DEMOGRAPHY, ECOLOGY, AND BEHAVIOR OF CHESTNUT-BACKED ANTBIRD (*MYRMECIZA EXSUL*) POPULATIONS IN FRAGMENTED NEOTROPICAL RAINFOREST

A DISSERTATION
SUBMITTED ON THE SEVENTEENTH DAY OF MAY 2015
TO THE DEPARTMENT OF ECOLOGY AND EVOLUTIONARY BIOLOGY
IN PARTIAL FULFILLMENT OF THE REQUIREMENTS
OF THE SCHOOL OF SCIENCE AND ENBINEERING
OF TULANE UNIVERSITY
FOR THE DEGREE OF
DOCTOR OF PHILOSOPHY

BY

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ABSTRACT

The understory insectivore guild is disproportionately affected by deforestation, and knowing the underlying mechanisms is critical to effective conservation. I investigated demographic, ecological, and behavioral responses of Chestnut-backed Antbird (*Myrmeciza exsul*) populations (a persistent understory insectivore) to a fragmented Costa Rican rainforest landscape where many ecologically similar species have declined. I estimated demographic rates to parameterize population models in three habitats differentially affected by forest fragmentation: contiguous, peninsular, and fragment. Models indicated that *M. exsul* are declining in the peninsula (λ=0.83), but increasing in fragments (λ=1.41). Sensitivity analyses suggested that population growth was most sensitive to adult survival and nesting success, suggesting these two variables as potentially important explanatory demographic parameters in this landscape. I studied nest predation using digital video and quantified breeding success and population density in each site. Nest predation rate was so high in the peninsula that few nests fledged any young, much lower in the fragments, and intermediate in the contiguous forest, inversely tracking *M. exsul* population density and corroborating population growth rate findings. Using 22,000 hours of active nest video recordings, one primary predator emerged, the bird-eating snake (*Pseustes poecilonotus*), responsible for 80% of nest attacks. *Pseustes'* prevalence in the peninsula where predation rates were highest implies possible predation-limitation. Populations both declining and growing locally provided unique insights into the mechanisms of change in a deforestation-impacted landscape, but represent only some fragmentation consequences. Therefore, I reviewed regional studies to assess other potential contributions to understory insectivorous bird decline in the Sarapiquí. Empirical studies supported effects of habitat area loss, dispersal limitation, reduced microhabitat availability, and low physiological tolerances to changing climates.

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ACKNOWLEDGEMENTS

I am fortunate to have many people to thank for helping make this accomplishment possible.

I first thank my dissertation advisor Thomas W. Sherry, who gave me the setting to develop a project and the freedom to lead it. Tom brims with ideas in the way only the most experienced ecologists can, and his endless enthusiasm for sharing these ideas and developing good hypotheses to test them helped build the core of this dissertation and train me as a scientist. It is hard to imagine that this project would be successful without his patience and skill for revising drafts, unwavering support, and encouragement to always go a little bit further, exchange one more draft, or add *just one more* test. My other committee members, Caz Taylor, Jordan Karubian, and Doug Robinson, were each critical to developing the ideas of this dissertation and improving it with constructive critiques, and advice.

Many others contributed to this project. Endless thanks goes to the small army of field assistants who volunteered their time to this project and their blood to the mosquitoes, and who accepted rice and beans as currency. I am grateful to the staff of my field sites and our host families in Costa Rica for their logistical support and hospitality, especially Carlos de la Rosa (Organization for Tropical Studies, OTS), Roldolfo Tenorio (MINAET), and the late Don Rigoberto Valveri. I am grateful to my lab mates Stefan Woltmann for teaching me the ropes of studying chestnut-backed antbirds, Nicole Michel

for statistical help and logistical advice for working at La Selva, and Ashley Peele for supporting and understanding me in ways that no other friend can. I thank my students Danielle Ferraro, Briana O'Malley, and Megan McWilliams for their enthusiasm and dedication to their projects. I recognize coauthors not mentioned above: Alice Boyle, and Bryan Sigel for their contributions to manuscripts developed from these chapters.

Funding from Louisiana Board of Regents Graduate Fellowship, multiple grants from the Organization for Tropical Studies (OTS), the American Ornithologists' Union, the Stone Center for Latin American Studies, the Wilson Ornithological Society, the Newcomb College Institute, Sigma Xi, and an NSF grant to TWS made this research possible.

Words cannot express my gratitude to my parents, Alfonse and Gail Visco, for unconditionally supporting my endeavors, no matter what jungle they took me to, so long as they made me happy. Possibly the best thing that came from this dissertation was meeting the love of my life, Djihbrihou Abibou, who has been my rock of support through all of the triumphs and tribulations. Through his support, he has proven himself worthy to become my husband many times over.

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Chapter One

Introduction: Understory insectivorous bird population responses to fragmented tropical landscapes

Background and rationale

The terrestrial tropics are the most important place for bird biodiversity, holding 79% of species in lowland and montane forests, making conservation in these regions disproportionately critical (Sodhi et al. 2011). One of the most species-rich groups, understory insectivorous birds, is globally recognized as vulnerable for reasons including their specialized diets (Sherry 1984), restricted habitat tolerances (Lees and Peres 2006), and life histories that increase their sensitivity to diverse fragmentation impacts (Şekercioğlu et al. 2002). Changes in the insectivore assemblage could be seriously disruptive both ecologically and economically, as these birds link trophic processes (Şekercioğlu 2006) and provide important ecosystem services including insect control in natural and agricultural environments (Şekercioğlu et al. 2004, Whelan et al. 2008).

Most forested tropical countries are experiencing deforestation as a result of cattle ranching and agricultural expansion (Wright 2005, Newbold et al. 2014). These disturbances affect animal populations in diverse ways, but concern for the fate of the understory insectivores is accumulating (Sodhi et al. 2011). Four long-term Neotropical studies have examined effects of forest fragmentation on avian communities, including the insectivores: Biological Dynamics of Forest Fragmentation Project (BDFFP) in

Brazil, Barro Colorado Island (BCI) in Panama, Lago Guri in Venezuela, and La Selva Biological Station (La Selva) and surrounding Sarapiquí, Costa Rica. Results from the BDFFP indicate that the understory insectivorous guild indeed often suffers the highest impacts of tropical forest fragmentation (Stratford and Stouffer 1999; Laurance et al. 2002), and that mechanisms beyond basic species/area relationships are operating given the lag in species abundance/density and area observed (Bierregaard and Lovejoy 1989, Stouffer and Bierregaard 1995). At BCI, insectivorous birds and ground or understory nesters have also been disproportionately extirpated in ways not predicted by basic colonization and extinction, confirming this trend on a different scale (Willis 1974, Sigel et al. 2010). Results from Lago Guri contributed evidence for indirect mechanisms of species loss, including effects on mesopredators and herbivores that could be mediated by the loss of top predators from the islands (Feeley and Terborgh 2008). Inferences from forest islands created by flooding are useful; however, whether or not they reflect the processes of dispersal in terrestrial systems is questionable (Sherry 2008). The Sarapiquí region in the northeastern lowlands of Costa Rica, once contiguous forest, has been heavily fragmented since the 1960s, and now consists of a patchwork of terrestrial islands with various degrees of isolation, connectivity, and human intrusion (Sesnie et al. 2008, Joyce 2011). Within this region and at La Selva, insectivore, understory, and small-bodied bird populations have declined alarmingly—and most continue to decline—despite proximity to a large contiguous forest reserve (Sigel et al. 2006, 2010, Roberts 2007, Boyle and Sigel 2015).

The foregoing studies effectively identified the problem and some of the patterns, and also inspired many new questions. To date, we fundamentally lack demographic or ecological explanations for most of these avian responses to tropical forest fragmentation (Robinson and Sherry 2012a). In addition to direct area effects, potential mechanisms of population decline include reduced habitat connectivity, loss of preferred microhabitats or microclimates, changing food abundance or access, agricultural pesticide drift, and altered abundances of competitors and predators. Hence, the broadest question inspiring this dissertation was; What are the ecological mechanisms largely responsible for declines of understory insectivores in fragmented rainforest?

Several dissertations would be necessary to test all these mechanisms effectively, although progress has been made on most (see Chapter 5). Addressing the question of mechanisms on a landscape scale requires comparative study. One scientific advantage of forest fragmentation is that it creates unusual ecological conditions—large scale, often replicated natural experiments—for comparative studies to tease apart the mechanisms behind population and community changes. Addressing this question also requires study species persistent enough to provide insights into the conditions affecting their survival, but not so ubiquitous as to be uninformative (Şekercioğlu et al. 2007). Many species disappear quickly from fragments, prohibiting study, but Woltmann et al. (2010) identified a suitable small-bodied understory insectivore in the Sarapiquí, the chestnut-backed antbird (*Myrmeciza exsul*). This species can be found in many of the region's fragments and at La Selva, but Sigel et al.'s (2006) long-term comparative study indicated that the *M. exsul* population could possibly be declining at La Selva. Woltmann's research investigated one of the above hypotheses, lack of connectivity, also known as dispersal limitation (Woltmann 2010). His landscape genetic approach showed that *M. exsul* is highly dispersal-limited, affecting their densities and genetic diversity, and effectively ruling out travel among forest patches as an explanation for their patterns of persistence (Woltmann and Sherry 2011, Woltmann et al. 2012b, 2012a). Michel's (2012) dissertation investigated mechanisms relating to the loss of preferred microhabitat by comparing several ecological factors across forests in Central America. Michel's studies support microhabitat loss mediated by mesoherbivores as a decline mechanism. Specifically, insectivores were found to forage in association with liana tangles, which are degraded by peccaries in some cases, leading to various ecological consequences (Michel and Sherry 2012, Michel et al. 2015).

The motivation for the present study was to address another potential mechanism of understory bird decline, increased nest predation, possibly as a consequence of mesopredator release (Crooks and Soule 1999, Fahrig 2003). Young et al. (2008) had documented increased nest predation rates for several species (pooled) in fragments compared with contiguous forest, so the premise of the present study was that increased nest predation in fragments reduces fecundity below the level needed to offset annual mortality. To obtain predator identities (which are more informative of mechanisms than rates alone), this line of research required video-monitoring nests (Lahti 2009).

Avian video monitoring in the tropics – a critical evaluation of current methods

Current strategies for documenting predators on avian nests have advanced our understanding of predator-prey interactions, yet the body of research has traditionally been limited in many ways. The most obvious shortcoming of nest predation literature is temperate bias of studies. Only within the past ten years have tropical species received much attention. The temperate literature provides an excellent and extensive video-monitoring framework (Ribic et al. 2012); however, the ecological differences between temperate and tropical systems are substantial, so we may not always expect similar patterns. For example, higher predator and prey diversities and more stable temperatures characterize the tropics (Stratford and Robinson 2005). Another consideration for videography is that tropical humidity can challenge electronic equipment.

Many nest predation studies and reviews involve inconsistent methods, such as limited nest stages, temporal windows, and artificial nest use, which confound comparisons. For example, experimental studies using artificial nests only examine the incubation phase, but predators on nestlings may differ. Biased temporal sampling is another issue: Debates regarding the time of day at which predation occurs cannot be resolved without photographic or videographic technology and appropriate lighting (Libsch et al. 2008). Artificial nest studies can be biased in other ways as well because they usually only consider predators of quail, chicken, or finch eggs, but it is doubtful that predators on real and artificial nests are the same (Roper 1992, Robinson et al. 2005b). Finding and monitoring real nests is the obvious solution; however, observational studies lack the precise controls and larger sample sizes provided by experiments. Many artificial studies also rely on indirect information to guess predator identities, but conducted without ground-truthing, these methods are likely biased and inaccurate (Zanette 2002, Moore and Robinson 2004).

Lastly, sample sizes of identified tropical nest predators have been inadequate to date. Tests of predation differences among habitats in fragmented landscapes has tended to focus on predation rate rather than predator identities, but the importance of identifying the predators to further understand mechanism cannot be overstated (Lahti 2009, Weidinger and Kocvara 2010). Anecdotal accounts of real depredation events provide a starting point, but they are rarely able to distinguish the relative importance of different predator species (Robinson and Robinson 2001). Study durations should be long enough to sample variable population distributions and abundances (Fleishman and Mac Nally 2007, Weidinger 2008). This information is particularly applicable to studies correlating avian declines with long-term ecological patterns like climate change or forest fragmentation (Stratford and Robinson 2005).

Despite these drawbacks, a body of tropical work is beginning to emerge. A recent Aftrotropical study was among the first to characterize nest predation rate for an entire suite of tropical species (Newmark and Stanley 2011). Anecdotes of predator identities in the tropics are accumulating (mostly in Panama) as technology improves and research interest grows (see below). Nevertheless, substantial monitoring of real nests comparatively, or even at sample sizes over 10 remains to be accomplished even in the Neotropics, and has only been accomplished once in another tropical region (Pierce and Pobprasert 2013).

Video monitoring is an accurate and reliable method for identifying tropical nest predators. New technologies make videographic studies more feasible and economical. Recent digital systems use reduced camera unit size, can allow for remote control, have improved memory capacity, and require less power (Bolton et al. 2007, Pierce and Pobprasert 2007, Stevens et al. 2008, Steen 2009). Setups also now use infrared light sources from light-emitting diodes (LEDs; e.g., Pierce and Pobprasert 2007) or lasers (Santos et al. 2008) for nocturnal or low-light diurnal monitoring. The increasing portability, reliability, and longevity of these camera systems make them practical and versatile. Using such systems, Robinson et al. (2005a) indicted one snake species

(*Pseustes poecilonotus*) as responsible for 80% of antbird nest predation in Panama, where raptors were previously presumed to be more important. Other documented Panamanian nest predators include toucans, snakes, kites, monkeys, and another antshrike (a novel observation) as predators at slaty antshrike (*Thamnophilus atrinucha*) nests (Tarwater 2008); oropendolas, raptors, a jay, and an opossum at lance-tailed manakin (*Chiroxiphia lanceolata*) nests (Reidy 2009); and snakes and monkeys at greater ani nests (Riehl and Jara 2009). In monsoon forest of Thailand—a wet environment very hard on electronic equipment—Pierce & Pobprasert (2013) used a researcher-built system to identify 87 nest predators. These goals are challenging to achieve in the tropics.

Ensuring accurate and reliable nest predator identification requires employing the most rigorous methods available. Studies should strive to (1) identify both diurnal and nocturnal predators via continuous imaging technology, (2) account for habitat heterogeneity, (3) span both the incubation and nestling stages, and (4) procure sample sizes of 50-100 observations (Weidinger 2008).

Synopsis of chapters: a demographic approach

In the course of my research, it became clear that a demographic perspective was useful for placing nest predation into its broader ecological context. I became interested in how *M. exsul*'s various demographic rates differed among habitats; how predators and other ecological contexts varied in ways that contributed to the demography; and how these various aspects influenced each population's behavior.

In Chapter 2, I addressed the question of how demographic parameters interact to determine whether a population persists or declines. Assessing and modeling population impacts from forest fragmentation demographically is an important tool to understand how and why populations respond to changing environments (Anders and Marshall 2005). I used comparative matrix modeling to (1) examine how the demographic components of survival and productivity vary across a fragmented landscape, (2) ask how habitat type affects population growth rate, and (3) evaluate how sensitive the population growth rate is to changes in each demographic parameter. A separate model estimated population growth rate for fragments, peninsula (La Selva), and contiguous forest habitats. These analyses revealed variable population dynamics. The population at La Selva had lower demographic rates (e.g, adult survival and nest success) than the fragments, and consequently, appears to be declining. The fragment populations on the other hand generally survived and reproduced at higher rates, and the model estimated growing fragment populations. Sensitivity analyses suggested that factors influencing adult survival and adult/juvenile nest success were good candidates for further investigation, as the population growth rates were most sensitive to changes in those parameters. In the next chapter, I examined one factor that could theoretically limit adult survival and adult/juvenile nest success: nest predation risk.

To understand the reasons we observed the nest success rates we did in each habitat, I quantified egg and nestling mortality risk in Chapter 3. Beyond just quantifying rates, I also identified predators at 46 nest predation events across the same set of habitats. I expected that nest predator taxa would vary spatially, that predation rates would be highest in fragments, and that the identity of primary nest predators would strongly influence breeding productivity. Results were surprising in light of expected trends in fragments from the nest predation literature (Wilcove 1985), but made sense in light of the population patterns described in Chapter 2. Indeed, nest predation rate varied inversely with population density. Nest predator identities suggested a dominant role of bird-eating snake (*P. poecilonotus*)—the same predator implicated by Robinson et al. (2005). What determines this snake's presence or activity is unknown. Further research is warranted into the natural history of this predator, its nest-searching behavior, and its potential influence on other Neotropical breeding birds with accessible nests (e.g., most birds).

Chapter 4 is a synthesis that scales back out to a regional view and asks what we know in aggregate regarding the causes of understory bird decline across the Sarapiquí's fragmented landscape. This chapter reviews and synthesizes findings from ~50 years of avian study. The evidence presented supports effects of direct loss of habitat area, limited dispersal among separated forest patches, reduced availability of preferred foraging microhabitat, elevated nest predation in association with bird-eating snake, and low physiological tolerances to changing climate.

Finally, in Chapter 5 I provide overall conclusions, along with recommendations for future research. Most ecological studies could benefit from larger sample sizes and more replication, and this dissertation is no exception. The contributions of the sum of these studies include, for the first time in a tropical understory insectivore, (1) development and application of a population model in a comparative demography framework, (2) challenges to dominant paradigms of population behavior in fragments and protected reserves, and (3) identification of an influential nest predator species across a landscape. These findings involving *M. exsul* further the understanding of several ways in which life history traits and demography in tropical forests differs from temperate forests. The regional synthesis contributes to the field by alerting tropical bird conservationists to relevant threats to understory birds in Central American rainforest.

Chapter Two[1]

Persistence and peril in fragmented tropical rainforest landscapes: comparative demography of an understory insectivorous bird

ABSTRACT

Despite many tropical passerine birds' long breeding season and long lifespan, the combination of small clutches, low nesting success, and a long nesting cycle leave many species with low productivity. How do these demographic parameters interact in fragmented landscapes to determine whether a population persists? We studied populations of chestnut-backed antbird (*Myrmeciza exsul*) in three landscapes, contiguous, peninsular (La Selva Biological Station, a protected forest reserve surrounded by pasture on three sides), and fragmented habitats to evaluate the relative importance of survival and productivity parameters to population growth rate. For each habitat type we built a two-stage annual population model including adult and juvenile survival, and productivity, almost completely parameterized with local field data. Our models indicate that the peninsular population is declining (λ=0.83), the contiguous population is nearly stable (λ=1.05), and the population in the fragmented landscape is growing (λ=1.41). Elasticity and sensitivity analyses showed that population growth in the peninsula was most sensitive to proportional variation in apparent adult survival and absolute changes in nesting success. Population growth in fragments was equally sensitive to proportional

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[1] A version of this manuscript is being prepared with coauthors C. Taylor and T.W. Sherry for submission to the Journal of Applied Ecology

change in all parameters and to absolute variation in juvenile nest success. Results from the peninsula suggest that mechanisms related to adult mortality and nest failure are important to population declines there. Residence within this well-protected reserve is not protecting this population. In the fragments on the other hand, adult survival may not be limiting; dwelling in small fragments has not prevented *M. exsul* from realizing growth. Overall we show that demographic parameters help identify different effects on population dynamics depending on their ecological context.

INTRODUCTION

Earth's biota is increasingly threatened by global anthropogenic disturbances. In the tropics the greatest threat is habitat loss and fragmentation (Newbold et al. 2014). Considerable effort has focused on impact assessments and conservation management relevant to tropical habitat fragmentation (Fleishman and Mac Nally 2007), but our knowledge is incomplete (Stutchbury 2007). Identifying the contributions of particular demographic phases to overall population dynamics is one way to address the mechanisms behind observed impacts (Brault and Caswell 1993), which is necessary to develop more targeted conservation measures. Despite much research on the effects of forest fragmentation in general, our current understanding of these mechanisms is limited, even for well-studied groups like birds (Lampila et al. 2005).

Mechanisms with the greatest impacts on avian population dynamics in fragmented tropical forest landscapes include area effects, dispersal limitation, microhabitat loss, nest predation, and physiological stress (Chapter 4; Robinson & Sherry 2012). These mechanisms affect multiple demographic processes for fragment-inhabiting wildlife. How do these demographic processes vary across a fragmented landscape, and how do they interact to determine whether a population persists? Addressing these questions rigorously requires a species-specific focus at relevant spatial scales rather than more crude taxa- and landscape-level assessments (Stutchbury 2007). Yet because many demographic factors contribute to population dynamics, understanding exactly why populations persist or perish remains challenging. Few studies gather comprehensive enough life history information to address such questions. Appropriately parameterized mathematical models are powerful tools to bridge these gaps in understanding how populations respond to disturbance.

Models help identify important processes that warrant further investigation, and are essential for addressing questions that are not as easily amenable to field or lab work. Population models in particular help evaluate the relative importance of specific demographic parameters to population growth rate. Assuming a closed population, in an annual cycle, productivity and survival interact to determine growth rate (Noon and Sauer 1992). These demographic components are determined by one or more demographic parameters, or vital rates estimable directly from a population. In fragmented forest landscapes a variety of demographic parameters could vary in ways that impact population dynamics. Moreover, some parameters influence population dynamics disproportionately. For instance, loggerhead sea turtle (*Caretta caretta*) population growth rate was most responsive to juvenile survival, prioritizing conservation efforts for juveniles more so than eggs (Crouse et al. 1987).

Many tropical bird species are declining globally, but for largely unknown reasons. Despite long breeding seasons, the combination of small clutches, low nesting success, and a long nesting cycle leaves many tropical passerines with low enough productivity to jeopardize population growth. Yet failure in one season does not preclude self-replacement in the next, because many tropical birds' have relatively high survival rate both as adults and juveniles (Russell 2000, Wilson et al. 2011, Woltmann and Sherry 2011). Thus, high survival can mitigate effects of low seasonal fecundity. However, fragmentation reducing survival rate can put a population at risk (Ruiz-Gutiérrez et al. 2008). Birds might also increase productivity (i.e., their odds of successfully raising a brood within a season) by shortening intervals between renestings after failure (Roper 2005). Therefore, we can better explain a group's response to ecological changes like forest fragmentation by knowing most, if not all these demographic rates.

Some tropical birds have life-history traits making them particularly sensitive to forest fragmentation. For example, understory insectivores, a guild of particular concern (Sodhi et al. 2004, Şekercioğlu and Sodhi 2007) are sensitive to fragmentation as a result of traits including large territory size, specialized diet, and small body size. However, while many understory insectivore populations have declined, some have not. In Costa Rica's Sarapiquí (Atlantic coastal lowlands) region the chestnut-backed antbird (*Myrmeciza exsul*; Thamnophilidae) persists in forest fragments, unlike many other understory insectivores (Woltmann et al. 2012a). *M. exsul* has sexually dimorphic plumage allowing sex-specific study, molt cycles that permit approximate ageing, accessible nests, and abundant and widely distributed lowland populations (primarily below 1000 m masl), making it amenable to demographic research in a fragmentation context (Skutch 1969, Woltmann et al. 2010).

M. exsul's persistence in a fragmented landscape presents an unusual opportunity to use comparative modeling to (1) examine how the demographic components survival and productivity vary in the landscape, (2) ask how habitat type affects population growth rate, and (3) evaluate how sensitive the population growth rate is to changes in each demographic parameter. Together, these analyses help pinpoint the factors most likely to tip the balance of an understory insectivore's population dynamics.

Here we determined the demographic components of *M. exsul* populations, and estimated relevant vital rates in each of three forest habitat types: fragmented, peninsular, and contiguous. Using these parameter estimates, we developed a matrix projection model for each type, and estimated its population growth rate (Caswell 2001). To interpret these results we used perturbation analyses to calculate sensitivity and elasticity of the growth rate to variation in the vital rate components (Caswell 2010). Results of these tests allowed us to identify relative influences of different demographic parameters on population growth.

SITE DESCRIPTION

The Sarapiquí watershed on Costa Rica's Caribbean slope includes a range of elevations—e.g., Braulio Carrillo National Park (BCNP) rises to almost 3,000 masl—but deforestation of what was until the 1950s essentially contiguous lowland and premontane tropical wet/rain forest has left much of the lowland landscape heavily fragmented (Fig. 2.1). More than 70% of this forest has now been converted to pasture, agriculture, or other uses, leaving a patchwork of variably sized forest fragments (Read et al. 2001, Fagan et al. 2013). This region receives nearly 4 m of rainfall annually, depending on elevation, with a season of less rain between February and April that coincides with the breeding activity of many birds (Skutch 1969).

We studied *M. exsul* at four sites, representing three landscape conditions: a contiguous site in BCNP (Quebrada Gonzalez), peninsular La Selva Biological Station, and two fragments (La Virgen and Rio Frio; Fig. 2.1). We used trails starting at the Quebrada Gonzalez ranger station, at 400 masl within the 46,000 ha BCNP, to survey an approximately 100 ha area. Connected to BCNP's northern end is La Selva Biological Station, where we surveyed an old-growth 300 ha focal area of the 1,600 ha biological reserve. La Selva is a flagship field station for tropical research extending back to the 1960s. Land conversion has left La Selva a peninsula of forest bordered by a matrix of pasture and agriculture on three sides (Joyce 2011). The two forest fragments are of similar size, age, composition, and surrounding matrix. Río Frío is a 90 ha fragment of old growth with evidence of some selective logging, of which we surveyed the southern 40 ha so the fragment sizes would be comparable. It is surrounded by pasture, a dirt road, and some mixed agriculture (e.g., heart of palm). La Virgen is a 41 ha fragment of old growth with some active selective logging, surrounded by pasture, a dirt road, and a pineapple plantation on one side.

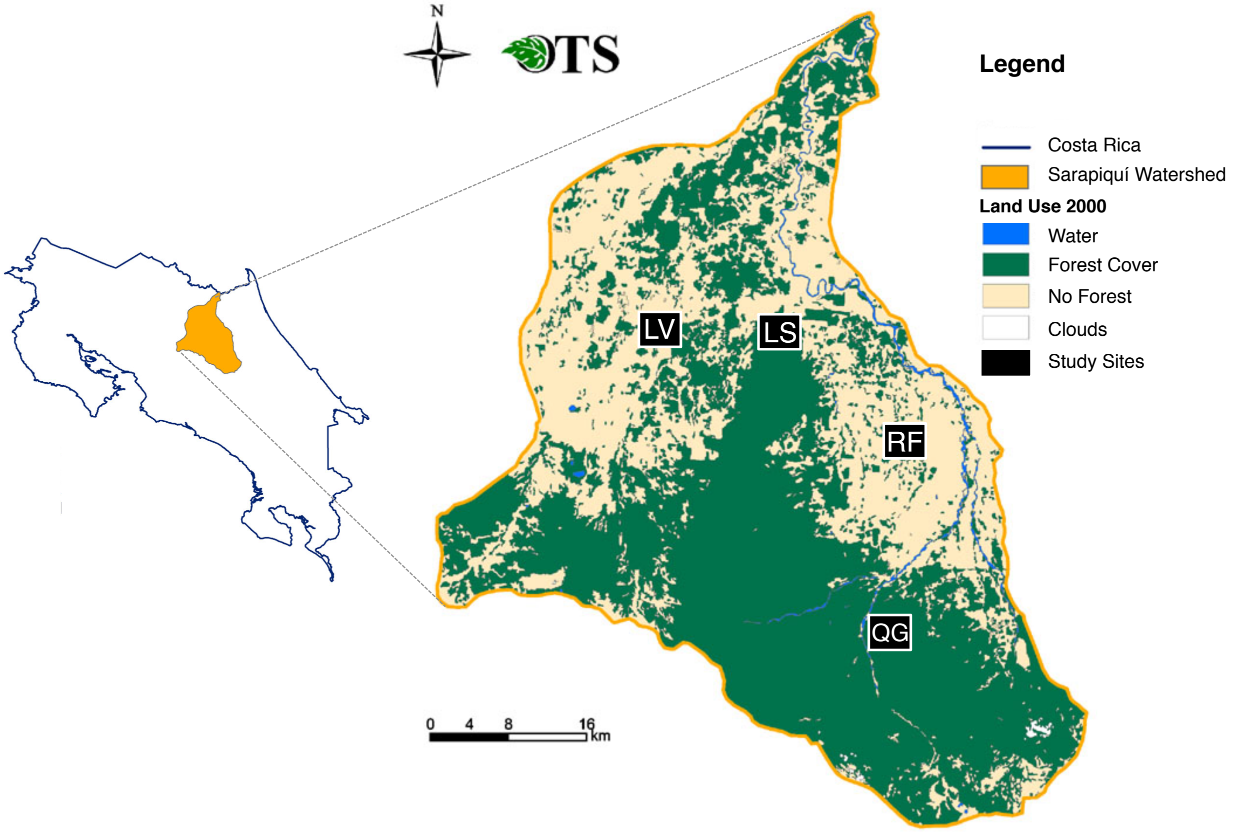

Figure 2.1. Field sites for surveying *Myrmeciza exsul* populations in Costa Rica's Sarapiquí region (see inset). QG = Quebrada Gonzalez in the 46,000 ha Braulio Carrillo National Park. LS = La Selva Biological Station, a 1,600 ha reserve peninsular to the park on one side. LV = La Virgen, a 41 ha fragment. RF = Río Frío, a 90 ha fragment.

MODEL DESCRIPTION

Our models are built from a deterministic population matrix model framework (Eq. 2.1):

$$N_{t+1} = \mathbf{M}N_t \ , \qquad (2.1)$$

where **M** is the projection matrix, N_t represents the population size at the initial time step (t), and N_{t+1} represents the population size one time step (in years) into the future (Caswell 1989). The dominant eigenvalue of the population projection matrix, **M**, estimates the asymptotic population growth rate, λ. Since a previous study indicated a lower survival rate for juveniles (Woltmann and Sherry 2011) and our field observations document birds breeding in their first year, we divided the population parameters to adult and juvenile groups to develop a two-stage model. Each time step then includes both the annual number of juveniles produced by both adults and juveniles and the annual number of juveniles and adults surviving (Fig. 2.2).

We thus describe each population as a two-stage, female-only matrix (Eq. 2.2):

$$\begin{pmatrix} J \\ A \end{pmatrix}_{t+1} = \begin{pmatrix} B_J & B_A \\ S_J & S_A \end{pmatrix} \begin{pmatrix} J \\ A \end{pmatrix}_t \qquad (2.2)$$

where A_t and A_{t+1} are the numbers of adult females (*M. exsul* in their 2nd breeding season or older) in the population at times t and t+1, respectively; B_A and B_J are the productivity of adult females and juvenile females, respectively; J_t and J_{t+1} are the numbers of juvenile females (*M. exsul* in their 1st breeding season) in the population at times t and t+1, respectively; and S_A and S_J are the apparent adult and juvenile survival, respectively.

Productivity (B) is the annual number of surviving female offspring produced per female parent. Thus, productivity includes fecundity, as well as the survival of offspring from an egg to an independent bird (Ricklefs and Bloom 1977). Fecundity (the number of eggs produced per female parent) includes the clutch size (c) divided by two (to reflect female offspring produced, assuming a 50:50 sex ratio), multiplied by the number of nests attempted in each breeding season (N_Y). Offspring survival begins in the nest for the first 26 days of life from egg laying to fledging (nest success, S_N). We estimated nest success separately for pairs where one or both parents were juveniles (S_{NJ}). Dependent fledgling survival (S_F) spans the approximately 8-week period from fledging to independence (DMV, *pers. obs.*). Between independence and the first breeding attempt (spanning 5-7 months depending on the site) we estimated immature survival (S_I). Thus, we express productivity as:

$$B_A = \frac{c}{2} N_Y S_N S_F S_I \qquad (2.3)$$

and

$$B_J = \frac{c}{2} N_Y S_{NJ} S_F S_I \qquad (2.4)$$

We constructed three models, each with different sets of parameters corresponding to *M. exsul* populations in contiguous, peninsular, and fragmented habitat types, combining data from both fragments. We calculated the dominant Eigenvalue of each matrix **M** as our estimate of λ for each site. The stable stage distribution, ***w***, is a vector characterizing the proportion of individuals in each stage class, calculated as **M*w*** = λ***w***, where ***w*** sums to one across all stages. The reproductive value, ***v***, is a vector representing the impacts of reproduction on λ, calculated as **M*v*** = λ***v***, where the smallest stage class is scaled to one. The structure of the stable stage distribution and reproductive value of each stage class in turn determine the sensitivities of the growth rate (Caswell 2010).

Our models assume a closed population. Available evidence supports this assumption for *M. exsul*: They likely avoid crossing large gaps due to lack of stamina (Moore et al. 2008), and landscape genetics show that breeding dispersal is local (<1km), as is natal dispersal (<2km; Woltmann & Sherry 2011; Woltmann, Sherry & Kreiser 2012). The models also assume that immigration balances emigration. Because dispersal among fragmented populations is essentially non-existent in this species, we can effectively eliminate source-sink dispersal as an explanation for observed patterns. To further justify this assumption, we compared average numbers of unbanded birds (i.e., immigrants) captured to offspring produced (i.e., potential emigrants) annually in each site. We excluded the first year of banding data from each site, and years in which we did not perform a complete survey. The mean ratio of unbanded birds to new offspring was 8:7 in QG (n=1 yr), 8.5:4.5 in LS (n=2 yrs), 5.5:6.5 in RF (n=2 yrs), and 11:15 in LV (n=1 yr). These ratios suggest a nearly balanced population in contiguous forest (QG) and one fragment site (RF). With a positive difference of 4, the possibility exists that the peninsular forest site (LS) could serve as a population sink. With a negative balance of 4, the other fragment (LV) could possibly serve as a population source, producing more offspring than it is recruiting; however, birds must disperse through at least 7 km of riparian corridor to reach the next suitable forest patch, which is unlikely given *M. exsul*'s typical dispersal range (Woltmann et al. 2012b).

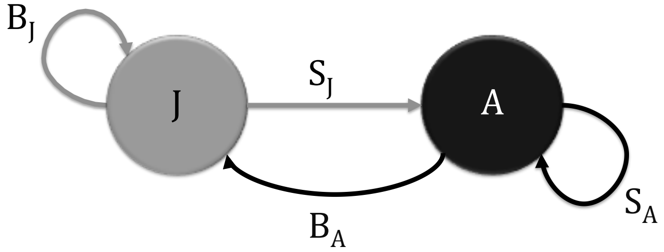

Figure 2.2. Two-stage life cycle graph of *Myrmeciza exsul*. B_A is adult seasonal productivity, B_J is juvenile seasonal productivity, S_A is adult apparent survival, and S_J is juvenile apparent survival.

