EFFECTS OF TROPICAL FOREST FRAGMENTATION ON ECOLOGY AND CONSERVATION OF MIGRANT AND RESIDENT BIRDS IN LOWLAND COSTA RICA

A Dissertation

Presented in Partial Fulfillment of the Requirements for the

Degree of Doctor of Philosophy

with a Major in Natural Resources

in the College of Graduate Studies

University of Idaho

and with a

Concentration in

Forests and Biodiversity

in the

Graduate School

Centro Agronómico Tropical de Investigación y Enseñanza

by

Dina L. Roberts

May 2007

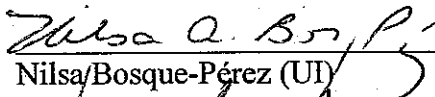Major Professors: Edward O. Garton, Ph.D. (UI),
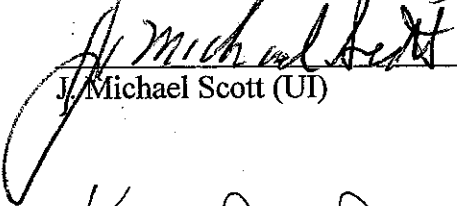
Celia A. Harvey, Ph.D. (CATIE)
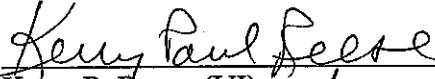
AUTHORIZATION TO SUBMIT DISSERTATION

This dissertation of Dina L. Roberts, submitted for the degree of Doctor of Philosophy with a major in Natural Resources and titled "Effects of tropical forest fragmentation on ecology and conservation of migrant and resident birds in lowland Costa Rica," has been reviewed in final form. Permission, as indicated by the signatures and dates given below, is now granted to submit final copies to the College of Graduate Studies at the University of Idaho (UI) for approval.
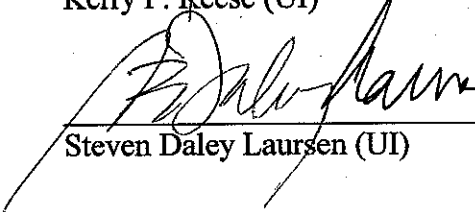
Major Professor _____ Date _3 May 2007_
Edward O. Garton (UI)

Co-Advisor _____ Date _8 May 2002_
Celia A. Harvey (CATIE)

Committee Members _____ Date _3 May 2007_
Nilsa Bosque-Pérez (UI)
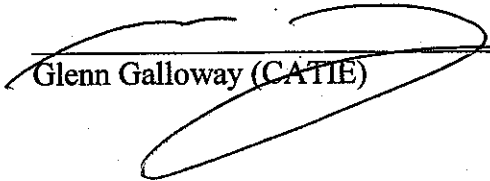
_____ Date _4 May, 2007_
J. Michael Scott (UI)

Department
Administrator (UI) _____ Date _5-4-07_
Kerry P. Reese (UI)

Discipline's
College Dean _____ Date _7/24/07_
Steven Daley Laursen (UI)

Final Approval and Acceptance by the College of Graduate Studies (UI)

_____ Date _____
Margrit von Braun (UI)

And by the Postgraduate School (CATIE)

_____ Date _14. May. 2007_
Glenn Galloway (CATIE)

ABSTRACT

Decades of forest loss throughout Central America have dramatically changed the

amount and configuration of winter habitat available for Neotropical-Nearctic migrant

songbirds and breeding habitat for resident birds. The overall objective of my research was

to understand the value of forest fragments to a diverse group of rainforest birds that depend

on lowland tropical rainforest for their survival at one part or all of their annual cycle. Using

both intensive research methods on a migrant songbird and extensive survey methods for

eight species of resident forest birds, results show that in general, remaining forest fragments

of the Sarapiquí region provide important habitat for all species studied, to varying degrees.

For the wintering Wood Thrush, *Hylocichla mustelina,* I surveyed forest fragments of

different sizes, and assessed the proportion of the population wintering outside of protected

forest reserves. Fragmentation effects on wintering Wood Thrush were further studied by

comparing over-winter survival, territorial fidelity, home range sizes, population structure

and indices of body condition and fitness, for birds in forest fragments versus intact forest.

Wood Thrushes were detected in all surveyed forest fragments ≥ 1 ha, and it was estimated

that 80% of the population winter in forest fragments outside of protected reserves. Forest

fragmentation affected sex ratios, with female Wood Thrush constituting 60% of birds

sampled in small fragments (< 20 ha), 25% in large (> 200 ha), and 35% in continuous

forests. Widespread presence even in fragments as small as 1 ha, along with evidence of

female-biased sex ratios in small fragments, may imply that available habitat for wintering

Wood Thrushes is saturated. For eight species of resident birds, we quantified changes in

species abundance and patch occupancy in forest fragments that exist across a continuum of

fragmentation, isolation and remaining forest cover. We detected all eight species within at least a subset of the fragments. The most abundant species, an understory wren, *Henicorhina leucosticta*, was observed in all 30 fragments. Two other common species, *Mionectes oleaginous* and *Myrmeciza exsul* were also found in a majority of surveyed fragments, a rather unexpected result. Abundances of two species, *Pipra mentalis*, a manakin, and *Thamnophilis atrinucha*, an antshrike, declined or the species disappeared entirely in fragments with decreasing patch size, isolation from a source, and low surrounding forest cover values. *R. sulfuratus* abundance was not significantly associated with any of the predictor variables. However, 4 of 6, or 67 % of the fragments lacking this species were < 25 ha. For *R. swansonii*, the largest toucan in the study region, highest abundances were associated with fragments embedded within areas of higher percent forest cover. Despite our predictions that species within the same foraging guild, or those with other shared life history strategies, would respond similarly to fragmentation, we found that species responded individualistically.

ACKNOWLEDGEMENTS

This dissertation is dedicated to my parents,

Steve and Barbara Roberts, who inspired me to believe in my abilities and use them in a

constructive way.   I thank them both for their friendship and for visiting me during both my

graduate field seasons in the jungles of Central America.

TABLE OF CONTENTS

LIST OF FIGURES

LIST OF TABLES

LIST OF ILLUSTRATIONS

CHAPTER 1

Tropical forest fragmentation and Wood Thrush winter ecology in lowland Costa Rica: "the known knowns, the unknown knowns, and the unknown unknowns"

Dina L. Roberts[1], Edward O. Garton[1], and Celia A. Harvey[2]

[1] Department of Fish and Wildlife Resources, College of Natural Resources, University of Idaho, Moscow, ID 83844

[2] Department of Agriculture and Agroforestry, CATIE, Turrialba, Costa Rica

ABSTRACT

In contrast to numerous studies on effects of temperate forest fragmentation on Wood Thrush (*Hylocichla mustelina*) breeding ecology, no studies to date have sought to understand how fragmentation affects Wood Thrush winter ecology. We hypothesized that forest fragments in Costa Rica would provide lower quality winter habitat as compared to continuous primary forest. We examined fragmentation effects on wintering Wood Thrush by comparing over-winter survival, territorial fidelity, home range sizes, as well as indices of body condition and fitness, for birds in forest fragments versus intact forest. In general, forest fragments, even those < 20 ha, provided important winter habitat for Wood Thrushes. No significant differences were detected for mean home range, estimated at 0.99 ha and 1.02 ha, for birds in continuous forest versus forest fragments, respectively, or between estimated survival rates between habitat types, and a majority of birds survived to migrate. These results contradicted our predictions. However, comparisons between fitness indices and spring departure date, although not significantly different, exhibited trends in the direction of our predictions. While fragmentation effects were nonexistent or subtle for the previously-mentioned traits, we did detect a significant difference between the site fidelity of birds, with Wood Thrushes in the smallest fragments showing lower rates of overwinter territory fidelity as compared to large forest fragments and continuous forests. Moreover, body condition was significantly lower for male birds in small fragments as compared to male birds occupying continuous forest and large fragments. Our research demonstrates that forest fragmentation effects may be more subtle for wintering Wood Thrushes as compared to effects on breeding populations of Wood Thrush. However, further study is justified to elucidate the degree to which forest

fragment size interacts with gender-specific demographic, physiological and behavioral traits of Wood Thrushes in lowland Costa Rica.

INTRODUCTION

Deforestation throughout Central America, historically occurring in dry forest habitats and shifting to wet forests within the last several decades (Sader and Joyce 1988, Sanchez-Azofeifa et al. 2001), has reduced once-expansive forest areas to forest fragments of varying sizes (Bryant et al. 1997). Tropical biologists have previously heralded the need to halt forest loss to prevent further population declines documented for many species of resident and migrant rainforest birds (Terborgh 1989, Hartshorn 1992, Petit et al. 1995, Brawn et al. 1998). But as Fahrig (2003) asserted, fragmentation involves both the loss and the breaking apart of habitat. Despite the efforts of a small group of tropical ornithologists to understand and document impacts of tropical forest loss on Neotropical-Nearctic songbird populations across broad scales (Powell et al. 1992, Rappole et al. 1992, Wunderle, Jr. and Latta 2000), little research currently exists to understand how forest fragmentation affects the wintering ecology of migrants.

