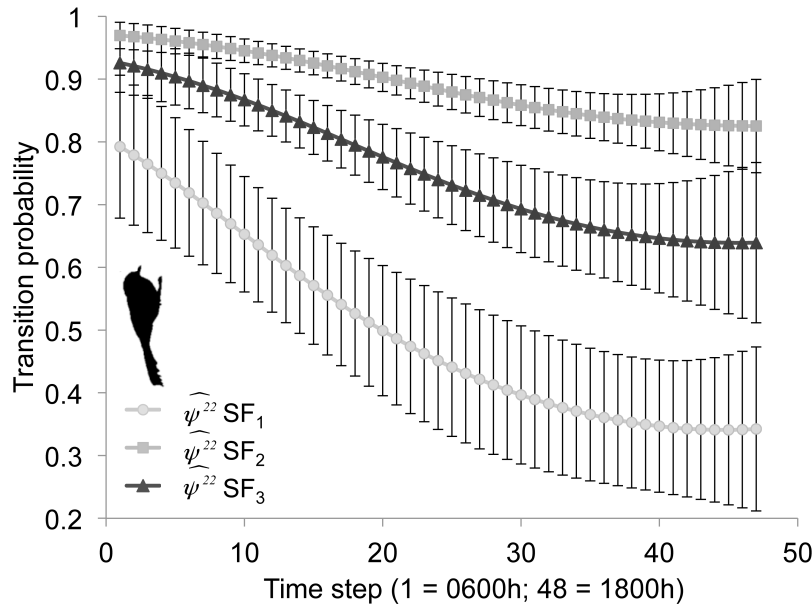


Figure 5.3. Model-averaged estimates of transition probability ($\widehat{\psi}^{rr} \pm \text{SE}$) over the course of the day for radio-tagged *Glyphorynchus spirurus* in secondary forest of three different age classes (SF₁–SF₃).

For *X. pardalotus*, habitat transition probability, $\widehat{\psi}^{rr}$, was state-specific (STATE) and affected by SF. Although three models including TIMEofDAY received some support, adding this variable reduced model fit (Table 5.2), and no model-averaged $\widehat{\psi}^{rr}$ estimate for this species varied more than 0.04 over the course of the day, indicating that TIMEofDAY had a negligible effect for this species. For *X. pardalotus* SF₁, $\widehat{\psi}^{11}$ was clearly greater than $\widehat{\psi}^{22}$ (Figure 5.4), but this effect was no longer evident for SF₂, as $\widehat{\psi}^{rr}$ was no different among states. Birds in SF₃ were surprisingly unlikely to remain there, as $\widehat{\psi}^{11}$ was more than twice as high as $\widehat{\psi}^{22}$. In SF₄, $\widehat{\psi}^{rr}$ estimates were essentially equal between states. TREND received little support for *X. pardalotus*.

Table 5.2. Candidate model set describing transition probabilities of radio-tagged *Xiphorhynchus pardalotus* occupying primary and secondary forest at the Biological Dynamics of Forest Fragments Project.

Model ^a	Deviance	<i>K</i>	ΔAIC_c ^b	w_i
STATE * SF	326	8	0.0	0.42
SF * STATE * TIMEofDAY	324	10	1.9	0.16
SF * STATE + TIMEofDAY ²	324	10	2.0	0.16
SF * STATE + TIMEofDAY	326	9	2.0	0.15
SF * STATE * TIMEofDAY ²	322	12	4.2	0.05
STATE	344	2	5.3	0.03
STATE + TIMEofDAY ²	341	4	6.6	0.02
STATE * TREND	343	4	8.8	0.01
STATE * TIMEofDAY ²	340	6	9.4	0.00
STATE * TREND + TIMEofDAY ²	339	8	12.6	0.00
NULL	354	1	13.5	0.00

^a Variables and column headings explained in Table 5.1.

^b AIC_c value of the best-fit model = 343.

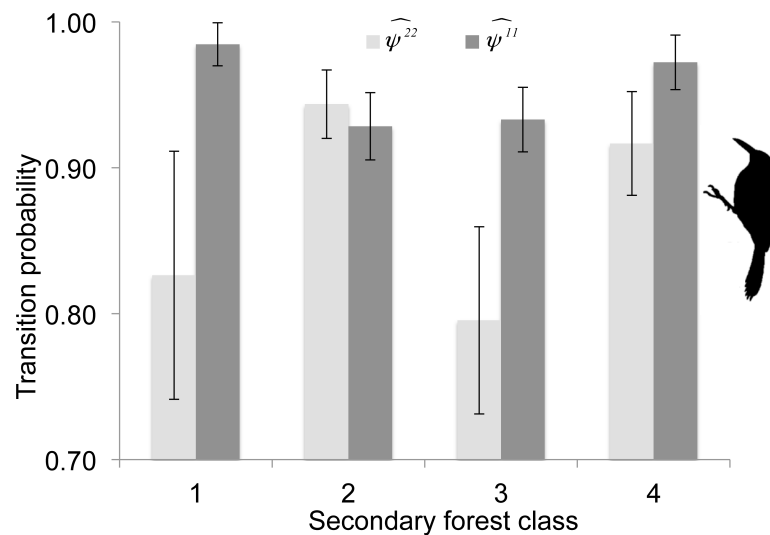


Figure 5.4. Model-averaged estimates of transition probability ($\widehat{\psi}^{rr} \pm \text{SE}$) for radio-tagged *Xiphorhynchus pardalotus* occupying primary forest and secondary forest of four different age classes. $\widehat{\psi}^{rr}$ did not vary by time of day for this species, so single estimates are shown for each secondary forest age class. See Figure 1 caption for definitions of $\widehat{\psi}^{rr}$

Transition probability of *Formicarius colma* was state-specific and affected by TIMEofDAY² and SF. TIMEofDAY showed a quadratic effect and little evidence for variation with STATE; model-averaged $\widehat{\psi}^{22}$ and $\widehat{\psi}^{11}$ were greatest during the middle of the day indicating few habitat transitions during this period relative to dawn and dusk (Figure 5.5). The variable SF was not included in the top model (it was included in the second best-fit model, $\Delta\text{AIC}_c = 0.9$; Table 5.3), but model-averaged parameter estimates indicated a considerable difference in point estimates, $\widehat{\psi}^{22}$, among secondary forest age classes (Figure 5.6). $\widehat{\psi}^{22}$ was relatively low in SF₁, and highest in SF₂ and SF₄ (Figure 5.6). Importantly, for most of the day, error bars for SF₄ $\widehat{\psi}^{11}$ and $\widehat{\psi}^{22}$ did not overlap (Figure 5.5c) suggesting that even in primary forest abutting 27–31 year-old secondary forest that was never burned, *F. colma* was more likely to remain in primary forest than to remain in secondary forest. Radio-tracked *F. colma* never entered SF₃, and I never detected any *F. colma* in SF₃—radio-tagged or not. The mean estimate of $\widehat{\psi}^{22}$ for group SF₃ was lower than other groups at 0.62 (range throughout the day: 0.58–0.63), but large standard errors (range: 0.41–0.44) reflected a lack of precision about this estimate. This pattern of variation in $\widehat{\psi}^{22}$ among SF groups certainly provided no support for models containing TREND (Table 5.3). Models including BIRD_AGE received essentially no support, indicating that age of *F. colma* as I defined it had little effect on $\widehat{\psi}^{rr}$. Null models for all three species received essentially no support ($\sum w_i = < 0.01$).