DEMOGRAPHIC PARAMETERS

Adult and juvenile apparent survival

Annual apparent survival is the annual probability of surviving and returning to the sampling area, independent of the probability of being encountered. We surveyed *M. exsul* for surviving adults using traditional capture-mark-recapture/resight methods. We target-netted in each pair's territory using conspecific vocalization playback. Upon capture, any unmarked individuals received a numbered aluminum band and unique Darvic leg band color combination to facilitate resighting. Birds were aged by plumage (Wolfe et al. 2009, Woltmann et al. 2010). Territories were only considered vacant after at least two separate capturing attempts. We incorporated 136 *M. exsul* live encounter histories from Woltmann and Sherry (2011) and Woltmann et al. (2012) with those from the present study for a total of 194 capture histories. Surveys were conducted in contiguous habitat in 2009, 2012, and 2013; in peninsular habitat in 2004 – 2012; and in the RF fragment in 2009, 2011, 2012, and 2013 (too few years of capture-recapture data from LV to estimate adult survival).

We used Program MARK 8.0, accessed via the RMark 2.1.8 interface in program R 3.1.2 (Laake 2013, R Core Team 2014) following the White and Burnham (1999) protocol to fit a set of Cormack-Jolly-Seber (CJS) models with various conditions to the data, and to estimate apparent survival (φ) of adults and juveniles and recapture probabilities (p) of adults (Lebreton et al. 1992). CJS models assume that marked animals (1) have equal recapture probabilities at each time step, (2) have equal probabilities of surviving to the next time step, (3) do not lose their marks, and (4) are sampled and released instantaneously. We never recaptured a bird missing one or more of its bands (assumption 3). Capture surveys took approximately the same amount of time each season, 1-3 months, and birds were released within 20 minutes of their capture (assumption 4). To test underlying model assumptions (1) and (2), we first fit the data to the most general (global) model φ (~age*sex*site*time) *p* (~sex*site*time) to assess goodness-of-fit using program RELEASE via RMark. There is no age effect of recapture because only adults are ever recaptured. Program RELEASE does not allow exclusion of the time effect, and thus tests often reported insufficient data. Therefore, we next removed the time effect and tested the new general model, φ (~age*sex*site) *p* (~sex*site), in program MARK to estimate a variance inflation factor ($\hat{c}$) with the median $\hat{c}$ approach, as this approach is not restricted to fully time-dependent models. If this value indicated over-dispersed data ($\hat{c} > 1$) we used it to adjust the statistics to account for extra-binomial variation. When we made $\hat{c}$ adjustments, we report the quasi-likelihood Akaike's Information Criterion for small sample sizes ($QAIC_C$). If no adjustments were made we used AIC_C for multi-model selection. Models were ranked by their difference from the best-fit model; those with $\Delta AIC_C < 2$ and differing by more than 1 parameter were considered to have strong support (Burnham and Anderson 2002).

Birds were grouped by site (peninsular, contiguous, or fragmented), sex (male or female), and age (adult or juvenile) to examine the effects of these factors and to generate appropriate estimates for input to the population model. Time effects in our models entailed a year-by-site interaction because each site was not sampled in each year. Our data were too sparse to include this time effect in addition to effects of sex and age (our effects of interest) in our models. To designate bird age, we binned years 0 to 1 (exclusive), as "juvenile" and years 1 to 10 (inclusive), as "adult". For model selection, time intervals were set to (0.25,1,1,1,1,1,1,1), to account for a December to February survey and annual surveys thereafter because these intervals reflect capture survey timing at site with the highest sample size. There was neither evidence of capture heterogeneity nor transience in our general model. The median $\hat{c}$ was 1.170 (SE 0.009), and we adjusted accordingly, although model rankings were unaffected. To determine the best recapture probability model to include with survival analyses, we performed a step-wise model selection: Keeping φ constant we ran all likely combinations of p, then performed model selection to determine the best-fit model, φ(~1) p(~sex). In all further models, p was set to this model.

Because all models provide some value, we used weighted model averages to derive our survival estimates where possible. We estimated survival separately for each site. The peninsular forest site (LS) included 128 individual capture histories, and time intervals were the same as in the initial general model. Goodness-of-fit was sufficient and the median $\hat{c}$ was 1.03 (SE 0.010), close enough to 1 to not require adjustment. For the contiguous forest site (QG), data were too sparse (n=27 individual capture histories) to satisfy goodness-of-fit assumptions. In the fragment (RF), 39 individual capture histories were recorded. We set the time intervals to (2, 1.25, 2) to match sampling initiation dates. Goodness-of-fit was only satisfied with a more basic set of candidate models, with only an age effect of survival and sex effect of recapture. The median $\hat{c}$ was 2.72 (SE 0.037), and we subsequently adjusted the models using this overdispersion estimate.

Adult and juvenile productivity

Seasonal productivity is defined as the number of female offspring produced per female per breeding season that survive to breeding age. Essentially, after determining the average number of eggs produced annually (factoring in clutch size and renesting attempts), productivity takes into account the chances of a successful nest, the subsequent survival of offspring while they are dependent, and finally the survival of independent offspring. Thus, our estimate of productivity includes fecundity (number of eggs per adult), nest survival, fledgling survival, and immature survival. Because birds breeding for the first time tend to have lower success, we estimated productivity during the first year separately from subsequent productivity to derive juvenile productivity estimates (Eberhard 1983).

Fecundity

Average clutch size (c) was estimated separately at each site from data collected during this study. We estimated the average number of nesting attempts per year (N_Y) per pair for each site by tracking the breeding activity of pairs over the season. We scaled the number of nesting attempts observed during the observation period (2.5–4 months) to match a 6-month long breeding season (Stiles & Skutch 1989; *pers. obs.*).

Nest success

Nest success (S_N) covers survival during the nesting cycle from egg laying to nestling fledgling, which is 26 days (±1 day) for this species (Visco and Sherry 2015). We define S_N as the daily nest survival rate (DSR) raised to the power of the number of days in the nesting cycle. *M. exsul* populations were systematically monitored for nest survival in peninsular forest (LS) in 2010 and 2011, in contiguous forest (QG) in 2012 and 2013, in fragment RF in 2011 and 2013, and fragment LV in 2012. We located nests by following parental behavioral cues and vegetation searching in active territories. Researchers monitored nests on foot and with continuously monitoring digital cameras (see Chapter

3). To estimate general nest success (S_N) and juvenile nest success (S_{NJ}) we used the nest survival model in Program MARK 8.0 (accessed via Program R 3.1.2 and the RMark 2.1.8 interface; Laake 2013; R Core Team 2014) to estimate DSR and overall nest success (White and Burnham 1999, Dinsmore and Dinsmore 2007). Grouping variables included habitat (peninsular, contiguous, or fragment), year (2010–2013), time (within-season linear pattern of survival), adult age (A=both parents were adults, J=at least one parent was a juvenile), and nest age (within-nest linear pattern of survival, varying from 0 to 26 days). We applied time-dependent and nest age covariates according to Program MARK protocols (Dinsmore et al. 2002, Rotella et al. 2004). All nests were used to estimate adult DSR, but only nests with definitively aged parents were used for estimating S_{NJ}. Visco and Sherry (2015) previously estimated daily predation rates (1 – DSR) from these data, but in the present study, abandoned or starved nests also counted as failures (in addition to nests that were depredated), and nests rearing one or more nestlings to fledging were considered successful. We ranked and evaluated models according to the same AICc criteria described above. We used the best-fit model to derive nest survival estimates.

Fledgling survival

Fledgling survival (S_F) spans the period from the time a nestling fledges to when young are independent of parents. For *M. exsul* this fledgling period lasts for approximately eight weeks based on weekly resightings and the length of time before parents attempted a second brood (parents will not renest until their offspring are depredated or independent; DMV *pers. obs.*), but some other Thamnophilids show substantial individual variation in the length of this period (e.g., Tarwater & Brawn 2010).

Fledglings received one numbered aluminum band and one colored Darvic leg band when their tarsi were of appropriate size, between Day 5 and Day 7 (see Chapter 4). After fledging, we attempted to resight fledglings weekly on their territories. Often, fledglings hid in dense or inaccessible vegetation and we could not identify them individually. In these cases, we inferred their presence (or not) by alarm vocalizations of the parents and movement in the vegetation. We resighted *n*=28 fledglings. Low nest success rates, difficult terrain in some habitats, and the onset of the rainy season prevented further sampling. We initially used Lukacs' "Young survival from marked adults" protocol in Program MARK 8.0, but Lukacs' models failed to converge. Therefore, we substitute an estimate from a related species, western slaty antshrike (*Thamnophilus atrinucha*), into all three population models as a reasonable placeholder. *T. atrinucha* fledgling survival (±SE) is 0.76 ± 0.07 (Tarwater et al. 2011) for the eight-week dependent period.

Immature survival

Between the time of independence from parents and their first breeding season as a juvenile, birds are "immatures" *sensu* Ricklefs (1997). We estimated survival of immature *M. exsul* (S_I) as the habitat-specific juvenile survival rate, raised to the power of the fraction of the year that they spend in this period. We determined the length of this period by converting dates to the Julian time scale and averaging the fledge dates for each habitat. All individuals transitioned from immature to juvenile on 1 March.

Among and within sites, we compared adult survival, juvenile survival, recapture rate, and nest survival estimates using program CONTRAST (Sauer and Hines 1989).

UNCERTAINTY, SENSITIVITY, AND ELASTICITY ANALYSES

We used several quantitative analyses to identify various patterns of increasing complexity in the relationship between model input parameters and responses, specifically, uncertainty, sensitivity, and elasticity analyses by habitat (peninsula, contiguous, and fragment). Uncertainty analyses quantify confidence in the estimates, given the probabilities of the model inputs. Sensitivity analyses (*sensu lato*) evaluate how sensitive the model output (λ) is to variation in specific demographic parameters, and include sensitivity (*sensu stricto*) and elasticity methods. Sensitivity analysis (hereafter *sensu stricto*) tests the relationship of a parameter to the model output as each parameter varies absolutely, in this case, within the distribution of its 95% confidence interval. Elasticity analysis differs in that each input parameter varies in proportion to itself, here by a -10% and +10% proportional change relative to the mean estimate, such that the values reflect relative contributions of each parameter (de Kroon et al. 1986, Caswell 1989).

We used global sampling-based techniques for our analyses rather than local methods (e.g., partial derivatives), as they better account for greater uncertainty in the input factors that is often the case in biological systems (Marino et al. 2008). These techniques involved parameter space sampling with Latin hypercubes. Latin hypercube sampling is a method of parameter space exploration that efficiently generates an even sample of a multidimensional space involving the variation of each input parameter, and then evaluates the model at each parameter combination (McKay et al. 1979). To sample parameters and evaluate model results with the analyses that follow, we implemented Latin hypercube parameter space sampling via Package ‘pse’ 0.3.4 (Chalom and Prado 2014) in Program R 3.1.2 (R Core Team 2014). We accounted for correlation among the input variables by defining and prescribing a correlation matrix to the parameters, and then using single-switch-optimized sample reordering as per the Huntington-Lyrintzis algorithm (Huntington and Lyrintzis 1998). The generated sample sets (n=200 per parameter) for each habitat were then applied to the population model function.

Uncertainty

First, we implemented uncertainty analyses to evaluate the probable distribution of the model output (the population growth rate, λ). We fit an empiric cumulative distribution function to the model results for sensitivity (ECDF; Helton & Davis 2003).

Sensitivity

To assess the nature of the relationship between each parameter and the model output, λ, we generated scatterplots of the Latin hypercube-sampled values of each parameter against its associated model outputs. We visually examined scatter plots of the values of each of the eight parameters in relation to λ; graphical assessments of the scatterplots identified emerging patterns and any nonlinear or nonmonotonic relationships (Kleijnen and Helton 1999).

We used multiple linear regression to assess the strength of nonlinear associations between the model output and each input parameter, after removing the linear effect of the other parameters. We rank transformed the data to obtain partial (rank) correlation coefficients (PRCC)–robust indicators of relationships that may be non-linear but still monotonic decreasing or increasing; Marino *et al.* 2008). These coefficients were tested for a significant relationship with λ using Spearman's rank correlation (Saltelli and Marivoet 1990). We bootstrapped the coefficients 1000 times to obtain each parameter's confidence intervals for sensitivity and elasticity.

We used a measure of concordance, the Symmetricized Blest Measure of Association (SBMA), to determine the sample sizes needed to achieve consistency among our PRCC results from different runs of the model (Genest and Plante 2003). We generated models with n=200 samples and n=300 samples of each parameter in the Latin hypercube (Chalom and Prado 2014). We considered models with agreements >0.75 to be acceptable (1 is perfect agreement, -1 is complete disagreement). The peninsula, contiguous, and fragment models had agreements of 0.85, 0.96, and 1.00, respectively, suggesting that further increasing the sample size over 200 does little to improve results, so the analyses presented here used n=200 samples.

Elasticity

Each of the above analyses described under "*Sensitivity*" (except ECDF) was repeated using the elasticity sampling scheme to assess how sensitive λ was to ± 10% proportional changes in each parameter, rather than over the range of the 95% confidence interval.

RESULTS

Population Model

The population model projected a substantially declining growth rate, λ, of 0.83 for the peninsula, a relatively stable λ of 1.05 for contiguous forest, and substantially increasing λ of 1.41 for the fragment (Table 2.1). Adults dominated the stable-stage distribution ($\boldsymbol{w}$) and reproductive values in all habitats (Table 2.1). The juvenile to adult ratio (indicated by the stable stage distribution) increased from the peninsula to contiguous to fragmented forest. Capture and territory mapping data confirm that in an average season, the surveyed population consisted of less than 20% juveniles in the peninsula, and less than 15% in the contiguous forest. In the fragments, however, juveniles typically represented between 25% and 30% of the surveyed population, qualitatively confirming the model results. The reproductive value (***v***) of adults relative to juveniles was highest in contiguous forest and lowest in the fragment, suggesting that population growth in the contiguous forest was highly sensitive to adult survival and that the effect of adult survival on the population growth rate was much smaller in fragments than in the other habitats.

Estimates of each demographic parameter were input into the population matrix model (Table 2.2). For each parameter estimate we calculated a 95% confidence interval and ± 10% proportional change for sensitivity and elasticity analyses, respectively (Table 2.2).

Adult and Juvenile Apparent Survival

The best-fit model from the peninsular forest (LS) model set was an age effect on survival and a sex effect on recapture (Table 2.3). We used model-averaged estimates for adult females and juvenile females in this site (Table 2.2), values not representing a significant difference (X^2=1.46, df=1, p=0.226). Adult and juvenile male survival estimates were 0.733 ± 0.031 and 0.586 ± 0.109, respectively. Adult female and male survival probabilities did not differ (X^2=0.0033, df=1, p=0.9542), and neither did those of juvenile females and males (X^2=0.0046, df=1, p=0.9461). Comparisons lacking significant differences could justifiably be grouped, if necessary. Model-averaged recapture probabilities (±SE) were 0.512 ± 0.081 for females and 0.830 ± 0.035 for males, the difference suggesting that females were significantly more difficult to recapture and resight (X^2=12.91, df=1, p=0.003).

Contiguous habitat models would not converge to derive reliable survival estimates, largely due to the low sample size there (e.g., *n*=3 juvenile female capture histories). Thus, we used general estimates pooled from the regional populations as conservative, but non-informative, placeholders in the population model. Thus, our results from contiguous forest should not be interpreted as site-specific, but rather as general comparative reference for the other two habitats. The best-fit model from the general model set was an age effect on survival and a sex effect on recapture (Table 2.4), but standard errors of juvenile survival were too high (>0.2) to use estimates from this model or an averaged model. Because we were interested in age by sex effects on survival, we used the φ(~age*sex) *p*(~sex) model to obtain generic *M. exsul* female adult and juvenile survival estimates with acceptable standard errors for use in the contiguous forest model (Table 2.2).

In the fragment site (RF), the best-fit model was a constant effect of survival and constant juvenile survival (Table 2.5). Other models receiving strong support showed age effects for φ and sex effects for *p*. Model-averaged estimates for adults and juveniles (Table 2.2) were not significantly different (X^2=0.5884, df=1, p=0.4430). Recapture probability also did not differ significantly between females and males: 0.560 ± 0.169 for females and 0.771 ± 0.090 for males, (X^2=0.9810, df=1, p=0.3219).

The peninsular and contiguous forest populations did not differ in their adult survival rates (X^2=0.4626, df=1, p=0.4964), and neither did the contiguous and fragment populations (X^2=1.188, df=1, p=0.2757), but the peninsula population had significantly lower adult survival than the fragment population (X^2=4.046, df=1, p=0.0443). There were no significant differences among juvenile survival rates.

Adult and Juvenile Productivity

Fecundity

We estimated clutch sizes in each habitat from a total of 95 nests with known initial clutch sizes (Table 2.6). We followed nesting attempts for 49 pairs at QG, LS, RF, and LV for a total of 145 nesting attempts to estimate mean seasonal nesting attempts for each habitat (Table 2.6). Some of the pairs were monitored twice in the same site in different years, so estimates are not completely independent.

Nest success

Our sample included 99 nests for estimating S_N for input into the adult productivity equation. Habitat was the only model with strong support according to our criteria for explaining nest success (S_N), thus we used this best-fit model to derive our estimates (Table 2.7). DSR was the lowest in peninsular forest 0.8886 ± 0.0175, which translates to only 4.6% of peninsular forest nests fledging offspring. Contiguous DSR was 0.9368 ± 0.0176, leading to an 18.3% S_N rate. Fragment DSR was the highest at 0.9472 ± 0.0101, giving an S_N of 24.4%. Nest survival was significantly lower in peninsular forest than in fragments (X^2=8.411, df=1, p=0.0037) and marginally lower than in contiguous forest (X^2=3.750, df=1, p=0.0528). Nest survival estimates did not differ between contiguous and fragmented forest (X^2=0.2604, df=1, p=0.6098).

A subset of 59 nests with definitively aged parents was used to estimate S_{NJ} for juvenile productivity (Table 2.8). Overall, nests with adult parents survived at a daily rate of 0.9332 ± 0.0111 for a 16.6% success rate, while nests with at least one juvenile parent survived at a daily rate of 0.8864 ± 0.0323 for a 4.3% success rate, a non-significant difference (X^2=1.882, df=1, p=0.1701). DSR of juvenile-parent nests in peninsular forest was 0.8595 ± 0.0398 (2.0% S_N) and in fragments was 0.9463 ± 0.0228 (23.8% S_N), representing a marginally significant difference (X^2=3.595, df=1, p=0.0580). Because we recorded no nests with juvenile parents in contiguous forest, we derived an average scaled estimate of S_{NJ} at 70% the S_N rate (S_{NJ} in connected forest was 42.4% the S_N rate, and S_{NJ} in fragments was 97.6% the S_N rate).

Immature Survival

Average dates of independence were 15 September for contiguous forest (QG), 1 July for peninsular forest (LS), and 1 August for fragmented forest (15 July for RF and 15 August for LV). Thus, the independent period was longest at 0.67 yr in peninsular forest (LS), the shortest at 0.46 yr in contiguous forest (QG, at a slightly higher elevation with cooler temperatures and more rain), and intermediate at 0.58 yr in fragments (RF and LV).

Sensitivity Analysis

Uncertainty

The empirical cumulative distribution function (ECDF) analysis gave a range of uncertainty for each population growth rate, λ (Table 2.1). The peninsular population is not viable (<1.0) for most parameter values in the parameter space. The contiguous population is viable over most of its range, but there is a chance it could also be stable or declining, reducing our confidence in estimates from this model. The ECDF of the fragment populations ranged widely, but did not include values less than one. Thus, we are less certain about the exact value our fragment population model produces, but fairly certain that the population is growing.

Sensitivity & Elasticity

There was no evidence of higher-order (e.g., quadratic, cubic) relationships in scatterplots from any of the populations. In the peninsula population, λ appeared most sensitive to nest survival and adult survival according to scatterplots (highest slopes; Fig. 2.3). The elasticity analysis of the peninsular population only identified a strong effect of adult survival on λ (Fig. 2.4).

In the contiguous population immature survival was the most influential parameter on λ, followed by juvenile and adult survival (Fig. 2.5). Adult survival showed the strongest proportional sensitivity (i.e., elasticity) effect on the contiguous λ, and all other parameters except S_{NJ} also displayed correlations (Fig. 2.6).

In the fragment populations, the parameter with the strongest linear correlation with λ was juvenile nest success, with immature survival and general nest success also playing strong roles (Fig. 2.7). Elasticity scatterplots for the fragment did not identify any clearly dominant parameter; clutch size, renesting, fledgling survival, and immature survival all had similar correlations (Fig. 2.8).

Partial Rank Correlation Coefficients (PRCC)

When the linear effects of the other variables were discounted, the sensitivity model for the peninsula identified nest success followed by adult survival as the most influential parameters to population growth, λ (Table A2.1; Fig. 2.9). The elasticity model only identified a significant effect of adult survival for this population (Table A2.2; Fig. 2.9).

The sensitivity model for contiguous forest indicated the strongest effect of immature survival on λ when all other linear effects were removed, but juvenile and adult survival also had large effects (Table A2.1; Fig. 2.9). Adult survival was the most influential proportional parameter effect identified via elasticity analysis (Table A2.2; Fig. 2.9).

Fragment populations differed from the others in that λ was not sensitive to adult survival; instead the populations were most sensitive to both adult and juvenile nest success (Table 1A; Fig. 2.9). Nevertheless, all parameters showed significant correlations with λ when varied proportionally, with no one parameter having a substantially greater influence than the others (Table A2; Fig. 2.9).

Table 2.1. Estimated population growth rates (λ) and their range of uncertainty given by empirical cumulative distribution functions (ECDF). Stable stage distribution (***w***) and reproductive value (***v***) vectors are also provided for populations in each habitat.

Habitat	λ	ECDF	Stage	***w***	***v***
Peninsula	0.829	0.7-1.2	*J*	0.147	1.000
			A	0.853	1.344
Contiguous	1.050	0.8-1.6	*J*	0.396	1.000
			A	0.604	1.740
Fragment	1.406	1.0-2.5	*J*	0.428	1.000
			A	0.573	1.115

Table 2.2. Population model parameters. Estimates without standard errors are rates derived from other parameter estimates, whose standard errors are reported elsewhere in the results.

Parameter	Estimate	St.Err.	Sensitivity		Elasticity	
			95% lcl	95% ucl	-10%	+10%
Peninsula						
S_A	0.7301	0.0422	0.6321	0.8281	0.6571	0.8031
S_J	0.5752	0.1210	0.3380	0.8124	0.5177	0.6327
c	1.8400	0.0614	1.7196	1.9604	1.6560	2.0240
N_Y	6.0000	0.5645	4.8936	7.1064	5.4000	6.6000
S_N	0.0460	.	0.0144	0.1100	0.0414	0.0506
S_{NJ}	0.0195	.	0.0037	0.1791	0.0176	0.0215
S_F	0.7600	0.0700	0.6228	0.8972	0.6840	0.8360
S_I	0.6904	.	0.4835	0.8700	0.6214	0.7594
Contiguous						
S_A	0.7785	0.0573	0.6662	0.8908	0.7007	0.8564
S_J	0.4134	0.1284	0	0.6651	0.3721	0.4547
c	1.8000	0.1069	1.5905	2.0095	1.6200	1.9800
N_Y	5.6600	0.7482	4.1935	7.1265	5.0940	6.2260
S_N	0.1830	.	0.1177	0.3834	0.1647	0.2013
S_{NJ}	0.1281	.	0.0037	0.1791	0.1153	0.1409
S_F	0.7600	0.0700	0.6228	0.8972	0.6840	0.8360
S_I	0.6661	.	0	0.8289	0.5995	0.7327
Fragment						
S_A	0.8611	0.0496	0.7639	0.9583	0.7750	0.9472
S_J	0.7296	0.1641	0.4080	1.0512	0.6566	0.8026
c	1.8400	0.0564	1.7294	1.9506	1.6560	2.0240
N_Y	4.3400	0.4532	3.4518	5.2282	3.9060	4.7740
S_N	0.2440	.	0.1266	0.3834	0.2196	0.2684
S_{NJ}	0.2381	.	0.0037	0.1791	0.2143	0.2619
S_F	0.7600	0.0700	0.6228	0.8972	0.6840	0.8360
S_I	0.8199	.	0.5945	1.0294	0.7379	0.9019

Table 2.3. Model selection results for the peninsular site (La Selva).

Model	K	AICc	ΔAICc	w	Dev
φ(~age) p(~sex)	4	544.2	0.0000	0.5116	242.50
φ(~age+sex) p(~sex)	5	546.2	2.0385	0.1846	242.46
φ(~1) p(~sex)	3	546.4	2.2116	0.1693	246.77
φ(~age*sex) p(~sex)	6	548.1	3.8925	0.0731	242.24
φ(~sex) p(~sex)	4	548.5	4.2429	0.0613	246.74

Table 2.4. Apparent survival model selection results for all data combined from all sites, for use in the contiguous site (Quebrada Gonzalez).

Model	*K*	QAICc	ΔQAICc	*w*	QDev	$\hat{c}$
φ(~age) *p*(~sex)	4	610.8	0.0000	0.3259	275.8	1.17
φ(~age*site) *p*(~sex)	8	611.8	0.9954	0.1981	268.5	1.17
φ(~age+site) *p*(~sex)	6	611.9	1.0996	0.1881	272.8	1.17
φ(~age+sex) *p*(~sex)	5	612.9	2.0323	0.1180	275.7	1.17
φ(~age+sex+site) *p*(~sex)	7	614.0	3.1638	0.0670	272.7	1.17
φ(~age*sex) *p*(~sex)	6	614.0	3.1781	0.0665	274.8	1.17
φ(~1) *p*(~sex)	3	616.7	5.8430	0.0176	283.7	1.17
φ(~site) *p*(~sex)	5	618.0	7.1440	0.0092	280.9	1.17
φ(~sex) *p*(~sex)	4	618.7	7.8717	0.0064	283.6	1.17
φ(~sex+site) *p*(~sex)	6	620.0	9.1902	0.0033	280.8	1.17

Table 2.5. Apparent survival model selection results for the fragment site (Río Frío).

Model	*K*	QAICc	ΔQAICc	w_i	QDev
φ(~1) *p*(~1)	2	44.89	0.0000	0.3541	23.67
φ(~1) *p*(~sex)	3	45.34	0.4498	0.2828	21.90
φ(~age) *p*(~1)	3	45.67	0.7870	0.2389	22.24
φ(~age) *p*(~sex)	4	46.98	2.0941	0.1243	21.23

Table 2.6. *Myrmeciza exsul* mean clutch size and nesting attempts.

Habitat	Parameter	Mean	StDev	*n*
Contiguous	c	1.84	0.37	37
Peninsular	c	1.80	0.41	15
Fragment	c	1.84	0.37	43
Contiguous	N_Y	5.66	2.37	10
Peninsular	N_Y	6.00	2.26	16
Fragment	N_Y	4.34	2.22	24

Table 2.7. Model selection results from 11 candidate models of *Myrmeciza exsul* nest success.

Model	*K*	AICc	ΔAICc	w_i	Dev
S(~Habitat)	3	498.4	0.000	0.4608	492.4
S(~Habitat + Time)	4	500.2	1.826	0.1849	492.2
S(~Habitat + NestAge)	4	500.3	1.888	0.1793	492.2
S(~Year)	4	502.0	3.615	0.0756	494.0
S(~Habitat:Year)	8	504.0	5.587	0.0282	487.8
S(~1)	1	504.0	5.651	0.0273	502.0
S(~Time)	2	505.0	6.595	0.0170	501.0
S(~NestAge)	2	505.9	7.460	0.0111	501.8
S(~Time + Habitat:Year)	9	506.0	7.561	0.0105	487.8
S(~NestAge + Habitat:Year)	10	508.0	9.579	0.0038	487.8
S(~Time + NestAge + Habitat:Year)	11	509.9	11.541	0.0014	487.7

Table 2.8. Model selection results of nest success of known-age *Myrmeciza exsul* parents.

Model	K	AICc	ΔAICc	w_i	Dev
S(~Habitat)	3	298.0	0.0000	0.8500	292.04
S(~AdAge * Habitat)	6	303.7	5.5868	0.0520	291.53
S(~AdAge)	2	304.9	6.8175	0.0281	300.88
S(~Year)	4	305.1	6.9977	0.0257	297.01
S(~1)	1	305.2	7.1285	0.0241	303.20
S(~Time)	2	306.7	8.6525	0.0112	302.71
S(~NestAge)	2	307.2	9.1301	0.0088	303.19

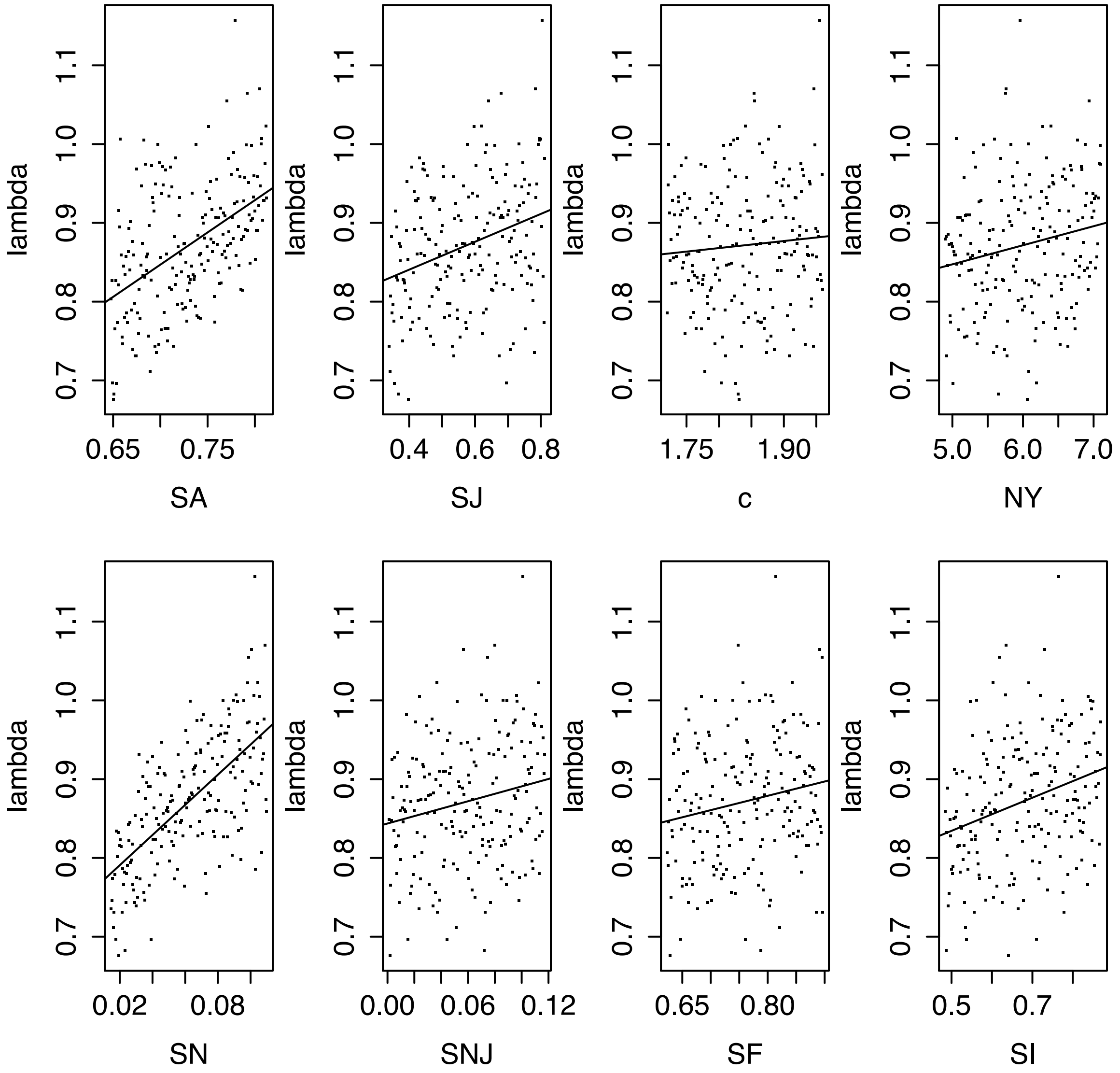

Fig. 2.3. Peninsular forest sensitivity scatterplots relating input parameter values to the model output, population growth rate (lambda, λ). Parameters are abbreviated as follows: SA = adult apparent survival, SJ = juvenile apparent survival, c = clutch size, NY = nests per year, SN = nest success, SNJ = juvenile nest success, SF = fledgling survival, SI = immature survival.