Many species of Neotropical-Nearctic songbirds breeding in eastern forests of the United States and Canada and over-wintering in Central and South America have exhibited population declines documented during the last 40 years (Robbins et al. 1989, Askins 1995, Sauer et al. 2004). Forest fragmentation and land use change in temperate breeding areas or deforestation and fragmentation of tropical forests on the wintering grounds are the most commonly-cited reasons for declines (Robinson et al. 1995, Sherry and Holmes 1996). Past

research has focused disproportionately on Neotropical-Nearctic songbird responses to temperate forest fragmentation (Robinson and Wilcove 1994, Mazerolle and Hobson 2002, Donovan and Flather 2002), leaving a dearth of information on songbird winter ecology.

One Neotropical-Nearctic songbird, the Wood Thrush (*Hylocichla mustelina*), provides a relevant example of how our current understanding of fragmentation effects is highly skewed towards breeding season ecology. Wood Thrushes breed in mixed deciduous and coniferous forests of eastern North America and migrate to their wintering range, from Mexico to Panama predominately below 1000 m in elevation, where they spend 5-7 months each year in tropical forest habitats (Roth et al. 1996). Wood Thrush populations have declined ca. 50 % over the last 40 years, based on surveys conducted across the breeding range (Sauer et al. 2004). A large body of research on temperate forest fragmentation contributes to our detailed understanding of how higher rates of both nest predation and parasitism decrease reproductive success of Wood Thrushes and other songbirds breeding in small, isolated fragments, as compared to birds breeding in large, continuous forest (Wilcove 1986, Robinson et al. 1995, Donovan and Flather 2002). Temperate forest fragmentation and indirect effects on breeding ecology have been linked to local and regional population declines of Wood Thrushes (Robinson et al. 1995, Roth et al. 1996). Contrastingly, earlier research on Wood Thrushes in the Neotropics was conducted at few sites, mostly within large intact forests, such as La Selva Biological Reserve in Costa Rica (Blake and Loiselle 1992, Powell et al. 1992, Blake and Loiselle 2001) and Los Tuxtlas Biological Reserve in Mexico (Winker 1990, Rappole et al. 1992). Studies in human-dominated tropical landscapes are lacking, where small and medium sized fragments (<200 m) are surrounded

by pastoral and agricultural land use.

The objectives of our research were to assess impacts of tropical forest fragmentation on over-winter survival, home range size, territorial fidelity, spring departure dates, and differences between indices of fitness and body condition of Wood Thrushes by comparing continuous forest of La Selva Biological Reserve and isolated forest fragments in lowland Costa Rica.

Until the 1940's, late-successional forests covered the entire Northeastern region of Costa Rica. We assumed for this study that La Selva Biological Reserve site, which contains the largest tract of primary lowland forest in the region, provides optimal habitat for Wood Thrushes. This assumption was based on past studies reporting widespread habitat use and site persistence of Wood Thrushes in lowland old-growth forest (Blake and Loiselle 1992, Powell et al. 1992). We hypothesized that forest fragments may provide sub-optimal habitat because 1) all forest fragments used for this study had some history of selective logging, as compared to our plots within La Selva and 2) landscape context of fragments as well as spatial limitations may hinder Wood Thrush movements to search out optimal territories.

As this study was the first to address fragmentation effects per se, we based our predictions about the direction of response for our objectives (Table 1) by gleaning from a growing body of literature reporting effects of differential winter habitat quality on demographics and body condition for thrushes and warblers (Rappole et al. 1989, Blake and Loiselle 1992, Conway et al. 1995, Sherry and Holmes 1995, Wunderle, Jr. and Latta 2000). Rappole et al. (1989) and Winker (1990) estimated lower survival and more frequent and longer movements in Wood Thrushes that occupied both higher elevation sites and secondary

habitats as compared to lower elevation and primary forest sites. Conversely, using intensive mist netting of banded birds, Conway et al. (1995) reported relatively low rates of over-winter survival, but found no habitat-specific variation in survival rates for 4 species of forest songbirds wintering in Belize.

Territorial fidelity, or site persistence, has been used to assess habitat quality by providing an indication of the adequacy of resources for wintering songbirds. Higher site fidelity has been observed in landscapes dominated by forest for several species of migrants (Wunderle and Latta 2000). Spring departure dates have also been shown to be later for birds occupying lower quality sites during the winter for at least two warbler species, American Redstarts (*Setophaga ruticilla*) (Runge and Marra 2005) and Black-throated Blue Warblers (*Dendroica caerulescens*) (Wunderle and Latta 2000).

Finally, fitness indices measure environmental stress during ontogeny and perhaps provide an early warning sign for impacts of stress on eventual survival or reproductive success (Clark and McKenzie 1992, Lens et al. 2002). For example, one index utilized in bird studies, fluctuating asymmetry (FA), or the difference between wing lengths or tarsus lengths in birds, has been used as an estimate of developmental stability (Palmer and Strobeck 1986). Lens and others (1999, 2002) reported that tarsus asymmetry was greater for Taita Thrushes (*Turdus helleri*) living in small, degraded forest fragments in Africa as compared with thrush populations in larger, moderately disturbed forests.

Using data collected from radio-marked Wood Thrushes, we addressed the following questions: 1) do Wood Thrushes wintering in forest fragments show different rates of within-season survival and territorial fidelity as compared to birds using continuous forest, 2) do

home range sizes of Wood Thrushes in forest fragments differ from birds wintering in continuous forest, 3) do body condition and fitness indices of Wood Thrushes differ for birds in forest fragments as compared to birds utilizing continuous forest habitats, and 4) does departure date differ for Wood Thrushes wintering in fragments verses continuous forest?

STUDY SITES

CONTINUOUS FOREST

La Selva Biological Station, Costa Rica (10° 26' N, 83° 59' W) is a private forest reserve owned by the Organization for Tropical Studies (OTS) and managed for scientific research, education and limited ecotourism development. La Selva reserve comprises 1,611 ha of lowland wet tropical forest on the Caribbean slope and is continuous with Braulio Carrillo National Park, which encompasses over 47,571 ha (La Selva Biological Station, OTS GIS Database). Average annual precipitation is approximately 4,000 mm and mean monthly temperatures range from 24.7º C in January to 27.1º C in August, consistent with a tropical wet-forest life zone (Holdridge 1947, McDade and Hartshorn 1994). About 850 hectares of old-growth lowland wet forest exists within the reserve (D. Roberts, *unpublished analysis*) with the remainder containing a variety of habitats, including secondary forest, native tree plantations and abandoned cacao plantations.

FOREST FRAGMENTS

Within the last 50 years, forest clearing in the area near La Selva Biological Station, Puerto Viejo de Sarapiquí, has been extensive (Butterfield 1994). Primary land uses today include cattle and dairy production, banana, heart of palm, pineapple and exotic flower cultivation.

We studied Wood Thrush in six forest fragments, ranging in size from 5 to 370 ha. Three fragments were < 20 ha in size, and three were > 200 ha. Fragments were chosen to represent two ends of a continuum across a gradient of fragment sizes that occur across the region. Small fragments, defined as < 20 ha, comprise a majority of fragments in the region (Bell and Donnelly 2006), particularly as one moves greater distances from the La Selva/Braulio Carrillo reserve complex (LSBCC). Larger fragments make significant contributions to overall forest area outside of the LSBCC and are often protected within an extensive system of private reserves used for ecotourism or selective logging, both of which receive environmental service payments (ESP) providing protection for both watershed functions, biodiversity conservation, and carbon storage. Small forest fragments are much less likely to be protected within the ESP system. We chose to study Wood Thrush in small and large fragments to find out if fragments provide habitat and if so, what quality of habitat. All forest fragments were isolated from other forest fragments by greater than 500 + m and were characterized by mid- to- late successional forest with large, emergent trees with a canopy closure of > 70% and a history of some selective forest logging. All fragments were surrounded predominantly by pasture, but two small fragments had flower cultivation or heart of palm and pasture as adjacent land uses. No fragments used for this study had any evidence of recent logging. Both La Selva and all forest fragments utilized in this study were below 150 m in elevation.

METHODS

FIELD SAMPLING METHODS

During two field seasons (November 2003 to April 2004 and December 2004 to April 2005),

we collected information on individual Wood Thrush survival, daily locations, movements,

and territorial fidelity, using radio telemetry techniques. Individual Wood Thrush were

initially located starting in late December of each year by walking trails within La Selva and

in forest fragments while playing recorded call notes. Thus, we ensured that birds had

completed post-migration jockeying for territories that occurred in November/early

December, and most individuals occupied established territories. Upon locating a bird,

targeted mist-netting, which involved erecting two, 12 m long x 3 m high nets and playing a

recorded call note, was used to capture the known bird/birds. Once a bird was captured, a

USFWS aluminum band (size 1A) was attached. For each individual Wood Thrush, we

collected an unflattened wing chord (to the nearest 0.5mm), tarsus length for both left and

right legs to the nearest 0.01 mm using a Fowler electronic caliper, following Pyle et al.