Table 5.3. Candidate model set describing transition probabilities of radio-tagged *Formicarius colma* occupying primary and secondary forest at the Biological Dynamics of Forest Fragments Project.

Model ^a	Deviance	<i>K</i>	ΔAIC_c ^b	w_i
STATE + TIMEofDAY ²	182	4	0.0	0.29
SF * STATE + TIMEofDAY ²	170	10	0.9	0.18
STATE	187	2	1.1	0.17
SF * STATE * TIMEofDAY ²	167	12	1.8	0.12
STATE * TIMEofDAY ²	180	6	2.8	0.07
STATE * BIRD_AGE ^c	186	4	4.0	0.04
STATE * TREND	186	4	4.5	0.03
SF * STATE * TIMEofDAY	174	10	5.1	0.02
STATE * SF	179	8	5.4	0.02
STATE * BIRD_AGE + TIMEofDAY ²	179	8	5.8	0.02
BIRD_AGE * STATE * TREND	180	8	6.6	0.01
STATE * TREND + TIMEofDAY ²	180	8	6.7	0.01
SF * STATE + TIMEofDAY	179	9	7.4	0.01
NULL	205	1	17.3	0.00

^a Variables and column headings explained in Table 5.1.

^b AIC_c value of the best-fit model = 190.

^c BIRD_AGE: whether individual was adult or young.

DISCUSSION

Forest type (both STATE and SF) was an important predictor of transition probability for the three species of Amazonian birds I radio-tracked, while time of day was also an important predictor for *G. spirurus* and *F. colma*. All three species were more likely to remain in primary forest than SF₁, strongly suggesting that 8–14-year-old secondary forest is of relatively poor quality, and that recovery of habitat quality begins after or at least towards the end of this successional stage. This pattern of recovery beyond 8–14 years generally matches well with estimates from mist netting studies at the BDFFP (Stouffer and Bierregaard 2007; Powell et al. 2013) as well as recovery estimates from the analysis of this same telemetry dataset in Chapter 4.

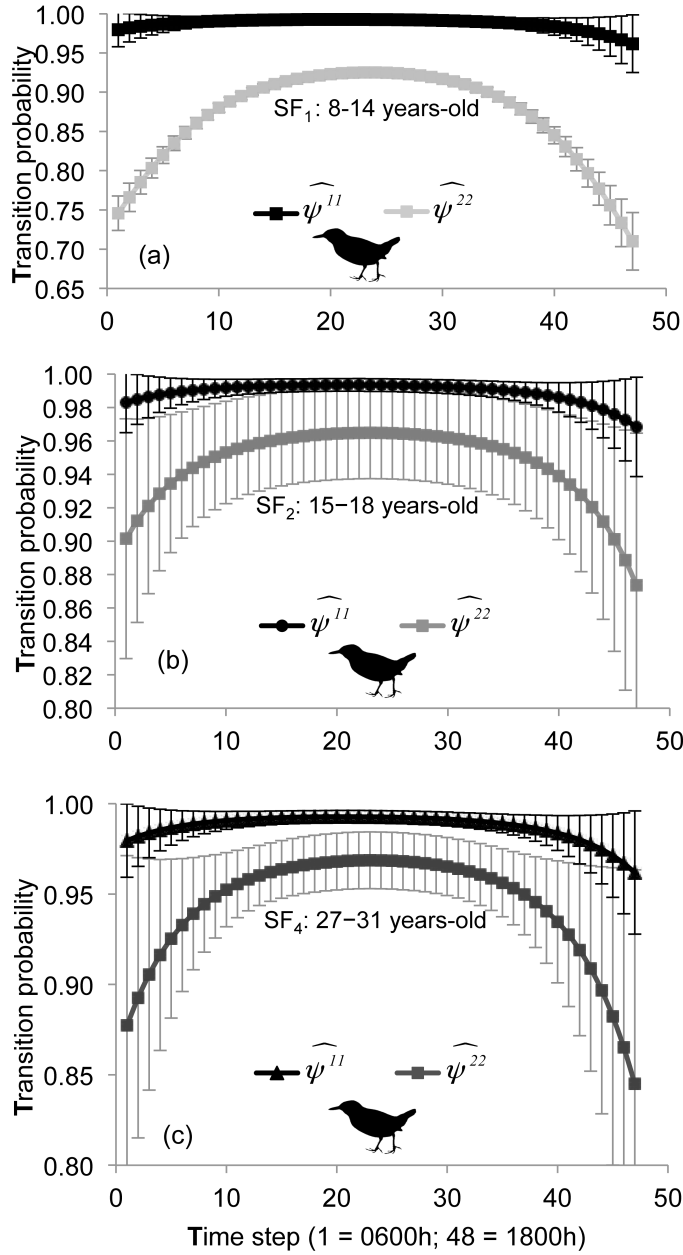


Figure 5.5. Model-averaged estimates of transition probability ($\widehat{\psi}^{rr} \pm \text{SE}$) over the course of the day for radio-tagged *Formicarius colma* occupying primary forest and secondary forest of three different age classes (SF₁, SF₂, SF₄). Secondary forest class three (21-24 years-old; $\widehat{\psi}^{11} = 0.99 \pm 0.01$, $\widehat{\psi}^{22} = 0.62 \pm 0.43$) not shown. See Figure 5.2 caption for definitions of $\widehat{\psi}^{rr}$

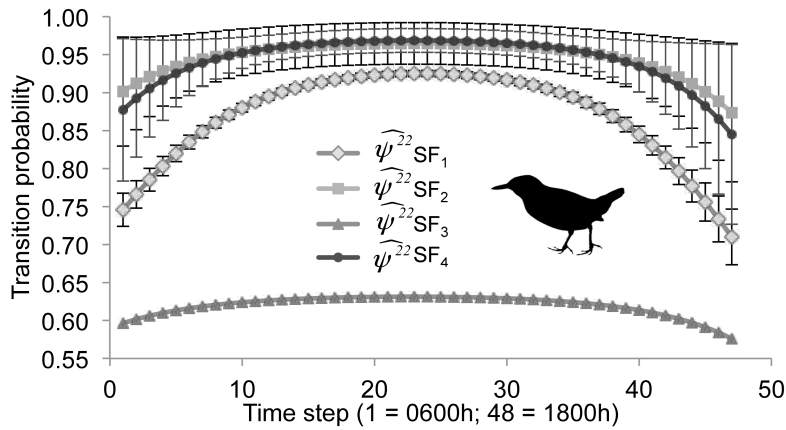


Figure 5.6. Model-averaged estimates of transition probability ($\widehat{\psi}^{rr} \pm \text{SE}$) over the course of the day for radio-tagged *Formicarius colma* occupying primary forest and secondary forest of four different age classes. Error bars for secondary forest class three (mean SE = 0.43) omitted for clarity. See Figure 5.2 caption for definitions of $\widehat{\psi}^{rr}$

Although I predicted that $\widehat{\psi}^{22}$ would increase with increasingly mature secondary forest, TREND received essentially no support in any species, suggesting that secondary forest age alone cannot predict movement among habitats or habitat quality. I believe the lack of support for TREND was driven primarily by the poor quality of SF₃ at the BDFFP. Due to logistical constraints, birds using SF₃ were only tracked at *fazenda* Dimona, the landscape with the most intensive human land use. Much of *fazenda* Dimona was burned multiple times before abandonment in the 1980s, and much of the landscape was used sporadically as cattle pasture for years. In contrast, locations within SF₄ that I radio-tracked were never burned (*e.g.* "Cidade Powell", Moreira 2003) and cattle grazing was minimal, which almost certainly contributed to substantial structural and resource availability differences between SF₃ and SF₄. Specifically, in the first years after the abandonment of clearcuts at the BDFFP, burned and unburned plots develop very different successional strategies, with *Vismia* shrubs dominating burned plots and