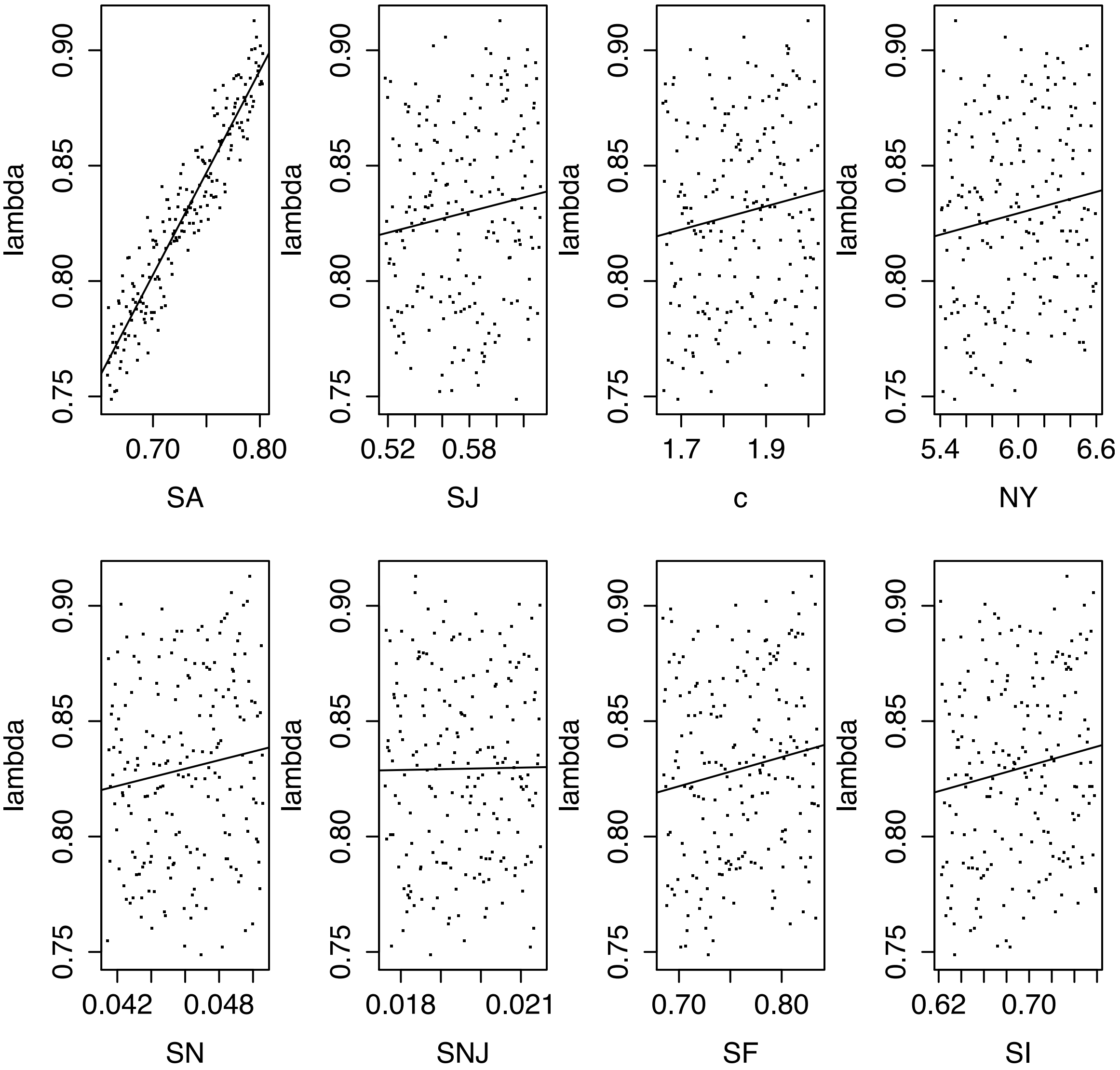

Fig. 2.4. Peninsular forest elasticity scatterplots relating input parameter values to the model output, population growth rate (lambda, λ). Parameters are abbreviated as follows: SA = adult apparent survival, SJ = juvenile apparent survival, c = clutch size, NY = nests per year, SN = nest success, SNJ = juvenile nest success, SF = fledgling survival, SI = immature survival.

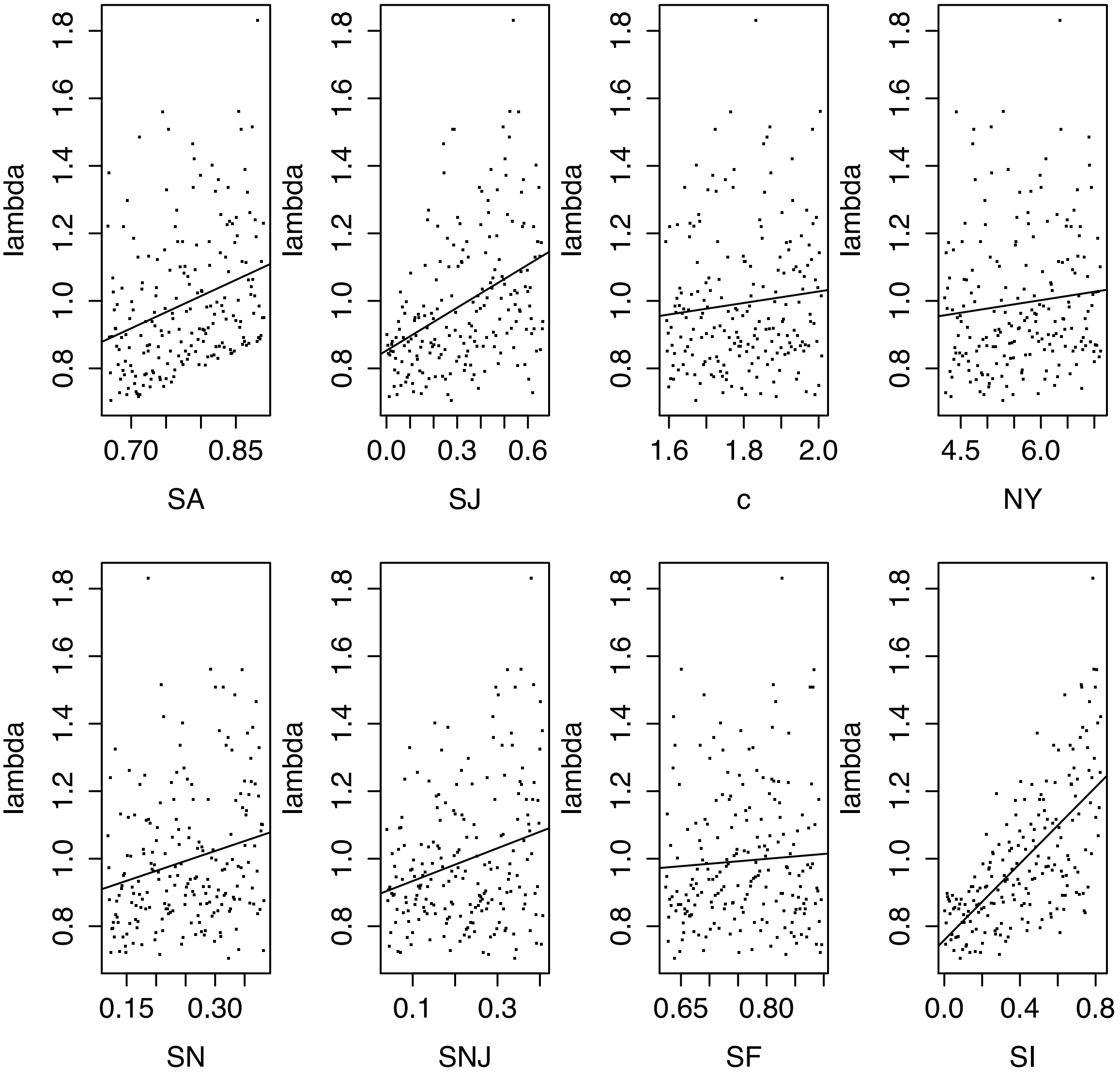

Fig. 2.5. Contiguous forest sensitivity scatterplots relating input parameter values to the model output, population growth rate (lambda, λ). Parameters are abbreviated as follows: SA = adult apparent survival, SJ = juvenile apparent survival, c = clutch size, NY = nests per year, SN = nest success, SNJ = juvenile nest success, SF = fledgling survival, SI = immature survival.

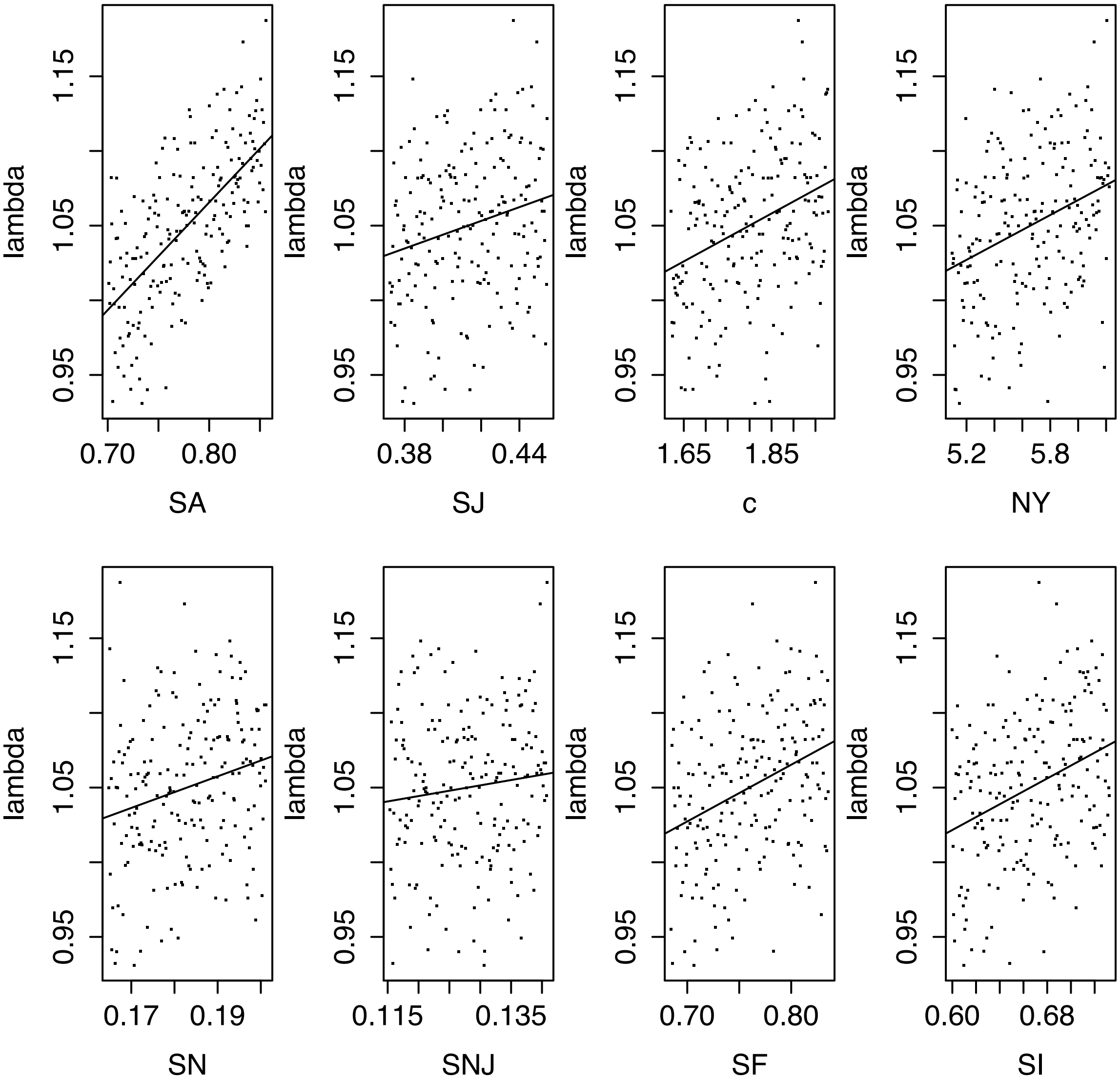

Fig. 2.6. Contiguous forest elasticity scatterplots relating input parameter values to the model output, population growth rate (lambda, λ). Parameters are abbreviated as follows: SA = adult apparent survival, SJ = juvenile apparent survival, c = clutch size, NY = nests per year, SN = nest success, SNJ = juvenile nest success, SF = fledgling survival, SI = immature survival.

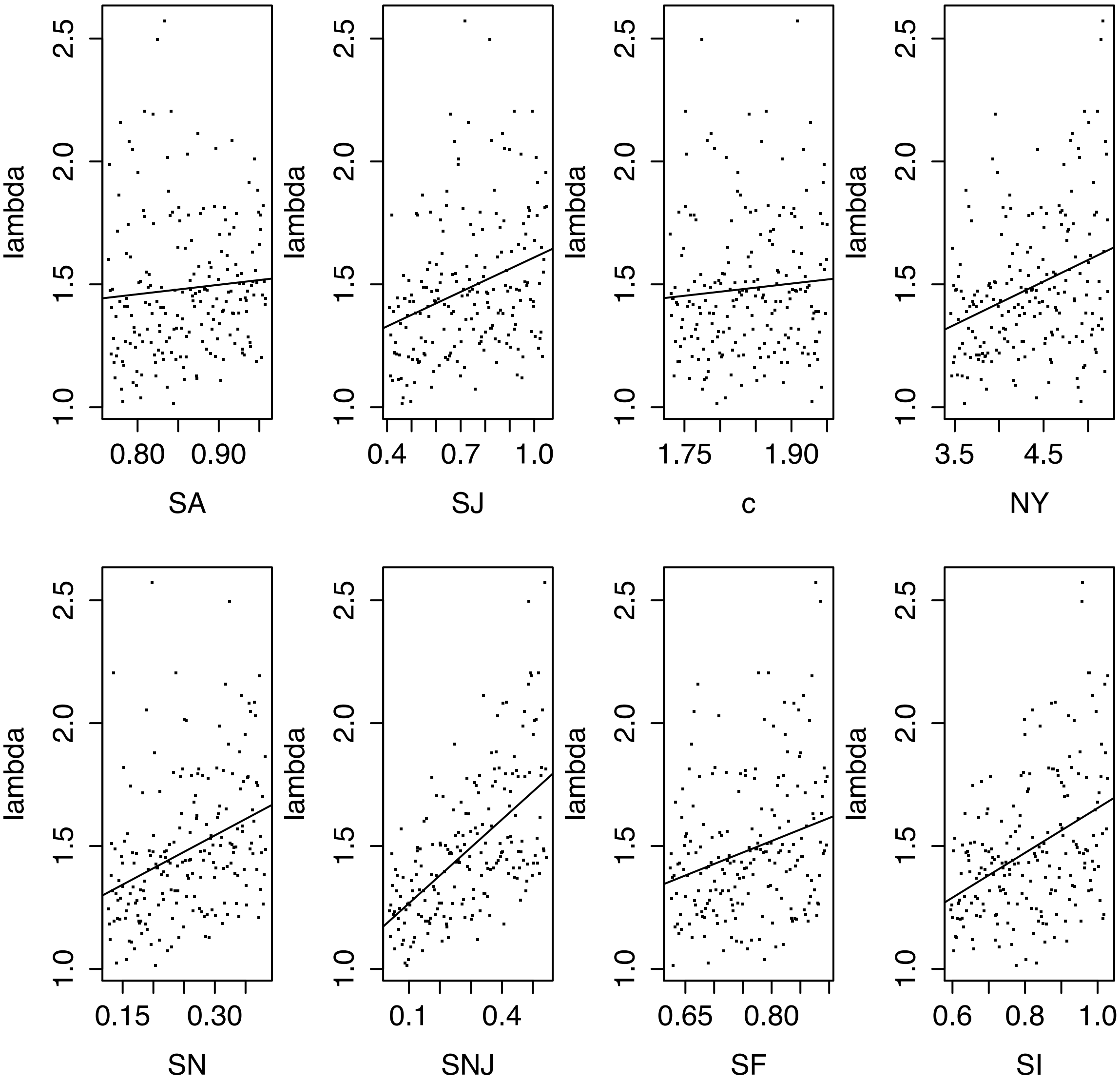

Fig. 2.7. Fragmented forest sensitivity scatterplots relating input parameter values to the model output, population growth rate (lambda, λ). Parameters are abbreviated as follows: SA = adult apparent survival, SJ = juvenile apparent survival, c = clutch size, NY = nests per year, SN = nest success, SNJ = juvenile nest success, SF = fledgling survival, SI = immature survival.

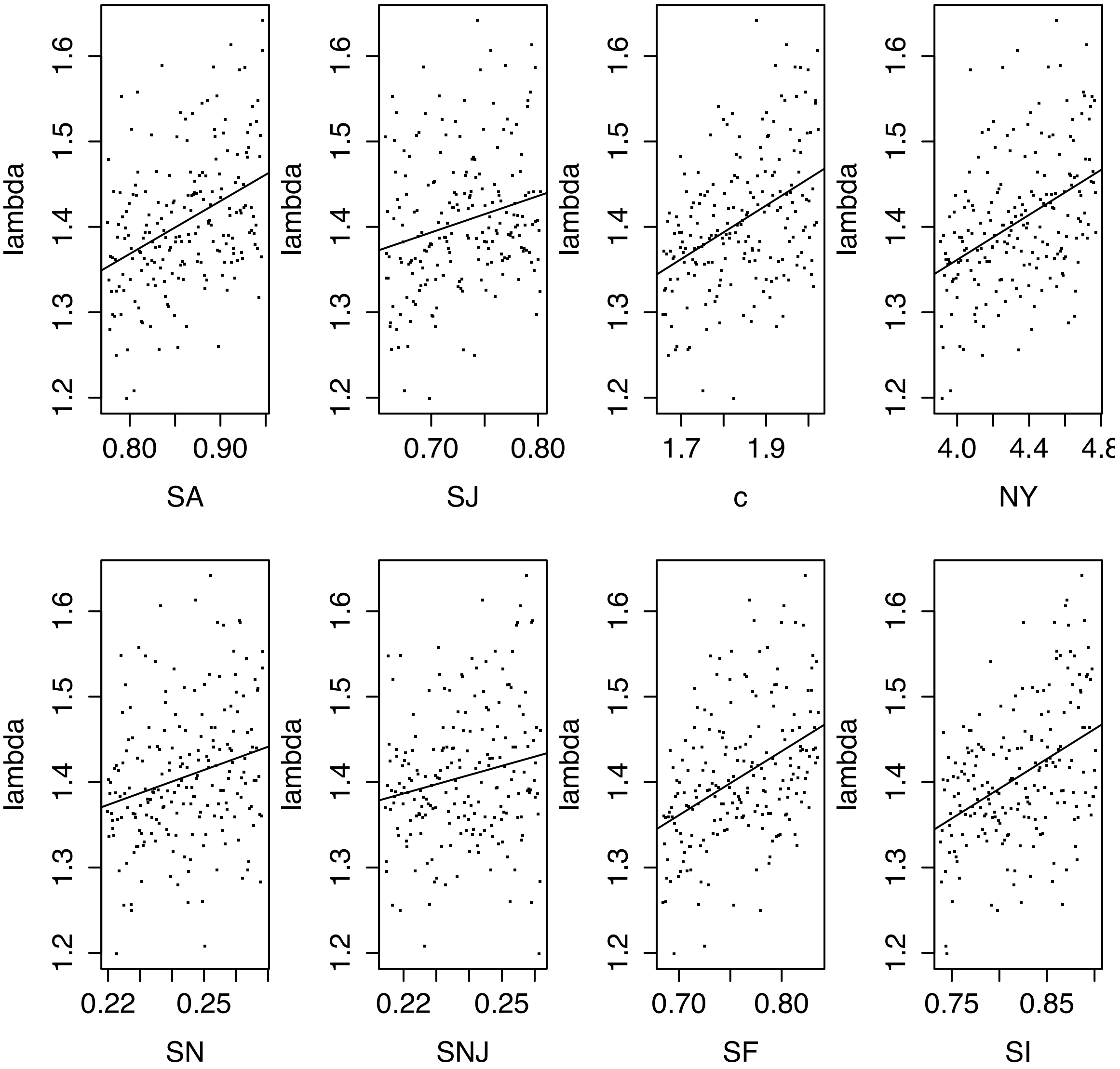

Fig. 2.8. Fragmented forest elasticity scatterplots relating input parameter values to the model output, population growth rate (lambda, λ). Parameters are abbreviated as follows: SA = adult apparent survival, SJ = juvenile apparent survival, c = clutch size, NY = nests per year, SN = nest success, SNJ = juvenile nest success, SF = fledgling survival, SI = immature survival.

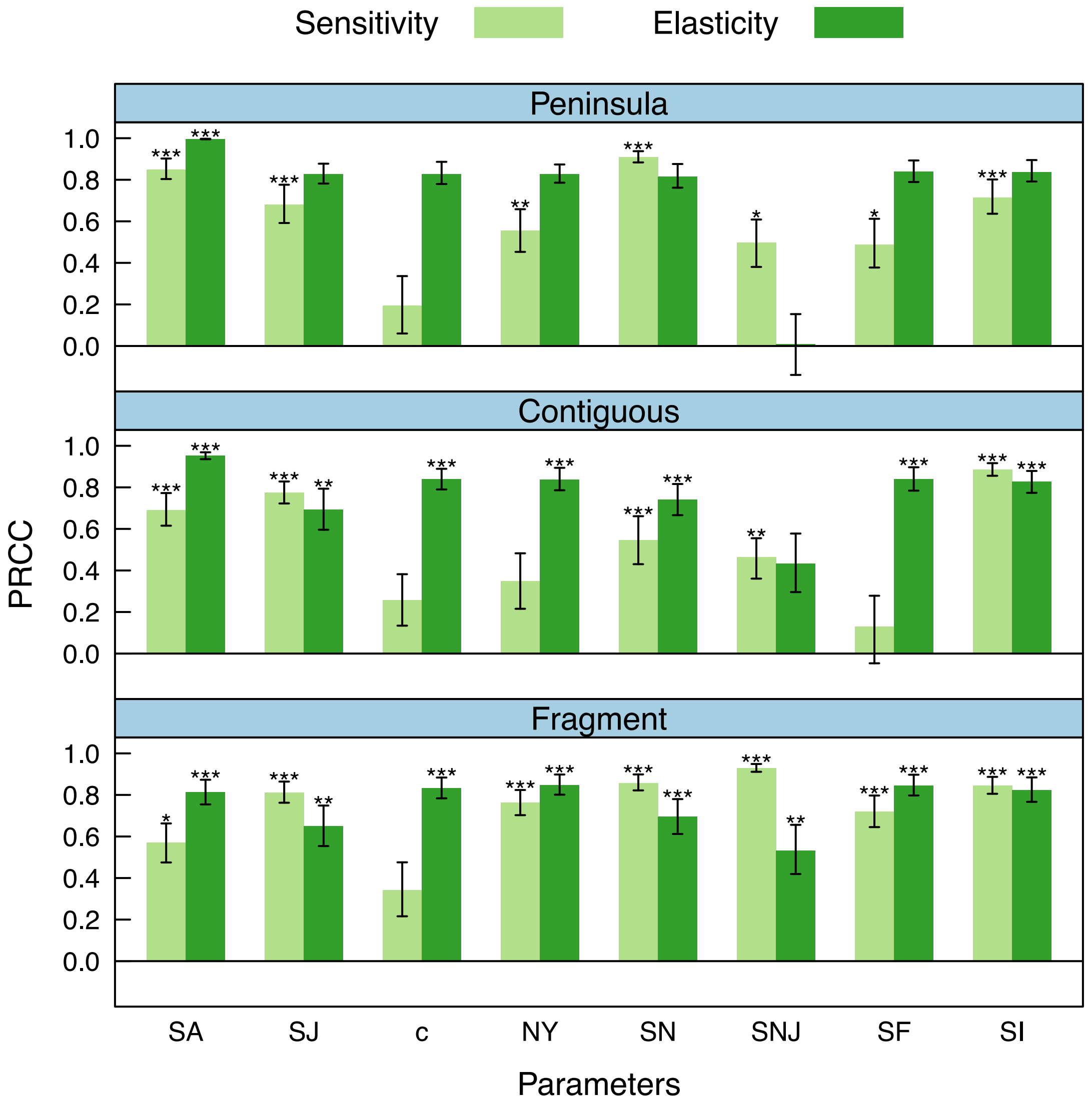

Figure 2.9. Partial Rank Correlation Coefficients (PRCC) show the monotonic relationship between absolute (sensitivity) and proportional (elasticity) changes in each parameter and the population growth rate, λ in the peninsula, contiguous, and fragment populations. Parameters are defined as follows: SA = adult survival, SJ = juvenile survival, c = clutch size, NY = nests initiated per year, SN = nest success, SNJ = juvenile nest success, SF = fledgling survival, SI = immature survival. Bars are 95% confidence intervals generated by bootstrapping 1000 times. Significance levels (‘*’ $p<0.05$, ‘**’ $p<0.01$, ‘***’ $p<0.001$) are indicated over each coefficient.

DISCUSSION

The population matrix model results indicate that estimated growth rates (λ) differ among *M. exsul* populations experiencing different degrees of anthropogenic disturbance and fragmentation. *M. exsul* are likely declining in the peninsular habitat (La Selva Biological Station) and increasing in the fragments sampled. Although we caution against interpreting the growth rate values strictly, results indicate reasonable confidence in the range and directionality. Considering the close proximity of these habitats (all within 40 km of each other), these differences are substantial, suggesting that population growth can vary locally in species that disperse little, such as tropical understory insectivorous birds (Moore et al. 2008, Woltmann et al. 2012b).

Decline in the peninsula corroborates Sigel et al. (2006) who observed a declining avifauna—including moderate declines of *M. exsul*—at La Selva over a 40-year period following heavy regional deforestation that left La Selva partially fragmented. Globally, tropical forest fragmentation has been found to influence many other understory insectivore populations, often leading to declines and extirpations (Stratford and Stouffer 1999, Lees and Peres 2006, Korfanta et al. 2012). The relative stability of the *M. exsul* population in contiguous forest compared to the decline in the peninsula fits with the expected response of understory insectivores to fragmentation. However, the directionality of the response in small fragments did not continue this pattern and contradicted typical understory insectivore behavior (Canaday 1997, Şekercioğlu et al. 2002). Instead of decline, we observed not only persistence of this species, but a λ substantially higher than one, indicating an advantage to dwelling in fragments compared to more connected habitat or even contiguous forest. Forest bird species succeeding in fragments relative to larger forest tracts may be uncommon, but *M. exsul* is not unique (Tewksbury et al. 1998, Friesen et al. 1999, Spanhove et al. 2009a, Sánchez et al. 2014). Thus, many forest remnants could have higher conservation value than initially appreciated, at least for some species—a potential that researchers have only recently attempted to understand (Turner and Corlett 1996, Şekercioğlu et al. 2007).

In the peninsula, the partial effect of adult survival on λ was strong. Consistent with this result, we found a high adult:juvenile stable-stage distribution, which translates to a large contribution of adult survival to the population's dynamics. We conclude that the declining λ there is primarily influenced by low adult survival—a typical feature of long-lived bird populations (Sæther and Bakke 2000) including tropical forest understory birds (Korfanta et al. 2012). We also observed a high sensitivity of the peninsula's λ to nest success, suggesting that the decline may also be related to the habitat's extremely high nest predation (Chapter 3). Nest success rates could be linked to abundance or behavior of nest predators or food availability, but nestlings only starved in 1 of the 99 nests sampled, suggesting that the population did not experience prohibitive food limitation (Martin 1995). On the other hand, there is strong evidence for predator community impacts: Video recordings revealed that bird-eating snakes (*Pseustes poecilonotus*) were responsible for at least 86% of nest depredations at the peninsula site, but only 63-75% of nest depredations in fragments (Visco and Sherry 2015), and this snake is not only a nest predator, but also capable of taking adults (Hayes 2002), making this predator a plausible cause of the population decline at La Selva.

Contiguous forest results were intermediate between peninsula and fragment populations. Its population growth rate showed the strongest sensitivity to adult survival, but many other parameters also showed significant correlations. Survival during the immature stage was also important. These results are less reliable than those of the other habitats because we included composite parameter estimates in the contiguous population model.

The demographic factors that contributed most to population growth in the fragments, and by inference the ecological causes, differed from those influencing peninsula and contiguous forest populations. Considering both sensitivity and elasticity results, fragment populations appeared almost equally sensitive to all contributing parameters, except perhaps slightly more strongly influenced by juvenile and general nest success. The absence of strong sensitivity of λ to adult survival compared to the other populations' sensitivities was notable, indicating that small perturbations of adult survival influenced population dynamics less there, a pattern usually associated with short-lived species (Noon and Sauer 1992). One explanation for this difference comes from the relatively low adult:juvenile ratio in the stable-stage distribution. A relatively high proportion of juveniles in the population could explain both the unusually low importance of adult survival and higher importance of juvenile nest success. Indeed, our population surveys indicate that there were relatively more juveniles in both fragments, corroborating this inference. This observation also makes sense in light of the relatively low reproductive value of adults, consistent with greater influence of juvenile reproduction.

Adult apparent survival (φ) was particularly influential in determining the population dynamics in two of three habitats. Our estimates were within the observed range of, or slightly higher than, previous φ estimates for *M. exsul* in Costa Rica

(0.62±0.11–0.80±0.05; Wilson et al. 2011, Woltmann and Sherry 2011), which are generally considered high for tropical forest birds (Blake and Loiselle 2008), but still varied substantially between the peninsular and fragment populations. What caused survival to differ among sites? Mechanisms theoretically influencing φ include adult predation, food availability, and dispersal (Lampila et al. 2005). Predators of adult birds such as snakes and forest hawks could vary across this landscape, as did nest predators of *M. exsul* (Visco and Sherry 2015). *P. poecilonotus* is not only a pervasive nest predator, but it is also a known predator of many adult bird species, so its prevalence could have a disproportionately large effect on adult survival generally, not just at La Selva (Savage 2002, Visco and Sherry 2015). Obtaining adequate nutrition is also key to survival. Food limitation can occur directly, e.g., due to low arthropod abundance (Rodenhouse and Holmes 1992), or indirectly due to lost foraging microhabitat (Michel and Sherry 2012, Michel et al. *in review*). Finally, dispersal limitation prohibits rescue of dwindling populations (Lees and Peres 2009), or can result in overcrowding if individuals cannot disperse out of isolated fragments to establish new territories (Frankham 1998). In overcrowded situations, higher competition, more frequent agonistic interactions among neighbors, and inbreeding could have detrimental impacts on survival (Bensch et al. 1994). Nevertheless, *M. exsul* adult survival was lowest in a site with large territories that is physically connected to a large forest reserve, and significantly higher in isolated fragments where territories were smaller (Woltmann and Sherry 2011, Visco and Sherry 2015). Thus, for *M. exsul* in this region, predation and food limitation mechanisms are probably most likely to drive adult mortality.

Unlike growth rates in peninsular and contiguous forest populations, fragment population growth rate was not strongly influenced by adult survival. In fragments, λ showed stronger sensitivity to factors relating to productivity (clutch size, renesting attempts, nest success, juvenile nest success, fledgling survival, and immature survival), which shared influence fairly equally. Despite higher adult and juvenile survival rates in fragments compared to the other habitats, the population's behavior ultimately did not respond strongly to them. Nest success of juveniles took on some importance in the sensitivity analysis, suggesting that when conditions are favorable for this species, the ability of birds to pair and produce offspring successfully in their first year can boost population growth. Another consideration is that high survival coupled with high nest success in the fragments is evidence of less selective pressure in general on survival and reproduction. For example*, P. poecilonotus* are a dominant nest predator of *M. exsul*, but video camera evidence suggests that snakes depredated nests in these fragments relatively infrequently, correlating with higher nest success there (Visco and Sherry 2015). If fragment populations are released from some of the important limiting factors elsewhere, it follows that other demographic components, and other nest predators, would be more influential. In other words, without strong selection for survival, there may be no single determinant of population dynamics. Surveys of predators and arthropods would advance understanding of the ecology of each habitat.

We have documented in this study how habitat fragmentation affects various aspects of an understory insectivore's demography and life history. For the first time in a Neotropical bird, we examined in depth how variation in demographic parameter estimates translated into population growth differences across the landscape. Depending on their ecological context, demographic parameters had different effects on population dynamics. Another surprise of our study was that two of the three local populations we studied appear to be experiencing ongoing population changes, both a decline and an increase, suggesting that these populations are not in equilibrium, and may take many years or decades to reach equilibrium given that we are unaware of any recent, strong ecological changes at any of our sites. Ornithologists have long recognized large-scale, including latitudinal, geographic patterns in life-history traits (Lack 1947, Martin 1996, Robinson et al. 2010), but local intraspecific variation, especially in tropical species, has attracted less attention until recently. The extent to which adult survival, nest success, and juvenile nest success parameters differed in such close proximity was surprising, but other tropical studies have recently substantiated intraspecific variation involving demographic parameters in fragmented landscapes (Karr et al. 1990, Githiru and Lens 2006, Ruiz-Gutiérrez et al. 2008, Newmark and Stanley 2011). Vital rates are often reported as fixed and predictable characteristics of a species (e.g., Karr et al. 1990), but this assumption does not acknowledge demographic rate heterogeneity (Sandercock et al. 2000). Inferences about a species based on vital rates from one geographical area may not apply generally, especially given global human impacts on diverse aspects of most, if not all environments.

We recognize that adequately sampling all major demographic and life history parameters for any one species in tropical forest is nearly prohibitive. Long tropical breeding seasons, well-hidden nests on large territories, and high predation rates mean that considerable investments of time and money are necessary to gather sufficient, representative data on nestling and post-fledging stages. Repeating this effort across fragmentation gradients is all too often infeasible. Yet we need more complete demographic data than generally available for at least some of the affected species in order to predict persistence or extirpation as land-use patterns change. Teasing apart the mechanisms determining population changes requires a thorough and comparative demographic analysis. Factors beyond what we analyzed in this study undoubtedly contribute to population outcomes as well, such as annual environmental conditions (Brawn et al. 2011). Nevertheless, our models illustrate how to compare population dynamics in disturbed landscapes by building on traditional avian population biology methodology. We not only accounted for all major life stages, incorporated transition probabilities between them, and estimated contributions to the next generation, but we also factored in realistic estimated ranges of parameter values in order to assess sensitivity meaningfully (see also Sheldon *et al.* 2012).

Effective conservation of understory insectivorous birds may require management of adult survival. The peninsular habitat, La Selva Biological Station, is a preeminent tropical reserve, but bird and leaf litter herpetofauna populations continue to decline (Sigel et al. 2006, Whitfield et al. 2007, Boyle and Sigel 2015). Reserves alone, depending on how managed, may be insufficient to achieve the necessary goals. On the other hand, despite habitat area loss, *M. exsul* populations are currently experiencing population growth in fragments. Nevertheless, over the long-term, habitats like forest fragments may not even protect such species, due to effects of crowding and resource limitation or inbreeding, all of which could decrease survival and productivity. For example, given the poor dispersal capability of *M. exsul* (reviewed above), inbreeding is inevitable in fragments, emphasizing the need for viable populations in reserves and large habitat expanses.