(1987) and body mass by placing the bird in a small bag and using a spring scale (Avinet,

Inc.). A radio transmitter (Model BD-2, 1.8 g, battery life ~ 16 weeks; Holohil Systems

LTD., Carp, Ontario, Canada) was attached to each bird with thin elastic using the thigh-loop

harness method (Rappole and Tipton 1991). Radio-telemetry techniques have been

established for *H. mustelina* and there is no evidence that attaching a small transmitter affects

survival or behavior of this species (Powell et al. 2000, Lang et al. 2002, Vega Rivera et al.

2006). Individual Wood Thrushes with transmitters were located on foot with an Osprey

waterproof receiver (H.A.B.I.T Research, LTD, Victoria, BC, Canada) and a Yagi 3-element

antenna (Titley Electronics, NSW, Australia). Permanent tracking stations were established

within La Selva and in forest fragments, and known latitude and longitude for each station

were acquired with a handheld Garmin GPS unit or from La Selva GIS grid/trail marker

UTM location data. Standard triangulation methods from the ground were used, with the aid

of program LOCATE II (Nams 2000), to obtain one UTM position per day or every other

day for each bird from date of capture (December/January of each season) until the bird

migrated (late March thru April), died or disappeared. To our knowledge, this study was the

first to use telemetry technology that allowed for tracking individual Wood Thrushes for 4

months, the longest period to date for a winter ecology telemetry study.

STATISTICAL ANALYSIS

We estimated survival rates of radiotagged birds using Kaplan-Meier analysis (Kaplan and

Meier 1958) in Program MARK (White 2006). We used a modification developed by

Pollock et al. (1989), allowing for staggered entry (not all animals are captured or radio

tagged at the same time) and for use of right-censored data resulting from an inability to

relocate a bird that disappeared from the study area. If fragment birds disappeared from a

fragment, we searched in all nearby fragments within 1 km of the initial capture location.

Because of the uncertainty of fates of some radiotagged birds in forest fragments, we used

two models to estimate survival (Ganey et al. 2006). In the first model ($\hat{S}_1$) we censored

those individuals that we presume left the fragment and were not relocated within 1000 m of

the capture location. In the second model ($\hat{S}_2$), we assumed that all birds that disappeared

and were not redetected had died. Utilizing two models was only necessary for fragment

birds because of unknown fates of birds that left fragments. During 2004, the one missing La

Selva bird was relocated in March from a permanent canopy tower and tracked until it

migrated. In 2005, fates of all birds in La Selva were known as they survived to migration or

were confirmed predation events without the use of the canopy tower.

Home range size was estimated using the fixed kernel method with an 80%

probability (with default smoothing parameter), on 20 individuals within La Selva and 15

individuals in forest fragments for a total of 35 thrushes. All calculations were performed

using Animal Movement Extension (Hooge et al. 1999) for Arcview 3.3 (ESRI). For the

analysis comparing home range size between La Selva and forest fragments, we used only

birds with a minimum of 20 independent locations; the average number was 37 locations per

bird. Home range size is reported as $\bar{x}$ +/- SE.

Territorial fidelity was defined by maintenance of a territory throughout the duration

of the winter without large (> 500 m) movements. We chose this distance as we had no

territories greater than 2.8 ha. Movements greater than 500 m were well outside the average

movement of birds holding territories and were thus assumed to signify non-territorial birds,

"floaters", unable to defend a territory. We determined the percentage of radio-marked birds

in each habitat type that were detected within the same territory from initial capture through

mid to late March of each year (Hooge et al. 1999, Koronkiewicz et al. 2006). We compared

percent territorial fidelity across continuous forest, large fragments and small fragments

using a Fisher's exact test.

One body condition index and one fitness index were developed from data collected

during the initial capture of each Wood Thrush individual. Body condition was defined here

as body mass corrected for structural size (henceforth standardized body mass).

Standardized body mass was obtained by regressing body mass against tarsus length and wing chord for each bird by gender and using the residual for each bird (observed body mass – predicted body mass) as a corrected measure of body condition. For male Wood Thrush, body mass was best correlated with tarsus length, and from the regression of body mass against tarsus length, we determined the equation: predicted body mass = (tarsus length x 1.37) + 5.32 ($F = 1.83$, $r^2 = 0.10$, df = 1 and 17, $P > 0.05$). For female Wood Thrush, body mass was best correlated with wing length, and we regressed body mass against wing chord to arrive at the following: predicted body mass = (wing chord x 0.45) + 0.84 ($F = 1.65$, $r^2 = 0.11$, df = 1 and 14, $P > 0.05$). Mean standardized values from the regression analysis for each sex were used to compare mean differences in body condition between habitats using t-tests. For the fitness index (fluctuating asymmetry) data, the same person measured each bird's left and right tarsus three times during the capture event. We calculated the mean difference between tarsi and compared the difference between habitats using a One-way ANOVA.

Spring departure dates from the winter grounds were ascertained for each radio-tagged bird during weekly periods beginning in late March to late April. Weekly intervals were chosen as birds often made longer movements prior to migration, but would return to the winter territory within one to two days of pre-migration forays. If a bird was not detected during one visit, we made daily visits for a week to that same territory. We verified that birds whose signals could not be detected from the ground were indeed gone from La Selva territories by ascending the 45 m canopy tower in late March and early April and searching for birds whose territories were within 2 km of the tower. The tower allowed us to verify

that our methods from the ground were indeed working. Also, behavioral cues of migration preparation were evident both years in La Selva and forest fragments. Wood Thrushes began using a quiet, non-aggressive call note around dusk before spring departure, possibly searching for conspecifics with which to begin the northward migration. To test for differences between mean departure date for La Selva and fragment birds, a two-sample Kolmogorov-Smirnov Test was used.

RESULTS

We captured and radiotagged 39 Wood Thrushes over two seasons (2003-2004, henceforth 2004; and 2004-2005, henceforth 2005) in continuous forests of La Selva (21 birds) and within six forest fragments (18 birds).

SURVIVAL RATES

Over-winter seasonal survival for Wood Thrushes wintering in both continuous forest and forest fragments was relatively high (Table 2). No birds died in La Selva during 2004, but two birds within La Selva were predated in 2005. One radio transmitter was relocated all season in the same tree adjacent to the birds' territory. It is possible that a forest raptor killed the bird and flew with it into the canopy where the transmitter was discarded. Alternatively, an arboreal snake, such a *Boa constrictor,* ate the bird and then passed the transmitter after ascending into a tree. We know this is possible from a second known predation event of a radiotagged bird by a *B. constrictor* just prior to a relocation event. We found the *Boa constrictor* on a small log 1.5 m above a small pile of feathers lying on the leaf litter, and noticed rectrices caught horizontally in the boa's mouth (Photo 1), as well as a strong signal coming from the belly of the snake. The boa was captured and held at La Selva's ambient

lab whereby it passed Wood Thrush feathers and a working transmitter one week after the predation event. The snake was released at the capture site unharmed.

Survival estimates for fragment birds were also high (Table 2). During the 2004 field season, only one of nine radio-tagged birds disappeared, from a small fragment (10 ha). The following year, three birds abandoned that same fragment, after several large movements were detected on previous visits. None of the birds that left were subsequently detected in the fragment or in any fragments within 1 km of the capture site.

HOME RANGE SIZE AND TERRITORIAL FIDELITY

Mean kernel home range estimates were within 3% of each other, with 0.99 ha ± 0.11 for Wood Thrushes wintering in continuous forest (La Selva) and 1.02 ha ± 0.18 for individuals over-wintering in forest fragments and did not differ significantly. More variation was observed between individual home range size within a habitat type than between habitats, and ranges (0.3 – 2.6 ha in La Selva versus 0.2 – 2.8 ha in forest fragments) spanned an order of magnitude in each habitat type. Birds were able to successfully defend territories in both habitats.

Despite strong territorial behavior by a majority of birds in both habitats, territorial fidelity was significantly lower in small forest fragments (Prob = 0.008) as compared to large fragments and continuous forests of La Selva (Table 3). However, large fragments had high territorial fidelity, while several birds in small fragments were unable to hold territories for the entire non-breeding season. From results of molecular sexing analysis (D. Roberts *unpublished manuscript*), we determined that each of the four birds that left the same small fragments both years were males. In fragments, male territories were on average larger than

female bird territories (Figure 1). Although we were not able to assess between-year site fidelity, one female was caught in the same net lane during both seasons in La Selva and successfully defended the territory both years. This bird was observed physically lunging at an intruder bird during the first season and dominated a second Wood Thrush that was caught and radiotagged during the same targeted mist netting the second year. No banded birds were recaptured in fragments during the second year.

BODY CONDITION and FITNESS INDICES

Mean standardized body mass was analyzed for each sex by habitat. Male Wood Thrushes (n=10) in La Selva, $\bar{x} = 1.09 \pm 0.88$ (SE), were much larger than male Wood Thrushes (n=8) in fragments, $\bar{x} = -0.87 \pm 0.83$ (SE). Mean standardized residuals were significantly different ($P = 0.07$) at alpha of 0.07, with male Wood Thrush in fragments having poorer body condition than males in continuous forests. While mean standardized body mass for female Wood Thrushes was not significantly different between La Selva birds, $\bar{x} = 0.84 \pm 0.78$ (SE), and fragment birds, $\bar{x} = 0.50 \pm 0.86$ (SE), $P = 0.78$, females showed the same tendency as males, with females wintering in fragments exhibiting lower body condition values.