Cecropia trees dominating unburned plots (Mesquita et al. 2001). Further, cattle grazing affects the recovery of secondary growth, as cattle compact the soil, heterogeneously consume recovering vegetation and affect nutrient levels in the soil (Fearnside 2005). Despite my best efforts, I did not detect any *F. colma* within SF₃, and none of my radio-tagged birds caught along edges ever entered SF₃; this likely contributed to the large error about the $\widehat{\psi}^{22}$ for this species in group SF₃. Powell et al. (2013, Chapter 2) estimated through capture rates that terrestrial insectivores at the BDFFP, including *F. colma*, take 13 years longer (54 vs 67) to move into secondary forest at pre-isolation rates when plots were burned. The authors speculate that terrestrial insectivores, which forage on the ground, may be affected by differences in the abundance of food resources (i.e. insects) on the forest floor when plots were burned. Given logistical constraints and the distribution of SF₃ at the BDFFP, I had little opportunity to quantify the effect of plot burning or cattle grazing on radio-tagged birds; however, I predict that with enough replication, models including the effects of cattle grazing and burning will account for much of the noise that likely prevented support for TREND in this analysis (e.g. Powell et al. 2013, Chapter 2). I maintain that transition probability likely increases with age of secondary forest, and suggest that the TREND model is not supported because variations in land use history practice were not carefully accounted for in the experimental design.

Glyphorhynchus spirurus was the most flexible species with respect to time of day and transition probabilities in young secondary forest. Unlike in the other species, there was good evidence for a quadratic effect of TIMEofDAY. The shape of the quadratic curve describing $\widehat{\psi}^{rr}$ over the course of the day varied between birds in primary and secondary forest (Figure. 5.2) *Glyphorhynchus spirurus* was most likely to remain in primary forest during midday, suggesting crepuscular behavior, perhaps due to avoidance of high light (and thus visibility to predators) and

temperature levels in less dense secondary forests during the middle of the day. On the other hand, $\widehat{\psi}^{22}$ was highest in the morning and tapered off over the course of the day, suggesting an advantage to remaining in secondary forest in the morning. It is not clear why $\widehat{\psi}^{22}$ did not increase again towards the end of the day as with *F. colma*. I speculate that *G. spirurus* transitioned back to night roosts at or just after 1800h, which was a bit too late to be detected by this analysis. When accounting for the effect of TIMEofDAY, it became clear that by 15–18 years after pasture abandonment, *G. spirurus* was already more likely to remain in secondary forest than remain in primary forest (i.e. $\widehat{\psi}^{22} > \widehat{\psi}^{11}$; Figure 5.2b). This suggests that by 15–18 years after abandonment, secondary forest has already passed the point of recovery for *G. spirurus*; recovery probably occurs at some point late in SF₁ or early in SF₂ i.e. approximately 12–15 years after abandonment. In Chapter 3 I speculated that *G. spirurus* may be released from competition in 1-ha forest fragments and young secondary growth because other woodcreepers are absent from this early successional stage, allowing them to exploit resources that are otherwise unavailable; this may help account for the high $\widehat{\psi}^{22}$ values in SF₂.

As was the case with *G. spirurus*, *X. pardalotus* showed a strong effect of SF on $\widehat{\psi}^{rr}$; although unlike in the other species, $\widehat{\psi}^{rr}$ was independent of TIMEofDAY. Among the species I radio-tracked, *X. pardalotus* was most closely associated with mixed-species understory flocks led by *Thamnomanes antshrikes* (Jullien and Thiollay 1998; Develey and Stouffer 2001; Marantz et al. 2003). Most individuals I tracked participated in mixed species flocks during the majority of the time I tracked them, so their willingness to enter secondary growth is undoubtedly affected by that of other flock members, particularly *Thamnomanes antshrikes*. Recovery was evident by 15–18 years after abandonment, as $\widehat{\Psi}_{22}$ in SF₂ was no different from $\widehat{\psi}^{11}$ (Figure 5.4). This

estimate for *X. pardalotus* and my recovery estimate of 12–15 years for *G. spirurus* matches well with estimates of Powell et al. (2013, Chapter 2), who calculated that after cutting, burning and land abandonment, mixed-species flock dropouts at the BDFFP (defined as *G. spirurus*, *X. pardalotus* and *Myrmotherula axillaris*) took 14 years to return to pre-isolation capture rates along edges of primary and secondary forest. My estimates also match well with my recovery estimates from the edge analysis in Chapter 4 (*G. spirurus*: 11–14 years; *X. pardalotus*: 15–20 years).

Formicarius colma showed a strong effect of SF and TIMEofDAY on $\widehat{\psi}^{rr}$, $\widehat{\psi}^{11}$ and $\widehat{\psi}^{22}$ were highest during midday and lowest early and late in all habitats (Figure 5.5), suggesting that the species' movements between habitats were crepuscular. The species generally avoids darker, cooler low-lying areas near streams, instead favoring areas on and near plateaus that are probably more exposed to high heat and light levels (Stratford and Stouffer 2013). I propose three non-mutually exclusive hypotheses for this pattern of less movement during midday: 1) high light levels agitate the birds' sensitive eyes, evolved to detect dark insects on dark leaves on the rainforest floor (Esteban Fernandez Juricic Purdue University, pers. comm.); 2) high light levels increase visibility by predators and thus predation risk (Patten and Smith-Patten 2012); 3) increased midday temperatures encourage thermoregulation via lethargy. This crepuscular habitat transition pattern suggests that it is light or heat that affect day-to-day movements of *F. colma*, rather than the structure of vegetation *per se* as suggested by Stratford and Robinson (2005). Prey availability is probably also associated with light and temperature levels, as insects may be less active during midday. Another non-mutually exclusive explanation is that birds leave their roosts at dusk, flying quickly to a spot where they will spend most of the day slowly foraging on the ground; they probably then fly back to their night roosts at dusk, producing a

pattern of relatively little movement (or habitat transitions) during midday. Hypotheses involving bird responses based on light, heat and vegetation structure could be tested in an aviary with manipulated environmental conditions. Regardless of the mechanism, the effect of TIMEofDAY² was absent in *X. pardalotus* and varied by habitat for *G. spirurus*, suggesting that movements of *F. colma*, and possibly other terrestrial insectivores may be particularly constrained by the effects of light or heat during midday.

Although the effect of habitat state on transition probability of *F. colma* was obvious, the effect of SF became clearer when graphing model-averaged parameter estimates (e.g. Figure 5.6). SF₁ and SF₃ were obviously inferior to other habitat options (Figure 5.5), and $\widehat{\psi}^{11}$ was at least marginally higher than $\widehat{\psi}^{22}$ in all secondary forest classes (Figure 5.5). $\widehat{\psi}^{22}$ of SF₂ was likely inflated by a very young individual (in pre-formative molt) that regularly moved between primary forest and SF₂. This one bird which was very young (likely < 6 months old) had its core home range within a 1-ha primary forest fragment, yet it regularly moved among habitat. However, as I have never caught or detected any adult *F. colma* in 1-ha fragments, I doubt that this individual will establish a territory in that location, and I instead suggest that the bird was in some phase of dispersal. Indeed, models including BIRD_AGE, which here I defined as binary (adult or young), were essentially without support, but based on plumage (Johnson 2010, Wolfe et al. 2010), this individual was likely the youngest in my analysis—suggesting that incorporating greater BIRD_AGE resolution, where available, may better explain the variability in ψ —particularly in these intermediate SFs. With a larger sample size, similar models could accommodate more resolution within BIRD_AGE and perhaps explain $\widehat{\psi}^{rr}$ for individuals that have not established territories.