ACKNOWLEDGEMENTS

We thank S. Woltmann for contributing to the dataset, and consulting on all things *M. exsul*. OTS, especially R. Vargas and C. de la Rosa, facilitated countless aspects of this study. We also thank the staff of Quebrada Gonzales, especially R. Tenorio; the staff of Río Frío Colegio, especially R. Vargas; and the local residents of Puerto Viejo de Sarapiquí and La Virgen for lodging, support, and their commitment to conservation. Invaluable field and lab assistance was provided by M. Aliaga, I. Ausprey, M. Brady, L. Cohen, A. Dufrene, D. Ferraro, D. Forthmann, H. Greeney, F. Newell, E. Nishikawa, B. O'Malley, L. Ormsby, S. Pack, A. Pizarro, C. Sedgewick, N. Sly, W. Tsai, R. Valveri, and E. L. Vasquez. This research was supported financially by a Louisiana Board of Regents Graduate Fellowship, the Organization for Tropical Studies (OTS), the American Ornithologists' Union, the Stone Center for Latin American Studies, the Wilson Ornithological Society, the Newcomb College Institute, and Sigma Xi. Animal care was approved by the Tulane University IACUC protocol No. 0394R. The La Selva Biological Station Advisory Committee; the Costa Rican Ministerio de Ambiente, Energía y Telecomunicaciones (MINAET), the Costa Rican Sistema Nacional de Áreas de Conservación (SINAC), and the Costa Rican Área de Conservación Cordillera Vólcanica Central (ACCVC) resolution No. 012-2013-ACCVC-PI; and the Costa Rican Comision Nacional para la Gestion de la Biodiversidad (CONAGEBIO) resolution No. R-016-2013-OT-CONAGEBIO approved of and logistically supported this research.

APPENDIX

Table A1.1 Sensitivity results for each parameter's nonlinear effect (with other linear effects removed) on *Myrmeciza exsul* populations in three habitats.

Parameter	**Partial Rank Correlation Coefficient**	**rho**	**p**
Peninsula Sensitivity			
S_A	0.8488	0.4768	<0.001
S_J	0.6808	0.2740	<0.001
c	0.1939	0.0580	0.415
N_Y	0.5557	0.1965	<0.01
S_N	0.9085	0.6467	<0.001
S_{NJ}	0.4966	0.1714	<0.05
S_F	0.4877	0.1650	<0.05
S_I	0.7128	0.3013	<0.001
Contiguous Sensitivity			
S_A	0.6899	0.3397	<0.001
S_J	0.7736	0.4331	<0.001
c	0.2561	0.0959	0.177
N_Y	0.3488	0.1337	0.059
S_N	0.5469	0.2325	<0.001
S_{NJ}	0.4638	0.1856	<0.01
S_F	0.1288	0.0432	0.543
S_I	0.8843	0.6732	<0.001
Fragment Sensitivity			
S_A	0.5695	0.1633	<0.05
S_J	0.8100	0.3279	<0.001
c	0.3424	0.0889	0.210
N_Y	0.7628	0.2844	<0.001
S_N	0.8574	0.3989	<0.001
S_{NJ}	0.9282	0.5989	<0.001
S_F	0.7192	0.2487	<0.001
S_I	0.8436	0.3773	<0.001

Table A1.2 Elasticity results for each parameter's nonlinear effect (with other linear effects removed) on *Myrmeciza exsul* populations in three habitats.

Parameter	**Partial Rank Correlation Coefficient**	**rho**	**p**
Peninsula Elasticity			
S_A	0.9960	0.9472	<0.001
S_J	0.8261	0.1251	0.078
c	0.8272	0.1256	0.076
N_Y	0.8259	0.1243	0.079
S_N	0.8148	0.1190	0.093
S_{NJ}	0.0076	0.0015	0.983
S_F	0.8377	0.1327	0.061
S_I	0.8368	0.1314	0.064
Contiguous Elasticity			
S_A	0.9514	0.6572	<0.001
S_J	0.6925	0.2039	<0.01
c	0.8386	0.3277	<0.001
N_Y	0.8367	0.3223	<0.001
S_N	0.7396	0.2333	<0.001
S_{NJ}	0.4335	0.1005	0.157
S_F	0.8395	0.3294	<0.001
S_I	0.8262	0.3112	<0.001
Fragment Elasticity			
S_A	0.8142	0.3707	<0.001
S_J	0.6503	0.2252	<0.01
c	0.8333	0.3969	<0.001
N_Y	0.8478	0.4219	<0.001
S_N	0.6949	0.25	<0.001
S_{NJ}	0.5316	0.1663	<0.01
S_F	0.8458	0.421	<0.001
S_I	0.8233	0.381	<0.001

Chapter Three[2]

Increased abundance, but reduced nest predation in the chestnut-backed antbird in Costa Rican rainforest fragments: surprising impacts of a pervasive snake species

ABSTRACT

Understory insectivorous birds often disappear from fragmented tropical rainforest landscapes before mechanisms such as increased rate of nest depredation can be evaluated. Here, we took advantage of chestnut-backed antbird (*Myrmeciza exsul*), a representative rainforest understory insectivore that persists in fragments (unlike many other understory species), to identify variables influencing nest predation rate and to test the hypothesis that nest predation underlies avian extirpation in tropical fragments. We compared nest predation rates, bird density, and predator identities in three habitats of lowland Caribbean Costa Rica: two fragments, a peninsular reserve (La Selva Biological Station), and unfragmented rainforest. Our results suggest an inversely density-dependent nest predation pattern: In fragments, chestnut-backed antbirds reached their highest density and—contrary to predictions—experienced their lowest nest predation rates; La Selva on the other hand experienced the lowest density and highest predation rate. Because nest predation decreased with fragmentation, it appears not to explain declines

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[2] A version of this chapter is published as: Visco, D.M., Sherry, T.W. 2015. Increased abundance, but reduced nest predation in the chestnut-backed antbird in Costa Rican rainforest fragments: surprising impacts of a pervasive snake species. Biological Conservation, *in press,* http://dx.doi.org/10.1016/j.biocon.2015.01.015

of understory insectivores from forest fragments generally. Nest survival models indicated that habitat best explained nest predation likelihood, whereas edge, annual, and nest age effects were unimportant. Video surveillance documented both bird-eating snake (*Pseustes poecilonotus*) causing 80% of nest loss overall (37 of 46 nests) and a larger variety of predators in fragments; thus, landscape factors influenced an understory bird's nest predation. Given the large effect on our focal species, *Pseustes* likely affects other understory nesters, a topic warranting further study. Tropical reserve conservation plans should consider potential impacts of specialized nest predators on vulnerable understory birds.

Keywords

Birds; Costa Rica; fragmentation; La Selva Biological Station; *Myrmeciza exsul*; nest predation; predators; *Pseustes*

INTRODUCTION

Animal extirpation in fragmented tropical forest landscapes is non-random; patterns of guild decline and loss following fragmentation are often predictable (Bierregaard and Lovejoy 1989, Ferraz et al. 2007). Larger animals, for example, tend to disappear first from fragments due to the bushmeat trade (Duffy 2003). Another highly vulnerable group includes understory insectivorous birds and ant-following birds (Stouffer and Bierregaard 1995, Stratford and Stouffer 1999, Şekercioğlu et al. 2002, Sigel et al. 2006). Whereas patterns of sensitivity have been identified, we still lack demographic or ecological explanations for most avian responses to tropical forest fragmentation or other global change phenomena, hampering conservation efforts (Robinson and Sherry 2012a).

Mechanisms affecting bird populations in fragmented landscapes typically reduce survival or reproduction. Nest predation is one such mechanism that may limit avian populations (Ricklefs 1969, Newton 2003) and has long been suspected as a factor threatening bird populations in temperate (Heske et al. 2001) and tropical forest fragments (Oniki 1979). However, it is generally difficult to generalize about nest predation over broad scales, among birds with different nest structures, or even among similar species (Brawn et al. 2011). Whereas some studies find relatively high nest predation for tropical birds (Robinson et al. 2000b), others—especially at higher elevations—find rates similar to those in temperate forests (Skutch 1985, Martin 1996). A potential influence on nest predation that remains understudied in the tropics is density dependence (but see Boyle, 2008). Dense territories can increase predators' ability to find the more closely-spaced nests (Page et al. 1983, Martin 1988, McKellar et al. 2014). Yet bird density and nest predation are not always positively correlated, and multiple life-history traits and contexts are relevant (Schmidt and Whelan 1999, Ricklefs 2000). Alternatively, in areas of low bird density (e.g., due to factors independent of nest predation), less prey would be available for nest predators, and therefore the nests they depredate would represent a greater proportion of the total, resulting in an inverse relationship.

Elevated nest predation rate may involve altered predator types in fragments or the loss of top down predation pressure, which releases middle-sized predator populations such as snakes, monkeys, or coatimundis; (i.e., mesopredator release; Crooks and Soule, 1999). Identifying predators is central to testing these hypotheses. Because of the infrequency of both predator identification and predictable patterns of nest predation, some have called for more research identifying predators (Robinson and Robinson 2001, Lahti 2009) and their ecology (Weatherhead and Blouin-Demers 2004, Spanhove et al. 2009c, Ribic et al. 2012). Predator identification connects bird demographic patterns with community ecology and trophic dynamics. Nest predator species may respond demographically and behaviorally to land-use change differently from their prey (Thompson, 2007). Predator diversity and abundance is often higher along habitat boundaries such as agriculture/forest edges because both forest-dwelling predators and generalist predators from agricultural habitat can access nests, and this may disproportionately affect small forest fragments (Møller 1989, Andrén 1992, Marini et al. 1995, Tewksbury et al. 2006). Nevertheless, Chalfoun et al. (2002) recognized how nest predator responses to fragmentation are complex, taxon-specific, and context-dependent. Explanations of nest predation rate patterns without both descriptive information of avian populations and predator identities are thus risky.

The temperate-zone literature has abundantly documented increased nest predation and brood parasitism in forest fragments (Donovan et al. 1995, Luck 2003, Tewksbury et al. 2006), in areas of decreased forest cover (Robinson et al. 1995), and closer to edges (Batary and Baldi 2004). Effects of the proximity of nests to the habitat border, or edge effects, are also frequently investigated. Recent reviews have both supported (Batary and Baldi 2004) and rejected (Lahti 2001) the existence of consistent edge effects on nest predation, but these reviews have often not distinguished between temperate and tropical forests. The relevant tropical literature tends to show either equivocal edge effects (Chiarello et al. 2008, Young et al. 2008) or inverse effects, with lower nest predation rates near edges than in forest interior (as documented in the

Afrotropics: Carlson and Hartman, 2001; Spanhove et al., 2009a). Despite invocations of nest predation to explain tropical forest bird population dynamics in fragmented landscapes (Sodhi et al., 2004; Stratford and Robinson, 2005), adequate tests of this mechanism are rare.

Some evidence suggests that tropical forest interior birds experience reduced nesting success in fragments, but most such studies have been criticized. Many have used artificial nests (e.g., Gibbs, 1991; Githiru et al., 2005; Sieving, 1992), which are now widely considered biased and unrepresentative of rates and predators on natural nests in the tropics (Roper 1992, Moore and Robinson 2004). Unfortunately, comparative tropical fragment nest predation studies using real nests are few (but see Laurance et al., 2002; Newmark and Stanley, 2011; Young et al., 2008), reflecting the challenge of finding adequate numbers of often cryptic nests on large territories (Robinson et al. 2000b). Rapid species loss from fragments exacerbates the problem by preventing tests in many landscapes. Indirect predator-identification techniques such as imprints on plasticine eggs, hair traps, and track plates are increasingly questionable in light of recent camera and video studies (Pietz and Granfors, 2005; Thompson and Burhans, 2003). In the Neotropics, no study to date has adequately identified nest predators with video camera sample sizes per species over ten (Weidinger, 2008), nor made comparisons at the landscape scale. Anecdotal data suggest the importance of snakes (e.g., *Pseustes poecilonotus*, *Boa constrictor*, and *Spilotes pullatus*) as nest predators, along with diverse birds (e.g., raptors, jays, toucans, oropendolas, antshrikes), monkeys, coatimundis, opossums, and army ants (Robinson and Robinson 2001, Robinson et al. 2005a, Tarwater 2008, Reidy 2009, Riehl and Jara 2009). Although these are invaluable documentations of nest predator diversity, many species were identified only once, and most knowledge comes from Panama.

The present study tested the nest predation decline mechanism within a fragmented Costa Rican landscape, the Sarapiquí (Caribbean) lowlands. Using the chestnut-backed antbird (*Myrmeciza exsul*), an understory insectivorous bird that persists in fragments, we compared nest predation rates and nest predator identities in habitats with varying degrees of fragmentation. We also quantified chestnut-backed antbird population density to test its potential impact on nest predation risk, as previous observations reported high density in a fragment (Woltmann et al. 2010). No single species represents an entire guild, as species are by nature unique, but they can help control for many variables. This single species' occurrence across a landscape along with evidence of moderate declines at La Selva (Sigel et al. 2006) made it a good choice for this investigation. To the extent that its nests and life histories are similar to other understory birds, chestnut-backed antbirds can help us understand, and perhaps even predict other species' persistence or declines. Here, we identified factors related to nest predation that might permit the persistence in fragments of chestnut-backed antbirds, and perhaps other understory birds in general. We hypothesized that nest predator taxa vary spatially and thus influence the nest predation rate. Because we expected nest predator taxa to be more diverse and bird populations to be denser in fragments, we expected nest predation rate also to be highest in fragments, and we predicted elevated nest predation rate near forest edges, based on potential exposure to more predator types.

METHODS

Study species

Chestnut-backed antbirds (family Thamnophilidae) are small, insectivorous understory passerines. Like many antbirds, they forage opportunistically at army-ant swarms, but more often solitarily (Willis and Oniki 1972). They are resident in lowland rainforests (generally <1 000 m elevation) from Honduras to Ecuador, where both sexes defend their territory year-round (Woltmann et al. 2010, Losada-Prado et al. 2014). Chestnut-backed antbirds are monogamous, and they build small, open-cup nests containing 1-2 eggs 10-40 cm off the ground (Greeney et al. 2013). Such nest types are vulnerable to various predators (Sieving 1992). Care of eggs and nestlings is biparental (Skutch 1969). Researchers may discover nests using a search image plus the birds' parental behaviors including distinctive alarm calls given near the nest. Genetic and experimental studies indicate that chestnut-backed antbirds disperse extremely poorly (Moore et al. 2008, Woltmann et al. 2012b), so colonization ability cannot explain their persistence in isolated forest fragments. *Unlike* most thamnophilids, chestnut-backed antbirds persist widely in small rainforest fragments (Roberts, 2007; Woltmann et al. 2010), making them suitable for comparative landscape study.

Site description

The Sarapiquí region of Costa Rica lies in the country's northern Caribbean slope of the Cordillera Central Mountains (Fig. 3.1). Until recently, the area was largely covered by lowland tropical wet forest, which is now a patchwork due to rapid deforestation following a settlement surge in the 1960s (Read et al. 2001, Joyce 2011). A large intact tract of old-growth forest, Braulio Carrillo National Park (46 000 ha), remains in this mountain range. Forest fragmentation in the region has now slowed, but its impact remains substantial with only 30% mature forest cover remaining (Fagan et al. 2013).

While the total extent of pasture has declined, it is generally being replaced by expanding pineapple plantations and other agriculture rather than by secondary forest that could provide wildlife habitat (Fagan et al. 2013).

Since the 1960s, understory bird populations in the Sarapiquí, and at La Selva Biological Station (hereafter La Selva) in particular, have declined alarmingly despite proximity to a large contiguous forest reserve (Braulio Carillo). Yet the declines are not strictly dependent on loss of habitat area; many of the same species persist in smaller reserves (e.g., Tirimbina 345 ha; Roberts, 2007; Sigel et al., 2010, 2006).

Two study fragments were selected based on presence of chestnut-backed antbirds, forest composition (minimally logged old-growth), size (40–100 ha), elevation (60–200 masl), isolation (no functional connectivity), and surrounding matrix type (pasture on 3 sides). Fragment sites were Río Frío Colegio (RF), a 92 ha forest remnant, and La Virgen (LV), a 41 ha fragment (Fig. 3.1). Most fragments in this region are 30-50 years old, isolated during a cattle ranching boom between 1960 and 1983 (Read et al. 2001).

La Selva (LS), a 1 600 ha Organization for Tropical Studies reserve, connects to Braulio Carrillo via a corridor on its southern end (Fig. 3.1). Whether La Selva should be considered contiguous forest or a fragment is debatable (Young et al. 2008). Land conversion has reduced La Selva to a peninsula largely surrounded by pasture and agriculture. La Selva (referred to here as peninsular forest) is a flagship field station for tropical research that has been monitored biologically for decades. The avifauna in particular is well documented, providing a baseline for understanding community change (Boyle and Sigel, this issue; Sigel et al., 2010, 2006). Here we sampled nests within a 300 ha focal area of older-growth forest, where the terrain is approximately 60 masl. Quebrada Gonzales (QG), a large forest area accessible from a ranger station located within Braulio Carillo at 400 masl, functioned as a contiguous forest control (Fig. 3.1).

Population density

Chestnut-backed antbird density was estimated using direct counts of color-banded birds plus a few unbanded territorial individuals. We ignored floaters (non-territorial birds), but counted lone males on a territory as a pair because females are typically much harder to detect. We roughly mapped territories of each pair within our focal areas to ensure discovering all mated pairs. We considered a previously occupied territory vacant when surveyed three times without detecting any individuals. Density estimates were averaged using 2-6 survey years, depending on the site. Average density differences grouped by site were tested using a one-way ANOVA with a Tukey's HSD post-hoc test to specify the differences. We conducted statistical analyses in Program R-3.1.1 (R Core Team, 2014).

Daily predation rate and nest predation probability

We used the nest survival model in Program MARK 7.1 to estimate daily predation rate (DPR) of nests and overall nest predation probabilities (White and Burnham 1999, Dinsmore and Dinsmore 2007). We accessed Program MARK via Program R-3.1.1 (R Core Team 2014) package RMark (Laake 2013) for model construction.

Grouping variables included an individual effect (n=45 unique breeding pairs, with n=27 pairs with multiple nests), year (2010–2013), habitat (fragment, peninsular, contiguous), time (linear temporal pattern of survival within the season), and nest age (a time-dependent individual nest covariate taking on values from 0-26 days). Time trends and nest age were applied according to the protocols for Program MARK (Dinsmore et al. 2002, Rotella et al. 2004). Because RMark does not allow nonlinear nest age models, we included a linear effect in the main data and subsequently analyzed two separate datasets to compare daily survival of the egg (laying plus incubation, Day 0-16) and nestling (Day 17-26) stages. Our a priori models included partial interactions (dropping one of the main effects) between habitat and year because not all habitat types were sampled in each year (factors with missing design data such as this cannot be fully crossed). Nest-specific covariates were added in the plausible remaining combinations to create twelve candidate models of nest predation risk.

We evaluated models for the edge covariate separately because of the need to use just nests from fragments, the only sites with edges. Nests were categorized as ≤75 (near) or >75 (far) meters from the forest/matrix interface—a distance consistent with previous edge effect studies that represents microclimate shifts and increased nonforest species prevalence (Laurance et al. 2002, Young et al. 2008).

We used Akaike's information criterion adjusted for small sample size (AIC_C; Burnham et al., 1995) to rank models by the difference (ΔAIC_C) from the best-fit model (AIC_{min}). Strength of support for each model was determined using evidence ratios of the AIC weights (w_i). Models with evidence ratios (w_j/w_i) <2.7 were considered to have strong support (Burnham and Anderson 2002). However, nested models with $\Delta AIC_C \leq 2$ and that differ by only one parameter from the best-fit model were considered uninformative because the log-likelihood is unchanged and hence they do not improve model fit (Burnham and Anderson 2002). We estimated daily nest survival rate from the parameters of the best-fit model because too few models had substantial enough support to justify using multimodel inference (Arnold 2010). After retrieving daily nest survival probabilities, we used Program CONTRAST to compare survival estimates (Hines and Sauer 1989).

Abandoned nests (*n*=9) were excluded from the "failed" fate so that we effectively estimated depredation rate rather than general nest failure. Control nests (not videoed) had similar abandonment rates (7.1%) as videoed nests (8.7%). Although human disturbance likely caused abandonment of at least two nests, we also observed infertility, a branch fall, and livestock disturbance causing abandonment. As MARK is designed to estimate daily survival rates (DSR) of nests, excluding nests lost to causes other than depredation means 1 – DSR reflects the parameter of interest, daily predation rate (DPR). Nest success was defined as DSR raised to the 26^{th} power (the number of days in the nesting cycle; *pers. obs.*). Its converse (1 – nest success) represents the depredation probability over the nesting cycle.

To test for a correlation between nest predation probability and bird population density across sites (*n*=4), we used the package lmPerm (Wheeler 2010) in Program R-3.1.1 (R Core Team 2014) to randomly resample all 24 possible data permutations for performing the regression. A permutation test allowed us to leverage a small sample size without assuming a normal distribution.

Predator identity and nest fates

Once a nest was found, we deployed user-built, continuously-imaging video systems to monitor their contents (Pierce and Pobprasert 2007). Effects of video cameras on nest survival are typically nonexistent or positive (Richardson et al. 2009). In 2010, we also used four Sony Hi8 TRV138 cameras during daytime hours, which recorded to analog tapes. Our digital system used small waterproof color security cameras with near-infrared Light-Emitting Diodes (LEDs) that permitted image recording at night and in low-light settings (e.g., shaded forest interior). Each configuration consisted of the security camera, situated ~ 1m distant from the nest, connected by a cable to a water-tight box housing a digital video recorder (DVR) and connectors, located at least 10m from the nest. Boxes were stored along with a sealed gel deep-cycle battery underneath a camouflage tarp to minimize disturbance by people, animals, or rain. The DVRs stored up to 30 gigabytes of video data, included a small viewing screen for checking camera images, and were easily carried and swapped out in the field every other day to maintain continuous monitoring without need for approaching nests. We uploaded video data onto hard drives in the lab. Nest videos containing depredation footage were reviewed using DiVx software. Predators were identified using Costa Rican field guides (Savage 2002, Guyer and Donnelly 2004, Wainwright 2007) and confirmed independently by a herpetologist familiar with the region's snakes (D. Wasko, Univ. Hartford).

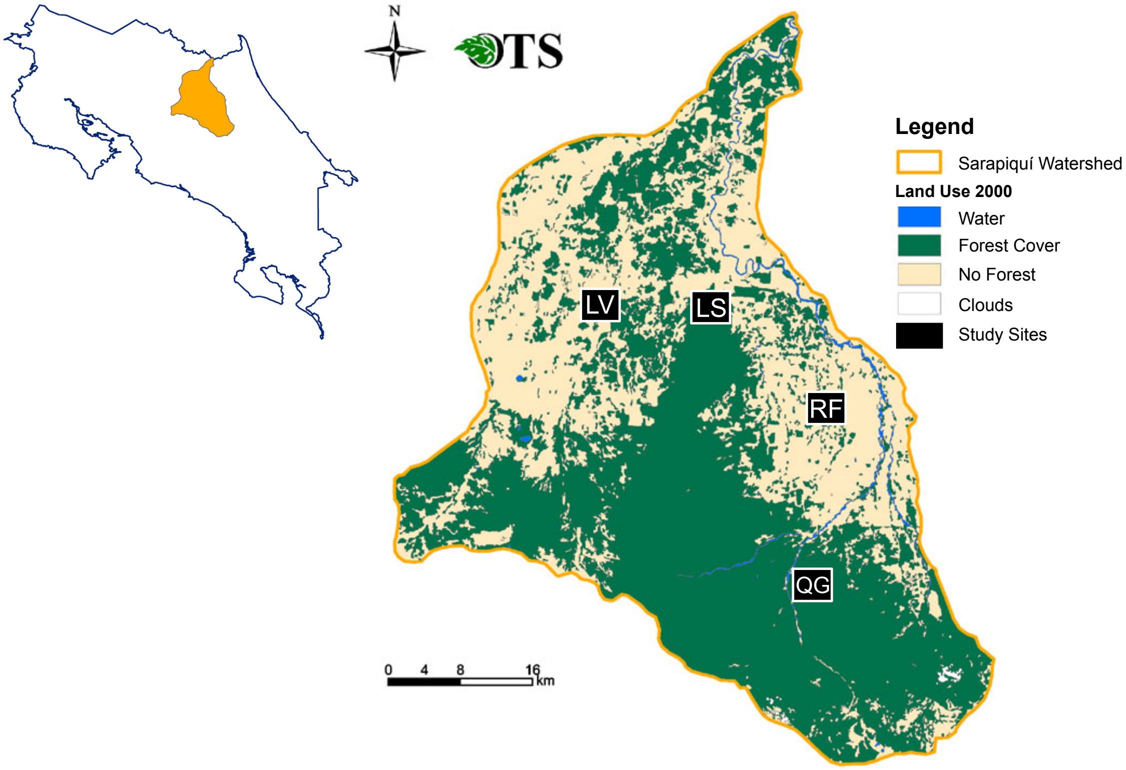

Figure 3.1. Inset shows the extent of the Sarapiquí watershed within Costa Rica. Study locations within the Sarapiquí region are abbreviated as follows: RF = Río Frío (Frag1), LV = La Virgen (Frag2), LS = La Selva (Peninsular), QG = Quebrada Gonzales (Contiguous).

RESULTS

We sampled a total of 99 nests and collected >22 098 hours of active-nest video footage. For perspective, an uninterrupted sample (with neither depredation nor video malfunction) of the laying (2 days), incubation (15 days), and nestling (9 days) periods from a single nest contains about 624 hours of data. We monitored 25 nests at fragment RF, 19 at fragment LV, 40 at peninsular forest LS, and 15 at contiguous forest QG. Sample sizes reflected renesting frequencies, and ease of movement through the terrain.

Population Density

Chestnut-backed antbirds not only persisted, but also reached significantly higher density (pairs/100 ha ±SE) in both isolated fragments (RF: 39.5±0.9, *n*=4 yr; LV: 46.9±1.8, *n*=2 yr) than in peninsular (9.3±0.2; *n*=6 yr) or contiguous forest (16.9±1.5; *n*=3 yr) (F=542, df=3, $p<0.001$; Fig. 3.2). All pair-wise comparisons differed (Tukey's HSD, $p<0.001$).

Daily nest predation rate (DPR)

Habitat was the strongest explanatory variable of nest predation likelihood, given our set of 12 candidate models (Table 3.1). The second and third models were considered unimproved versions of the first model (nearly identical log-likelihoods). The evidence ratio of the Habitat model (Akaike weight of Habitat divided by respective Akaike weights) was >2.7 when compared with the remaining nonnested models. Temporal (among and within years) and nest age effects did not receive strong support (Table 3.1). Lack of support for the Pair model suggests that individual effects fail to explain nest predation.

Daily nest predation rate (DPR) ±SE was 0.047±0.013 in RF fragment, 0.038±0.012 in LV fragment, 0.109±0.017 in LS peninsula, and 0.058±0.017 in QG contiguous forest (Fig. 3.2). Rates for the two fragments were statistically indistinguishable (χ^2=0.250, df=1, p=0.617), thus there is no evidence of any site effect, and we report the combined DPR for fragment habitats: 0.043±0.009. Depredation rate was significantly lower in fragments than in the peninsular forest site (χ^2=11.3, df=1, p<0.001), and higher in peninsular forest than in all other sites combined (χ^2=9.97, df=1, p=0.002). Contiguous forest depredation rate was significantly lower than peninsular forest rate (χ^2=4.29, df=1, p=0.038), but no different from fragmented forest (χ^2=0.648, df=1, p=0.421).

DPR correlated negatively with pair density (Fig. 3.2; N=4, R^2=0.607, p=0.042) and slightly decreased with nest age and time (Fig. 3.3), but the nest age and time models lacked support. Over the course of a 26-day nesting cycle, the probability of a nest being depredated was 72% and 64% in the fragments, 95% at La Selva, and 79% in contiguous forest. Independent analyses of null models of the egg and nestling stages yielded indistinguishable daily nest predation rates of 0.066±0.009 and 0.069±0.015, respectively, in line with little support for a linear nest age effect.

Edge effect

Of nests in fragments (*n*=44), estimated DPR ±SE was 0.038±0.011 for interior nests and 0.050±0.015 for edge nests, not a significant difference (χ^2=0.416, df=1, p=0.519).

Predator identity

We identified 46 independent predation events: 41 snakes, 2 mammals, 2 fire ant swarms, and 1 forest hawk (Table 3.2; Fig. 3.4). Ninety percent of snake individuals were a single species, the bird-eating snake (*Pseustes poecilonotus,* hereafter *Pseustes*). We recorded juvenile, subadult, and adult *Pseustes* depredating both eggs and nestlings. Other nest predator snakes included *Chironius grandisquamus*, and *Leptophis sp.*, both at La Selva. We observed another snake (*Dendrophidion percarniatum*) attempt to depredate eggs, but the female chestnut-backed antbird successfully defended the nest—the only successful nest defense we observed. We were unable to identify two snakes due to poor camera views. Two mammalian predators, both in fragment site LV, were four-eyed opossum (*Philander opossum*) and ocelot (*Leopardus pardalis*). Fire ants (*Solenopsis sp.*) only depredated eggs, and both events occurred in the RF fragment. The single avian nest predator, semiplumbeus hawk (*Leucopternis semiplumbeus*), depredated a nestling in the RF fragment.

Pseustes (Fig. 3.5) emerged as the dominant nest predator, as it was responsible for 80% of nest depredations overall. Most nest predators were snakes regardless of habitat (89%), but more diverse predator taxa were video-recorded in fragments—the only sites with mammalian, avian, and insect predators (Table 3.2). The two sites with exclusively snake predators (LS and QG) also had the highest estimated nest predation probabilities.

Table 3.1. Model selection results of twelve candidate models for estimation of daily predation rate (DPR) of chestnut-backed antbird (*Myrmeciza exsul*) nests. The bolded model is the best-fit model (AIC$_{\text{min}}$).

Model	[a]***K***	[b]**ΔAIC$_C$**	[c]w_i
$S_{(^{d}\text{HABITAT})}$	3	0.000	0.464
$S_{(^{e}\text{NESTAGE + HABITAT})}$	4	1.797	0.189
$S_{(\text{HABITAT + }^{f}\text{TIME})}$	4	2.001	0.171
$S_{(\text{HABITAT:}^{g}\text{YEAR})}$	8	3.091	0.099
$S_{(\text{TIME + HABITAT:YEAR})}$	9	5.107	0.036
$S_{(\text{NESTAGE + HABITAT:YEAR})}$	10	7.013	0.014
$S_{(\text{YEAR})}$	4	7.237	0.012
$S_{(^{h}\text{NULL})}$	1	9.003	0.005
$S_{(\text{TIME + NESTAGE + HABITAT:YEAR})}$	11	9.047	0.005
$S_{(\text{TIME})}$	2	10.692	0.002
$S_{(\text{NESTAGE})}$	2	10.789	0.002
$S_{(^{i}\text{PAIR})}$	45	39.232	0.000

[a] Number of parameters in the model.

[b] Difference between current model and best-fit model; AIC$_C$ of best-fit model = 465.30; AIC$_C$ is Akaike's Information Criterion for small samples.

[c] Akaike weights

[d] Spatial survival variation (fragment, peninsular, or contiguous habitat)

[e] Within-nest linear temporal pattern of survival (0-26 days)

[f] Season-long linear temporal pattern of survival (144 day season)

[g] Annual survival variation (years 2010, 2011, 2012, 2013)

[h] Constant nest survival

[i] Individual effect on nest survival (45 unique breeding pairs)

Table 3.2. Frequencies of nest predator identities grouped by taxa across four sites. 90% of the snake predators were bird-eating snakes (*Pseustes poecilonotus*).

	Fragment		Peninsula	Contiguous
	Río Frío	La Virgen	La Selva	Quebrada Gonzalez
Total Depredations	**8**	**8**	**22**	**8**
[a]Snakes Total	5	6	22	8
Pseustes	5	6	19	7
[b]Mammals	0	2	0	0
[c]Birds	1	0	0	0
[d]Fire Ants	2	0	0	0

[a] Non-*Pseustes* snakes included *Chironius grandisquamus*, *Leptophis sp.*, and an unknown at LS, and 1 unknown at QG.

[b] Mammals included a four-eyed opossum (*Philander opossum*) and an ocelot (*Leopardus pardalis*).

[c] The avian nest predator was a semiplumbeus hawk (*Leucopternis semiplumbeus*).

[d] Genus *Solenopsis*.

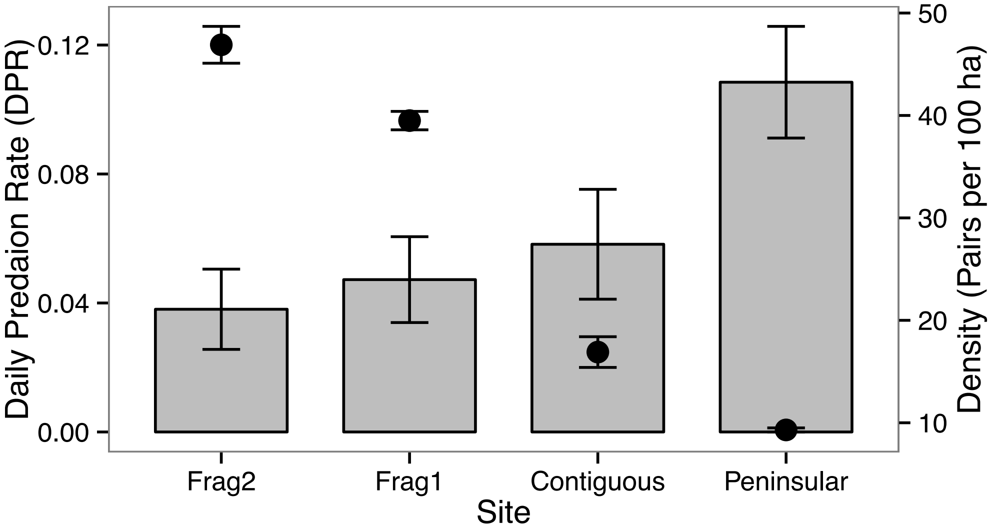

Figure 3.2. Daily predation rate (DPR) ±SE (gray bars, left axis) estimates of chestnut-backed antbird (*Myrmeciza exsul*) nests by site. See section *3.2* for statistical differences. Nest sample sizes in each site were: Frag1=25, Frag2=19, Contiguous=15, Peninsular=40. Mean population density ±SE (black dots, right axis) differed strongly by site (F=542, df=3, $p<0.001$), and all pair-wise comparisons differed according to Tukey's HSD ($p>0.001$). DPR negatively correlates with bird density. Site names, nest sample sizes, and their number of population survey samples (one per year) are as follows: Frag1 = Río Frío (25 nests, 4 surveys), Frag2 = La Virgen (19 nests, 2 surveys), Contiguous = Quebrada Gonzales (15 nests, 3 surveys), Peninsular = La Selva (40 nests, 6 surveys).