Comparisons of levels of fluctuating asymmetry between birds in La Selva and the two fragment classes, while not significantly different ($F = 1.44$, $P = 0.252$, df = 2), showed a trend towards higher asymmetry in birds utilizing small fragments (Figure 2).

DEPARTURE DATE

La Selva birds tended to leave earlier than birds occupying forest fragments (Figure 3), but differences were not significant (K-S = 0.013, $P = 0.35$).

DISCUSSION

"THE KNOWN KNOWNS"

Our results provide the first evidence that tropical forest fragments of all sizes, even those

< 5 ha provide winter habitat for Wood Thrushes. From this study, our "known knowns"

include the results that a majority of birds wintering across the gradient of habitats from

continuous forest to small fragments survived to migrate. High estimates of survival and

territorial fidelity in La Selva and large fragments suggest that fragments > 200 ha provide

habitat comparable to large, intact forest areas, but even small fragments seem to provide

suitable habitat for Wood Thrushes. High rates of over-winter survival have been

documented for other Neotropical-Nearctic migrants, as was reported for *Empidonax*

flycatchers in Mexico and Costa Rica (Rappole and Warren 1980, Koronkiewicz et al. 2006).

We are confident that our high survival estimates, especially for birds in large fragments and

within La Selva, provides additional evidence that winter survival can be high for many

individuals within populations of Neotropical-Nearctic migrants.

Additional known knowns included the ability of birds to maintain territories in both

intact and fragmented forest habitats and occupy equally sized home ranges between the

habitats. Our mean home range estimates of approximately 1 ha were slightly larger than

averages from one previous study conducted on wintering Wood Thrushes by Winker and

others (1990), but both studies documented a wide range in estimates between individuals.

Winker et al. (1990) estimated average home-range size of Wood Thrushes in Mexico at 0.44

ha, which was calculated using the minimum area method of home range estimation.

Differences in our average estimates as compared to theirs could be explained by methods of

estimation and the fact that we included all individuals in our analysis that had a minimum number of locations. Winker et al. (1990), on the other hand, described a population structured by both a substantial wandering class of individuals forced to move from higher elevations during inclement weather and a sedentary class of Wood Thrushes wintering at lower elevations, and thus did not include any wandering birds in their analysis. We encountered few birds that we defined as "wandering" birds during our study. Our study design of capturing birds with targeted playbacks all below 150 m in elevation as opposed to passive netting was used to assess fragmentation effects on largely sedentary birds and thus we did not specifically address this aspect of Wood Thrush winter ecology. However, some birds in small forest fragments that could not establish territories for the duration of the winter could be classed possibly as secondary wanderers.

Generally high survival rates for most birds across all habitats, and similar home range estimates for birds in both intact and fragmented habitats went against our original predictions that fragmentation would negatively impact these aspects of Wood Thrush winter ecology in lowland Costa Rica. Despite these encouraging results, however, the remaining ecological traits measured followed our predictions (Table 1) that support a hypothesis of differential quality among habitats. Significantly lower site fidelity, and for males birds, poorer body condition, coupled with trends in later departure and higher fluctuating asymmetry for fragment birds, often driven by small fragment data, suggests that small fragments may provide sub-optimal habitat for some individuals. Based on removal experiments and over-winter fidelity and territoriality, Winker et al. (1990) concluded that Wood Thrushes exhibited behavior similar to that predicted by Brown's (1969) critical

density and Fretwell-Lucas despotic models, whereby lower suitability habitat would be occupied when population demands exceed available resources in higher quality habitat (Winker et al. 1990). For other species of Neotropical-Nearctic warblers, poorer body condition and later departures have been associated with lower habitat quality (Marra and Holmes 2006). Our data, at least for Wood Thrushes wintering in small fragments, support these earlier conclusions.

"UNKNOWN KNOWNS"

Poorer indices of body condition and fitness, as well as later departure dates for migrant birds from fragments during spring migration both indicate that something more subtle than effects on outright survival may be occurring. How these effects may manifest themselves during migration or subsequent breeding effects are as yet unknown for Wood Thrush. For more extensively studied warbler species, individuals over-wintering in suboptimal habitat have been shown to arrive later on breeding grounds and have lower reproductive output (Marra et al. 1998).

Higher levels of asymmetry in birds wintering in small fragment displayed a pattern predicted by fitness arguments and supports previous research showing small, more degraded fragments, while providing habitat, may in certain cases, provide sub-optimal habitat. Wood Thrushes breed in North America and their tarsi are formed upon fledging the nest. This measurement may then reflect a pattern of later arrival onto the breeding ground of birds in poorer condition or that small fragment birds get excluded from higher quality habitat by behaviorally dominant birds. Thus, better quality habitat was settled first, and birds exhibited behavioral dominance to maintain territories and excluded sub-dominate birds. There may

be a threshold in terms of fragment size settled by most individual Wood Thrush. Intraspecific competition based on observational behavioral data appeared to be intense in one, 20-hectare fragment in a highly degraded landscape. Alternatively, fewer birds appeared to settle in the smallest fragments, < 10 ha, in the first place and intraspecific competition may be less, but we have yet to quantify densities across fragment sizes. These aspects of Wood Thrush winter ecology remain little understood, but based on body condition data and decreased territorial fidelity, one could conclude that fragment habitats are poorer quality habitat for some members of this population and are settled by birds arriving later on the wintering grounds or by birds unable to occupy territories in larger forest areas. To our knowledge, settlement patterns upon arrival on the wintering grounds are not well understood for this species. Future research could address this issue.

Other questions remain unanswered for wintering Wood Thrushes in fragmented and continuous forests. What are the rates of between-year site fidelity? We recaptured only one Wood Thrush in La Selva both years, but given that our overall sample size was under 50 birds, the odds of recapturing more birds would be small given our capture methods. Another unknown includes why Wood Thrushes use small forest fragments within heavily modified agricultural landscapes if such habitat is sub-optimal? One, they may have no choice, as available habitats may be saturated. Second, physiological needs to maintain wintering Wood Thrushes may be met with a diet of litter arthropods mixed with fruit readily obtained by most individuals in small fragments. Several small fragment birds were observed consuming fruit mid-winter, especially from large shrubs of *Miconia* sp., that grew along the edges of many fragments.

"UNKNOWN UNKNOWNS"

Our results indicate that many important winter ecology questions remain unanswered for Wood Thrush, one of the most well-studied Neotropical-Nearctic migrants. What are the things we don't know we don't know? Continued land use change patterns and unknown climate scenarios could affect migratory ranges and ecological responses. Intensification of agricultural production in lowland Costa Rica and the increased input of chemicals on crops adjacent to forest fragments may have affects on physiology, fitness or survival of birds wintering in fragments, but this is largely unknown. Collecting baseline data in tropical habitats across a range of Neotropical-Nearctic songbird families will provide critical data for future comparative studies and as yet unknown unknowns.

CONCLUSION

Widespread forest fragmentation and continued land change throughout Central America, both historical and present-day, affect declining species of migrants during the winter phase of the life cycle and likely during subsequent seasons. Our conclusions of widespread use of forest fragments of all sizes by wintering Wood Thrushes support continued efforts to retain remaining forest fragments across the lowland tropics of Central America as necessary to provide critical winter habitat for Wood Thrush populations. However many questions remain unanswered about Wood Thrush winter ecology, especially for birds using small fragments (< 20 ha) and medium-sized fragments (between 20 and 200 ha). Future studies with larger samples sizes of both fragments and individual Wood Thrush are necessary to confirm our results and provide additional insight for managers. Fragmentation and winter

ecology of Wood Thrushes deserves further investigation, especially as differential usage by juvenile or sexual segregation may force certain individuals to occupy sub-optimal habitat. How these differences play out across the annual life cycle of migratory birds or affect the population regulation of Wood Thrushes is important to sound land use management at both ends of the journey.

LITERATURE CITED

Askins, R. A. 1995. Hostile landscapes and the decline of migratory songbirds. Science 267:1956-1957.

Bell, K. E., and M. A. Donnelly. 2006. Influence of forest fragmentation on community structure of frogs and lizards in Northeastern Costa Rica. Conservation Biology 20: 1750-1760.

Blake, J. G., and B. A. Loiselle. 1992. Habitat use by Neotropical migrants at La Selva Biological Station and Braulio Carrillo National Park, Costa Rica, p. 257-272. *In* J. M. I. Hagan, and D. W. Johnston [EDS.], Ecology and conservation of Neotropical migrant landbirds. Smithsonian Institution Press, Washington D.C.

Blake, J. G., and B. A. Loiselle. 2001. Bird assemblages in second-growth and old-growth forest, Costa Rica: perspectives from mist nets and point counts. The Auk 118:304-326.

Brawn, J. D., S. K. Robinson, D. F. Stotz, and W. D. Robinson. 1998. Research needs for the conservation of Neotropical birds, p. 323-335. *In* J. M. Marzluff, and R. Sallabanks [EDS.], Avian Conservation: Research and Management. Island Press, Washington, D.C.