Given the difference between model-averaged $\widehat{\psi}^{11}$ and $\widehat{\psi}^{22}$ for *F. colma* in SF₄ (Figure 5.5c), my results suggest that even SF₄, which was never burned, is still of lower quality than primary forest for *F. colma*. Error bars were least likely to overlap at times other than dawn and dusk, suggesting that primary forest may be particularly suitable during midday—perhaps because it buffers the effect of light and heat better than secondary forest as explained above. The apparent low quality of SF₄ compared to primary forest fits with the estimates of Powell et al. (n.d.) who estimated that terrestrial insectivores at the BDFFP (including *F. colma*) would take 54 years to recover to pre-isolation capture rates along edges of primary forest after abandonment of unburned clearcuts. The species is also associated with thick trunked trees and avoids areas dense with thin trees (Stratford and Stouffer 2013), which further suggests that vegetation structure takes considerable time to recover to the point when *F. colma* prefers those conditions, even if the canopy has recovered to primary-forest-like heights.

More generally, my models using data collected from radio-tagged birds permitted useful inferences about transition probabilities. Using only time of day and age of secondary forest, I was able to account for much of the variation around transition probabilities, and for two woodcreepers, estimate the point during the succession of secondary forest at which differences in transition probabilities between primary and secondary forest are essentially absent. Once the ability to transition among habitats is quantified, estimates can help estimate habitat quality and parameterize more complex models of metapopulation dynamics and ultimately informing conservation planning (e.g. Stevens et al. 2006; Castellón and Sieving 2007; Knowlton and Graham 2010). Given rates of deforestation and secondary forest accumulation in Amazonia and other tropical rainforests, there is a great need to quantify habitat transition probabilities and

connectivity—particularly for the species and guilds thought to be most sensitive to disturbance, such as terrestrial insectivores.

LITERATURE CITED

- Bierregaard Jr., R. O., C. Gascon, T. E. Lovejoy, and R. Mesquita. 2001. Lessons from Amazonia: the ecology and conservation of a fragmented forest. Yale Univ Press, Ann Arbor, MI.
- Bierregaard Jr., R. O., and C. Gascon. 2001. The Biological Dynamics of Forest Fragments Project: Overview and history of a long-term conservation project. Pages 5–12 in R. O. Bierregaard Jr., C. Gascon, T. E. Lovejoy, and R. Mesquita, editors. Lessons from Amazonia: The Ecology and Conservation of a Fragmented Forest. Yale University Press, New Haven.
- Brawn, J. D., G. Angehr, N. Davros, W. D. Robinson, J. N. Styrsky, and C. E. Tarwater. 2011. Sources of variation in the nesting success of understory tropical birds. *Journal of Avian Biology* 42:61–68.
- Brook, B. W., C. J. A. Bradshaw, L. P. Koh, and N. S. Sodhi. 2006. Momentum drives the crash: mass extinction in the tropics. *Biotropica* 38:302–305.
- Brownie, C., J. E. Hines, J. D. Nichols, K. H. Pollock, and J. B. Hestbeck. 1993. Capture-recapture studies for multiple strata including non-Markovian transitions. *Biometrics* 49:1173–1187.
- Burnham, K. P., and D. R. Anderson. 2002. Model selection and multimodel inference: a practical information-theoretical approach. Second edition. Springer-Verlag, New York, New York, USA.
- Castellón, T. D., and K. E. Sieving. 2007. Patch network criteria for dispersal-limited endemic birds of South American temperate rain forest. *Ecological Applications* 17:2152–2163.
- Cohn-Haft, M., A. Whittaker, and P. C. Stouffer. 1997. A new look at the “species-poor” central Amazon: the avifauna north of Manaus, Brazil. *Ornithological Monographs* 48:205–235.
- Develey, P. F., and P. C. Stouffer. 2001. Effects of roads on movements by understory birds in mixed-species flocks in central Amazonian Brazil. *Conservation Biology* 15:1416–1422.
- Fearnside, P. M. 2005. Deforestation in Brazilian Amazonia: history, rates, and consequences. *Conservation Biology* 19:680–688.
- Fretwell, S. D. 1972. *Populations in a Seasonal Environment*. Princeton University Press.

- Fretwell, S. D., and H. L. Lucas. 1969. On territorial behavior and other factors influencing habitat distribution in birds. *Acta Biotheoretica* 19:16–36.
- Gradwohl, J., and R. Greenberg. 1980. The formation of antwren flocks on Barro Colorado Island, Panama. *The Auk*:385–395.
- Hestbeck, J. B., J. D. Nichols, and R. A. Malecki. 1991. Estimates of movement and site fidelity using mark-resight data of wintering Canada geese. *Ecology* 72:523–533.
- Howell, S. N. G., C. Corben, P. Pyle, and D. I. Rogers. 2003. The first basic problem: a review of molt and plumage homologies. *The Condor* 105:635–653.
- Johnson, E. I. 2010. Banding guide to the birds of The Biological Dynamics of Forest Fragments Project. School of Renewable Resources, Louisiana State University, Baton Rouge, LA.
- Johnson, E. I., P. C. Stouffer, and C. F. Vargas. 2011a. Diversity, biomass, and trophic structure of a central amazonian rainforest bird community. *Revista Brasileira De Ornitologia* 19:1–16.
- Johnson, E. I., J. D. Wolfe, T. Brandt Ryder, and P. Pyle. 2011b. Modifications to a molt-based ageing system proposed by Wolfe et al.(2010). *Journal of Field Ornithology* 82:422–424.
- Jullien, M., and J.-M. Thiollay. 1998. Multi-species territoriality and dynamic of neotropical forest understory bird flocks. *Journal of Animal Ecology* 67:227–252.
- Knowlton, J. L., and C. H. Graham. 2010. Using behavioral landscape ecology to predict species' responses to land-use and climate change. *Biological Conservation* 143:1342–1354.
- Krabbe, N., and T. S. Schulenberg. 2003. Family Formicariidae (ground-antbirds). Pages 682–731 *Handbook of the Birds of the World Volume 8. Broadbills to Tapaculos*. Lynx Edicions Barcelona, Spain.
- Laurance, S. G. W., P. C. Stouffer, and W. F. Laurance. 2004. Effects of road clearings on movement patterns of understory rainforest birds in central Amazonia. *Conservation Biology* 18:1099–1109.
- Laurance, W. F., J. L. C. Camargo, R. C. C. Luizão, S. G. Laurance, S. L. Pimm, E. M. Bruna, P. C. Stouffer, G. Bruce Williamson, J. Benítez-Malvido, and H. L. Vasconcelos. 2011. The fate of Amazonian forest fragments: A 32-year investigation. *Biological Conservation* 144:56–67.
- Levey, D. J. 1988. Tropical wet forest treefall gaps and distributions of understory birds and plants. *Ecology* 69:1076–1089.