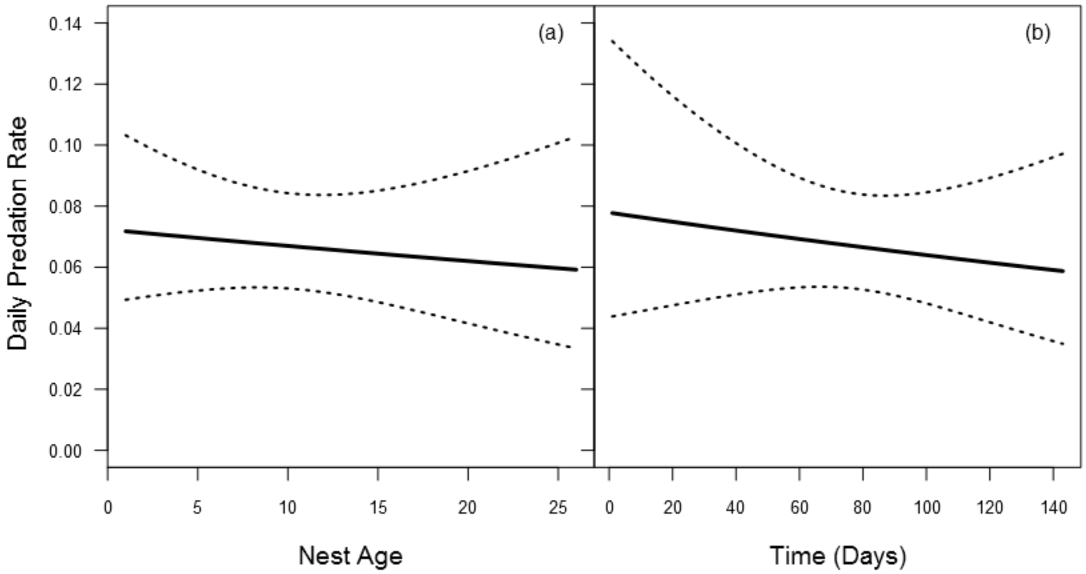

Figure 3.3. The daily predation rate (DPR, solid line) of chestnut-backed antbird (*Myrmeciza exsul*) nests slightly decreases, but does not show a strong linear trend with (a) increasing nest age over the 26-day nesting cycle, nor with (b) time over the 144-day breeding season. Dotted lines represent upper and lower 95% confidence intervals.

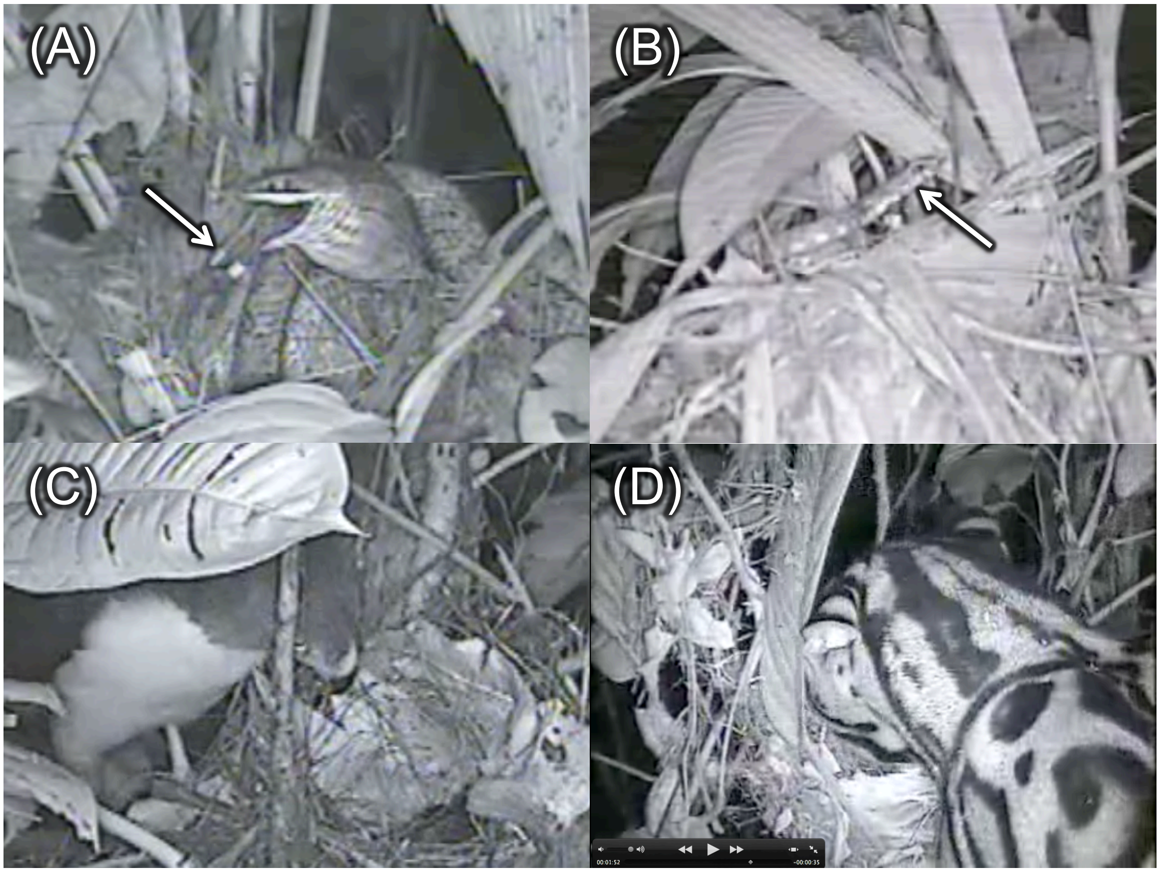

Figure 3.4. Video stills from chestnut-backed antbird (*Myrmeciza exsul*) nest depredations. Nest cup diameter averages 7.1cm (0.5 SD) for visual reference. (A) An adult *Pseustes poecilonotus*, the only identified predators in the contiguous forest of Quebrada Gonzalez, here consuming a nearly full-grown nestling (arrow indicates nestling's leg bands). (B) Juvenile *Pseustes*—identified by their distinct dorsal and ventral markings (indicated by arrow)—were common predators of eggs and occasionally nestlings. (C) A semiplumbeus hawk (*Leucopternis semiplumbeus*)—here depredating a nest in the Río Frío fragment—was the lone avian predator recorded. (D) This ocelot (*Leopardus pardalis*), was one of only two mammals (both in fragments) that depredated nests during the course of the study.

Figure 3.5. The bird-eating snake (*Pseustes poecilonotus*) consumed chestnut-backed antbird (*Myrmeciza exsul*) nest contents in 80% of depredation cases, highlighting the need to understand its biology better so as to improve understanding of its impacts on bird populations in human-modified landscapes. Photo credit: Maxime Aliaga.

DISCUSSION

This study used real nests on a landscape-scale to test the nest-predation hypothesis in a Neotropical understory insectivore, while systematically identifying predators. Our hypothesis that nest predator taxa vary spatially, and thus influence the daily nest predation rate (DPR) was partially supported. Predator frequencies did not permit formal tests, but support the notion that more diverse predator taxa affected nests in fragments. Snakes were clearly dominant—*Pseustes* in particular—supporting the idea that snakes are primary nest predators in Central American tropical forests (Robinson et al. 2005a, Delhey et al. 2010, Brawn et al. 2011). However, some nest depredation patterns countered our expectation; specifically, greater nest predation rates did not correspond with where the predator pool was most diverse nor where antbird populations were most dense.

Dense populations in fragments

The observed population density trends are atypical for most, but not all, understory insectivores (Robinson 2001, Laurance et al. 2011). High chestnut-backed antbird population density in fragments suggests that nest depredation may not cause understory bird declines in fragments, at least in this species; but that fragments may instead provide refuge from nest predation, allowing population increase. Alternatively, chestnut-backed antbirds may have benefitted from reduced niche overlap following release from competitors like western slaty antstrikes (*Thamnophilus artinucha*) and spotted antbirds (*Hylophylax naeviodies*) that rapidly disappeared from fragments (Sigel et al. 2006, Roberts 2007, Touchton and Smith 2011). Other considerations include effects of altered trophic dynamics and habitats on understory bird abundance. Food availability could have increased following fragmentation, a hypothesis that could be tested by quantifying arthropods directly, or indirectly via food provisioning rates and biomass delivery to nests. Lack of dispersal from fragments could also lead to more dense populations, and genetic information shows that chestnut-backed antbirds in this region disperse poorly (Woltmann et al. 2012b). In fragments, understory-adapted birds may also fare poorly due to higher-light conditions (Patten and Smith-Patten, 2012; but see Pollock et al., this issue), deeper leaf litter (Stratford and Stouffer, this issue), or other aspects of forest structure (Pavlacky et al., this issue). Another possibility is that increased collared peccary (*Pecari tajacu*) abundance at La Selva has reduced liana tangle abundances, a preferred foraging and nesting substrate for many specialized forest interior insectivores (Michel and Sherry, 2012; Michel et al., *in review*).

Nest predation differences

The negatively density-dependent DPR trend was unexpected (although not unheard of; Robinson, 2001), and suggests that in chestnut-backed antbirds high nest predation fails to correspond with high density, but could instead possibly contribute to low population density. Central American understory bird nest failure probabilities are typically close to 70% (comparable to the predation probability in the fragments), although nest predation rate varies spatially and temporally, and thus should not be treated as characteristic of a species (Robinson et al. 2000b). With 95% of chestnut-backed antbird nests failing to fledge offspring at La Selva, high nest predation pressure there might contribute to declines of some understory bird populations. Another possibility is that high predation rate reflects nest scarcity. For instance, there may be fewer total bird nests available to predators at La Selva because so many species have declined there. Thus, if the predator populations have remained stable, they may simply be consuming a greater proportion of the total nests available to them. Conversely, the predators' effect would be more spread out where the bird community is more dense, such as in upslope areas like QG or in fragments.

Nest success is only one of several demographic parameters that determine population status; higher annual productivity (via multiple nesting attempts), as well as adult and juvenile survival, could compensate for nest losses, and competition could factor into fecundity (Sofaer et al. 2014). Aspects of parental care such as nest defense and investment in fledglings could also prove informative (Roper et al. 2010, Tarwater and Brawn 2010). Evidence for limited habitat area, dispersal ability, microhabitat availability, and microclimatic conditions all exist as well, so any nest predation effects would not act alone (Michel et al., 2015; Pavlacky Jr. et al., *this issue*; Stratford and Stouffer, *this issue*; Woltmann et al., 2012). Adult and natal dispersal among fragments or subpopulations, for example, is very limited for chestnut-backed antbirds, so empty territories may not be quickly filled from a source population (Woltmann et al. 2012b). Comprehensive demographic studies of Neotropical species are needed to understand how these various factors combine and interact (see Tarwater et al., 2011).

Habitat type best explained nest predation rate in our study, suggesting that habitat-scale ecological factors should be considered a likely influence on regional understory bird nest predation. Indeed, nests were less likely to be depredated in fragments and contiguous sites than in peninsular La Selva, suggesting that fragments and very large reserves may function as refugia for this species, and perhaps for other understory nesters that survive initial fragmentation effects. We suspect that the lack of a significant difference between the fragmented and contiguous sites could be related to the latter having the smallest sample size (n=15). Skutch (1966) and Snow and Snow (1963) were among the first to predict relief from nest predation in disturbed sites like fragments, where predators have disappeared. But because lower nest predation in fragments is not typical in temperate systems, the notion has gained little attention (but see Friesen et al., 1999; Tewksbury et al., 1998). This result of reduced nest predation in fragments was also unexpected considering another Sarapiquí study: Young et al. (2008) estimated higher and nearly equal DPRs in fragments (0.052±0.008) and La Selva (0.052±0.009) compared to contiguous forest (0.023±0.008). A key difference is that Young et al. (2008) monitored real nests of many species pooled together, obscuring species-level variation found in the present study (see also Brawn et al., 2011).

The idea that generalist nest predators readily access forest fragments from the surrounding matrix seems increasingly unlikely in tropical forests. We detected no effect of edge proximity on DPR. In light of our primary nest predator's success at depredating nests in more intact forest (see also Robinson et al. 2005), one might sooner expect to find an inverse rather than traditional edge effect in this region (e.g., Spanhove et al., 2009a, 2009c). Edge effects may ultimately be more habitat- or predator-specific than intrinsic to edges per se (Robinson 2009).

Varying nest predators among sites

Our results confirm the value of identifying nest predators. Given that 89% of nest predators were snakes (see also Robinson et al. 2005), this predator may have a major influence on the region's avifauna. Different predator groups seemed to respond to habitat fragmentation in different ways, and perhaps at different spatial or temporal scales. *Pseustes'* dominant influence at the site with by far the highest DPR (La Selva) points to their potential importance, although the control forest also had exclusively snake predators. That sites with mixed predator taxa had the lowest DPR suggests an alternative hypothesis: the low nest predation rate in fragments could theoretically result from low snake abundance there, which would also afford other predators a better chance of finding the nests.

Our observed nest predator identifications do not eliminate the mesopredator release hypothesis; it is possible that *Pseustes'* predators might be rare in connected/protected forest like La Selva, leaving their population unchecked. Population release of snakes is not unheard of (Savidge 1987, Laurance 1997). Not only are *Pseustes* protected from hunting at La Selva, but most of their known and potential predators, especially large raptors, have experienced declines or extirpation there (e.g., crested eagle *Morphnus guianensis*, Hawk Eagle *Spizaetus ornatus*, Swainson's Hawk *Buteo swainsoni*, and Harpy Eagle *Harpia harpyja*; Bierregaard, 1984; Klein et al., 1988; Muñiz-López et al., 2007; Rodríguez-Estrella, 2000; Sigel et al., 2006). While we also observed exclusively snake predators at the contiguous forest site, one notable difference is that some large raptors that could keep *Pseustes* in check, such as ornate hawk-eagles, still occur there (*pers. obs.*). However, why the snakes would not have also undergone release in smaller fragments (where the largest raptors are almost certainly absent) is not clear. Surveys are needed of edge-tolerant raptor populations.

Lower snake abundance or activity in fragments could also explain chestnut-backed antbird nest predation patterns. Indiscriminate persecution of snakes by humans in unprotected fragments could theoretically reduce snake populations, but unfortunately no data on snake persecution exist to validate this idea. Snake activity patterns is another potentially important factor. For example, passerine nest predation in Illinois and Texas increases with Texas ratsnake (*Elaphe obsoleta*) activity (Sperry et al. 2008, Weatherhead et al. 2010). Snakes in slightly cooler, higher elevation Costa Rican sites like QG might be less active than those in the warmer lowlands (Bennett 1982). We could learn much from future investigations that simultaneously monitor *Pseustes* abundance and activity along with other nesting Sarapiquí bird species.

Conservation implications and future directions

Focused study of a representative understory insectivore here exemplifies how nest predation can vary widely across fragmented tropical forests, inversely with population density, and thus could influence both population persistence and density. Our results emphasize considering habitat type (size and degree of connection) and primary predators as potential explanatory factors for declining populations. To further understand bird persistence disparities in fragments, much more demographic information is needed. We recommend including phases of avian annual cycles beyond the nest to include all factors relating to population growth rates. Specifically, we need to learn how adult and juvenile survival, and season-long productivity vary across fragmented landscapes.

The identification of *Pseustes* as the major nest predator on a widespread rainforest understory bird raises questions about what controls the snake's abundance and activity, and what other species it affects. *Pseustes* also remains a compelling explanation for why many of the insectivorous bird populations declined at La Selva—a major tropical research hub. Unfortunately, forest snakes are difficult to survey, but if captured, snakes of *Pseustes'* size can readily be implanted with Passive Integrated Transponder

(PIT) tags and radio transmitters (Wasko and Sasa 2009, O'Malley 2014). Nevertheless, better understanding of threats to understory birds will come from research on predator biology, including the under-studied subjects of tropical nest predator movements, home ranges, diet, and prey consumption rates (Weatherhead and Blouin-Demers 2004, Lahti 2009).

Video identification revealed a largely expected suite of nest predators, but nest predation rate displayed an unexpected pattern: nest predation may not threaten some species in fragments, but might threaten some in larger forest tracts. Learning the mechanisms generating these patterns could contribute to our ecological understanding of understory bird population declines in the Sarapiquí. Future research into avian decline/persistence in other tropical regions should consider rigorous tests of this nest-predation hypothesis to assess its generality.

ACKNOWLEDGEMENTS

This research was supported financially by a Louisiana Board of Regents Graduate Fellowship, the Organization for Tropical Studies (OTS), the American Ornithologists' Union, the Stone Center for Latin American Studies, the Wilson Ornithological Society, the Newcomb College Institute, Sigma Xi, and an NSF grant to TWS. OTS, especially R. Vargas and C. de la Rosa, facilitated countless aspects of this study. We also thank the staff of Quebrada Gonzales, especially R. Tenorio; the staff of Río Frío Colegio, especially R. Vargas; and the local residents of Puerto Viejo de Sarapiquí and La Virgen for lodging, support, and their commitment to conservation. J. P. Kelley lent us hand-held video cameras in 2010. D. Dierick provided electrical engineering help for video camera construction. D. Wasko provided herpetological expertise. S. Wilson advised on nest survival models. Invaluable field and lab assistance was provided by M. Aliaga, I. Ausprey, M. Brady, L. Cohen, A. Dufrene, D. Ferraro, D. Forthmann, H. Greeney, F. Newell, E. Nishikawa, B. O’Malley, L. Ormsby, S. Pack, A. Pizarro, C. Sedgewick, N. Sly, W. Tsai, R. Valveri, and E. L. Vasquez. Animal care was approved by the Tulane University IACUC protocol No. 0394R. The La Selva Biological Station Advisory Committee; the Costa Rican Ministerio de Ambiente, Energía y Telecomunicaciones (MINAET), the Costa Rican Sistema Nacional de Áreas de Conservación (SINAC), and the Costa Rican Área de Conservación Cordillera Vólcanica Central (ACCVC) resolution No. 012-2013-ACCVC-PI; and the Costa Rican Comision Nacional para la Gestion de la Biodiversidad (CONAGEBIO) resolution No. R-016-2013-OT-CONAGEBIO approved of and logistically supported this research.

Chapter Four[3]

Patterns and causes of understory bird declines in human-disturbed tropical forest landscapes: a case study from Central America

ABSTRACT

Tropical forest understory birds are declining globally for unknown reasons, indicating an urgent need to understand the causes. We review and synthesize studies investigating causes of these declines focusing on the Sarapiquí region of the Caribbean slope of Costa Rica. We discuss evidence for five potential causes of population declines motivated by current understanding of the effects of fragmentation, disturbance of remnant forests, climate change, and their possible interactions: (1) reduced forest area increases the probability of stochastic extirpation; (2) reduced connectivity among forest patches decreases population rescue opportunities; (3) degradation of preferred microhabitats due to, for example, abundant large mammals, jeopardizes specialized birds' foraging opportunities; (4) high nest predation rates reduce productivity below replacement levels; and (5) changes in macro- and microclimate increase energetic demands and reduce survival. Our review documents how tropical forest loss and degradation likely impact understory birds through a variety of direct, indirect, and interrelated causes spanning multiple temporal and spatial scales and levels of biological organization. We propose

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[3] A version of this chapter, written with coauthors N.L. Michel, W.A. Boyle, B.J. Sigel, S. Woltmann, and T.W. Sherry, is in revisions for the journal *Biological Conservation*.

that the processes affecting understory birds in the Sarapiquí region may be broadly representative of threats experienced by rainforest understory birds pantropically. Effective conservation will require consideration of such diverse and interacting factors.

Keywords

climate change; fragmentation; Neotropics; population decline; understory birds

INTRODUCTION

Tropical communities are threatened globally (Newbold et al. 2014). Effective conservation of tropical species requires determining why their populations are declining and identifying the ecological and life history traits associated with persistence or loss. Although many correlates of extinction risk have been identified, mechanistic studies of declines are surprisingly infrequent. Considerable recent interest has focused on avian declines in particular. While we recognize that tropical forests are losing their avifaunas, the causes of these extirpations are poorly understood (Sodhi et al. 2004, 2011). The biodiversity stakes are high because these communities are diverse and provide essential ecosystem services such as insect control (Blake and Loiselle, 2009; Maas et al., *in review*; Şekercioğlu, 2006; Terborgh et al., 1990).

Insectivorous birds have emerged as a guild of particular concern in tropical rainforest understory (Robinson 1999, 2001, Şekercioğlu et al. 2002, Sigel et al. 2006, 2010). Many of these species possess traits that increase sensitivity to disturbance including having large territories (and thus, low population density and large area requirements), poor dispersal capabilities, and preferences for old growth or interior forest habitat (Stouffer and Bierregaard 1995, Robinson 1999, Şekercioğlu et al. 2002, Sodhi et al. 2004, Şekercioğlu 2007, Lees and Peres 2008, 2010). Microhabitat specialization resulting from diet and/or foraging specialization is also common in this guild, including reliance on dense understory vegetation, sparse leaf litter, or particular types of arthropods or fruits (Fitzpatrick, 1980; Marra and Remsen, 1997; Michel et al., *in review*; Michel et al., 2015; Sherry, 1984; Stratford and Stouffer, 2013). Nest type and placement by many of these birds (e.g., open-cup, ground, and pendulous nests) may elevate predation risk from a variety of predators (Oniki, 1979; Sieving, 1992; Sigel et al., 2010; but see Sigel et al., 2006; Young et al., 2008). Finally, the tropical forest understory guilds contain many small-bodied birds (Karr, 1971) that must feed frequently due to high mass-specific metabolic rate exacerbated by large surface area to body mass ratio. A consequence of such physiological traits is sensitivity to climatic change (Karr and Freemark 1983, Canaday 1997, Stratford and Robinson 2005) and thus greater vulnerability to extinction (Boyle and Sigel, *in review*; Owens and Bennett, 2000).

Here we take advantage of a well-studied tropical region, the Sarapiquí River watershed on the Caribbean slope of Costa Rica, as a case study to examine the causes of understory bird population declines in fragmented and otherwise disturbed tropical forests. Given the correlates of avian declines listed above and this region's ecological history, five core hypotheses (grouped into four categories) emerge as likely causes of decline: (1a) Loss of intact old-growth forest has reduced available habitat for bird species with strong preferences for this habitat type. (1b) Fragmentation also prevents dispersal-limited understory birds from moving between isolated habitat patches. (2) Microhabitat availability has declined even within intact forest; specifically, increased abundance of collared peccaries (*Pecari tajacu*, a native omnivorous mammal) has reduced an important microhabitat (dense liana tangles) needed by many specialized insectivores, including mixed-species flock participants. (3) Nest predation by a specialized predator, the bird-eating snake (*Pseustes poecilonotus*) has disproportionately impacted ground/understory nesters in connected forest more than in fragments or contiguous forest. (4) Physiological stressors linked to changing temperature and rainfall regimes are resulting in declines of small-bodied birds. In the following sections we review evidence from the Sarapiquí region of Costa Rica for each of these hypotheses, and consider each of these causes in a broader tropical perspective. Finally, in order to develop comprehensive conservation recommendations, we interpret causes in terms of their associated spatio-temporal scales and levels of biological organization.

METHODS

We reviewed published literature by searching Web of Science, Google Scholar, Science Direct, and the Searchable Ornithological Research Archive. Search terms included combinations of the following: Sarapiquí, Costa Rica, forest, rainforest, disturb*, fragment*, climate change, avian, understory, bird*, decline, mechanis*, cause*. We supplemented these searches with targeted efforts to locate references recommended by colleagues or otherwise identified during the literature search.

We assessed recent (1997-2012) land use in the Sarapiquí River watershed through analysis of land cover datasets in ArcMap 10.1 (ESRI, Redlands, CA). We merged the 1997-2000 Land Use dataset from the Earth Observation Systems Laboratory and Fondo Nacional de Financiamento Forestal (http://cro.ots.ac.cr/en/laselva/gis/laselva_gis/index.html) with the 2012 MODIS Land Cover type dataset (MCD12Q1). The MCD12Q1 data product was obtained through the online Data Pool at the NASA Land Processes Distributed Active Archive Center (LP

DAAC), USGS/Earth Resources Observation and Science (EROS) Center, Sioux Falls, South Dakota (https://lpdaac.usgs.gov/data_access). Additional spatial data layers (rivers, reserve boundaries, and a digital elevation model) were obtained from the La Selva Biological Station Geographic Information Systems Laboratory (http://cro.ots.ac.cr/en/laselva/gis/laselva_gis/index.html).

CAUSES OF UNDERSTORY BIRD DECLINE

Land use history and the Sarapiquí avifauna

The Sarapiquí region was historically forest-covered, but declined to approximately 70% forest cover by 1963 and ~55% today (Fig. 4.1). Mature forest loss slowed following a 1996 ban on deforestation, but agricultural expansion into pasture and secondary forest interferes with forest regeneration (Fagan et al. 2013). The remaining mature forest is largely restricted to ecological reserves, including Braulio Carrillo National Park, which now encompasses 47 000 ha of primarily old-growth forest that extends up to ~3 000 masl (McDade and Hartshorn 1994), La Selva Biological Station (hereafter La Selva), Tirimbina Biological Reserve (hereafter Tirimbina), and several other private reserves as well as scattered forest fragments in a matrix of pasture and cropland (Read et al. 2001).

Besides regional deforestation, local landscapes also affect the avifaunal community both directly and indirectly (Sigel et al. 2010). For example, corridors can facilitate forest bird movements, just as pastures and agricultural crops inhibit movements. Elevational corridors are thought to enhance altitudinal migration (Blake and Loiselle 2000). Despite La Selva's connection to Braulio Carrillo National Park's large area of forest by an elevational corridor, its rapid rise in elevation and extensive deforestation along La Selva's southern and western edges (Read et al. 2001) may have effectively isolated some lowland-restricted species. Where present, secondary forest provides additional habitat and dispersal opportunities for some understory species, but even older secondary forest may be unsuitable for many forest-dependent birds (Barlow et al. 2007).

The bird community in the Sarapiquí region of Costa Rica's Caribbean slope was first described by Slud (1960) at La Selva. The first systematic bird censuses were conducted there in the late 1970s by TWS, and repeated by Bruce Young in the 1990s (Sigel et al. 2006). Together with other qualitative assessments of the bird community through the end of the twentieth century (Stiles 1983, Levey and Stiles 1994, Zook et al. 1999) a picture emerged of the responses of birds at La Selva and throughout Sarapiquí to regional landscape changes. Specifically, understory insectivores and species that participate in mixed-species flocks declined significantly between 1960 and 1999, concurrent with regional forest loss (Sigel et al. 2006).

Reduced Habitat Area and Connectivity

Habitat loss

Tropical deforestation often leaves islands of forest surrounded by non-forest matrix, such as pastures, plantations, buildings, and roads. In forest fragments, as on islands, area and isolation from continuous forest influence species richness and composition (Watling and Donnelly 2006). In forest fragments, however, processes such as edge effects and matrix composition also influence species richness, and it is challenging to tease these processes apart from area effects (Lees and Peres 2006, Laurance 2008). Habitat loss and fragmentation inevitably reduce bird population size, increasing the likelihood of stochastic extirpation. Many Neotropical forest species have large territory sizes (e.g., 53 ha for *Phaenostictus mcleannani* and 200 ha for *Lipaugus unirufus*; Chaves-Campos and DeWoody, 2008; Sigel, 2007), and consequently low population densities making such species susceptible to area effects (Terborgh et al. 1990, Robinson et al. 2000a).

In the Sarapiquí region, forest loss has created forested islands of varying size. Sigel (2007) compared bird diversity in four sites in the region (La Selva, Tirimbina, and two small fragments surrounded by banana plantations), using Refugio Bartola connected to the 260 000 ha Indio Maíz Biosphere Reserve in southeastern Nicaragua as a control site. As predicted by the species-area relationship, estimated bird species richness—estimated by point counts for a subset of each reserve—was highest in the control site (111 spp), followed by La Selva (77 spp, 1 200 ha of primary forest) and Tirimbina (65 spp, 345 ha), and significantly lower in small fragments surrounded by banana plantations (58 spp, 35.4 ha and 53 spp, 24.6 ha; Matlock et al., 2002; Sigel, 2007). Species may continue to decline and disappear from these sites, as time lags in extirpations may occur up to 100 years after isolation (Brooks et al., 1999) and regional deforestation occurred 30-40 years ago. Continued monitoring is necessary to assess the effects of time lags and evaluate the impact of local reforestation projects (Matlock et al. 2002, Pagiola 2008).

Dispersal limitation

The dispersal-limitation hypothesis was developed from island biogeography and metapopulation concepts, and posits that organisms may be unable or unwilling to cross hostile matrix to re-colonize fragments undergoing extirpation (MacArthur and Wilson 1967). However, it is difficult to test. Although birds' flight may generally reduce vulnerability to dispersal barriers, we know little about their dispersal, and some tropical understory birds disperse surprisingly poorly. A problem testing the dispersal-limitation hypothesis is that patterns of species occurrence in terrestrial landscapes may be misleading, saying little about processes like population resilience and likelihood of recolonization and rescue. For example, a frequent assumption is that species occupying a majority of fragments in a landscape must be good dispersers (With and King 1999, Uezu et al. 2005, Boscolo and Metzger 2011), but this pattern may arise instead because species persist at a site for long periods due to high survival and strong site-faithfulness (e.g., Gill and Stutchbury, 2006; Morton and Stutchbury, 2000; Woltmann and Sherry, 2011). Also, natal dispersal may be greater than breeding dispersal, and thus more important for understanding the impacts of fragmentation on adult distributions in tropical forest birds. Unfortunately, natal dispersal is poorly studied in all birds, not just tropical, and low nesting success in many tropical birds makes natal dispersal challenging to study in practice (Ricklefs and Bloom, 1977; Robinson, 2009; Robinson et al., 2000b; Rompré and Robinson, 2008; With and King, 1999; D.M.V. *unpubl. data*).

Despite the challenges associated with studying dispersal limitation, mounting evidence suggests that poor dispersal ability reduces the persistence of tropical understory birds in fragmented landscapes. Rigorous tests of dispersal limitation come from three main types of data: mark-recapture, displacement trials, and molecular genetics. Mark-recapture studies reveal that some tropical birds regularly move between forest fragments, clearly not limited in their movements by the matrix (Stouffer and Bierregaard 1995, 2007, Barlow et al. 2006). Importantly, in two of these studies the matrix was secondary forest, which may be more permeable to birds than agricultural or human-inhabited landscapes.

Displacement trials entail capturing, releasing, and observing whether individual birds return to their home range. Compelling evidence for limited flight capacity of tropical birds comes from Panama, where a number of species were shown to be physically incapable of flying 200-300m over open water, thereby demonstrating that Barro Colorado Island (a true island) contains closed populations of several understory species (Moore et al. 2008). Similarly, in more typical terrestrial contexts, some understory birds were hesitant to cross even 50 m of non-forest habitat despite strong motivation to do so (Ibarra-Macias et al. 2011). Nevertheless, a number of studies have demonstrated the propensity for some understory individuals to return after being displaced at distances up to 1.4 km, provided that there are minimal gaps and at least some forest cover (Laurance et al. 2004, 2005, Castellón and Sieving 2006, Kennedy and Marra 2010).

Molecular genetic data (e.g., microsatellites) are increasingly valuable for providing evidence of genetically-relevant dispersal processes over larger geographic and time scales than typical for behavioral studies such as displacement trials (Haig et al. 2011, Sunnucks 2011). In the Sarapiquí, high mean pairwise relatedness in isolated fragments suggests that individuals produced in fragments infrequently emigrate, implying that most individuals did not disperse into those fragments (Woltmann et al., 2012a; W.D. Robinson and S.W., *unpubl. data*). Consequently, individuals must be breeding with related individuals. Over time, such inbreeding will inevitably have negative demographic consequences (Frankham 1998, 2005).

Combining genetic data with information about the movement behavior of adults and juvenile birds reveals dispersal patterns at fine spatial scales. In the Sarapiquí lowlands, adult chestnut-backed antbirds were unlikely to disperse (~32% switched territories or left the study area in 5 yr). Furthermore, juveniles were capable of acquiring and defending territories within the same site as their parents (Woltmann and Sherry 2011), and genetic parentage assignment techniques enabled Woltmann et al. (2012b) to infer natal dispersal distances in chestnut-backed antbirds of typically <2 km. Thus, even within intact forest, this understory bird disperses little.

Microhabitat and dietary specialization

Many tropical understory forest-interior birds specialize in microhabitats for foraging and feeding. For example, frugivores often feed from many plant species, but some specialize on substrates (e.g., fruits of epiphytes or hemiepiphytes; Boyle et al., 2011) and others forage on only one or a few plant families, exemplified by olive-backed euphonia (*Euphonia gouldi*) and white-vented euphonia (*E. minuta*) specialization on mistletoe berries (Snow, 1971). Similarly, many understory insectivores are stereotyped foragers or diet specialists (Fitzpatrick 1980, Sherry 1984, Marra and Remsen 1997). For example, some insectivores consume diverse arthropods from one substrate, such as dead leaves in the case of checker-throated antwren (*Epinecrophylla fulviventris*; Gradwohl and Greenberg, 1980; Rosenberg, 1993).

Many tropical forest-interior birds forage in a limited number of microhabitats (Sherry 1984, Marra and Remsen 1997, Stratford and Stouffer 2013). For example, at least 457 bird species forage, nest, and/or roost in tangles of lianas (i.e., woody vines; Michel et al., 2015). Lianas support abundant and diverse arthropod resources such as planthoppers (Sherry, 1984; Wolda, 1979). Dense liana tangles also trap falling dead leaves that shelter arthropods, creating food pockets attractive to antwrens and other understory insectivores (Gradwohl and Greenberg 1980, Michel et al. 2015).

Dietary and microhabitat specialization should make forest-interior birds relatively vulnerable to altered vegetation structure or food availability. Indeed, species with narrow trophic-niche widths are less likely to persist following logging and fragmentation than species that feed on a wider range of prey types (Edwards et al., 2013). At La Selva, the forest-interior understory birds that continue to decline (Boyle and Sigel, *in review*) include many mixed-species flocking insectivores (Sigel et al. 2006, 2010), many of which specialize on liana tangles (Michel et al., *in review*). Many of these same Sarapiquí species persist in nearby, smaller forest reserves (e.g., Tirimbina; B.J.S., *unpubl. data*; Michel et al., *in review*). This pattern of regionally patchy decline hints at causes that affect vegetation locally, rather than direct effects of limited forest area.