Brown, J. L. 1969. Territorial behavior and population regulation in birds. Wilson Bulletin 81: 293-330.

Bryant, D., D. Nielsen, and L. Tangley. 1997. The last frontier forests: ecosystems and economies on the edge. World Resources Institute Report, Washington, D.C.

Butterfield, R. P. 1994. The regional context: land colonization and conservation in Sarapiqui, p. 299-306. *In* L. A. McDade, K. S. Bawa, H. Hespenheide, and G. S. Hartshorn [EDS.], La Selva: ecology and natural history of a Neotropical rain forest. University of Chicago Press, Chicago and London.

Clark, G. M., and N. L. McKenzie. 1992. Fluctuating asymmetry as a quality control indicator for insect mass rearing processes. Journal of Economic Entomology 85:2045-2050.

Conway, C. J., G. V. N. Powell, and J. D. Nichols. 1995. Over-winter survival of Neotropical migratory birds in early successional and mature tropical forests. Conservation Biology 9:855-864.

Donovan, T. M., and C. H. Flather. 2002. Relationships among North American songbird trends, habitat fragmentation, and landscape occupancy. Ecological Applications 12:364-374.

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

Ganey, J. L., W. M. Block, J. K. Dwyer, B. E. Strohmeyer, and J. S. Jenness. 2006. Dispersal movements and survival rates of juvenile Mexican Spotted Owls in northern Arizona. Wilson Bulletin 110:206-217.

Hartshorn, G. S. 1992. Forest loss and future options in Central America, p. 13-19. *In* J. M. I. Hagan, and D. W. Johnston [EDS.], Ecology and conservation of Neotropical migrant landbirds. Smithsonian Institution Press, Washington D.C.

Holdridge, L. R. 1947. Determination of world plant formations from simple climatic data. Science 105: 367-368.

Hooge, P. N., W. Eichenlaub, and E. Solomon. The animal movement program. (2.04 beta). 1999. Glacier Bay Field Station, USGS Alaska Biological Science Center.

Kaplan, E. L., and P. Meier. 1958. Nonparametric estimation from incomplete observations. Journal of the American Statistical Association 53:457-481.

Koronkiewicz, T. J., M. K. Sogge, C. Van Riper III, and E. H. Paxton. 2006. Territoriality, site fidelity, and survivorship of Willow Flycatchers wintering in Costa Rica. Condor 108:558-570.

Lang, J. D., L. A. Powell, D. G. Krementz, and M. J. Conroy. 2002. Wood Thrush movements and habitat use: effects of forest management for Red-cockaded Woodpeckers. Auk 119:109-124.

Lens, L., S. Van Dongen, C. M. Wilder, T. M. Brooks, E. Matthysen. 1999. Fluctuating asymmetry increases with habitat disturbance in seven bird species of a fragmented afrotropical forest. Proceedings of the Royal Society of London: 266:1241-1246.

Lens, L., S. Van Dongen, and E. Matthysen. 2002. Fluctuating asymmetry as an early warning system in the critically endangered Taita Thrush. Conservation Biology 16:479-487.

Marra, P. P., K. A. Hobson, and R. T. Holmes. 1998. Linking winter and summer events in a migratory bird by using stable-carbon isotopes. Science 282:1884-1886.

Marra, P. P., and R. T. Holmes. 2006. Consequences of dominance-mediated habitat segregation in American Redstarts during the wintering season. The Auk 118:92-104.

Mazerolle, D. F., and K. A. Hobson. 2002. Consequences of forest fragmentation on territory quality of male Ovenbirds breeding in western boreal forests. Canadian Journal of Zoology 80:1841-1848.

McDade, L. A. and G. S. Hartshorn. 1994. La Selva Biological Station, p. 6-14. *In* L.A. McDade [ED.], La Selva: ecology and natural history of a Neotropical rainforest. The University of Chicago Press, Chicago.

Nams, V.O. 2000. LOCATE II User's guide. Pacer Computer Software, Truro, NS.

Palmer, A. R. and C. Strobeck. 1986. Fluctuating asymmetry: measurement, analysis and patterns. Annual Review of Ecology and Systematics 17:391-421.

Petit, D. R., J. F. Lynch, R. L. Hutto, J. G. Blake, and R. B. Waide. 1995. Habitat use and conservation in the Neotropics, p. 145-200. *In* T. E. Martin, and D. M. Finch [EDS.], Ecology and Management of Neotropical Migratory Birds. Oxford University Press, New York.

Pollock, K. H., S. R. Winterstein, C. M. Bunck, and P. D. Curtis. 1989. Survival analysis in telemetry studies: the staggered-entry design. Journal of Wildlife Management 53:7-15.

Powell, L. A., D. G. Krementz, J. D. Lang, and M. J. Conroy. 2000. Effects of radio transmitters on migration Wood Thrushes. Journal of Field Ornithology 69:306-315.

Powell, G. V. N., J. H. Rappole, and S. A. Sader. 1992. Neotropical migrant landbird use of lowland Atlantic habitats in Costa Rica: A test of remote sensing for identification of habitat, p. 287-298. *In* J. M. I. Hagan, and D. W. Johnston [EDS.], Ecology and conservation of Neotropical migrant landbirds. Smithsonian Institution Press, Washington, D.C.

Pyle, P., S. Howell, R. P. Yunick, and D. DeSante. 1987. Identification guide to North American passerines. Slate Creek Press, Bolinas, CA.

Rappole, J. H., and C. E. Warren. 1980. Ecological aspects of migrant bird behavior in

Veracruz, Mexico, p. 353-393. *In* A. Keast, and E. S. Morton [EDS.], Migrant birds in the Neotropics: ecology, behavior, distribution, and conservation. Smithsonian Institution Press, Wasington, D.C.

Rappole, J. H., M. A. Ramos, and K. Winker. 1989. Wintering Wood Thrush mortality in southern Veracruz. Auk 106:402-410.

Rappole, J. H., and A. R. Tipton. 1991. New harness design for attachment of radio transmitters to small passerines. Journal of Field Ornithology 62:335-337.

Rappole, J. H., E. S. Morton, and M. A. Ramos. 1992. Density, philopatry, and population estimates for songbird migrants wintering in Veracruz, p. 337-344. *In* J. M. I. Hagan, and D. W. Johnston [EDS.], Ecology and conservation of Neotropical migrant landbirds. Smithsonian Institution Press, Washington D.C.

Robbins, C. S., J. R. Sauer, R. S. Greenberg, and S. Droege. 1989. Population declines in North American birds that migrate to the Neotropics. Proceedings of the National Academy of Sciences 86:7658-7662.

Robinson, S. K., and D. S. Wilcove. 1994. Forest fragmentation in the temperate zone and its effects on migratory songbirds. Bird Conservation International 4:233-249.

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

Roth, R. R., M. S. Johnson, and T. J. Underwood. 1996. Wood Thrush (*Hylocichla mustelina*), *In* A. Poole, and F. Gill [EDS.], Birds of North America. The Academy of Natural Sciences and The American Ornithologists' Union, Philadelphia, PA.

Runge, M., and P. P. Marra. 2005. A demographic model for a migratory passerine bird: population dynamics of the American Redstart, p. 375-389. *In* R. Greenberg, and P. P. Marra [EDS.], Johns Hopkins University Press, Baltimore.

Sader, S. A., and A. T. Joyce. 1988. Deforestation rates and trends in Costa Rica, 1940-1983. Biotropica 20:11-19.

Sanchez-Azofeifa, G. A., R. C. Harriss, and D. L. Skole. 2001. Deforestation in Costa Rica: a quantitative analysis using remote sensing imagery. Biotropica 33:378-384.

Sauer, J. R., J. E. Hines, and J. Fallon. 2004. The North American breeding bird survey results and analysis 1966-2003. Patuxent Wildlife Research Center, Laurel, MD.

Sherry, T. W., and R. T. Holmes. 1995. Summer versus winter limitation of populations: what are the issues and what is the evidence, p. 85-120. *In* T. E. Martin, and D. M. Finch [EDS.], Ecology and management of Neotropical migratory birds. Oxford University Press, New York.

Sherry, T. W., and R. T. Holmes. 1996. Winter habitat quality, population limitation, and conservation of Neotropical-Nearctic migrant birds. Ecology 77:36-48.

Terborgh, J. W. 1989. Where have all the birds gone? Princeton University Press, Princeton, New Jersey.

Vega Rivera, J. H., J. H. Rappole, W. J. McShea, and C. A. Haas. 2006. Wood Thrush postfledging movements and habitat use in northern Virginia. Condor 100:69-78.

White, G.C. and K. P. Burnham. 1999. Program MARK: Survival estimation from populations of marked animals. Bird Study 46 Supplement, 120-138.

Wilcove, D. 1986. Habitat fragmentation in the temperate zone, p. 237-256. *In* M. E. Soule [ED.], Conservation Biology. Sinauer Associates, Inc., Sunderland, MA.

Winker, K., J. H. Rappole, and M. A. Ramos. 1990. Population dynamics of the Wood Thrush in Southern Veracruz, Mexico. The Condor 92:444-460.