- Marantz, C. A., A. Aleixo, L. Bevier, R., and M. A. Patten. 2003. Family Dendrocolaptidae (Woodcreepers). Pages 358–447 in J. A. del Hoyo, A. Elliott, and D. A. Christie, editors. *Handbook of the Birds of the World. Volume 8. Broadbills to Tapaculos*. Lynx Edicions. Barcelona, Spain.
- Martin, J., J. D. Nichols, W. M. Kitchens, and J. E. Hines. 2006. Multiscale patterns of movement in fragmented landscapes and consequences on demography of the snail kite in Florida. *Journal of Animal Ecology* 75:527–539.
- Mesquita, R. C. G., K. Ickes, G. Ganade, and G. B. Williamson. 2001. Alternative successional pathways in the Amazon Basin. *Journal of Ecology* 89:528–537.
- Moreira, M. P. 2003. Uso de sensoriamento remoto para avaliar a dinâmica de sucessão secundária na Amazônia central. Universidade Federal do Amazonas / UFAM, Manaus, Brazil.
- Neeff, T., R. M. Lucas, J. R. Santos, E. S. Brondizio, and C. C. Freitas. 2006. Area and age of secondary forests in Brazilian Amazonia 1978–2002: an empirical estimate. *Ecosystems* 9:609–623.
- Nichols, J. D. 1996. Sources of variation in migratory movements of animal populations: statistical inference and a selective review of empirical results. Pages 147–197 in O. E. Rhodes, R. K. Chesser, and M. H. Smith, editors. *Population Dynamics in Ecological Space and Time*. University of Chicago Press, Chicago, IL.
- Nichols, J. D., and W. L. Kendall. 1995. The use of multi-state capture-recapture models to address questions in evolutionary ecology. *Journal of Applied Statistics* 22:835–846.
- Otis, D. L., and G. C. White. 1999. Autocorrelation of location estimates and the analysis of radiotracking data. *Journal of Wildlife Management* 63:1039–1044.
- Patten, M. A., and B. D. Smith-Patten. 2012. Testing the microclimate hypothesis: Light environment and population trends of Neotropical birds. *Biological Conservation* 155:85–93.
- Powell, L. L., P. C. Stouffer, and E. I. Johnson. 2013. Recovery of understory avian movement across the interface of primary and secondary Amazon Rainforest. *The Auk* 130(3):459–468.
- Rappole, J. H., and A. R. Tipton. 1991. New harness design for attachment of radio transmitters to small passerines. *Journal of Field Ornithology* 62:335–337.
- Ruiz-Gutiérrez, V., P. F. Doherty Jr, E. S. C, S. C. Martínez, J. Schondube, H. V Munguía, and E. Iñigo-Elias. 2012. Survival of resident Neotropical birds: Considerations for sampling and analysis based on 20 years of bird-banding efforts in Mexico. *The Auk* 129:500–509.

- Sberze, M., M. Cohn-Haft, and G. Ferraz. 2009. Old growth and secondary forest site occupancy by nocturnal birds in a neotropical landscape. *Animal Conservation* 13:3–11.
- Sekercioglu, C. H., P. R. Ehrlich, G. C. Daily, D. Aygen, D. Goehring, and R. F. Sandi. 2002. Disappearance of insectivorous birds from tropical forest fragments. *Proceedings of the National Academy of Sciences of the United States of America* 99:263–7.
- Skutch, A. F. 1969. Life histories of Central American birds. III. Families Cotingidae, Pipridae, Formiariidae, Furnariidae, Dendrocolaptidae, and Picidae. *Pacific Coast Avifauna* 35.
- Stevens, V. M., C. Verkenne, S. Vandewoestijne, R. A. Wesselingh, and M. Baguette. 2006. Gene flow and functional connectivity in the natterjack toad. *Molecular Ecology* 15:2333–2344.
- Stouffer, P. C. 2007. Density, territory size, and long-term spatial dynamics of a guild of terrestrial insectivorous birds near Manaus, Brazil. *Auk* 124:291–306.
- Stouffer, P. C., and R. O. Bierregaard Jr. 1995. Effects of forest fragmentation on understory hummingbirds in Amazonian Brazil. *Conservation Biology* 9:1085–1094.
- Stouffer, P. C., and R. O. Bierregaard Jr. 2007. Recovery potential of understory bird communities in Amazonian rainforest fragments. *Revista Brasileira De Ornitologia* 15:219–229.
- Stouffer, P. C., R. O. Bierregaard Jr., C. Strong, and T. E. Lovejoy. 2006. Long-term landscape change and bird abundance in Amazonian rainforest fragments. *Conservation Biology* 20:1212–1223.
- Stouffer, P. C., and R. O. Bierregaard Jr. 1993. Spatial and temporal abundance patterns of Ruddy Quail-doves (*Geotrygon montana*) near Manaus, Brazil. *Condor* 95:896–903.
- Stouffer, P. C., E. I. Johnson, and R. O. Bierregaard. 2013. Breeding seasonality in Central Amazonian rainforest birds. *The Auk* 130(3):529–540.
- Stratford, J. A., and W. D. Robinson. 2005. Gulliver travels to the fragmented tropics: geographic variation in mechanisms of avian extinction. *Frontiers in Ecology and the Environment* 3:91–98.
- Stratford, J. A., and P. C. Stouffer. 2001. Reduced feather growth rates of two common birds inhabiting central Amazonian forest fragments. *Conservation Biology* 15:721–728.
- Stratford, J. A., and P. C. Stouffer. 2013. Microhabitat associations of terrestrial insectivorous birds in Amazonian rainforest and second-growth forests. *Journal of Field Ornithology* 84:1–12.

- Van Horne, B. 1983. Density as a misleading indicator of habitat quality. *The Journal of Wildlife Management*:893–901.
- White, G. C., and K. P. Burnham. 1999. Program MARK: survival estimation from populations of marked animals. *Bird study* 46:120–139.
- Willis, E. O. 1977. Lista preliminar das aves da parte noroeste e áreas vizinhas da Reserva Ducke, Amazonas, Brasil. *Revista Brasileira de Biologia* 37:585–601.
- Wolfe, J. D., T. B. Ryder, and P. Pyle. 2010. Using molt cycles to categorize the age of tropical birds: an integrative new system. *Journal of Field Ornithology* 81:186–194.
- Wright, S. J., and H. C. Muller-Landau. 2006a. The future of tropical forest species. *Biotropica* 38:287–301.
- Wright, S. J., and H. C. Muller-Landau. 2006b. The uncertain future of tropical forest species. *Biotropica* 38:443–445.