Changes in vegetation structure and, consequently, avian microhabitat frequently occur at fragment edges (Didham and Lawton 1999). Yet vegetation structure responds to multiple drivers even within large, intact forest reserves far from edges (Michel and Sherry 2012). Global climate change may also alter vegetation structure; elevated night-time temperatures are linked to increased tree mortality at La Selva, although there are no directional trends to date (Clark et al. 2010). Yet vegetation structure varies within the Sarapiquí region: canopy cover as well as palm cover, liana cover, and vine density are significantly lower at La Selva than nearby Tirimbina, again suggesting site-specific processes (Michel 2012).

Large mammals, particularly ungulates, shape vegetation structure locally through both trophic (e.g., eating leaves, roots, seeds) and non-trophic (e.g., trampling, wallowing) effects (Paine 2000, Beck 2005). By reducing vegetation biomass and changing vegetation structure, abundant native large mammals impact a wide variety of other animals, including birds (Foster et al. 2014). At La Selva, the collared peccary has rebounded from near-extirpation in the 1970s (unlike the now extirpated white-lipped peccary) to become unusually abundant today (Michel et al., *in review*; Romero et al., 2013), concurrent with understory bird declines. Collared peccaries are far more abundant at La Selva (14-66/km^2) than either Tirimbina (3/km^2) or Bartola (4/km^2; Michel et al., *in review*; Romero et al., 2013). La Selva's omnivorous collared peccaries reduced the frequency of dense liana tangles used by many understory insectivorous birds by 57% and also reduced vine density by 30% and liana cover by 41% relative to experimental mammal exclosures (Michel, 2012; Fig. 4.2). La Selva also has fewer liana tangles than Barro Colorado Island (Michel et al., *in review*). Furthermore, lianas comprise >30% of total rainforest canopy cover (Avalos and Mulkey 1999). By reducing lianas, peccaries have also significantly reduced canopy cover (Michel et al., *in review*), thus likely exposing understory birds to increased light levels and warmer, drier microclimates at La Selva (see Section 3.5).

Eight of La Selva's declining understory insectivorous bird species forage selectively and/or nest in liana and vine tangles (Michel et al., 2015; Michel et al., *in review*; Sigel et al., 2010). For example, checker-throated antwrens, dot-winged antwrens (*Microrhopias quixensis*), and ruddy-tailed flycatchers (*Terenotriccus erythrurus*) have declined severely at La Selva (Sigel et al., 2010) where populations are lower (0.60–1.3 birds/100ha) than Tirimbina (2.2–28.3 birds/100ha) or Barro Colorado Island (BCI; 25.6–256 birds/100ha; Michel et al., *in review*; Robinson, 2001). Structural equation models reveal that, across six sites in Costa Rica, Nicaragua, and Panama, collared peccaries have strong negative direct and indirect effects (i.e., mediated by vine and liana density and cover) on abundance of these same three species (Michel et al., *in review*). Moreover, other common causes of tropical understory bird decline cannot explain the spatial patterns observed in these species: dispersal limitation is greater at BCI (a true island) than La Selva despite higher abundance of many forest interior insectivores in the former; and climatic conditions are similar at La Selva, Tirimbina, and Bartola, while drier and more seasonal at BCI (Michel et al., *in review*). Research suggests that collared peccary alteration of understory and canopy vegetation structure likely contributes to declines of understory birds through a combination of preferred foraging microhabitat loss and microclimatic change (Michel and Sherry, 2012; Michel, 2012; Michel et al., *in review*). These interactions illustrate how changing abundances of an ecologically important species such as the collared peccary may potentially lead to complex and arguably eccentric ecological results. Such effects could be representative of keystone species loss in other Neotropical forests.

Elevated nest predation

At temperate latitudes nest predation tends to be higher in fragmented forest relative to contiguous forest (Donovan et al. 1995, Luck 2003, Tewksbury et al. 2006) and in forest edges relative to interiors (Batary and Baldi 2004). Reasons for this pattern include reduced vegetation cover in degraded and fragmented forest reducing availability of well-camouflaged nesting sites (Martin 1992). The greater edge-to-interior ratio of fragments is also generally thought to allow predator influx from surrounding habitats (Tewksbury et al. 2006, Thompson 2007). Mesopredators—usually mid-trophic level mammals (e.g., foxes)—are often opportunistic nest predators (Crooks and Soule, 1999). More abundant nest predators may result from mesopredator release in temperate forest fragments that have lost apex predators.

In fragmented tropical landscapes, elevated nest predation can also reduce avian productivity causing population declines (Willis 1974, Stratford and Stouffer 1999, Sodhi et al. 2004, Stratford and Robinson 2005). However, we often fail to see the same relationships between fragmentation and predation in Neotropical forest as we do in temperate forests (Stratford and Robinson 2005, Lahti 2009). For example, several Neotropical studies have found no evidence of edge effects on nesting birds (e.g., Carlson and Hartman, 2001; Chiarello et al., 2008; Cooper and Francis, 1998). Tropical forest fragmentation can affect the vegetation and physical environment up to 400 m from the edge (Laurance et al. 2002), potentially modifying nest site vulnerability nearer to edges. Yet the few Neotropical studies that have demonstrated elevated predation risk in fragments or near edges are all based on data from artificial nests (i.e., Carlson and Hartman, 2001; Chiarello et al., 2008; Cooper and Francis, 1998; Galetti et al., 2009; Gibbs, 1991; Sieving, 1992). Such results may not reflect true risk to nesting birds (Roper 1992, Zanette 2002, Moore and Robinson 2004). Studies using real nests are infrequent because finding sufficient tropical bird nests is often logistically challenging (Robinson et al. 2000b). Two recent studies from the Sarapiquí region using real nests found no evidence of elevated nest predation near edges (Visco and Sherry, *in review*; Young et al., 2008). These findings suggest that tropical nest predators are likely neither edge species nor elevated in abundance in the surrounding matrix. Young et al.'s (2008) study also found higher nest predation rates in fragments and at La Selva (80%) relative to contiguous forest of Braulio Carrillo National Park (BCNP, 50%) for several understory species pooled together. However, pooling species may obscure important species-specific patterns; for example, chestnut-backed antbird experiences nest predation rates of 64-72% in fragments compared to 95% at La Selva and 79% in contiguous forest (Visco and Sherry, *in review*).

Such spatial patterns of nest predation offer a potential demographic explanation for why some understory species have declined at La Selva relative to contiguous forest, although nest predation apparently cannot explain losses from smaller fragments. The causes of high nest predation at La Selva remain unclear, potentially resulting from higher predator abundance or foraging activity compared to both the fragments and higher-elevation contiguous forest. Alternatively, densities of understory birds may be so much lower at La Selva than other habitats (due to decline and/or elevational patterns) that there are fewer total bird nests, so the predators depredate a greater proportion of the available nests.

Sarapiquí's understory nesting birds are primarily depredated by a specialized nest predator, *Pseustes poecilonotus*, the bird-eating snake. *P. poecilonotus* was responsible for 80% of video-documented chestnut-backed antbird nest predations (N=46; Visco and Sherry, *in review*; see also Robinson et al., 2005). Snakes in general were responsible for all recorded nest predations in both lowland La Selva (60-100 masl) and higher-elevation (400 masl) forest in BCNP (Visco and Sherry, *in review*). Considering the lower predation rate in BCNP, perhaps its cooler climate limits ectothermic snakes' abundance or activity levels (see Sperry et al., 2008). Despite this regional variation, *P. poecilonotus*' disproportionate influence on nest success implies that the presence, absence, or activity of a single predator species can influence nesting bird populations.

While high nest predation rates at La Selva could help explain understory bird declines there, low nest predation rates in other fragments—opposite to the expected pattern—fail to explain regional understory bird declines. One possibility is that predators, and specifically *P. poecilonotus,* have also declined in fragments. Because tropical forest birds tend to be long-lived (Johnston et al., 1997; Moreau, 1944; but see Karr et al., 1990), relatively high nest predation rates alone should rarely doom populations to extirpation. Demographic models reveal that typical adult annual survival rates of 0.75±0.07 can overcome nest predation rates as high as 73% to maintain a stable population (Young et al. 2008, Wilson et al. 2011, Woltmann and Sherry 2011). However, high survival may not be enough: additive effects of habitat loss, reduced foraging opportunities, and climate change could tip the population balance, resulting in declines (Sodhi et al. 2004).

Physiological tolerances to changing environments

Changing climate is another factor that could explain rainforest understory bird declines. Exposure to even sublethal climatic conditions could alter behavior, increase stress, and increase energy expenditure, resulting in reduced survival or reproductive success. Climate can also affect avian demography indirectly via food availability. How birds cope with these environmental changes depends on physiological processes such as thermoregulatory capacity and metabolic rates—factors that covary with body size.

Changing climate and microclimate of the Sarapiquí lowlands

In the northern Neotropics, both temperature and precipitation have increased in recent years, and sites influenced by Caribbean precipitation patterns are experiencing more severe precipitation events (Aguilar et al. 2005). Since 1983, La Selva's maximum and minimum temperatures have increased by an average of 0.2°C per decade (Fig. 4.3a,b). Mean daily maxima in 2005 and 2008 peaked at nearly 32°C, approaching the upper critical threshold of 37°C for some small birds (Weathers and Riper 1982, Powers 1992). Over the same 30-year period, rainfall has also increased by an average of 307mm per decade (Fig. 4.3d; Clark and Clark, 2011), while the number of days with no precipitation have declined by 20-40 days per decade (Fig 4.3c; Whitfield et al., 2007). However, total annual precipitation appears not to have changed significantly over the past 50 years (Clark and Clark 2011, OTS 2014).

Independent of global climate processes, local changes to the understory microclimate may have occurred due to vegetation structure change. A common consequence of tropical forest fragmentation is warming and drying of forest edges (Laurance et al. 2002, Stratford and Robinson 2005). Most forested areas of the Sarapiquí have experienced increased fragmentation and edge:forest ratio since the 1960s (Joyce 2011). However, in some areas of Sarapiquí, deforested land surrounding old-growth has reforested (Drake et al. 2002), buffering adjacent understory (Didham and Lawton 1999). Thus, although edge effects might have contributed to population declines at La Selva and in forest fragments, this probably cannot explain regional avifaunal changes.

Other microclimatic changes may be driven by changing vegetation in Sarapiquí, including tree mortality, reduced tree growth, and the effects of collared peccaries on vegetation structure (Section 3.2). Canopy openings could increase understory light levels—an important factor for light-sensitive species (Patten and Smith-Patten 2012)—potentially accompanied by increased temperature and decreased humidity. Unfortunately, we lack the data to evaluate these vegetation-dependent microclimate changes.

Direct physiological consequences of changing climate

Body size and understory habitat use are the strongest predictors of current decline in La Selva's avifauna (Boyle and Sigel, *in review*). Contrary to predictions from island-biogeography theory, small-bodied birds are more likely to be declining in the Sarapiquí region, and are declining faster than larger-bodied birds, independent of habitat. The covariation between insectivory and small body size, and the stronger predictive power of body size relative to diet suggest that associations between insectivory and decline may be driven by factors differentially affecting small-bodied species (Boyle and Sigel, *in review*).

How might higher temperatures and altered humidity, including more severe rainfall events, affect Sarapiquí birds physiologically? Tropical birds often have narrower temperature optima than temperate counterparts (Stratford and Robinson 2005). Furthermore, avian temperature tolerance is mediated by humidity: Under dry conditions, some desert birds can cope with temperatures >45°C, but with even slight increases in humidity their ability to dissipate heat declines dramatically, elevating metabolic costs (Gerson et al. 2014). Tropical birds can detect and respond behaviorally to spatial variation in microclimate (Karr and Freemark 1983), even when these differences are small (e.g., 0.8°C, 4.2% humidity; Şekercioğlu et al., 2007). However, doing so may be costly, if not impossible. Obligate understory species typically experience even narrower diurnal swings in temperature and humidity than do birds living in the canopy or forest edge (Stratford and Robinson 2005). Thus, just as tropical and temperate birds differ in their abilities to survive swings in climatic conditions (Janzen 1967, Ghalambor et al. 2006), understory birds may have relatively narrow thermal niches and suffer greater adverse consequences of changing climates than birds in other tropical habitats.

Unfortunately, measurements of the breadth and plasticity of thermal neutral zones in tropical forest birds are few. Thermal tolerance in birds is better studied in more extreme environments (McKechnie and Erasmus 2006, McKechnie 2008, McKechnie and Wolf 2010) or exposed non-forested habitats (Weathers 1997). Deviance from allometric relationships helps identify those guilds with reduced capacity to cope metabolically with climatic variation as a function of body size (Bernardo et al. 2007). Smaller birds, regardless of their habitat, are more sensitive to temperature fluctuations due to well-established relationships between body size and conductance (a measure of the ease of heat exchange between a birds' body and the environment) (Weathers 1997). For small Neotropical birds, thermal extremes of 37°C may approach lethal or near-lethal limits, particularly if such species have evolved relatively low and narrow thermal optima (Weathers and Riper 1982). Weathers (1997) reports a thermal neutral zone of 28.9-39.2°C for the 10.9g variable seedeater (*Sporophila corvina*), a bird commonly found in deforested Neotropical regions. Thermal neutral zones of wet forest understory birds may be even more restricted; conductance of two manakin species is far higher than predicted by allometric equations, and basal metabolic rate (BMR) is far lower (Weathers 1997). High conductance and low BMR reduce birds' abilities to regulate internal temperature and consequently to tolerate thermal fluctuations (Bucher and Worthington 1982).

Frugivores and granivores typically have higher BMRs than insectivores independent of body size relationships, suggesting a direct link between diet and physiology that could explain declines of the insectivore foraging guild (Sabat et al. 2009).

A variety of tropical forest birds also facultatively drop metabolic rate at night when temperatures cool off to conserve energy (Bucher and Worthington 1982, Bartholomew et al. 1983, Downs and Brown 2002, Steiger et al. 2009). If night-time temperatures increase (Fig. 4.3b; Clark and Clark, 2011), warm nights could deprive understory birds of energy savings from heterothermy. While it appears that selection will likely favor thermal generalists (Boyles et al. 2011), we have few data with which to evaluate the relationship between climatic tolerances and patterns of species decline in Neotropical forests.

As little as we understand the physiological consequences of variation in temperature on tropical understory birds, we know even less regarding the consequences of variation in precipitation regime. Both too much and too little rain likely adversely affects fitness, but we lack empirical or theoretical data to identify precipitation optima—the equivalent of the thermal neutral zone for rain and humidity. In some more seasonally dry Neotropical forests, positive deviations in rainfall have positive demographic effects (Brawn, 2012; but see Dugger et al., 2004) which are likely mediated by food abundance (Brown and Sherry 2006, Studds and Marra 2007, Williams and Middleton 2008). However, in wetter forests, the reverse may be true. Mounting evidence suggests that in the context of high annual rainfall, further increases in rainfall are stressful to birds; extreme rainfall events trigger facultative short-term movements of tropical birds (Ramos-Olmos 1983), and both synchronize and influence the magnitude of downhill movements by seasonal altitudinal migrants (Boyle et al. 2010, Boyle 2011). Severe rainfall in the Sarapiquí region raises corticosterone levels and necessitates short-term fasting (Boyle et al. 2010). Severe rainfall also alters patterns of energy acquisition and storage elsewhere, as observed in rainforest birds in Sarawak (Fogden, 1972) and the Cocos Finch (*Pinaroloxias inornata*; T.W.S. and T. Werner Sherry, *unpubl. data*). Behavioral and physiological responses occur independently of local food availability (Boyle 2008b), suggesting that heavy rain impedes foraging directly rather than altering food abundance. Heavy rainfall influences reproductive behavior via this same mechanism; foraging and feeding rates decline during torrential rains elsewhere in Central America (Foster 1974). Due to the allometric relationships between body size, metabolic rate, and capacity for energy storage, small birds run out of energy reserves more quickly than do large birds (Calder 1974). Thus, precipitation-induced fasts are most likely to penalize small birds.

Because precipitation is the major axis of seasonality in tropical forests, it stands to reason that changes to rainfall regimes will have profound consequences for tropical avifauna. We know, for instance, that rainfall seasonality regulates the timing of breeding in some Neotropical species (Wikelski et al. 2000). While widely hypothesized to reflect an indirect effect of climate on reproduction via food availability, it may be the direct effects of rainfall that limit the ability of tropical birds to nest during the wettest times of the year (Dowsett-Lemaire 1989, Tye 1992).

Unfortunately, there are very few mechanistic studies of physiological consequences of climate change on tropical birds (Harris et al. 2011). While slower life histories mean that the longevity of tropical birds could buffer populations from stochastic weather-related events, their low reproductive rates will limit populations' capacity to recover from mortality events (Morris et al. 2008). If we take a regional perspective to species conservation efforts, we might worry less about lowland Central American birds under climate change than birds with no possibility for upslope range shifts such as central Amazonian species. However, until we understand the basis for the losses and declines of lowland avifauna, and the patterns of population change at higher elevations, we will not be able to predict further changes or mitigate on-going losses. We echo the call for more studies of tropical birds' physiological responses to climate (Şekercioğlu et al. 2012).

Figure 4.1. Land use in the Sarapiquí River watershed, compiled from data sets collected during 1997-2012.

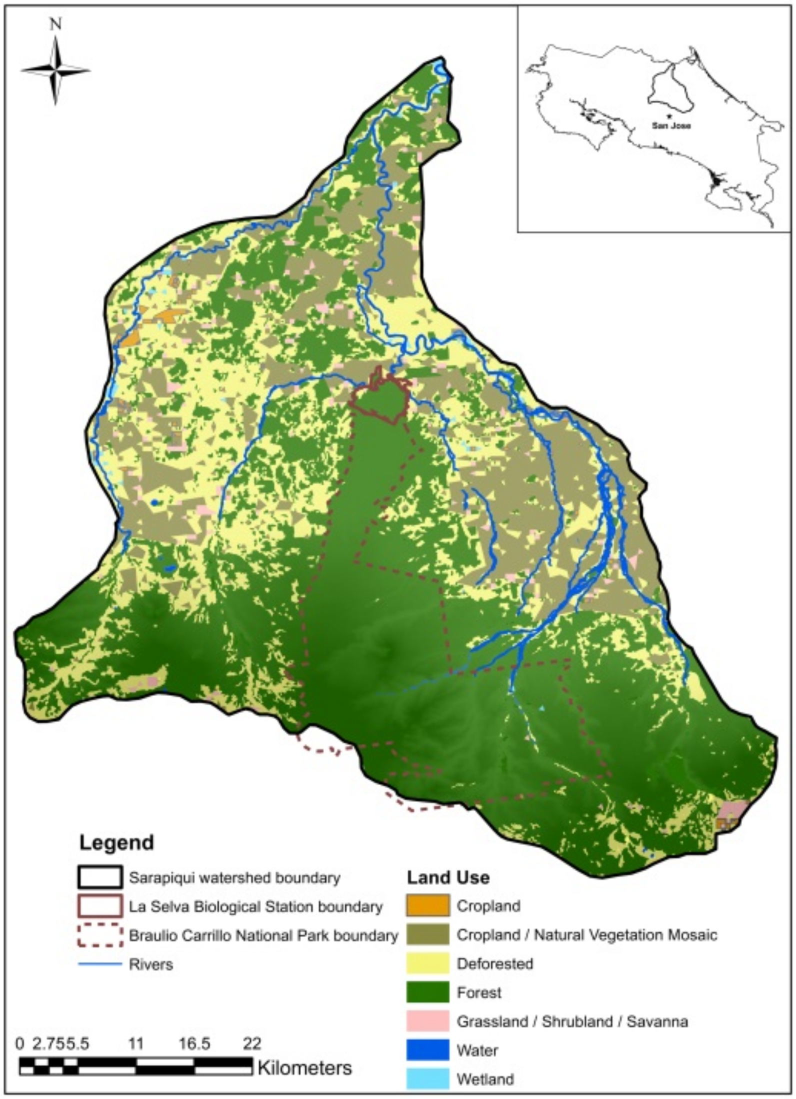


Figure 4.2. Proposed direct (solid arrows) and indirect (dashed arrow) effects of abundant collared peccaries (*Pecari tajacu*; top left) on lianas (bottom center) and understory birds (checker-throated antwren, *Epinecrophylla fulviventris*; top right) in the Sarapiquí River watershed. Potential effects of peccaries on lianas are described in the bottom left, and benefits lianas provide to birds are described in the bottom right.
(Photo attribution – peccary: Nicole Michel; checker-throated antwren: Dominic Sherony; liana tangle: Nicole Michel. This work is licensed under the Creative Commons Attribution 3.0 Unported License. To view a copy of this license, visit http://creativecommons.org/licenses/by/3.0/.)

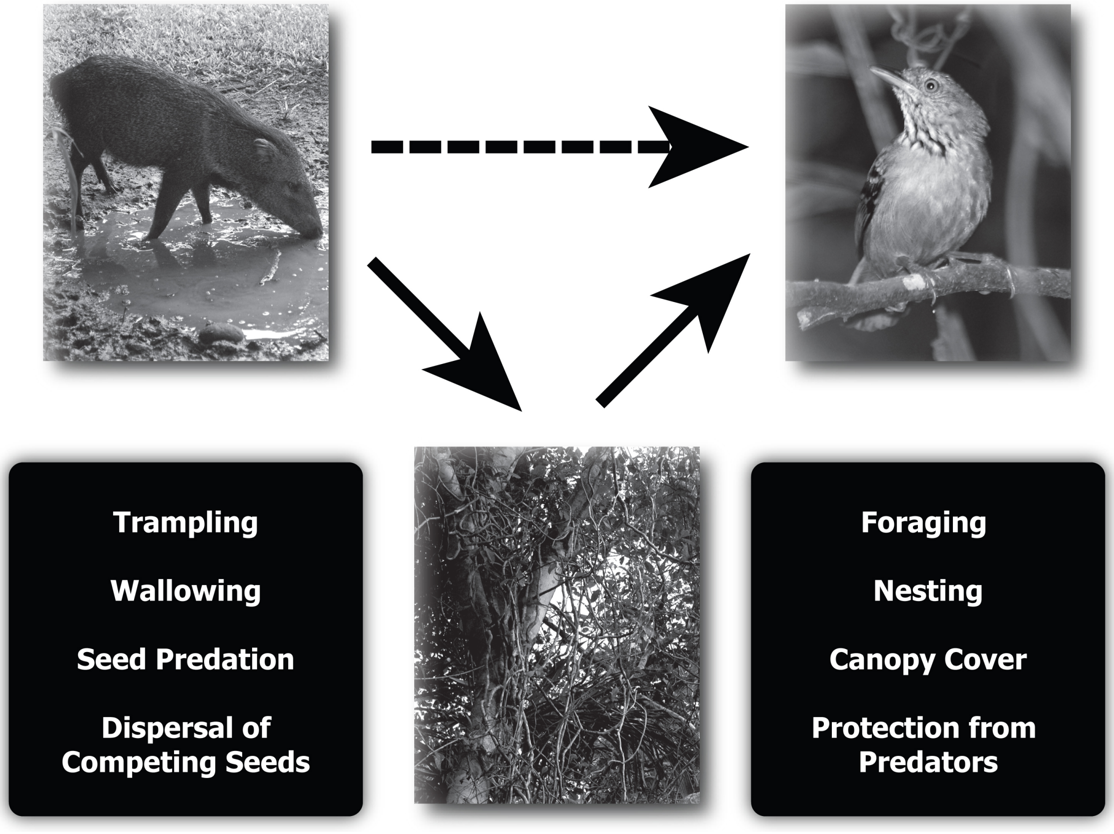
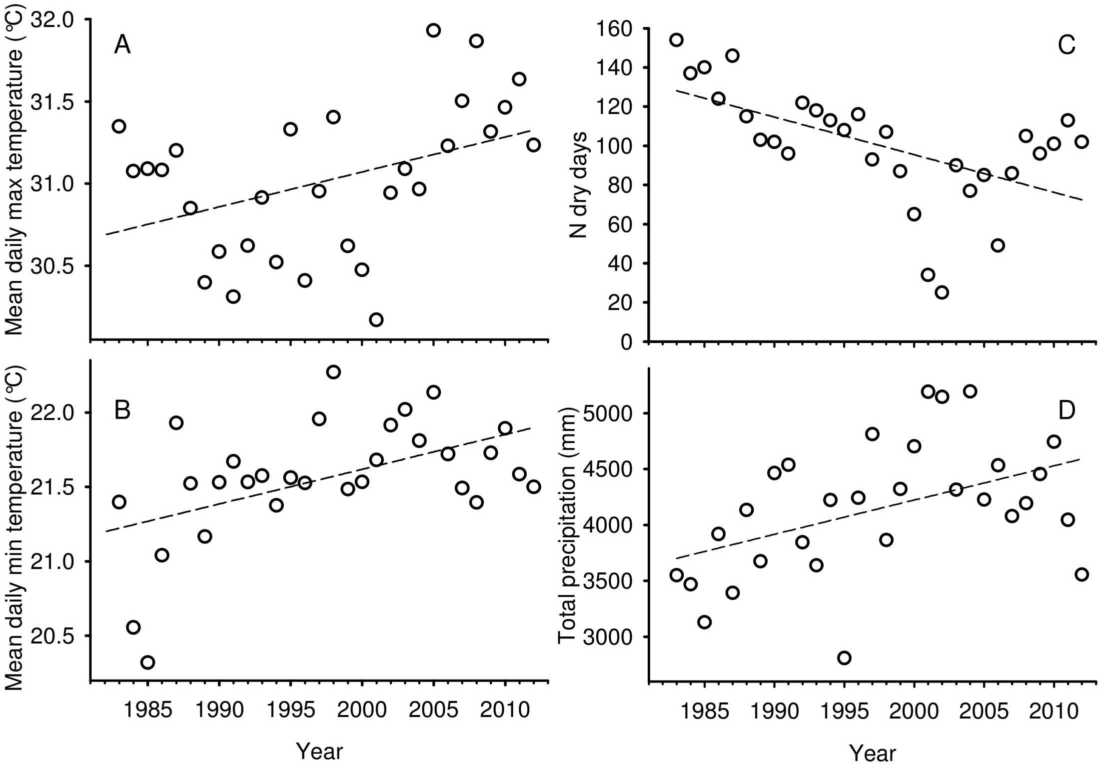


Figure 4.3. Organization for Tropical Studies (OTS) Meteorological Data from 1983 to 2012 (OTS 2014). During this time, mean daily maximum temperatures increased (Panel A, $R^2=0.17$, $p=0.024$), mean daily minimum temperatures increased (Panel B, $R^2=0.26$, $p=0.004$), the number of dry days decreased (Panel C, $R^2=0.33$, $p=0.001$), and total precipitation has increased (Panel D, $R^2=0.21$, $p=0.01$). Data from http://www.ots.ac.cr/meteoro/default.php?pestacion=2.

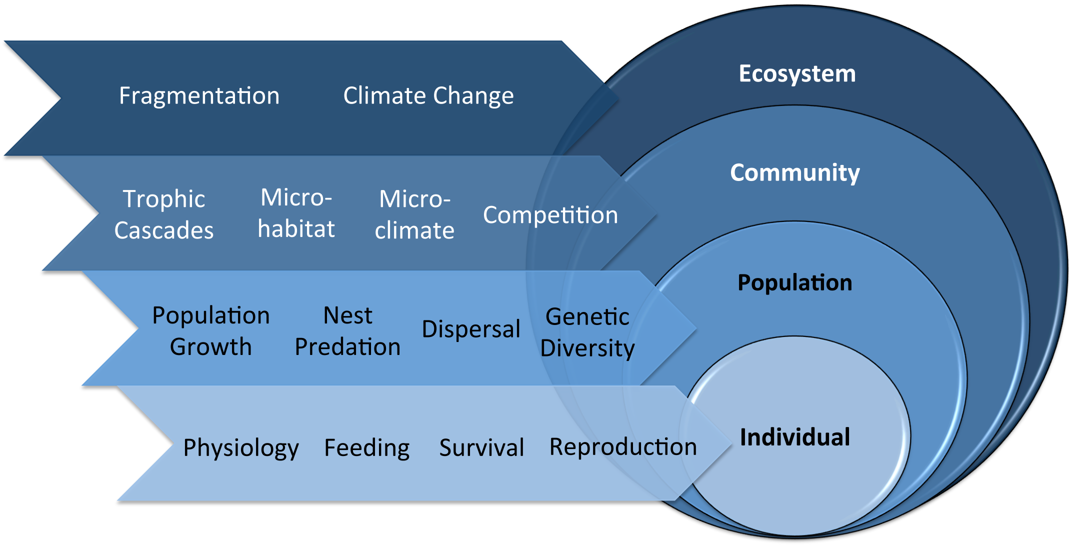


SYNTHESIS: CHARACTERIZING THE CAUSES OF DECLINE

The foregoing review identifies several likely causes of understory bird decline in disturbed tropical forest, but we must consider that these factors rarely operate in isolation. Due to the complexity of ecological networks and high biodiversity, tropical forests may be particularly susceptible to “ecological meltdown” (sensu Terborgh et al., 2001) when disturbed. Inter-specific relationships often depend on particular biotic or abiotic conditions that vary across the tropics, even within wet forested regions. Heavy forest fragmentation coupled with human-modified climate disrupts these ecological relationships at multiple levels of organization, which in turn affect each other (Fig. 4.4). For example, causes of decline that operate at the population level, such as inbreeding depression resulting from limited natal dispersal opportunities, will exert the strongest effects when individuals are simultaneously stressed by individual-level factors such as body condition (Delgado et al. 2010). To make inferences to other regions, we must consider that the structure of these relationships has two consequences: (1) populations of tropical forest birds are vulnerable to a diverse set of disruptions in their interactions, making them particularly vulnerable to human impacts; and (2) forest fragmentation and climate change entail many predictable impacts at particular ecological levels, but the interrelationships among these levels largely depend on the local context.

Time lags also likely play a greater role in persistence of understory bird populations than currently understood. We know that time lags occur between the isolation of populations in fragments and subsequent inbreeding and loss of heterozygosity. Such genetic effects can take decades to hundreds of years to manifest in birds depending on fragment size (Keyghobadi 2007). Similarly, direct or indirect climatic effects, or changes to vegetation triggering complex trophic interactions that affect individual fitness, could take decades to manifest themselves as population-level effects (Davis 1986). Over longer timescales, populations with small habitat areas, low genetic diversity, limited food and microhabitat availability, and limited reproduction, or that include physiologically stressed individuals, are likely to be more vulnerable to stochastic disturbance events.

Figure 4.4. How causes of understory bird decline primarily act on ecological structure in human-disturbed tropical forest.



CONSERVATION AND RESEARCH RECOMMENDATIONS

Our review highlights diverse independent and interacting threats to Neotropical understory birds. The studies featured here suggest that understory bird populations may persist temporarily in forested reserves and even some fragments, but remain vulnerable to multiple threats to persistence. Although not a sustainable solution for most species, fragments are valuable to land managers, as many fragments contain thriving wildlife populations (Şekercioğlu et al. 2007, Mendenhall et al. 2014) and present opportunities for achieving conservation goals via education and community engagement (e.g., Tirimbina; Tirimbina Biological Reserve, 2010; Turner and Corlett, 1996). Nevertheless, we advocate setting aside large relatively intact tropical forest reserves and increasing connectivity between them, as exemplified by the San Juan-La Selva Biological Corridor that connects multiple lowland and highland forest areas (Fagan et al., 2013; see also Ripple et al., 2014). Importantly, however, even large reserves need ongoing monitoring to ensure that key ecological processes remain intact.

Regardless of global human impacts, faunal communities inevitably change over time, forming novel ecosystems, so goals to restore ecosystems to “pre-human” states are both unrealistic and ill-advised (Jackson and Hobbs 2009). If instead our goal is to conserve existing diversity and functioning ecosystems, then tangible solutions exist. Our assessment from this Sarapiquí case study indicates that large, unfragmented reserves with genetically diverse populations, diverse microhabitats, monitored populations of keystone species (e.g., top carnivores, ungulates, and nest predators), and connectivity with climate-buffered high-altitude forests may provide understory birds the best odds for surviving on-going human-caused disturbances.

Undoubtedly we have oversimplified some causes and missed other important threats. Nevertheless, this case study of the Sarapiquí region embodies key ideas prevalent in the broader field of tropical forest biodiversity conservation. Common themes include the fact that research focused on single species may overlook threats to other species in the community. Additionally, across-taxa, research is needed on basic demography and long-term genetic prospects of isolated populations. Despite the difficulty of teasing apart stochastic from more deterministic ecological changes given the necessarily restricted temporal and spatial perspective, insights from Sarapiquí likely apply to tropical forests generally. Indeed, many hypotheses explaining declines arose from results from other sites such as the Biological Dynamics of Forest Fragments Project in Brazil (Laurance et al. 2011), and Barro Colorado Island in Panama (e.g., Robinson, 1999). Our work also highlights where future research is strategically important to advance understanding of threats to tropical taxa generally.

Efforts to understand threats to tropical taxa are hindered by substantial logistical challenges. For example, quantifying dispersal distances in large, unfragmented landscapes is a priority, but the undisturbed landscapes in which such studies would be possible are extremely scarce. Another logistic challenge is financially supporting the resource- and time-intensive monitoring work required to characterize fragment and reference landscape population trends. Long-term data such as mark-recapture studies are critical to understanding the demographic bottlenecks in declining populations, yet funding for such studies is notoriously difficult to obtain. Funding presently tends to favor large-scale meta-analyses, molecular analyses, and modeling over long-term ecological field research (Sodhi et al., 2011; but see the Stability of Altered Forest

Ecosystems project in Borneo, Ewers et al., 2011). Incentivizing the long-term effort and financial commitment involved in targeted experimental studies is crucial for understanding the causes of tropical forest biodiversity loss (Lindenmayer et al. 2012).