Wunderle, J. M., Jr., and S. C. Latta. 2000. Winter site fidelity of Nearctic migrants in shade coffee plantations in different sizes in the Dominican Republic. Auk 117: 596-614.
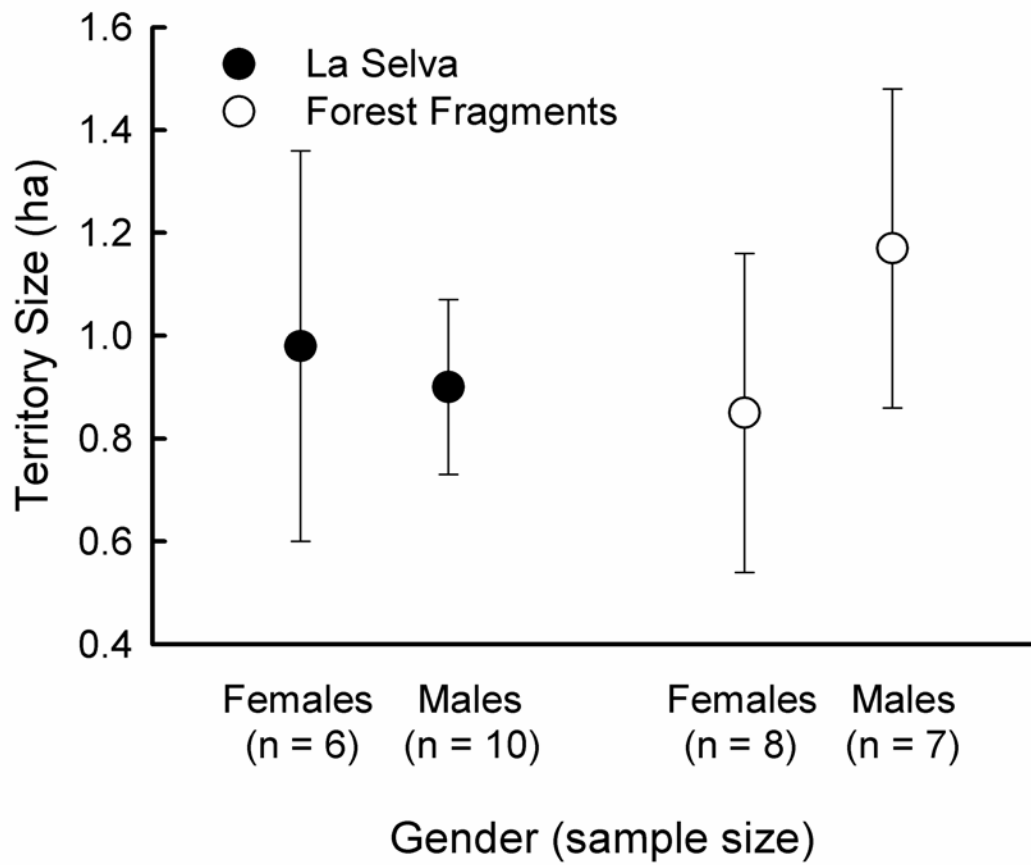
FIGURE 1. Winter territory sizes ($\bar{x}$ +/- SE) by gender of Wood Thrush in two forested habitat types in Costa Rica.
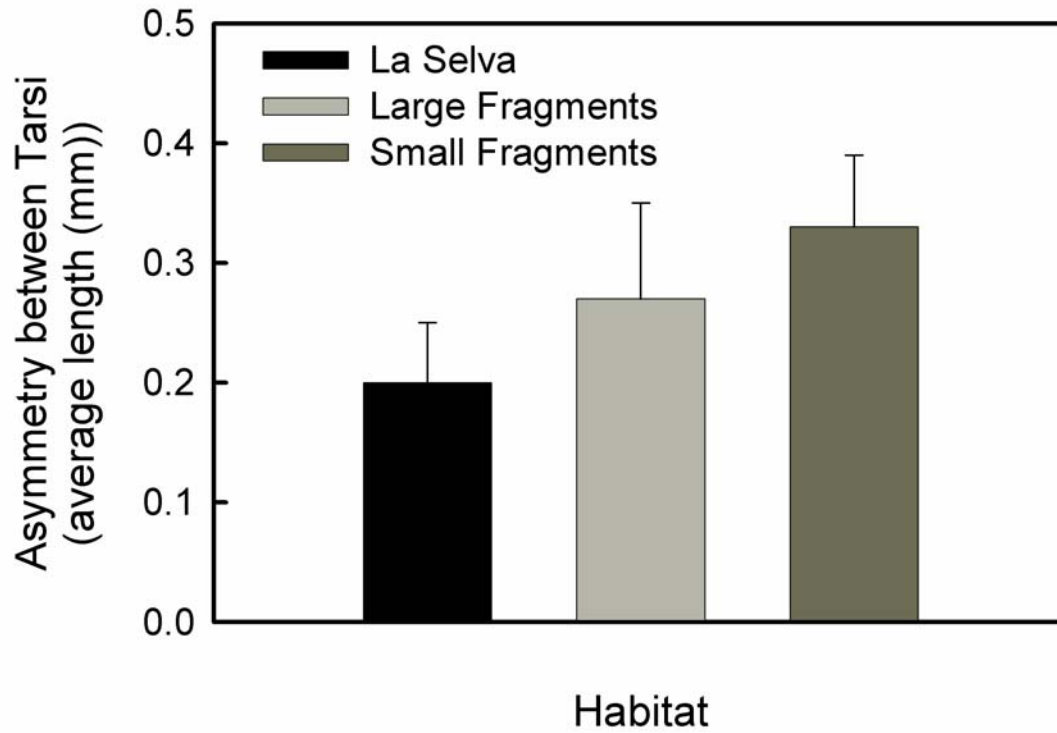
FIGURE 2. Comparison of fluctuating asymmetry ($\bar{x}$ +/- SE) for Wood Thrush wintering in La Selva, large fragments (> 200 ha) and small fragments (< 20 ha).
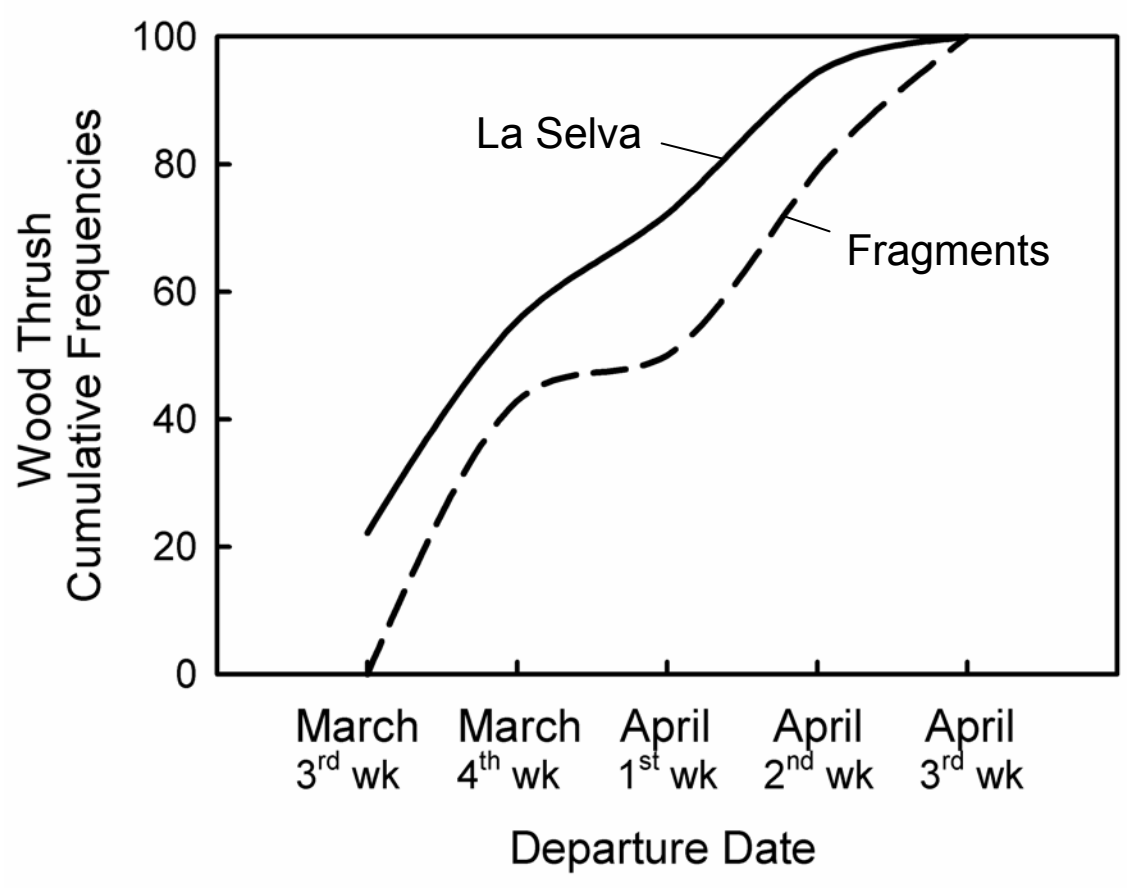
FIGURE 3. Spring departure date by week for Wood Thrushes wintering in La Selva

versus forest fragments in lowland Costa Rica during 2004 and 2005.