APPENDIX A: GUILD ASSIGNMENTS AND COMPLETE MODEL SELECTION RESULTS FROM CHAPTER 2

Table A.1. Guild assignments of species included in repeated-measures or information-theoretic analyses.	
Species ^a	Guild ^b
<i>Notharchus tectus</i>	Insectivore, solitary sallier
<i>Bucco tamatia</i>	Insectivore, solitary sallier
<i>Malacoptila fusca</i>	Insectivore, solitary sallier
<i>Galbula albirostris</i>	Insectivore, solitary sallier
<i>Sclerurus mexicanus</i>	Insectivore, terrestrial
<i>S. rufigularis</i>	Insectivore, terrestrial
<i>S. caudacutus</i>	Insectivore, terrestrial
<i>Certhiasomus stictolaemus</i>	Insectivore, flock obligate
<i>Sittasomus griseicapillus</i>	Insectivore, solitary bark forager
<i>Deconychura longicauda</i>	Insectivore, solitary bark forager
<i>Dendrocincla fuliginosa</i>	Insectivore, solitary bark forager
<i>D. merula</i>	Insectivore, ant follower
<i>Glyphorhynchus spirurus</i>	Insectivore, flock dropout
<i>Hylexetastes perrotii</i>	Insectivore, solitary bark forager
<i>Dendrocolaptes certhia</i>	Insectivore, solitary bark forager
<i>D. picumnus</i>	Insectivore, solitary bark forager
<i>Xiphorhynchus pardalotus</i>	Insectivore, flock dropout
<i>Campylorhamphus procurvovides</i>	Insectivore, solitary bark forager
<i>Xenops minutus</i>	Insectivore, flock obligate
<i>Philydor erythrocercum</i>	Insectivore, flock obligate
<i>Automolus infuscatus</i>	Insectivore, flock obligate
<i>A. ochrolaemus</i>	Insectivore, edge
<i>Thamnomanes ardesiacus</i>	Insectivore, flock obligate
<i>T. caesioides</i>	Insectivore, flock obligate
<i>Isleria guttata</i>	Insectivore, near-ground
<i>Epinecrophylia gutturalis</i>	Insectivore, flock obligate
<i>Myrmotherula axillaris</i>	Insectivore, flock dropout
<i>Myrmotherula longipennis</i>	Insectivore, flock obligate
<i>M. menetriesii</i>	Insectivore, flock obligate
<i>Hypocnemis cantator</i>	Insectivore, edge
<i>Pernostola rufifrons</i>	Insectivore, edge
<i>Myrmeciza ferruginea</i>	Insectivore, terrestrial
<i>Pithys albifrons</i>	Insectivore, ant follower
<i>Gymnopithys rufigula</i>	Insectivore, ant follower
<i>Hylophylax naevius</i>	Insectivore, near-ground
<i>Willisornis poecilinotus</i>	Insectivore, near-ground
<i>Formicarius colma</i>	Insectivore, terrestrial

<i>F. analis</i>	Insectivore, terrestrial
<i>Myrmornis torquata</i>	Insectivore, terrestrial
<i>Grallaria varia</i>	Insectivore, terrestrial
<i>Hylopezus macularius</i>	Insectivore, terrestrial
<i>Conopophaga aurita</i>	Insectivore, terrestrial
<i>Mionectes macconnelli</i>	Frugivore, core
<i>Corythopis torquatus</i>	Insectivore, terrestrial
<i>Lophotriccus galeatus</i>	Non-forest
<i>Rhynchocyclus olivaceus</i>	Insectivore, flock obligate
<i>Platyrinchus saturatus</i>	Insectivore, solitary sallier
<i>P. coronatus</i>	Insectivore, solitary sallier
<i>P. platyrhynchos</i>	Insectivore, solitary sallier
<i>Onychorhynchus coronatus</i>	Insectivore, solitary sallier
<i>Terenotriccus erythrurus</i>	Insectivore, solitary sallier
<i>Myiobius barbatus</i>	Insectivore, flock obligate
<i>Schiffornis olivacea</i>	Frugivore, core
<i>Corapipo gutturalis</i>	Frugivore, core
<i>Lepidothrix serena</i>	Frugivore, core
<i>Dixiphia pipra</i>	Frugivore, core
<i>Ceratopipra erythrocephala</i>	Frugivore, core
<i>Hylophilus ochraceiceps</i>	Insectivore, flock obligate
<i>Pheugopedius coraya</i>	Non-forest
<i>Troglodytes aedon</i>	Non-forest
<i>Microcerculus bambla</i>	Insectivore, near-ground
<i>Cyphorhinus arada</i>	Insectivore, terrestrial
<i>Turdus albicollis</i>	Frugivore, core
<i>Microbates collaris</i>	Insectivore, near-ground
<i>Cyanocompsa cyanooides</i>	Frugivore, core
<i>Tachyphonus surinamus</i>	Frugivore, core
<i>Ramphocelus carbo</i>	Non-forest
<i>Oryzoborus angolensis</i>	Non-forest
^a Sequence follows Cohn-Haft et al. (1997), with taxonomy reflecting Remsen et al. (2013). The first entry under guild represents a bird's primary categorization. The second entry indicates that within the first category that species fits, secondarily, in the category mentioned or some other category. ^b Insectivores include species that eat almost no fruit; frugivores include species that often eat fruit.	

Table A.2. Complete list of Akaike's information criterion (AIC _c) model selection results for capture rates of non-forest species as a function of landscape characteristics at the Biological Dynamics of Forest Fragments Project, 1991–2011.				
Model	–2 Log Likelihood	<i>K</i> ^a	ΔAIC _c ^b	<i>w_i</i>
BorderYrs*BorderUnburned ^c	278.3	5	0.0	0.73
BorderYrs BorderUnburned	284.0	4	3.4	0.13
BorderYrs MatrixYrs BorderUnburned	283.2	5	4.9	0.06
BorderYrs MatrixYrs	287.5	4	7.0	0.02
BorderYrs	290.1	3	7.4	0.02
BorderYrs InteriorCapRate	288.1	4	7.6	0.02
BorderYrs MatrixYrs MatrixUnburned	287.5	5	9.2	0.01
BorderYrs MatrixUnburned	289.8	4	9.3	0.01
MatrixYrs MatrixUnburned	300.4	4	19.9	0.00
InteriorCapRate	308.9	3	26.2	0.00
NULL	313.4	2	28.5	0.00
^a <i>K</i> = number of parameters; AIC _c = AIC adjusted for small sample size; ΔAIC _c = difference in AIC _c in relation to the most parsimonious value; <i>w_i</i> = Akaike weight.				
^b AIC _c value of the best-fit model = 289.0.				
^c Interactive models also include non-interactive effects of the variables involved in the interaction.				

Table A.3. Complete list of Akaike's information criterion (AIC _c) model selection results for capture rates of edge species as a function of landscape characteristics at the Biological Dynamics of Forest Fragments Project, 1991–2011.				
Model	–2 Log Likelihood	<i>K</i> ^a	ΔAIC _c ^b	<i>w_i</i>
BorderYrs*BorderUnburned ^c	285.3	5	0.0	0.58
BorderYrs MatrixYrs	289.9	4	2.4	0.17
BorderYrs MatrixYrs BorderUnburned	288.5	5	3.2	0.12
BorderYrs MatrixYrs MatrixUnburned	289.6	5	4.3	0.07
BorderYrs BorderUnburned	293.7	4	6.1	0.03
BorderYrs	297.7	3	8.0	0.01
BorderYrs InteriorCapRate	295.4	4	7.8	0.01
NULL	301.0	2	9.1	0.01
InteriorCapRate	299.5	3	9.7	0.01
MatrixYrs MatrixUnburned	297.2	4	9.7	0.00
BorderYrs ² MatrixYrs	297.3	4	9.8	0.00
BorderYrs MatrixUnburned	297.5	4	10.0	0.00
BorderYrs ²	300.9	3	11.1	0.00
^a <i>K</i> = number of parameters; AIC _c = AIC adjusted for small sample size; ΔAIC _c = difference in AIC _c in relation to the most parsimonious value; <i>w_i</i> = Akaike weight.				
^b AIC _c value of the best-fit model = 296.0.				
^c Interactive models also include non-interactive effects of the variables involved in the interaction.				

Table A.4. Complete list of Akaike's information criterion (AIC_c) model selection results for capture rates of core frugivores as a function of landscape characteristics at the Biological Dynamics of Forest Fragments Project, 1991–2011.