ACKNOWLEDGEMENTS

Support during the research and writing of this article was provided by NSF grant DEB-1242588 to TWS. NM was supported during the writing of this article by Environment Canada and the School of Environment and Sustainability at the University of Saskatchewan]. This is contribution no. 15-095-J of the Kansas Agricultural Experiment Station. Although this review was not conducted in Costa Rica, we wish to acknowledge the Organization for Tropical Studies for their continued support of the authors, as well as the Costa Rican Ministerio de Ambiente, Energía y Telecomunicaciones (MINAET), Sistema Nacional de Áreas de Conservación (SINAC), Área de Conservación Cordillera Vólcanica Central (ACCVC), and the Costa Rican Comision Nacional para la Gestion de la Biodiversidad (CONAGEBIO) for their facilitation of conservation research efforts.

Chapter Five

Conclusions: What have we learned about understory insectivore population biology in the fragmented tropics?

Sifting through the various ecological factors that might play a role in producing different population growth trends is complicated, especially in biodiverse tropical forests where food resources are unquantified, competitors are diverse, and predators are largely undocumented. Even for well-studied taxa like birds, tropical life histories are incompletely documented, so there is less knowledge to build on compared with temperate species (Robinson et al. 2010). Demographic rate data are even scarcer (and we often have no appreciation of the extent to which they may vary), and population growth rate estimates are almost nonexistent. Essentially, many Neotropical bird studies must start from scratch, and like much of science, take a leap of faith that the nests can be found and the birds can be captured. Collecting comprehensive population data is made even more challenging by the logistics of Neotropical rainforest work; long breeding seasons, large territories, dense vegetation, venomous snakes, and expensive travel and field station fees dissuade many researchers from undertaking the long-term projects necessary to collect sufficient demographic data on Neotropical birds species (but see Styrsky and Brawn 2011, Tarwater et al. 2011). Add to this the multiple sites necessary for comparative studies in fragmented landscapes, and now a small army of keen field assistants is also necessary. It is thus unsurprising that comprehensive demographic and ecological studies of any tropical birds in fragmented landscapes are few (but see Githiru and Lens 2006, Korfanta et al. 2012, Bierregaard et al. 2014). The option to just collect one-time blood samples and go becomes much more appealing. Narrowing the focus to a single species is one way to make the logistical limitations of tropical fieldwork more manageable.

In-depth study of a single species has the advantage of controlling many aspects of life-history, such as habitat requirements, dispersal tendencies, diet, and nest structure, allowing elimination of several otherwise plausible explanations early on. But in-depth focus on a single species runs the risk of producing results with limited applicability. So is the investment in such projects worth it? For species belonging to certain groups, the answer is yes. Considering the gaps in our knowledge, large-scale declines, and the continued pervasive effects of human disturbance to tropical forests, studies of sensitive guilds such as insectivores and small-bodied birds are desperately needed (Şekercioğlu et al. 2002, Sodhi et al. 2004). Because of their sensitivity, the health of these understory bird populations indicates the health of their tropical forest homes, and likewise, their declines may be among the first signals that the state of their environment is deteriorating (Bregman et al. 2014). Species-specific observations can help tease apart the causes behind those declines. As we collect more case studies over various spatial scales, we can shed light on the proximate causes of population changes.

Within close proximity (~35 km as the toucan flies) in a landscape fragmented by deforestation, I observed populations of chestnut-backed antbird (*Myrmeciza exsul*) exhibit considerably different behavior. Such species on the cusp of persistence or decline are in a unique position to inform us about the ecological constraints operating to produce those trends in fragmented forests (Şekercioğlu et al. 2007). The research presented in this dissertation is among the first studies to take advantage of an understory insectivorous bird species persisting both in undisturbed tropical rainforest and fragments, allowing comparative demographic and ecological study. To our knowledge, it is the first such study specifically in the Neotropics.

The populations of *M. exsul* that I examined in the Sarapiquí region of Costa Rica differed considerably in demography, including population density, nest survival, and adult survival (Chapter 2, 3). These populations were located in either small and isolated forest remnants (i.e., fragments Río Frío, RF, and La Virgen, LV), a forest reserve connected to the 40,000 ha Braulio Carrillo National Park (BCNP), but deforested on its other three sides (i.e., forest peninsula La Selva Biological Station, hereafter La Selva), and a location within the park itself (i.e., contiguous forest Quebrada Gonzalez, QG). Demographically, contiguous forest site QG usually fell somewhere in between the other two habitats, not differing significantly from either. Although QG is one of the lowest accessible locations within BCNP, our low sample sizes there (largely representing the difficulties of navigating its steep and rocky terrain) reduced statistical power. The differences in vital rates were most pronounced between La Selva and the fragments, with lowest nest success and lower adult survival at La Selva.

To investigate the effects of these vital rate differences to the demography of each population as a whole, I estimated population growth rate (λ) by inputting demographic rates from each habitat type into three separate matrix population models (Chapter 2). This represents the first comprehensive comparative demographic model of a Neotropical rainforest bird, and it is among the first such models of a tropical bird in general (see

Tarwater et al. 2011, Korfanta et al. 2012 for two other examples). Given my initial predictions based on avian fragmentation studies from mostly temperate (but some tropical) studies, the directionality of the results was surprising. According to the models, the peninsula population (in a well studied ecological reserve) was declining, the fragment populations were increasing, and the contiguous forest population was intermediate given its relative stability. A particularly exciting aspect of these findings is that these methods suggest that the system remains in a state of flux, in which case it may take many decades for any kind of population stabilization in anthropogenically-disturbed landscapes. These results also ran contrary to the expected declines of understory insectivore populations in forest fragments (Canaday 1997). Clearly, something about *M. exsul* is different, allowing them not only to hang on, but to grow relatively dense populations in forest remnants. They are not, however, invulnerable to human impacts in the region, as indicated by their decline at La Selva (Sigel et al. 2006).

The populations' behavior fails to follow a consistent trend from the most to the least connected, so factors other than area effects alone must be operating to explain the demographic differences—factors that might be linked to other ecological aspects of the habitats. Sensitivity and elasticity analyses of the population models helped tease apart the relative importance of various demographic factors to the population growth rate (Chapter 2; Caswell 2010). Key findings were that La Selva's λ was most responsive to perturbations of adult survival and nest success, and the fragment λ to juvenile and general nesting success, but the elasticity response was not clearly associated with any one parameter. Another clue to explain the differences among habitats came from the stable stage distributions and reproductive values, which were consistent with a strong effect of low adult survival at La Selva, and a lesser influence of adult survival but higher influence of juvenile reproduction in the fragments. Thus the models help us understand that even within nearby populations of one species, the factors most likely to tip the population balance can differ among habitats, and may therefore depend on several ecological features.

What are the factors that could explain different adult survival and nest success rates? Ultimately, the main limitations involved are food and mortality from predators (Martin 1996), although we still know little about parasites and diseases. To explore one of these limitations further, I next investigated mortality of young in the nest (Chapter 3). The probability of daily nest predation was significantly lower at La Selva than in each of the other habitats. Videography revealed the cause of nest predation in 80% of cases was the bird-eating snake, *Pseustes poecilonotus*. That *Pseustes* is a nest predator of Neotropical understory birds was not novel (Robinson and Robinson 2001, Robinson et al. 2005a, Tarwater 2008, Riehl and Jara 2009), but its dominance in every site was surprising. Furthermore, no Neotropical bird species has had its predators documented on the scale of the present study (*n*=46 compared to *n*≤10 in other studies), and thanks to >22,000 hours of continuously-monitoring video, this study also represents the second-largest tropical nest predation dataset globally (Pierce and Pobprasert 2013). For *M. exsul,* the relative dominance of *Pseustes*' as a nest predator corresponded with the severity of daily predation rates among sites; they represented 86% of the predators at La Selva, where predation rates were 95%, but 69% of predators in fragments where predation rates were 32%. *Pseustes* predation of adult *M. exsul* could be a plausible explanation for the La Selva population's relatively low survival (Hayes 2002). While nest predation by *Pseustes* fails to explain the decline of other understory insectivores in fragments where the snake is less prevalent, its potential impact in areas like La Selva warrants further study. *Pseustes* is a wide-ranging and likely specialized predator of many other bird species, so it could potentially impact entire communities of understory birds throughout large areas of the Neotropics (Savage 2002). This aspect of my research has led to one preliminary investigation focused on *Pseustes* (O'Malley 2014), although far more research on *Pseustes* is needed.

The implications of these results for the fields of tropical ecology and avian population biology are that more intraspecific variation exists in demographic rates than previously appreciated. Nest predators, especially snakes, need further investigation so as to understand their abundances, activity levels, and potential roles in tropical bird declines (Weatherhead and Blouin-Demers 2004). Availability of food resources for insectivores is poorly documented in the tropics, and such information could greatly increase our ability to diagnose the causes of population declines (Sánchez et al. 2014). I have demonstrated the application of videographic methods to reveal nest predation rates, nest predator identifications, and variation of predation across a landscape, but it can also be applied to other aspects of tropical forest bird ecology and behavior such as food provisioning. Future video work could quantify *M. exsul*'s diet by estimating provisioning rate and biomass delivered to nestlings, testing the accuracy of provisioning rate as a food estimate (Omland and Sherry 1994). Further video applications include understanding other life-history decisions made by adults, such as how they manage the tradeoff between their own survival versus that of their offspring when defending the nest (Pietz and Granfors 2005).

The sum of the evidence reported and inferences made in this dissertation support the potential for nest predation to explain understory bird declines in some habitats (such as La Selva of the Sarapiquí). Yet these represents only one of the likely causes of understory bird decline in Costa Rica's Sarapiquí region (Robinson and Sherry 2012b). A review of regional evidence supports effects of (1) habitat area loss, (2) limited forest habitat connectivity associated with the fragmentation coupled with poor dispersal ability across non-forest habitat, (2) reduced microhabitat availability, (3) elevated nest predation, and (4) low physiological tolerances to changing climates (Chapter 4). This work in the Sarapiquí lowlands of Costa Rica is among the first regional syntheses of diverse anthropogenic factors impacting tropical rainforest understory birds, providing novel perspectives on the scales and interactions of factors (Githiru and Lens 2007). In light of these causes, managing for understory bird conservation means more than setting aside protected forest. Effective management should mitigate these threats as much as possible by striving to provide large, unfragmented reserves with genetically diverse populations, intact microhabitats, monitored populations of keystone species, established populations of top predators, and connections to climate-buffered forests.

In addition to the scientific advances described in this dissertation, the project as a whole made broader impacts on students and communities both in the United States and Costa Rica. While conducting field research, I have given bird banding demonstrations and forest tours to classes at the Río Frío high school. In a larger effort to teach students about local effects of forest fragmentation, local wildlife conservation activities, and the part they can play, I partnered with wildlife documentary producers Wild Lens to make an educational video in Spanish, which I distributed to three local schools, a local church, and the education coordinator of La Selva Biological Station. Thus far, I have disseminated my research by giving invited talks at three scientific meetings in the U.S., and two tropical meetings in Costa Rica, in association with societies for the study of ecology, ornithology, tropical biology, and conservation. I have contributed to the future of these fields by training and mentoring students both in the field and the lab, including 4 Latin American field assistants, 13 other assistants, and 4 Tulane undergraduate women, 3 of whom pursued independent projects which are all being prepared for publication. Because we lived and worked away from research stations for the majority of the project, I also fostered cross-cultural learning and understanding (and vastly improved my Spanish) among my crew, officials such as park guards, and most importantly, local residents.

LIST OF REFERENCES

Aguilar, E., T. C. Peterson, P. R. Obando, R. Frutos, J. A. Retana, M. Solera, J. Soley, I. G. García, R. M. Araujo, A. R. Santos, V. E. Valle, M. Brunet, L. Álvarez, M. Bautista, C. Castañón, L. Herrera, E. Ruano, J. J. Sinay, E. Sánchez, G. I. H. Oviedo, F. Obed, J. E. Salgado, J. L. Vázquez, M. Baca, M. Gutiérrez, C. Centella, J. Espinosa, D. Martínez, B. Olmedo, C. E. O. Espinoza, R. Núñez, M. Haylock, H. Benavides, and R. Mayorga. 2005. Changes in precipitation and temperature extremes in Central America and northern South America, 1961–2003. Journal of Geophysical Research 110:D23107.

Anders, A. D., and M. R. Marshall. 2005. Increasing the accuracy of productivity and survival estimates in assessing landbird population status. Conservation Biology 19:66–74.

Andrén, H. 1992. Corvid Density and Nest Predation in Relation to Forest Fragmentation: A Landscape Perspective. Ecology 73:794–804.

Arnold, T. W. 2010. Uninformative Parameters and Model Selection Using Akaike's Information Criterion. Journal of Wildlife Management 74:1175–1178.

Avalos, G., and S. S. Mulkey. 1999. Seasonal changes in liana cover in the upper canopy of a Neotropical dry forest. Biotropica 31:186–192.

Barlow, J., L. A. M. Mestre, T. A. Gardner, and C. A. Peres. 2007. The value of primary, secondary and plantation forests for Amazonian birds. Biological Conservation 136:212–231.

Barlow, J., C. A. Peres, L. M. P. Henriques, P. C. Stouffer, and J. M. Wunderle. 2006. The responses of understorey birds to forest fragmentation, logging and wildfires: An Amazonian synthesis. Biological Conservation 128:182–192.

Bartholomew, G. A., C. M. Vleck, and T. L. Bucher. 1983. Energy metabolism and nocturnal hypothermia in two tropical passerine frugivores, Manacus vitellinus and Pipra mentalis. Physiological Zoology 56:370–379.

Batary, P., and A. Baldi. 2004. Evidence of an edge effect on avian nest success. Conservation Biology 18:389–400.

Beck, H. 2005. Seed predation and dispersal by peccaries throughout the Neotropics and its consequences: a review and synthesis. Pages 77–115 *in* P. Forget, J. E. Lambert, P. E. Hulme, and S. B. Vander Wall, editors. Seed fate: predation, dispersal and seedling establishment. CABI, Wallingford, UK.

Bennett, A. F. 1982. The Energetics of Reptilian Activity. Pages 155–199 Biology of the Reptilia. 13th edition.

Bensch, S., D. Hasselquist, and T. von Schantz. 1994. Genetic similarity between parents predicts hatching failure: nonincestuous inbreeding in the Great Reed Warbler? Evolution 48:317–326.

Bernardo, J., R. J. Ossola, J. Spotila, and K. A. Crandall. 2007. Interspecies physiological variation as a tool for cross-species assessments of global warming-induced endangerment: validation of an intrinsic determinant of macroecological and phylogeographic structure. Biology letters 3:695–698.

Bierregaard, R. O. 1984. Observations of the nesting biology of the Guiana crested eagle (Morphnus guianensis). The Wilson Bulletin 96:1–5.

Bierregaard, R. O., and T. E. Lovejoy. 1989. Effects of forest fragmentation on Amazonian understory bird communities. Acta amazonica 19:215–241.

Bierregaard, R. O., T. E. Lovejoy, V. Kapos, A. Augusto, R. W. Hutchings, and R. B. Jr. 1992. The Biological Dynamics of Tropical Rainforest Fragments: A prospective comparison of fragments and continuous forest. BioScience 42:859–866.

Blake, J. G., and B. A. Loiselle. 2000. Diversity of birds along an elevational gradient in the Cordillera Central, Costa Rica. The Auk 117:663–686.

Blake, J. G., and B. A. Loiselle. 2008. Estimates of apparent survival rates for forest birds in eastern Ecuador. Biotropica 40:485–493.

Blake, J. G., and B. A. Loiselle. 2009. Species composition of Neotropical understory bird communities: local versus regional perspectives based on capture data. Biotropica 41:85–94.

Bolton, M., N. Butcher, F. Sharpe, D. Stevens, and G. Fisher. 2007. Remote monitoring of nests using digital camera technology. Journal of Field Ornithology 78:213–220.

Boscolo, D., and J. P. Metzger. 2011. Isolation determines patterns of species presence in highly fragmented landscapes. Ecography 34:1018–1029.

Boyle, W. A. 2008a. Can variation in risk of nest predation explain altitudinal migration in tropical birds? Oecologia 155:397–403.

Boyle, W. A. 2008b. Partial migration in birds: tests of three hypotheses in a tropical lekking frugivore. The Journal of Animal Ecology 77:1122–1128.

Boyle, W. A. 2011. Short-distance partial migration of Neotropical birds: a community-level test of the foraging limitation hypothesis. Oikos 120:1803–1816.

Boyle, W. A., D. R. Norris, and C. G. Guglielmo. 2010. Storms drive altitudinal migration in a tropical bird. Proceedings. Biological sciences / The Royal Society 277:2511–2519.

Boyle, W. A., and B. J. Sigel. 2015. Ongoing changes in the avifauna of La Selva Biological Station, Costa Rica: twenty-three years of Christmas bird counts. Biological Conservation.

Boyles, J. G., F. Seebacher, B. Smit, and A. E. McKechnie. 2011. Adaptive thermoregulation in endotherms may alter responses to climate change. Integrative and comparative biology 51:676–90.

Brault, S., and H. Caswell. 1993. Pod-specific demography of killer whales (*Orchinus orca*). Ecology 74:1444–1454.

Brawn, J. D. 2012. Population growth rates in tropical understory birds and their prospects under climate change. North American Ornithological Conference, Vancouver, Canada.

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.

Bregman, T. P., Ç. H. Şekercioğlu, and J. A. Tobias. 2014. Global patterns and predictors of bird species responses to forest fragmentation: Implications for ecosystem function and conservation. Biological Conservation 169:372–383.

Brown, D. R., and T. W. Sherry. 2006. Food supply controls the body condition of a migrant bird wintering in the tropics. Oecologia 149:22–32.

Bucher, T. L., and A. Worthington. 1982. Nocturnal hypothermia and oxygen consumption in manakins. The Condor 84:327–331.

Burnham, K. P., and D. R. Anderson. 2002. Model selection and multimodel inference: A practical information-theoretic approach. Second. Springer, New York.

Burnham, K. P., G. C. White, and D. R. Anderson. 1995. Model selection strategy in the analysis of capture-recapture data. Biometrics 51:888–898.

Calder, W. A. 1974. Consequences of body size for avian energetics. Pages 86–144 *in* R. A. Paynter, editor. Avian Energetics. Nuttall Ornithological Club Publication 15, Cambridge, MA.

De Camargo Barbosa, K. V., A. Uezu, C. Knogge, and P. F. Develey. *in press*. Effects of matrix type and patch proximity on the use of the small fragments by Atlantic Forest birds in the Cantareira-Mantiqueira corridor of Southeastern Brazil. Biological Conservation.

Canaday, C. 1997. Loss of insectivorous birds along a gradient of human impact in Amazonia. Biological Conservation 77:63–77.

Carlson, A., and G. Hartman. 2001. Tropical forest fragmentation and nest predation–an experimental study in an Eastern Arc montane forest, Tanzania. Biodiversity and Conservation 10:1077–1085.

Castellón, T. D., and K. E. Sieving. 2006. An experimental test of matrix permeability and corridor use by an endemic understory bird. Conservation Biology 20:135–145.

Caswell, H. 1989. Matrix Population Models. Sinauer Assoc. Inc., Sunderland, MA.

Caswell, H. 2010. Reproductive value, the stable stage distribution, and the sensitivity of the population growth rate to changes in vital rates. Demographic Research 23:531–548.

Chalfoun, A. D., F. R. Thompson, and M. J. Ratnaswamy. 2002. Nest predators and fragmentation: a review and meta-analysis. Conservation Biology 16:306–318.

Chalom, A., and P. I. Prado. 2014. pse: Parameter space exploration with Latin Hypercubes. R package version 0.3.4. http://CRAN.R-project.org/package=pse.

Chaves-Campos, J., and J. A. DeWoody. 2008. The spatial distribution of avian relatives: do obligate army-ant-following birds roost and feed near family members? Molecular ecology 17:2963–74.

Chiarello, A. G., A. C. Srbek-Araujo, H. J. Del Duque, and E. Rodrigues Coelho. 2008. Ground nest predation might not be higher along edges of Neotropical forest remnants surrounded by pastures: evidence from the Brazilian Atlantic forest. Biodiversity and Conservation 17:3209–3221.

Clark, D. A., and D. B. Clark. 2011. Assessing tropical forests' climatic sensitivities with long-term data. Biotropica 43:31–40.

Cooper, D. S., and C. M. Francis. 1998. Nest predation in a Malaysian lowland rain forest. Biological Conservation 85:199–202.

Crooks, K. R., and M. E. Soule. 1999. Mesopredator release and avifaunal extinctions in a fragmented system. Nature 400:563–566.

Crouse, D. T., L. B. Crowder, and H. Caswell. 1987. A Stage-based population model for loggerhead sea turtles and implications for conservation. Ecology 68:1412–1423.

Davis, M. B. 1986. Climatic instability, time lags, and community disequilibrium. Pages 269–284 *in* J. Diamond and T. Case, editors. Community Ecology. Harper & Row.

Delgado, M. D. M., V. Penteriani, E. Revilla, and V. O. Nams. 2010. The effect of phenotypic traits and external cues on natal dispersal movements. The Journal of Animal Ecology 79:620–632.

Delhey, K., M. Carrizo, L. Verniere, B. Mahler, and A. Peters. 2010. Seasonal Variation in reproductive output of a Neotropical temperate Suboscine, the firewood-gatherer (*Anumbius annumbi*). The Auk 127:222–231.

Didham, R. K., and J. H. Lawton. 1999. Edge structure determines the magnitude of changes in microclimate and vegetation structure in tropical forest fragments. Biotropica 31:17–30.

Dinsmore, S. J., and J. J. Dinsmore. 2007. Modeling avian nest survival in program MARK. Studies in Avian Biology 34:73–83.

Dinsmore, S. J., G. C. White, and F. L. Knopf. 2002. Advanced Techniques for Modeling Avian Nest Survival. Ecology 83:3476–3488.

Donovan, T. M., F. R. Thompson, J. Faaborg, and J. R. Probst. 1995. Reproductive success of migratory in habitat birds sources and sinks. Conservation Biology 9:1380–1395.

Downs, C. T., and M. Brown. 2002. Nocturnal heterothermy and torpor in the Malachite Sunbird (*Nectarinia famosa*). The Auk 119:251–260.

Dowsett-Lemaire, F. 1989. Ecological and biogeographical aspects of forest bird communities in Malawi. Ornithological Sub-Committee of the East Africa Natural History Society.

Drake, J. B., R. O. Dubayah, D. B. Clark, R. G. Knox, J. B. Blair, M. A. Hofton, R. L. Chazdon, J. F. Weishampel, and S. Prince. 2002. Estimation of tropical forest structural characteristics using large-footprint lidar. Remote Sensing of Environment 79:305–319.

Duffy, J. E. 2003. Biodiversity loss, trophic skew and ecosystem functioning. Ecology Letters 6:680–687.

Dugger, K. M., J. Faaborg, W. J. Arendt, and K. A. Hobson. 2004. Understanding survival and abundance of overwintering warblers: does rainfall matter? The Condor 106:744–760.

Eberhard, C. 1983. Why do young birds reproduce less well? Ibit 125:400–404.

Edwards, D. P., P. Woodcock, R. J. Newton, F. A. Edwards, D. J. R. Andrews, T. D. S. Docherty, S. L. Mitchell, T. Ota, S. Benedick, S. H. Bottrell, and K. C. Hamer. 2013. Trophic flexibility and the persistence of understory birds in intensively logged rainforest. Conservation biology 27:1079–1086.

Ewers, R. M., R. K. Didham, L. Fahrig, G. Ferraz, A. Hector, R. D. Holt, V. Kapos, G. Reynolds, W. Sinun, J. L. Snaddon, and E. C. Turner. 2011. A large-scale forest fragmentation experiment: the Stability of Altered Forest Ecosystems Project. Philosophical transactions of the Royal Society of London. Series B, Biological sciences 366:3292–3302.

Fagan, M. E., R. S. DeFries, S. E. Sesnie, J. P. Arroyo, W. Walker, C. Soto, R. L. Chazdon, and a Sanchun. 2013. Land cover dynamics following a deforestation ban in northern Costa Rica. Environmental Research Letters 8:034017.

Fahrig, L. 2003. Effects of habitat fragmentation on biodiversity. Annual Review of Ecology Evolution and Systematics 34:487–515.

Feeley, K. J., and J. W. Terborgh. 2008. Direct versus indirect effects of habitat reduction on the loss of avian species from tropical forest fragments. Animal Conservation 11:353–360.

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.

Fitzpatrick, J. W. 1980. Foraging behavior of Neotropical tyrant flycatchers. The Condor 82:43–57.

Fleishman, E., and R. Mac Nally. 2007. Measuring the response of animals to contemporary drivers of fragmentation. Canadian Journal of Zoology 85:1080–1090.

Fogden, M. P. L. 1972. The seasonality and population dynamics of equatorial forest birds in Sarawak. The Ibis 114:307–343.

Foster, C. N., P. S. Barton, and D. B. Lindenmayer. 2014. Effects of large native herbivores on other animals. Journal of Applied Ecology 51:929–938.

Foster, M. S. 1974. Rain, feeding behavior, and clutch size in tropical birds. The Auk 91:722–726.

Frankham, R. 1998. Inbreeding and extinction: Island populations. Conservation Biology 12:665–675.

Frankham, R. 2005. Genetics and extinction. Biological Conservation 126:131–140.

Friesen, L., M. D. Cadman, and R. J. Mackay. 1999. Nesting success of Neotropical migrant songbirds in a highly fragmented landscape. Conservation Biology 13:338–346.

Galetti, M., R. S. Bovendorp, R. F. Fadini, C. O. A. Gussoni, M. Rodrigues, A. D. Alvarez, P. R. Guimaraes, and K. Alves. 2009. Hyper abundant mesopredators and bird extinction in an Atlantic forest island. Zoologia 26:288–298.

Genest, C., and J.-F. Plante. 2003. On Blest's measure of rank correlation. The Canadian Journal of Statistics 31:35–52.

Gerson, A. R., E. K. Smith, B. Smit, A. E. McKechnie, and B. O. Wolf. 2014. The impact of humidity on evaporative cooling in small desert birds exposed to high air temperatures. Physiological and Biochemical Zoology 87.

Ghalambor, C. K., R. B. Huey, P. R. Martin, J. J. Tewksbury, and G. Wang. 2006. Are mountain passes higher in the tropics? Janzen's hypothesis revisited. Integrative and comparative biology 46:5–17.

Gibbs, J. P. 1991. Avian nest predation in tropical wet forest: an experimental study. Oikos 60:155–161.

Gill, S. A., and B. J. M. Stutchbury. 2006. Long-term mate and territory fidelity in neotropical buff-breasted wrens (*Thryothorus leucotis*). Behavioral Ecology and Sociobiology 61:245–253.

Githiru, M., and L. Lens. 2006. Demography of an Afrotropical passerine in a highly fragmented landscape. Animal Conservation 9:21–27.

Githiru, M., and L. Lens. 2007. Application of fragmentation research to conservation planning for multiple stakeholders: An example from the Taita Hills, southeast Kenya. Biological Conservation 134:271–278.

Githiru, M., L. Lens, and W. Cresswell. 2005. Nest predation in a fragmented Afrotropical forest: evidence from natural and artificial nests. Biological Conservation 123:189–196.

Gradwohl, J., and R. Greenberg. 1980. The formation of antwren flocks on Barro Colorado Island, Panamá. The Auk 97:385–395.

Greeney, H. F., C. Sánchez, J. E. Sánchez, and E. Carman. 2013. A review of nest and egg descriptions for the genus Myrmeciza, with the first description of nests and eggs of the dull-mantled antbird (*M. laemosticta*). Journal of Ornithology 154:1049–1056.

Guyer, C., and M. A. Donnelly. 2004. Amphibians and Reptiles of La Selva, Costa Rica, and the Caribbean Slope: a Comprehensive Guide. University of California Press, Oakland.

Haig, S. M., W. M. Bronaugh, R. S. Crowhurst, J. D. Elia, C. A. Eagles-Smith, C. W. Epps, B. Knaus, M. P. Miller, M. L. Moses, S. Oyler-McCance, W. D. Robinson, and B. Sidlauskas. 2011. Genetic applications in avian conservation. The Auk 128:205–229.

Harris, J. B. C., Ç. H. Şekercioğlu, N. S. Sodhi, D. A. Fordham, D. C. Paton, and B. W. Brook. 2011. The tropical frontier in avian climate impact research. Ibis 153:877–882.

Hayes, F. E. 2002. Predation on birds by snakes in Trinidad and Tobago. Living World, Trinidad and Tobage Field Naturalists' Club:59–61.

Helton, J. C., and F. J. Davis. 2003. Latin hypercube sampling and the propagation of uncertainty in analyses of complex systems. Reliability Engineering & System Safety 81:23–69.

Heske, E. J., S. K. Robinson, and J. D. Brawn. 2001. Nest predation and Neotropical migrant songbirds: piecing together the fragments. Wildlife Society Bulletin 29:52–61.

Huntington, D. E., and C. S. Lyrintzis. 1998. Improvements to and limitations of Latin hypercube sampling. Prob. Engng. Mech. 13:245–253.

Ibarra-Macias, A., W. D. Robinson, and M. S. Gaines. 2011. Experimental evaluation of bird movements in a fragmented Neotropical landscape. Biological Conservation 144:703–712.

Jackson, S. T., and R. J. Hobbs. 2009. Ecological restoration in the light of ecological history. Science 325:567–569.

Janzen, D. H. 1967. Why mountain passes are higher in the tropics. The American Midland Naturalist 101:233–249.

Johnston, J. P., W. J. Peach, R. D. Gregory, and S. A. White. 1997. Survival rates of tropical and temperate passerines: a Trinidadian perspective. The American Naturalist 150:771–789.

Joyce, A. T. 2011. Land Use Change in Costa Rica: Updated to Year 2011. Litografia y Imprenta LIL, San Jose, Costa Rica.

Karr, J. R., and K. E. Freemark. 1983. Habitat selection and environmental gradients: dynamics in the “stable” tropics. Ecology 64:1481–1494.

Karr, J. R., J. D. Nichols, M. K. Klimkiewicz, and J. D. Brawn. 1990. Survival rates of birds of tropical and temperate forests: Will the dogma survive? The American Naturalist 136:277–291.

Kennedy, C. M., and P. P. Marra. 2010. Matrix mediates avian movements in tropical forested landscapes: Inference from experimental translocations. Biological Conservation 143:2136–2145.

Keyghobadi, N. 2007. The genetic implications of habitat fragmentation for animals. Canadian Journal of Zoology 85:1049–1064.

Kleijnen, J. P. C., and J. C. Helton. 1999. Statistical analyses of scatterplots to identify important factors in large-scale simulations, 1: Review and comparison of techniques. Reliability Engineering & System Safety 65:147–185.

Klein, B. C., L. H. Harper, R. O. Bierregaard, and G. V. N. Powell. 1988. The nesting and feeding behavior of the ornate hawk-eagle near Manaus, Brazil. The Condor 90:239–241.

Korfanta, N. M., W. D. Newmark, and M. J. Kauffman. 2012. Long-term demographic consequences of habitat fragmentation to a tropical understory bird community. Ecology 93:2548–2559.

De Kroon, H., A. Plaisier, J. van Groenendael, and H. Caswell. 1986. Elasticity: the relative contribution of demographic parameters to population growth rate. Ecology 67:1427–1431.

Laake, J. L. 2013. RMark: An R Interface for Analysis of Capture-Recapture Data with MARK. AFSC Processed Rep 2013-01, 25p. Alaska Fish. Sci. Cent., NOAA, Natl. Mar. Fish. Serv., 7600 Sand Point Way NE, Seattle WA 98115.

Lack, D. 1947. The significance of clutch size. The Ibis 89:302–352.

Lahti, D. C. 2001. The "edge effect on nest predation" hypothesis after twenty years. Biological Conservation 99:365–374.

Lahti, D. C. 2009. Why we have been unable to generalize about bird nest predation. Animal Conservation 12:279–281.

Lampila, P., M. Monkkonen, and A. Desrochers. 2005. Demographic responses by birds to forest fragmentation. Conservation Biology 19:1537–1546.

Laurance, S. G. W., M. S. Gomez, S. Biotropica, and N. Mar. 2005. Clearing width and movements of understory rainforest birds. Biotropica 37:149–152.

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. 1997. Responses of mammals to rainforest fragmentation in tropical Queensland: a review and synthesis. Wildlife Research 24:603–612.

Laurance, W. F. 2008. Theory meets reality in fragmented forests. Animal Conservation 11:364–365.

Laurance, W. F., J. L. C. Camargo, R. C. C. Luizão, S. G. W. 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, S. G. W. Laurance, and E. Sampaio. 2002. Ecosystem decay of Amazonian forest fragments: a 22-year investigation. Conservation Biology 16:605–618.

Lebreton, J.-D., K. P. Burnham, J. Clobert, and D. R. Anderson. 1992. Modeling survival and testing biological hypotheses using marked animals: a unifed approach with case studies. Ecological Monographs 62:67–118.

Lees, A. C., and C. a Peres. 2009. Gap-crossing movements predict species occupancy in Amazonian forest fragments. Oikos 118:280–290.

Lees, A. C., and C. A. Peres. 2006. Rapid avifaunal collapse along the Amazonian deforestation frontier. Biological Conservation 133:198–211.

Lees, A. C., and C. A. Peres. 2008. Avian life-history determinants of local extinction risk in a hyper-fragmented Neotropical forest landscape. Animal Conservation 11:128–137.

Lees, A. C., and C. A. Peres. 2010. Habitat and life history determinants of antbird occurrence in variable-sized Amazonian forest fragments. Biotropica 42:614–621.

Levey, D. J., and F. G. Stiles. 1994. Birds: ecology, behavior, and taxonomic affinity. Pages 217–228 *in* L. A. McDade, K. S. Bawa, H. A. Hespenheide, and G. S.

Hartshorn, editors. La Selva: ecology and natural history of a neotropical rain forest. University of Chicago Press, Chicago, Illinois.

Libsch, M. M., C. Batista, D. Buehler, I. Ochoa, J. D. Brawn, and R. E. Ricklefs. 2008. Nest predation in a neotropical forest occurs during daytime. The Condor 110:166–170.

Lindenmayer, D. B., G. E. Likens, A. Andersen, D. Bowman, C. M. Bull, E. Burns, C. R. Dickman, A. A. Hoffmann, D. A. Keith, M. J. Liddell, A. J. Lowe, D. J. Metcalfe, S. R. Phinn, J. Russell-Smith, N. Thurgate, and G. M. Wardle. 2012. Value of long-term ecological studies. Austral Ecology 37:745–757.