TABLE 1. Predicted responses of Wood Thrush to forest fragmentation on wintering grounds in Costa Rica.

	Habitat	
	Continuous Forest	Forest fragments
Predictions		
Survival	Higher	Lower
Home range	Smaller	Larger
Territorial fidelity	Higher	Lower
Body condition index	Better	Poorer
Fluctuating Asymmetry	Lower	Higher
Spring Departure	Earlier	Later

TABLE 2. Estimated survival rates of radio-tagged Wood Thrush in lowland continuous forest and forest fragments in Costa Rica, 2004 and 2005.

		Habitat	
Year	n LS/FF	La Selva (LS)	Forest fragments (FF) $\hat{S}_1$ $\hat{S}_2$
2004	11/9	1.0	1.0 or 0.87
2005	9/9	0.77 ± 0.13	1.0 or 0.66
Average over both seasons		$\hat{s} = 0.89$	$\hat{s} = 1.0$ or 0.77

$\hat{S}_1$ – survival estimate model one, unknown fate Wood Thrush censored
$\hat{S}_2$ – survival estimate model two, all birds that left the small fragments were treated as dead

TABLE 3. Wood Thrush telemetry sample sizes and territory fidelity by habitat types in lowland Caribbean Costa Rica. Territory fidelity is the percentage of birds that remained on the same territory for the entire season, from time of capture to migration.

Habitat Type	Total Wood Thrush With Transmitters (Females/Males/Unk)	Within-season Territorial Fidelity (%)
La Selva (continuous forest)	21 (7/11/3)	95
Forest Fragments	18	
Large fragments only (> 200 ha)	8 (2/6/0)	100
Small fragments only (< 20 ha)	10 (6/4/0)	60

Illustration 1. First record of *Boa constrictor* depredating an adult Wood Thrush. Besides rectrices lodged in the snakes mouth, other evidence included a strong signal emitted from the radio-tagged Wood Thrush inside the snake. The radio transmitter survived the week-long trip through the snake, and came out the other end still ticking.

CHAPTER 2

Large conservation value of small forest fragments for Wood Thrush populations in

Costa Rica's Atlantic lowlands

Dina L. Roberts

Department of Fish and Wildlife Resources, College of Natural Resources, University of

Idaho, Moscow, ID 83844

ABSTRACT

Decades of forest loss throughout Central America have dramatically changed the amount and configuration of winter habitat available for Nearctic-Neotropical songbirds, yet little is known about the minimum patch sizes of tropical forest fragments settled or used by migrant songbirds. This information is critical for making sound forest management and conservation decisions in the fragmented landscapes that dominate the region. I assessed the relative value of forest fragments of varying size for wintering Wood Thrushes, *Hylocichla mustelina,* by examining three aspects of their winter ecology: 1) presence and densities, 2) proportion of the population wintering outside of protected forest reserves, and 3) sex ratio of the population across a gradient of continuous forest, large and small forest fragments. To obtain presence and density data, playback surveys were conducted. Using a classified Landsat image and home range data collected from the same population, Wood Thrush population size was estimated in both forest fragments and continuous forest in northeastern Costa Rica. To ascertain if fragmentation influenced sex ratios, I used genetic techniques to determine gender of birds occupying forest fragments and continuous forest. Wood Thrushes used all surveyed forest fragments that were $> = 1$ ha, but were not detected in the 0.5 ha fragment. It was estimated that 80% of the population winter in and depend on forest fragments. Tropical forest fragmentation influenced sex ratio patterns by habitat, with female Wood Thrush constituting 60% of birds sampled in small fragments (< 20 ha), only 25% in large (> 200 ha), and 35% in continuous forests, however this difference was not significant. Widespread presence in fragments and a trend towards female-biased sex ratios in small fragments may imply that available habitat for wintering Wood Thrushes is

saturated. Strategies for conserving Wood Thrush populations should include the protection of remaining tropical forest fragments, including small fragments embedded within agricultural matrices, often ignored in conservation planning. Such protection will require developing new alliances with farmers and landowners throughout Central America's Atlantic lowlands.

INTRODUCTION

Forest loss and fragmentation affect the ecology of Nearctic-Neotropical migrant songbirds on both their breeding and wintering grounds (Powell et al. 1992, Robinson et al. 1995, Roth et al. 1996, Ross et al. 1996). A recent review, however, suggests that the skew toward breeding (temperate) studies from across the spectrum of behavioral and ecological studies is so high as to be "almost embarrassing" (Webster 2005). The lack of studies collecting basic information such as minimum tropical forest patch size requirements settled and used by wintering migrant songbirds hampers informed forest management and conservation strategies.

Decades of forest loss throughout Central America have dramatically changed the amount and configuration of winter habitat available for species of Nearctic-Neotropical migrant songbirds (Harcourt and Sayer 1996). Cross-national comparisons of tropical rainforest fragmentation report that Central American countries along with regions of West Africa had the highest global fragmentation levels between 1975-1990 (Rudel and Roper 1997). Where large reductions in forest cover have occurred, such as along the Caribbean

slope of Costa Rica, forest fragments are more numerous, reduced in size and more isolated as compared to historical forest extent (Sanchez-Azofeifa et al. 1999).

To understand the effects of reduced forest size and increased isolation (fragmentation) on a wintering Nearctic-Neotropical songbird, I chose to study the Wood Thrush, *Hylocichla mustelina.* This species was selected because it is forest dependent, yet tolerant of intermediate habitat modification. While Wood Thrush populations are still abundant and widespread across most of the breeding range, populations have exhibited declines of ca. 50% between 1966-2004 (Sauer et al. 2004).

Wood Thrushes are the most intensively studied of North American forest thrushes, as their reproductive ecology is highly vulnerable to indirect effects of temperate forest fragmentation (Robinson et al. 1995, Donovan et al. 1995, Roth et al. 1996, Trine 1998, Donovan and Flather 2002). Guidelines for maintaining viable Wood Thrush populations include suggested minimum forest patch size requirements in landscapes with varying percent forest cover and such recommendations exist for the entire breeding range of Wood Thrush (Trine 1998, Rosenberg et al. 2003). Generally, to maintain Wood Thrush populations in the Midwestern U.S., it has been shown that forest fragments embedded in agricultural landscapes with low forest cover may need to be > 2500 ha in size (Trine 1998, Rosenberg et al. 2003). Even if small forest fragments maintain viable populations at local or patch scales, there is no evidence that local source populations can compensate for abundant sinks in agricultural regions of the Midwestern U.S. (Fauth 2001). Only in areas where Brown-headed Cowbirds (*Molothrus ater*) are rare and forest cover is high can smaller fragments (20-60 ha) provide quality habitat for Wood Thrushes, such as in areas of the

northeastern U.S. (Roth et al. 1996, Rosenberg et al. 2003). Based on temperate-based breeding studies, our thinking about Wood Thrush population maintenance and forest fragments in highly deforested, agricultural landscapes is that small fragments are population sinks and large fragments are population sources (Donovan et al. 1995).

The wealth of information about Wood Thrush breeding ecology and fragmentation contrasts starkly with the paucity of information from the wintering grounds. While forest loss in Central America has been suggested to contribute to population declines of migrants generally (Rappole et al. 1992), and Wood Thrush in particular (Powell et al. 1992), I am aware of only one study that assessed habitat use of Wood Thrush in a tropical forest fragment, and this was in a single large fragment > 400 ha in Costa Rica (Powell et al. 1992). Habitat use and diet research have been conducted on Wood Thrushes within continuous forests of La Selva Biological Station and adjacent Braulio Carrillo National Park in Costa Rica (Blake 1992, Blake and Loiselle 1992, Loiselle and Blake 1999, Blake and Loiselle 2000, Blake and Loiselle 2001), but no such information is available for forest fragments. In addition, no population estimates are available for wintering Wood Thrush within La Selva or outside this protected area.

A recent study of non-breeding Wood Thrushes across a gradient of fragment sizes in lowland Costa Rica (Roberts et al. in review) found that Wood Thrushes maintained winter territories in fragments < 20 ha in size. However, the extent to which Wood Thrushes will settle in tropical forest fragments of different sizes embedded within agricultural landscapes is still unknown. It is also unclear what the minimum patch size is that Wood Thrushes will

use in winter or what proportion of the population uses forest fragments versus large continuous forest areas.