Model	–2 Log Likelihood	<i>K</i> ^a	ΔAIC _c ^b	<i>w_i</i>
BorderYrs InteriorCapRate	230.8	4	0.0	0.54
BorderYrs Area InteriorCapRate	229.9	5	1.3	0.28
InteriorCapRate	235.3	3	2.3	0.17
BorderYrs*Area ^c	245.2	5	16.6	0.00
BorderYrs Area CF800	246.3	5	17.7	0.00
BorderYrs*Area CF800	244.7	6	18.4	0.00
BorderYrs Area	254.1	4	23.3	0.00
BorderYrs	256.9	3	23.9	0.00
BorderYrs CF800	255.0	4	24.2	0.00
BorderYrs MatrixYrs	255.8	4	24.9	0.00
Area	258.1	3	25.0	0.00
Area CF800	256.6	4	25.7	0.00
Area MatrixYrs	257.7	4	26.8	0.00
BorderYrs ²	260.6	3	27.6	0.00
NULL	263.9	2	28.8	0.00
BorderYrs ² MatrixYrs	259.9	4	29.0	0.00
^a <i>K</i> = number of parameters; AIC _c = AIC adjusted for small sample size; ΔAIC _c = difference in AIC _c in relation to the most parsimonious value; <i>w_i</i> = Akaike weight.				
^b AIC _c value of the best-fit model = 239.3.				
^c Interactive models also include non-interactive effects of the variables involved in the interaction.				

Table A.5. Complete list of Akaike's information criterion (AIC_c) model selection results for capture rates of obligate ant-following species as a function of landscape characteristics at the Biological Dynamics of Forest Fragments Project, 1991–2011.

Model	–2 Log Likelihood	<i>K</i> ^a	ΔAIC _c ^b	<i>w_i</i>
BorderYrs InteriorCapRate	284.5	4	0.0	0.69
BorderYrs Area InteriorCapRate	284.5	5	2.3	0.22
BorderYrs*BorderUnburned ^c	288.3	5	6.1	0.03
BorderYrs MatrixYrs MatrixUnburned	288.7	5	6.8	0.02
BorderYrs MatrixYrs	293.6	4	9.1	0.01
BorderYrs*Area	291.8	5	9.6	0.01
BorderYrs MatrixUnburned	294.2	4	9.7	0.01
BorderYrs	296.4	3	9.8	0.01
BorderYrs BorderUnburned	294.8	4	10.3	0.00
BorderYrs MatrixYrs BorderUnburned	293.0	5	10.8	0.00
BorderYrs Area	295.7	4	11.2	0.00
InteriorCapRate	316.3	3	29.6	0.00
MatrixYrs MatrixUnburned	330.2	4	45.8	0.00
Area MatrixYrs	336.3	4	51.8	0.00
Area	339.9	3	53.3	0.00
NULL	347.5	2	58.8	0.00
^a <i>K</i> = number of parameters; AIC _c = AIC adjusted for small sample size; ΔAIC _c = difference in AIC _c in relation to the most parsimonious value; <i>w_i</i> = Akaike weight.				
^b AIC _c value of the best-fit model = 292.9.				
^c Interactive models also include non-interactive effects of the variables involved in the interaction.				

Table A.6. Complete list of Akaike's information criterion (AIC _c) model selection results for capture rates of sallying insectivores as a function of landscape characteristics at the Biological Dynamics of Forest Fragments Project, 1991–2011.				
Model	–2 Log Likelihood	<i>K</i> ^a	ΔAIC _c ^b	<i>w_i</i>
BorderYrs MatrixUnburned	273.3	4	0.0	0.27
BorderYrs MatrixYrs MatrixUnburned	271.4	5	0.3	0.23
BorderYrs Area	275.3	4	1.9	0.10
BorderYrs*Area ^c	273.4	5	2.3	0.08
BorderYrs Area InteriorCapRate	273.4	5	2.3	0.08
Area MatrixYrs	276.6	4	3.3	0.05
BorderYrs MatrixYrs	276.8	4	3.5	0.05
BorderYrs*BorderUnburned	275.1	5	4.0	0.04
BorderYrs InteriorCapRate	277.2	4	3.9	0.04
MatrixYrs MatrixUnburned	278.8	4	5.4	0.02
BorderYrs MatrixYrs BorderUnburned	276.8	5	5.7	0.02
BorderYrs	281.6	3	6.1	0.01
Area	282.7	3	7.2	0.01
BorderYrs BorderUnburned	280.7	4	7.4	0.01
InteriorCapRate	289.1	3	13.6	0.00
NULL	294.7	2	17.0	0.00
^a <i>K</i> = number of parameters; AIC _c = AIC adjusted for small sample size; ΔAIC _c = difference in AIC _c in relation to the most parsimonious value; <i>w_i</i> = Akaike weight.				
^b AIC _c value of the best-fit model = 281.8.				
^c Interactive models also include non-interactive effects of the variables involved in the interaction.				

Table A.7. Complete list of Akaike's information criterion (AIC_c) model selection results for capture rates of bark foraging insectivores as a function of landscape characteristics at the Biological Dynamics of Forest Fragments Project, 1991–2011.

Model	–2 Log Likelihood	<i>K</i> ^a	ΔAIC _c ^b	<i>w_i</i>
BorderYrs MatrixYrs	246.0	4	0.0	0.40
BorderYrs MatrixYrs MatrixUnburned	244.6	5	0.9	0.25
BorderYrs MatrixYrs BorderUnburned	245.4	5	1.7	0.17
BorderYrs*Area ^c	246.5	5	2.8	0.10
BorderYrs BorderUnburned	251.6	4	5.7	0.02
BorderYrs	254.2	3	6.0	0.02
BorderYrs*BorderUnburned	250.1	5	6.4	0.02
BorderYrs InteriorCapRate	254.0	4	8.1	0.01
BorderYrs Area	254.2	4	8.2	0.01
BorderYrs MatrixUnburned	254.2	4	8.2	0.01
BorderYrs Area InteriorCapRate	254.0	5	10.3	0.00
NULL	260.8	2	10.6	0.00
MatrixYrs MatrixUnburned	257.7	4	11.8	0.00
Area	259.9	3	11.8	0.00
InteriorCapRate	260.2	3	12.0	0.00
Area MatrixYrs	258.4	4	12.5	0.00
^a <i>K</i> = number of parameters; AIC _c = AIC adjusted for small sample size; ΔAIC _c = difference in AIC _c in relation to the most parsimonious value; <i>w_i</i> = Akaike weight.				
^b AIC _c value of the best-fit model = 254.4.				
^c Interactive models also include non-interactive effects of the variables involved in the interaction.				

Table A.8. Complete list of Akaike's information criterion (AIC_c) model selection results for capture rates of flock dropouts as a function of landscape characteristics at the Biological Dynamics of Forest Fragments Project, 1991–2011.

Model	–2 Log Likelihood	<i>K</i> ^a	ΔAIC _c ^b	<i>w_i</i>
BorderYrs MatrixUnburned	267.6	4	0.0	0.32
BorderYrs MatrixYrs MatrixUnburned	266.3	5	1.0	0.19
BorderYrs	271.5	3	1.7	0.13
BorderYrs InteriorCapRate	270.0	4	2.4	0.10
BorderYrs Area	271.0	4	3.4	0.06
BorderYrs BorderUnburned	271.4	4	3.7	0.05
BorderYrs MatrixYrs	271.3	4	3.7	0.05
BorderYrs Area InteriorCapRate	269.6	5	4.2	0.04
BorderYrs*BorderUnburned ^c	270.2	5	4.8	0.03
BorderYrs*Area	271.0	5	5.6	0.02
BorderYrs MatrixYrs BorderUnburned	271.3	5	5.9	0.02
BorderYrs ²	279.8	3	9.9	0.00
BorderYrs ² MatrixYrs	279.2	4	11.6	0.00
MatrixYrs MatrixUnburned	290.4	4	22.8	0.00
Area MatrixYrs	292.2	4	24.6	0.00
InteriorCapRate	298.7	3	27.9	0.00
NULL	302.0	2	30.1	0.00
Area	300.6	3	30.8	0.00
^a <i>K</i> = number of parameters; AIC _c = AIC adjusted for small sample size; ΔAIC _c = difference in AIC _c in relation to the most parsimonious value; <i>w_i</i> = Akaike weight.				
^b AIC _c value of the best-fit model = 276.1.				
^c Interactive models also include non-interactive effects of the variables involved in the interaction.				