Losada-Prado, S., B. Finegan, F. DeClerck, F. Casanoves, and J. Dunning. 2014. Home-range size of Chestnut-backed Antbird (Myrmeciza exsul) in fragmented landscapes in southwestern Costa Rica. Ornitología Neotropical 25:1–11.

Luck, G. W. 2003. Differences in the reproductive success and survival of the rufous treecreeper (*Climacteris rufa*) between a fragmented and unfragmented landscape. Biological Conservation 109:1–14.

MacArthur, R. H., and E. O. Wilson. 1967. The Theory of Island Biogeography. Princeton University Press, Princeton, NJ.

Marini, M. A., S. K. Robinson, and E. J. Heske. 1995. Edge effects on nest predation in the Shawnee National Forest, southern Illinois. Biological Conservation 74:203–213.

Marino, S., I. B. Hogue, C. J. Ray, and D. E. Kirschner. 2008. A methodology for performing global uncertainty and sensitivity analysis in systems biology. Journal of theoretical biology 254:178–96.

Marra, P. P., and J. V Remsen. 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:445–483.

Martin. 1992. Breeding productivity considerations: what are the appropriate habitat features for management? Pages 455–473 *in* J. M. Hagan and D. W. Johnston, editors. Ecology and Conservation of Neotropical Migrant Land Birds. Smithsonian Institution Press, Washington, DC.

Martin, T. E. 1988. Processes organizing open-nesting bird assemblages: competition or nest predation? Evolutionary Ecology 2:37–50.

Martin, T. E. 1995. Avian life history evolution in relation to nest sites, nest predation, and food. Ecological Monographs 65:101–127.

Martin, T. E. 1996. Life history evolution in tropical and south temperate birds: What do we really know? Journal of Avian Biology 27:263–272.

Matlock, R. B., D. Rogers, P. J. Edwards, and S. G. Martin. 2002. Avian communities in forest fragments and reforestation areas associated with banana plantations in Costa Rica. Agriculture, Ecosystems and Environment 91:199–215.

McDade, L. A., and G. S. Hartshorn. 1994. La Selva Biological Station. Pages 6–14 *in* L. A. McDade, K. S. Bawa, H. A. Hespenheide, and G. S. Hartshorn, editors. La Selva: Ecology and Natural History of a Neotropical Rain Forest. The University of Chicago Press, Chicago, Illinois.

McKay, M. D., R. J. Beckman, and W. J. Conover. 1979. A comparison of three methods for selecting values of input variables in the analysis of output from a computer code. Technometrics 21:239–245.

McKechnie, A. E. 2008. Phenotypic flexibility in basal metabolic rate and the changing view of avian physiological diversity: a review. Journal of comparative physiology. B, Biochemical, systemic, and environmental physiology 178:235–47.

McKechnie, A. E., and B. Erasmus. 2006. Climate change and birds in hot deserts: the impacts of increased demand for thermoregulatory water on survival and reproduction. Journal of Ornithology 147:209–210.

McKechnie, A. E., and B. O. Wolf. 2010. Climate change increases the likelihood of catastrophic avian mortality events during extreme heat waves. Biology letters 6:253–256.

McKellar, A. E., P. P. Marra, P. T. Boag, and L. M. Ratcliffe. 2014. Form, function and consequences of density dependence in a long-distance migratory bird. Oikos 123:356–364.

Mendenhall, C. D., D. S. Karp, C. F. J. Meyer, E. A. Hadly, and G. C. Daily. 2014. Predicting biodiversity change and averting collapse in agricultural landscapes. Nature 509:213–217.

Michel, N. L. 2012. Mechanisms and consequences of avian understory insectivore population decline in fragmented Neotropical rainforest. Tulane University, New Orleans, LA.

Michel, N. L., W. D. Robinson, and T. W. Sherry. 2015. Liana-bird relationships: a review. Pages 362–397 *in* S. A. Schnitzer, F. Bongers, R. J. Burnham, and F. E. Putz, editors. The Ecology of Lianas. Wiley-Blackwell Publlishing, Hoboken, NJ.

Michel, N. L., and T. W. Sherry. 2012. Human-altered mesoherbivore densities and cascading effects on plant and animal communities in fragmented tropical forests.

Pages 177–202 *in* P. Sudarshana, M. Nageswara-Rao, and J. R. Sonegi, editors. Tropical Forests. InTech Open Access Publisher, New York.

Michel, N. L., T. W. Sherry, and W. P. Carson. *in review*. Do collared peccaries negatively impact understory insectivorous rainforest birds indirectly via lianas and vines? Biotropica.

Møller, A. P. 1989. Nest site selection across field-woodland ecotones: the effect of nest predation. Oikos 56:240–246.

Moore, R. P., and W. D. Robinson. 2004. Artificial bird nests, external validity, and bias in ecological field studies. Ecology 85:1562–1567.

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.

Moreau, R. E. 1944. Clutch-size: a comparative study, with special reference to African birds. Ibis 86:286–347.

Morris, W. F., C. A. Pfister, S. Tuljapurkar, C. V Haridas, C. L. Boggs, M. S. Boyce, E. M. Bruna, D. R. Church, T. Coulson, D. F. Doak, S. Forsyth, J. Gaillard, C. C. Horvitz, S. Kalisz, B. E. Kendall, T. M. Knight, C. T. Lee, and E. S. Menges. 2008. Longevity can buffer plant and animal populations against changing climatic variability. Ecology 89:19–25.

Morton, E. S., and B. J. M. Stutchbury. 2000. Demography and reproductive success in the Dusky Antbird, a sedentary tropical passerine. Journal of Field Ornithology 71:493–500.

Muñiz-López, R., O. Criollo, and A. Mendúa. 2007. Results of five years of the "Harpy Eagle (Harpia harpyja) Research Program" in the Ecuadorian tropical forest. Pages 23–32 *in* K. L. Bildstein, D. R. Barber, and A. Zimmerman, editors. Neotropical Raptos. Hawk Mountain Santuary, Orwigsburg, PA.

Newbold, T., L. N. Hudson, H. R. P. Phillips, S. L. L. Hill, S. Contu, A. Blandon, S. H. M. Butchart, H. L. Booth, J. Day, A. De Palma, M. L. K. Harrison, L. Kirkpatrick, E. Pynegar, A. Robinson, J. Simpson, G. M. Mace, J. P. W. Scharlemann, A. Purvis, P. R. S. B, I. Lysenko, and P. W. Scharlemann. 2014. A global model of the response of tropical and sub-tropical forest biodiversity to anthropogenic pressures. Proceedings of the Royal Society B-Biological Sciences 281:20141371.

Newmark, W. D., and T. R. Stanley. 2011. Habitat fragmentation reduces nest survival in an afrotropical bird community in a biodiversity hotspot. Proceedings of the National Academy of Sciences of the United States of America 108:11488–11493.

Newton, I. 2003. Population Limitation in Birds. 2nd edition. Academic Press, San Diego, California, USA.

Noon, B., and J. R. Sauer. 1992. Population models for passerine birds: structure, parameterization, and analysis. Wildlife:441–464.

O'Malley, B. 2014. Natural history of the bird-eating snake (*Pseustes poecilonotus*) and its impact on Neotropical understory nesting birds. Tulane University.

Omland, K. E., and T. W. Sherry. 1994. Parental care at nests of two age classes of male American Redstart: Implications for female mate choice. Condor 96:606–613.

Oniki, Y. 1979. Is nesting success of birds low in the tropics? Biotropica 11:60–69.

OTS. 2014. Organization for Tropical Studies meteorlogical data. http://www.ots.ac.cr/meteoro/default.php?pestacion=2.

Owens, I. P., and P. M. Bennett. 2000. Ecological basis of extinction risk in birds: habitat loss versus human persecution and introduced predators. Proceedings of the National Academy of Sciences of the United States of America 97:12144–12148.

Page, G. W., L. E. Stenzel, D. W. Winkler, C. W. Swarth, and S. Url. 1983. Spacing out at Mono Lake: breeding success, nest density, and predation in the snowy plover. The Auk 100:13–24.

Pagiola, S. 2008. Payments for environmental services in Costa Rica. Ecological Economics 65:712–724.

Paine, R. T. 2000. Phycology for the mammalogist: marine rocky shores and mammal-dominated communities - how different are the structuring processes? Journal of Mammalogy 81:637–648.

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.

Pavlacky Jr., D. C., H. P. Possingham, and A. W. Goldizen. *in press*. Integrating life history traits and forest structure to evaluate the vulnerability of rainforest birds along gradients of landscape change in Eastern Australia. Biological Conservation.

Pierce, A. J., and K. Pobprasert. 2007. A portable system for continuous monitoring of bird nests using digital video recorders. Journal of Field Ornithology 78:322–328.

Pierce, A. J., and K. Pobprasert. 2013. Nest predators of southeast Asian evergreen forest birds identified through continuous video recording. Ibis 155:419–423.

Pietz, P. J., and D. Granfors. 2005. Parental nest defense on videotape: more reality than "myth." The Auk 122:701–705.

Pollock, H. S., Z. A. Cheviron, and J. D. Brawn. (n.d.). Why do tropical understory insectivores avoid disturbed habitats? The role of microclimates and light environments in habitat selection in Panama. Biological Conservation.

Powers, D. R. 1992. Effect of temperature and humidity on evaporative water loss in Anna's hummingbird (*Calypte anna*). Journal of Comparative Physiology B, Biochemical, Systemic, and Environmental Physiology 162:74–84.

R Core Team. 2014. R: A language and environment for statistical computing. R Foundation for Statistical Computing, Vienna, Austria. URL http://www.r-project.org/. R Foundation for Statistical Computing, Vienna, Austria.

Ramos-Olmos, M. A. 1983. Seasonal movements of bird populations at a Neotropical study site in southern Veracruz, Mexico. University of Minnesota, Minneapolis, MN.

Read, J. M., J. S. Denslow, and S. M. Guzman. 2001. Documenting land cover history of a humid tropical environment in northeastern Costa Rica using time-series remotely sensed data. Pages 69–89 GIS and remote sensing applications in biogeography and ecology. Boston; Kluwer Academic Publishers.

Reidy, J. L. 2009. Nest predators of lance-tailed manakins on Isla Boca Brava, Panama. Journal of Field Ornithology 80:115–118.

Ribic, C. A., F. R. Thompson, and P. J. Pietz (Eds.). 2012. Video Surveillance of Nesting Birds. Page 244 Studies in Avian Biology No. 43. University of California Press, Berkeley, CA.

Richardson, T. W., T. Gardali, and S. H. Jenkins. 2009. Review and meta-analysis of camera effects on avian nest success. Journal of Wildlife Management 73:287–293.

Ricklefs, R. E. 1969. An analysis of nesting mortality in birds. Smithsonian Contributions to Zoology:1–48.

Ricklefs, R. E. 1997. Comparative demography of new world populations of thrushes (*Turdus spp.*). Ecological Monographs 67:23–43.

Ricklefs, R. E. 2000. Density dependence, evolutionary optimization, and the diversification of avian life histories. The Condor 102:9–22.

Ricklefs, R. E., and G. Bloom. 1977. Components of avian breeding productivity. The Auk 94:86–96.

Riehl, C., and L. Jara. 2009. Natural history and reproductive biology of the communally breeding greater ani (*Crotophaga major*) at Gatun Lake, Panama. The Wilson Journal of Ornithology 121:679–687.

Ripple, W. J., J. A. Estes, R. L. Beschta, C. C. Wilmers, E. G. Ritchie, M. Hebblewhite, J. Berger, B. Elmhagen, M. Letnic, M. P. Nelson, O. J. Schmitz, D. W. Smith, A. D. Wallach, and A. J. Wirsing. 2014. Status and ecological effects of the world's largest carnivores. Science 343:1–11.

Roberts, D. 2007. Effects of Tropical Forest Fragmentation on Ecology and Conservation of Migrant and Resident Birds in Lowland Costa Rica. University of Idaho.

Robinson, S. K., F. R. T. III, T. M. Donovan, D. R. Whitehead, and J. Faaborg. 1995. Regional forest fragmentation and the nesting success of migratory birds. Science 267:1987–1990.

Robinson, W. D. 1999. Long-term changes in the avifauna of Barro Colorado Island, Panama, a tropical forest isolate. Conservation Biology 13:85–97.

Robinson, W. D. 2001. Changes in abundance of birds in a Neotropical forest fragment over 25 years: a review. Animal Biodiversity and Conservation 24:51–65.

Robinson, W. D. 2009. Avian reproductive failure in tropical forest fragments. Animal Conservation 12:276–278.

Robinson, W. D., J. D. Brawn, and S. K. Robinson. 2000a. Forest Bird Community Structure in Central Panama: Influence of Spatial Scale and Biogeography. Ecological Monographs 70:209–235.

Robinson, W. D., M. Hau, K. C. Klasing, M. Wikelski, J. D. Brawn, S. H. Austin, C. E. Tarwater, and R. E. Ricklefs. 2010. Diversification of life histories in New World birds. The Auk 127:253–262.

Robinson, W. D., and T. R. Robinson. 2001. Observations of predation events at bird nests in central Panama. Journal of Field Ornithology 72:43–48.

Robinson, W. D., T. R. Robinson, S. K. Robinson, and J. D. Brawn. 2000b. Nesting success of understory forest birds in central Panama. Journal of Avian Biology 31:151–164.

Robinson, W. D., G. Rompré, and T. R. Robinson. 2005a. Videography of Panama bird nests shows snakes are principal predators. Ornitologia Neotropical 16:187–195.

Robinson, W. D., and T. W. Sherry. 2012a. Mechanisms of avian population decline and species loss in tropical forest fragments. Journal of Ornithology 7.

Robinson, W. D., and T. W. Sherry. 2012b. Mechanisms of avian population decline and species loss in tropical forest fragments. Journal of Ornithology 153:141–152.

Robinson, W. D., J. N. Styrsky, J. D. Brawn, and P. C. Stouffer. 2005b. Are artificial bird nests effective surrogates for estimating predation on real bird nests? A test with tropical birds. The Auk 122:843–852.

Rodenhouse, N. L., and R. T. Holmes. 1992. Results of experimental and natural food reductions for breeding Black-Throated Blue Warblers. Ecology 73:357–372.

Rodríguez-Estrella, R. 2000. Breeding success, nest-site characteristics, and diet of Swainson's hawk (*Buteo swainsoni*) in a stable population in northern México. Canadian Journal of Zoology 78:1052–1059.

Romero, A., B. J. O'Neill, R. M. Timm, K. G. Gerow, and D. McClearn. 2013. Group dynamics, behavior, and current and historical abundance of peccaries in Costa Rica's Caribbean lowlands. Journal of Mammalogy 94:771–791.

Rompré, G., and W. D. Robinson. 2008. Predation, nest attendance, and long incubation periods of two Neotropical antbirds. Ecotropica 14:81–87.

Roper, J. J. 1992. Nest predation experiments with quail eggs: too much to swallow? Oikos 65:528–530.

Roper, J. J. 2005. Try and try again: Nest predation favors persistence in a neotropical bird. Ornitologia Neotropical 16:253–262.

Roper, J. J., K. A. Sullivan, and R. E. Ricklefs. 2010. Avoid nest predation when predation rates are low, and other lessons: testing the tropical-temperate nest predation paradigm. Oikos 119:719–729.

Rosenberg, K. V. 1993. Diet selection in Amazonian antwrens: consequences of substrate specialization. The Auk 110:361–375.

Rotella, J. J., S. J. Dinsmore, and T. L. Shaffer. 2004. Modeling nest–survival data: a comparison of recently developed methods that can be implemented in MARK and SAS. Animal Biodiversity and Conservation 27:187–205.

Ruiz-Gutiérrez, V., T. A. Gavin, and A. A. Dhondt. 2008. Habitat fragmentation lowers survival of a tropical forest bird. Ecological Applications 18:838–846.

Russell, E. M. 2000. Avian life histories: Is extended parental care the southern secret? Emu 100:377–399.

Sabat, P., G. Cavieres, C. Veloso, M. Canals, and F. Bozinovic. 2009. Intraspecific basal metabolic rate varies with trophic level in rufous-collared sparrows. Comparative biochemistry and physiology. Part A, Molecular & integrative physiology 154:502–7.

Sæther, B.-E., and Ø. Bakke. 2000. Avian life history variation and the contribution of demographic traits to the population growth rate. Ecology 81:642–653.

Saltelli, A., and J. Marivoet. 1990. Non-parametric statistics in sensitivity analysis for model output: a comparison of selected techniques. Reliability Engineering & System Safety 28:229–253.

Sánchez, N. V, L. E. Vargas-Castro, G. Avalos, and F. Paniagua. 2014. Effect of prey availability on the abundance of White-breasted Wood-Wrens, insectivorous birds of tropical lowland forests. Journal of Field Ornithology 85:347–354.

Sandercock, B. K., S. R. Beissinger, S. H. Stoleson, R. R. Melland, and C. R. Hughes. 2000. Survival rates of a Neotropical parrot: implications for latitudinal comparisons of avian demography. Ecology 81:1351–1370.

Santos, C. D., P. M. Lourenco, A. C. Miranda, J. P. Granadeiro, and J. M. Palmeirim. 2008. Birds after dark: an efficient and inexpensive system for making long-range observations at night. Journal of Field Ornithology 79:329–335.

Sauer, J. R., and J. E. Hines. 1989. Testing for differences among survival or recovery rates using Program CONTRAST. Wildlife Society Bulletin 17:549–550.

Savage, J. M. 2002. The Amphibians and Teptiles of Costa Rica: A Herpetofauna Between Two Continents, Between Two Seas. University of Chicago Press, Chicago.

Savidge, J. A. 1987. Extinction of an island forest avifauna by an introduced snake. Ecology 68:660–668.

Schmidt, K. a., and C. J. Whelan. 1999. Nest predation on woodland songbirds: When is nest predation density dependent? Oikos 87:65.

Şekercioğlu, Ç. H. 2006. Increasing awareness of avian ecological function. Trends in Ecology & Evolution 21:464–471.

Şekercioğlu, Ç. H. 2007. Conservation ecology: area trumps mobility in fragment bird extinctions. Current Biology 17:R283–R286.

Şekercioğlu, Ç. H., G. C. Daily, and P. R. Ehrlich. 2004. Ecosystem consequences of bird declines. Proceedings of the National Academy of Sciences of the United States of America 101:18042–18047.

Şekercioğlu, Ç. 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 99:263–267.

Şekercioğlu, Ç. H., S. R. Loarie, F. O. Brenes, P. R. Ehrlich, and G. C. Daily. 2007. Persistence of forest birds in the Costa Rican agricultural countryside. Conservation Biology 21:482–494.

Şekercioğlu, Ç. H., R. B. Primack, and J. Wormworth. 2012. The effects of climate change on tropical birds. Biological Conservation 148:1–18.

Şekercioğlu, Ç. H., and N. S. Sodhi. 2007. Conservation biology: Predicting birds' responses to forest fragmentation. Current Biology 17:R838–R840.

Sesnie, S. E., P. E. Gessler, B. Finegan, and S. Thessler. 2008. Integrating Landsat TM and SRTM-DEM derived variables with decision trees for habitat classification and change detection in complex neotropical environments. Remote Sensing of Environment 112:2145–2159.

Sheldon, R. D., J. Kamp, M. a. Koshkin, R. S. Urazaliev, T. K. Iskakov, R. H. Field, A. R. Salemgareev, V. V. Khrokov, V. A. Zhuly, S. L. Sklyarenko, and P. F. Donald. 2012. Breeding ecology of the globally threatened Sociable Lapwing Vanellus gregarius and the demographic drivers of recent declines. Journal of Ornithology 154:501–516.

Sherry, T. W. 1984. Comparative dietary ecology of sympatric, insectivorous Neotropical flycatchers. Ecological Monographs 54:313–338.

Sherry, T. W. 2008. Community approach to tropical forest fragmentation gets us closer to understanding mechanisms by revealing strong indirect effects. Animal Conservation 11:361–363.

Sieving, K. E. 1992. Nest predation and differential insular extinction among selected forest birds of Central Panama. Ecology 73:2310–2328.

Sigel, B. J. 2007. The susceptibility of tropical forest bird communities to habitat fragmentation. Tulane University.

Sigel, B. J., W. D. Robinson, and T. W. Sherry. 2010. Comparing bird community responses to forest fragmentation in two lowland Central American reserves. Biological Conservation 143:340–350.

Sigel, B. J., T. W. Sherry, and B. E. Young. 2006. Avian community response to lowland tropical rainforest isolation: 40 Years of change at La Selva Biological Station, Costa Rica. Conservation Biology 20:111–121.

Skutch, A. F. 1966. A breeding bird census and nesting success in Central America. The Ibis 108:1–16.

Skutch, A. F. 1969. Life Histories of Central American Birds III. Pacific Coast Avifauna.

Skutch, A. F. 1985. Clutch size, nesting success, and predation on nests of Neotropical birds, reviewed. Neotropical Ornithology:575–594.

Slud, P. 1960. The birds of finca "La Selva," Costa Rica: a tropical wet forest locality. Bulletin of the American Museum of Natural History 121:53–146.

Snow, D. W. 1971. Evolutionary aspects of fruit-eating by birds. Ibis 113:194–202.

Snow, D. W., and B. K. Snow. 1963. Breeding and the annual cycle in three Trinidad thrushes. Wilson Bulletin 75:27–41.

Sodhi, N. S., L. H. Liow, and F. A. Bazzaz. 2004. Avian extinctions from tropical and subtropical forests. Annual Review of Ecology, Evolution, and Systematics 35:323–345.

Sodhi, N. S., Ç. H. Şekercioğlu, J. Barlow, and S. K. Robinson. 2011. Conservation of Tropical Birds. Wiley-Blackwell, West Sussex, UK.

Sofaer, H. R., T. S. Sillett, K. M. Langin, S. A. Morrison, and C. K. Ghalambor. 2014. Partitioning the sources of demographic variation reveals density-dependent nest predation in an island bird population. Ecology and Evolution 4:2738–2748.

Spanhove, T., V. Lehouck, P. Boets, and L. Lens. 2009a. Forest fragmentation relaxes natural nest predation in an Afromontane forest. Animal Conservation 12:267–275.

Spanhove, T., V. Lehouck, and L. Lens. 2009b. Inverse edge effect on nest predation in a Kenyan forest fragment: an experimental case study. Bird Conservation International 19:367–378.

Spanhove, T., V. Lehouck, and L. Lens. 2009c. Edge effects on avian nest predation: the quest for a conceptual framework. Animal Conservation 12:284–286.

Sperry, J. H., R. G. Peak, D. A. Cimprich, and P. J. Weatherhead. 2008. Snake activity affects seasonal variation in nest predation risk for birds. Journal of Avian Biology 39:379–383.

Steen, R. 2009. A Portable digital video surveillance system to monitor prey deliveries at raptor nests. Journal of Raptor Research.

Steiger, S. S., J. Kelley, W. W. Cochran, and M. Wikelski. 2009. Low metabolism and inactive lifestyle of a tropical rain forest bird investigated via heart-rate telemetry. Physiological and Biochemical Zoology 82:580–589.

Stevens, D. K., G. Q. A. Anderson, P. V Grice, K. Norris, and N. Butcher. 2008. Predators of Spotted Flycatcher Muscicapa striata nests in southern England as determined by digital nest-cameras. Bird Study 55:179–187.

Stiles, F. G. 1983. Checklist of birds. Pages 530–544 *in* D. H. Janzen, editor. Costa Rican natural history. The University of Chicago Press, Chicago, Illinois.

Stouffer, P. C., and R. O. Bierregaard. 1995. Use of Amazonian forest fragments by understory insectivorous birds. Ecology 76:2429–2445.

Stouffer, P. C., and R. O. Bierregaard. 2007. Recovery potential of understory bird communities in Amazonian rainforest fragments. Revista Brasileira de Ornitologia 15:219–229.

Stouffer, P. C., C. Strong, and L. N. Naka. 2009. Twenty years of understorey bird extinctions from Amazonian rain forest fragments: consistent trends and landscape-mediated dynamics. Diversity and Distributions 15:88–97.

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. *(in press).* The role of vegetation structure in the distribution of terrestrial insectivores in a fragmented Amazonian forest. Biological Conservation.

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. 2013. Microhabitat associations of terrestrial insectivorous birds in Amazonian rainforest and second-growth forests. Journal of Field Ornithology 84:1–12.

Studds, C., and P. P. Marra. 2007. Linking fluctuations in rainfall to nonbreeding season performance in a long-distance migratory bird, Setophaga ruticilla. Climate Research 35:115–122.

Stutchbury, B. J. M. 2007. The effects of habitat fragmentation on animals: gaps in our knowledge and new approaches. Canadian Journal of Zoology 85:1015–1016.

Styrsky, J. N., and J. D. Brawn. 2011. Annual Fecundity of a Neotropical Bird During Years of High and Low Rainfall. The Condor 113:194–199.

Sunnucks, P. 2011. Towards modelling persistence of woodland birds: the role of genetics. Emu 111:19–39.

Tarwater, C. E. 2008. Predators at nests of the western slaty antshrike (*Thamnophilus atrinucha*). Wilson Journal of Ornithology 120:620–624.

Tarwater, C. E., and J. D. Brawn. 2010. The post-fledging period in a tropical bird: patterns of parental care and survival. Journal of Avian Biology 41:479–487.

Tarwater, C. E., R. E. Ricklefs, J. D. Maddox, and J. D. Brawn. 2011. Pre-reproductive survival in a tropical bird and its implications for avian life histories. Ecology 92:1271–1281.

Terborgh, J. W., L. Lopez, P. Nunez, M. Rao, G. Shahabuddin, G. Orihuela, M. Riveros, R. Ascanio, G. H. Adler, T. D. Lambert, and L. Balbas. 2001. Ecological meltdown in predator-free forest fragments. Science 294:1923–1926.

Terborgh, J. W., S. K. Robinson, T. A. Parker III, C. A. Munn, and N. Pierpont. 1990. Structure and organization of an Amazonian forest bird community. Ecological Monographs 60:213–238.

Tewksbury, J. J., L. Garner, S. Garner, J. D. Lloyd, V. Saab, and T. E. Martin. 2006. Tests of landscape influence: nest predation and brood parasitism in fragmented ecosystems. Ecology 87:759–68.

Tewksbury, J. J., S. J. Hejl, and T. E. Martin. 1998. Breeding productivity does not decline with increasing fragmentation in a western landscape. Ecology 79:2890–2903.

Thompson, F. R. 2007. Factors affecting nest predation on forest songbirds in North America. Ibis 149:98–109.

Thompson, F. R., and D. E. Burhans. 2003. Predation of songbird nests differs by predator and between field and forest habitats. Journal of Wildlife Management 67:408–416.

Tirimbina Biological Reserve. 2010. Tirimbina Rainforest Center, Sarapiquí, Costa Rica. http://www.tirimbina.org/.

Touchton, J. M., and J. N. M. Smith. 2011. Species loss, delayed numerical responses, and functional compensation in an antbird guild. Ecology 92:1126–1136.

Turner, I. M., and R. T. Corlett. 1996. The conservation value of small, isolated fragments of lowland tropical rain forest. Trends in Ecology & Evolution 11:330–333.

Tye, H. 1992. Reversal of breeding-season by lowland birds at higher altitudes in Western Cameroon. Ibis 134:154–163.

Uezu, A., J. P. Metzger, and J. M. E. Vielliard. 2005. Effects of structural and functional connectivity and patch size on the abundance of seven Atlantic Forest bird species. Biological Conservation 123:507–519.

Visco, D. M., N. L. Michel, W. A. Boyle, B. J. Sigel, S. Woltmann, and T. W. Sherry. *(in review).* Patterns and causes of understory bird declines in human-disturbed tropical forest landscapes: a case study from Central America. Biological Conservation:In revision.

Visco, D. M., and T. W. Sherry. *in press*. Increased abundance, but reduced nest predation in the chestnut-backed antbird in costa rican rainforest fragments: surprising impacts of a pervasive snake species. Biological Conservation.

Wainwright, M. 2007. The Mammals of Costa Rica: A Natural History and Field Guide. Cornell University Press, Ithaca, NY.

Wasko, D. K., and M. Sasa. 2009. Activity Patterns of a Neotropical Ambush Predator: Spatial Ecology of the Fer-de-lance (*Bothrops asper*, Serpentes: Viperidae) in Costa Rica. Biotropica 41:241–249.

Watling, J. I., and M. A. Donnelly. 2006. Fragments as islands: a synthesis of faunal responses to habitat patchiness. Conservation Biology 20:1016–1025.

Weatherhead, P. J., and G. Blouin-Demers. 2004. Understanding avian nest predation: why ornithologists should study snakes. Journal of Avian Biology 35:185–190.

Weatherhead, P. J., G. L. F. Carfagno, J. H. Sperry, J. D. Brawn, and S. K. Robinson. 2010. Linking snake behavior to nest predation in a Midwestern bird community. Ecological Applications 20:234–241.

Weathers, W. W. 1997. Energetics and thermoregulation by small passerines of the humid, lowland tropics. The Auk 114:341–353.

Weathers, W. W., and C. Van Riper. 1982. Temperature regulation in two endangered Hawaiian honeycreepers: the Palila (*Psittirostra bailleui*) and the Laysan Finch (*Psittirostra cantans*). The Auk 99:667–674.

Weidinger, K. 2008. Identification of nest predators: a sampling perspective. Journal of Avian Biology 39:640–646.

Weidinger, K., and R. Kocvara. 2010. Repeatability of nest predation in passerines depends on predator species and time scale. Oikos 119:138–146.

Wheeler, B. 2010. lmPerm: Permutation tests for linear models. R package version 1.1-2. http://cran.r-project.org/package=lmPerm.

Whelan, C. J., D. G. Wenny, and R. J. Marquise. 2008. Ecosystem services provided by birds. Pages 25–60 Year in Ecology and Conservation Biology 2008.

White, G. C., and K. P. Burnham. 1999. Program MARK: survival estimation from populations of marked animals. Bird Study 46:S120–S139.

Whitfield, S. M., K. E. Bell, T. Philippi, M. Sasa, F. Bolanos, G. Chaves, J. M. Savage, and M. A. Donnelly. 2007. Amphibian and reptile declines over 35 years at La Selva, Costa Rica. Proceedings of the National Academy of Sciences of the United States of America 104:8352–8356.

Wikelski, M., M. Hau, and J. C. Wingfield. 2000. Seasonality of reproduction in a Neotropical rain forest bird. Ecology 81:2458–2472.

Wilcove, D. S. 1985. Nest predation in forest tracts and the decline of migratory songbirds. Ecology 66:1211–1214.

Williams, S. E., and J. Middleton. 2008. Climatic seasonality, resource bottlenecks, and abundance of rainforest birds: implications for global climate change. Diversity and Distributions 14:69–77.

Willis, E. O. 1974. Populations and local extinctions of birds on Barro Colorado Island, Panama. Ecological Monographs 44:153–169.

Willis, E. O., and Y. Oniki. 1972. Ecology and nesting behavior of the Chestnut-backed Antbird (Myrmeciza exsul). The Condor 74:87–98.

Wilson, S., D. M. Collister, and A. G. Wilson. 2011. Community composition and annual survival of lowland tropical forest birds on the Osa Peninsula, Costa Rica. Ornitologia Neotropical 22:421–436.

With, K. A., and A. W. King. 1999. Extinction thresholds for species in fractal landscapes. Conservation Biology 13:314–326.

Wolda, H. 1979. Abundance and diversity of Homoptera in the canopy of a tropical forest. Ecological Entomology 4:181–190.

Wolfe, J. D., P. Pyle, and C. J. Ralph. 2009. Breeding Seasons, Molt Patterns, and Gender and Age Criteria for Selected Northeastern Costa Rican Resident Landbirds. Wilson Journal of Ornithology 121:556–567.

Woltmann, S. 2010. Dispersal of a tropical rainforest understory bird, the Chestnut-backed Antbird (*Myrmeciza exsul*). Tulane University, New Orleans.

Woltmann, S., B. R. Kreiser, and T. W. Sherry. 2012a. Fine-scale genetic population structure of an understory rainforest bird in Costa Rica. Conservation Genetics 13:925–935.

Woltmann, S., and T. W. Sherry. 2011. High apparent annual survival and stable territory dynamics of chestnut-backed antbird (*Myrmeciza exsul*) in a large Costa Rican rain forest preserve. The Wilson Journal of Ornithology 123:15–23.

Woltmann, S., T. W. Sherry, and B. R. Kreiser. 2012b. A genetic approach to estimating natal dispersal distances and self-recruitment in resident rainforest birds. Journal of Avian Biology 43:33–42.

Woltmann, S., R. S. Terrill, M. J. Miller, and M. L. Brady. 2010. Chestnut-backed Antbird (Myrmeciza exsul). http://neotropical.birds.cornell.edu/portal/species/overview?p_p_spp=393811.

Wright, S. J. 2005. Tropical forests in a changing environment. Trends in Ecology & Evolution 20:553–560.

Young, B. E., T. W. Sherry, B. J. Sigel, and S. Woltmann. 2008. Nesting success of Costa Rican lowland rain forest birds in response to edge and isolation effects. Biotropica 40:615–622.

Zanette, L. 2002. What do artificial nests tells us about nest predation? Biological Conservation 103:323–329.

Zook, J. R., J. Alvarado Ch., O. Vargas R., A. Downs V., E. Castro V., and G. Vega Ch. 1999. Checklist of the birds of La Selva. Organization for Tropical Studies, Costa Rica.

BIOGRAPHY

Deborah Marie Visco was born in Huntington Station, New York on April 18th, 1984. She grew up on Long Island, where she developed life-long interests in dance, horses, and exploring the natural world. In 2002 she graduated from Walt Whitman High School in 2002 with a 4.0 and a penchant for overachievement. She went on to earn a Bachelor of Science in Environmental and Forest Biology at the State University of New York College of Environmental Science and Forestry (SUNY ESF), graduating *summa cum laude*. Field courses in Dominica of the West Indies and tropical Australia ignited her interests in tropical ecology and ornithology. After graduating, Deborah gained ornithological skills by working various field jobs including on Acorn Woodpeckers, California Condors, and Black-throated Blue Warblers. In 2008 she joined Thomas W. Sherry's research lab at Tulane as a PhD student. She currently teaches an introductory biology course, Diversity of Life, at Tulane and looks forward to continuing her teaching and research. Deborah currently lives in New Orleans with her fiancé Djihbrihou and they hope to make the best of it before the sea level rises too high.