Table A.9. Complete list of Akaike's information criterion (AIC_c) model selection results for capture rates of obligate mixed flock species as a function of landscape characteristics at the Biological Dynamics of Forest Fragments Project, 1991–2011.

Model	–2 Log Likelihood	<i>K</i> ^a	ΔAIC _c ^b	<i>w_i</i>
BorderYrs*Area ^c	266.9	5	0.0	0.48
BorderYrs Area InteriorCapRate	267.8	5	1.0	0.29
BorderYrs InteriorCapRate	271.5	4	2.4	0.14
BorderYrs Area	272.7	4	3.5	0.08
BorderYrs	282.9	3	11.6	0.00
BorderYrs BorderUnburned	281.7	4	12.6	0.00
BorderYrs MatrixUnburned	281.8	4	12.7	0.00
BorderYrs MatrixYrs	282.3	4	13.2	0.00
BorderYrs MatrixYrs MatrixUnburned	280.4	5	13.5	0.00
BorderYrs*BorderUnburned	281.0	5	14.1	0.00
BorderYrs MatrixYrs BorderUnburned	281.5	5	14.6	0.00
InteriorCapRate	306.0	3	34.7	0.00
Area	306.5	3	35.2	0.00
Area MatrixYrs	305.1	4	35.9	0.00
MatrixYrs MatrixUnburned	307.8	4	38.6	0.00
NULL	327.0	2	53.6	0.00

^a *K* = number of parameters; AIC_c = AIC adjusted for small sample size; ΔAIC_c = difference in AIC_c in relation to the most parsimonious value; *w_i* = Akaike weight.

^b AIC_c value of the best-fit model = 277.6.

^c Interactive models also include non-interactive effects of the variables involved in the interaction.

Table A.10. Complete list of Akaike's information criterion (AIC _c) model selection results for capture rates of near-ground insectivores as a function of landscape characteristics at the Biological Dynamics of Forest Fragments Project, 1991–2011.				
Model	–2 Log Likelihood	<i>K</i> ^a	ΔAIC _c ^b	<i>w_i</i>
BorderYrs Area InteriorCapRate	253.0	5	0.0	0.43
BorderYrs InteriorCapRate	255.6	4	0.3	0.37
BorderYrs MatrixYrs	258.9	4	3.7	0.07
BorderYrs	263.1	3	5.7	0.03
BorderYrs MatrixYrs BorderUnburned	258.7	5	5.7	0.03
BorderYrs MatrixYrs MatrixUnburned	258.9	5	5.9	0.02
BorderYrs BorderUnburned	261.9	4	6.7	0.02
BorderYrs*BorderUnburned ^c	260.4	5	7.4	0.01
BorderYrs MatrixUnburned	263.0	4	7.7	0.01
BorderYrs Area	263.1	4	7.9	0.01
BorderYrs*Area	261.3	5	8.4	0.01
InteriorCapRate	283.3	3	25.8	0.00
MatrixYrs MatrixUnburned	284.3	4	29.1	0.00
Area MatrixYrs	298.6	4	43.3	0.00
Area	301.6	3	44.2	0.00
NULL	305.2	2	45.7	0.00
^a <i>K</i> = number of parameters; AIC _c = AIC adjusted for small sample size; ΔAIC _c = difference in AIC _c in relation to the most parsimonious value; <i>w_i</i> = Akaike weight.				
^b AIC _c value of the best-fit model = 263.7.				
^c Interactive models also include non-interactive effects of the variables involved in the interaction.				

Table A.11. Complete list of Akaike's information criterion (AIC_c) model selection results for capture rates of terrestrial insectivores as a function of landscape characteristics at the Biological Dynamics of Forest Fragments Project, 1991–2011.

Model	–2 Log Likelihood	<i>K</i> ^a	ΔAIC _c ^b	<i>w_i</i>
BorderYrs MatrixYrs BorderUnburned	198.4	5	0.0	0.42
BorderYrs BorderUnburned	201.1	4	0.3	0.36
BorderYrs*BorderUnburned ^c	201.0	5	2.5	0.12
BorderYrs MatrixYrs	205.2	4	4.5	0.04
BorderYrs*Area	204.2	5	5.7	0.02
BorderYrs MatrixYrs MatrixUnburned	204.8	5	6.3	0.02
BorderYrs	211.5	3	8.6	0.01
BorderYrs MatrixUnburned	209.6	4	8.8	0.01
BorderYrs Area	210.8	4	10.1	0.00
BorderYrs InteriorCapRate	211.3	4	10.6	0.00
BorderYrs Area InteriorCapRate	210.8	5	12.3	0.00
MatrixYrs MatrixUnburned	221.4	4	20.7	0.00
NULL	235.1	3	32.2	0.00
InteriorCapRate	236.7	3	33.8	0.00
Area MatrixYrs	235.0	4	34.3	0.00
Area	240.9	2	35.8	0.00

^a *K* = number of parameters; AIC_c = AIC adjusted for small sample size; ΔAIC_c = difference in AIC_c in relation to the most parsimonious value; *w_i* = Akaike weight.

^b AIC_c value of the best-fit model = 209.2.

^c Interactive models also include non-interactive effects of the variables involved in the interaction.

APPENDIX B: PERMISSION FROM THE AUK TO REPRINT PREVIOUSLY PUBLISHED CHAPTER 2

 **AOU Executive Director** <executivedirector@aou.org> Aug 10 (2 days ago) ☆  

to Michael, me 

Hi Luke,

You have the permission of the American Ornithologists' Union to republish your *Auk* article as you requested. Let me know if you need anything else.

Congratulations and best wishes,
Scott

Scott W. Gillihan
Executive Director
American Ornithologists' Union
5405 Villa View Drive
Farmington, NM 87402
[505-326-1579](tel:505-326-1579)
ExecutiveDirector@aou.org
www.aou.org

VITA

Luke Losada Powell was born in Sea Cliff, NY in 1981. He left home at 17 to pursue a Bachelor of Science degree at Tufts University in biology and environmental studies, which included a semester in Madrid, Spain. After college, Luke spent two years working as an itinerant technician, including stints in Berkeley, CA, Manomet, MA, Puerto Maldonado, Peru, and Smithtown, NY. He then returned to academia in 2005, completing a Master of Science in Ecology and Environmental Studies from the University of Maine in 2008 under Dr. William E. Glanz, during which he studied Rusty Blackbird breeding biology. Drawn back to the tropics by Dr. Phil Stouffer's advertisement, Luke moved to Louisiana and began his PhD in January 2009, where he would spend more than a year studying tropical birds in the field near Manaus, Brazil. He will receive his doctorate in Wildlife and Fisheries Sciences from Louisiana State University in December 2013.