For this study, I examined three aspects of Wood Thrush winter ecology: 1) presence and densities across fragments of different sizes, 2) proportion of the population wintering outside of protected forest reserves, and 3) sex ratio of the population in continuous, large and small fragments. Wood Thrushes have highly compressed winter ranges, with an estimated 18% winter range size relative to breeding range size (Mills 2006). If Wood Thrush populations are limited by the amount of overall habitat, remaining forest fragments might provide essential winter habitat, complementing habitat within protected areas. Wood Thrushes of both sexes are strongly territorial during the winter period and social dominance may be exerting influence on population structure in this population. By examining winter patch occupancy and population structure, as well as modeling population size, this study assessed the relative value of forest fragments of different sizes in lowland Costa Rica for wintering Wood Thrush

METHODS

STUDY SITES and FIELD SAMPLING METHODS

Surveys for Wood Thrush were conducted in 25 forest fragments, ranging in size from 0.5 ha to 373 ha, and within primary forests of La Selva Biological Station (Figure 1). La Selva Biological Reserve (10° 26' N, 83° 59' W) is a private forest reserve owned by the Organization for Tropical Studies (OTS). The reserve comprises 1,611 ha and is continuous with the Braulio Carrillo National Park, which encompasses over 47,571 ha (La Selva

Biological Station, OTS GIS Database). Average annual precipitation in the region is approximately 4,000 mm and mean monthly temperatures range from 24.7º C in January to 27.1º C in August, consistent with a tropical wet-forest life zone (Holdridge 1947; McDade and Hartshorn 1994).

Forest fragments were chosen based on the following criteria: 1) isolation from other forest patches or continuous forest on all sides (minimum distance was 100m, varying from 100 to >500 m, 2) a closed canopy (on average > 75 %), with generally open understory, and 3) covering a range of size classes. The general purpose of the surveys was to assess the importance of forest fragments; however, determining the minimum size used required sampling several small patches. Logistical constraints, such as contacting each landowner to obtain permission to survey their land, not only limited the number of fragments that could be surveyed but also contributed to the combination of random and non-random fragment selection methods. The distribution of class sizes was skewed towards the smaller size classes (Figure 2). A bias towards small fragments (<20 ha) is representative of fragment size distribution within several parts of the study area. Small fragments made up the majority of overall fragments in both the Rio Frio region (Brenes 2003), as well as within a 177-km^2 area around La Selva (Bell and Donnelly 2006). A large proportion of the smallest fragments were chosen at random from all available fragments using a 1 by 1 km^2 classification based on high-resolution imagery (Brenes 2003) for the Rio Frio region (Figure 1) as this landscape is characterized by low forest cover with numerous forest fragments embedded within a predominantly agricultural matrix. However, larger fragments (>50 ha) were often chosen

non-randomly as fewer large fragments were available in the Rio Frio region and the landscape in general.

To obtain presence/absence data and an estimate of the number of Wood Thrushes, all forest sites were surveyed during January and February 2005. In forest fragments, 210 playback surveys were conducted across the 25 fragments. The number of surveys per fragment depended on fragment area; thus, different fragment classes had between 55 and 80 survey points (Table 1) located 150 m from each other and 100 m from the fragment edge. A complete census was conducted in small patches (<20 ha), thus an absolute density of Wood Thrush was obtained. In medium to large patches, 10 to 20 playback points were established in each fragment. Within La Selva, 120 playback surveys were conducted every 150 m along trails at randomly chosen signposts throughout primary forest habitat.

To detect presence of Wood Thrushes, playback tape recordings from handheld recorders with portable external speakers were used to project aggressive call notes. Recorded call notes of Wood Thrush were broadcast for 2 minutes at each point. Upon detection of the first bird and any subsequent birds, the tape recorder was stopped and an azimuth direction and distance were noted. The broadcast was then continued for the remaining two minutes. The recorder was then turned off and the observer continued to listen for another 1 min. Additionally, if one or more Wood Thrush responded and kept calling aggressively, the broadcast was stopped and the observer listened for other individual Wood Thrush responses.

Blood samples for sexing monomorphic Wood Thrush were collected from individuals captured within a subset of six fragments (three large and three small) as part of a

telemetry study during 2004 and 2005 (Roberts et al., unpublished manuscript). Wood Thrushes were captured using targeted mist netting. Upon capture, one to two capillary tubes of blood were collected via the brachial vein with a 26-gauge precision glide needle. Each tube was then emptied into a nunc vial with lysis buffer following a standard recipe (White and Densmore 1992). Blood was stored at room temperature in lysis buffer until DNA extraction procedures were completed, from a few months to > one year for first year samples.

LABORATORY METHODS

DNA extraction was completed at the University of Idaho Conservation Genetics Laboratory, College of Natural Resources, Moscow, ID. DNEasy Qiagen kits were used to extract DNA from each blood sample. PCR analysis to determine gender of each individual Wood Thrush was completed under the guidance of Dr. M. S. Webster's genetics laboratory at Washington State University, Pullman, WA. CHD genes located on the avian sex chromosomes were amplified by polymerase chain reaction (PCR) using primers 1237L and 1272H following the protocol developed by Kahn et al. (1998). PCR reactions contained the following: 1μL extracted DNA, 1μL of 10X PCR buffer, 0.15mM dNTP mix, 0.5uM each primer, 2.0mM MgCl2, and 2.5 U Taq polymerase. The thermal profile consisted of initial heating at 94ºC for three minutes, followed by 30 cycles of denaturation at 94 ºC for one minute, annealing at 60 ºC for one minute, and extension at 72 ºC for 45 s. A final extension for 5 minutes at 72 ºC followed the last thermal cycle. PCR products were then electrophoresed in a 3 % agarose gel stained with ethidium bromide at constant 100 volts for one hour.

After electrophoresis, PCR products were visualized under UV light and individuals were scored as male (single band) or female (two bands). PCR product size was estimated between 210-285 bp, by running samples with a ladder (Kahn et al. 1998). Images were transferred via Kodak digital camera to a computer for gender determination (Figure 3).

STATISTICAL ANALYSIS

A Fisher's Exact Test (SAS) was used to test for differences in the frequency of each sex between the following three habitat levels: 1) continuous forest, 2) large forest fragments (> 80 ha) and 3) small forest fragments (< 20 ha). This design represents a subset (six) of the fragments surveyed with playback (25), as part of the intensive telemetry portion of this Wood Thrush research (Roberts et al. in review).

POPULATION MODELING

Wood Thrush populations were estimated for the primary forest area of La Selva Biological Station and for the extent of closed canopy forests at a semi-regional scale (1433 km^2 area) in Costa Rica's lowlands.

La Selva Model

To determine the overall area of primary forest, I used a classification of La Selva available from the GIS laboratory (OTS, La Selva 2000). Area calculations were made using ArcView 3.3 (ESRI 2005). Approximately 850 ha of primary forest (excluding inundated swamp forest) exist within the biological reserve and this calculation was used in model projections. Two separate models of population estimation of Wood Thrushes were developed for La Selva. The first consisted of a population estimate based on a GIS

extrapolation model of playback surveys. For this model, I used the total count of birds

within an effective area (60 m perpendicular to the point) calculated in Program DISTANCE

(Thomas et al. 2004). A 60-m radius circular buffer was placed around each of the points

along a GIS layer of trail signposts available from La Selva's GIS laboratory (OTS, La

Selva). The Clip tool within ArcView 3.2 Geoprocessing Wizard extension was used to join

the intersection of the buffered survey points with the forest layer (Figure 4). Once an

estimate of number of birds within the effective survey area was calculated, I extrapolated

the estimated Wood Thrush population to the entire 850 ha primary forest area.

The second modeling approach involved the use of home range data collected from

the same population of Wood Thrushes within La Selva's primary forest. Mean winter home

range was estimated at 1.02 ha (Roberts et al. in review). I obtained the second population

estimate by dividing the total forest area available (850 ha) by the mean home range size.

Regional Population Projections

To estimate available habitat for Wood Thrush populations in the Sarapiquí, Costa

Rica, the amount of late-successional (primary) forest and partially cut regenerated forest in

fragments with closed canopy and age > 20 years below 600 m was calculated from a 2001

land use classification derived from Landsat TM data (Sesnie 2006). The minimum mapping

unit for this classification was 1 ha. The cutoff elevation of 600 m was chosen because

although Wood Thrush are found up to 1000 m in elevation, the largest numbers of

individuals winter below 600 m (Blake and Loiselle 2000).

The three spatial layers used in the analysis were the outline of forest reserves, the

extent of Braulio Carrillo National Park, (Figure 5) and the land use classification. Using the

Spatial Analyst extension for ArcGIS 9.1 (ESRI 2005), I first calculated the overall forest

amount (in ha) within the forest reserves, La Selva and Braulio Carrillo below 600 m in

elevation and then determined the amount of late-successional forest outside of the reserves

using ArcGIS 9.1 (ESRI 2005). I estimated the number of Wood Thrush present in the

region based on amount of forest habitat and the fact that the mean winter home range size of

Wood Thrush is 1 ha in both fragmented and continuous forest habitats (Roberts et al. in

review). In this coarse approach to estimate the proportion of the population outside of the

forest reserve network, I assumed one Wood Thrush per hectare across the area of natural

forest within the study area extent.

RESULTS

FIELD POPULATION SURVEYS

Wood Thrush were detected in all fragments surveyed that were >= 1 ha in area, but not

within a 0.5 ha fragment. The number of survey points where Wood Thrushes were detected

was high across the fragmentation gradient, with detections of Wood Thrush in over half of

all points in small fragments (Table 1). Likewise, detection rates were high for medium and

large fragments. Densities varied across fragment size classes (Table 1), with the highest

densities in the smallest fragments; however, all densities in fragments were lower than those

estimated within L Selva using both playback survey data and telemetry data (see results

under "Population modeling" reported below).

SEX RATIO ANALYSIS

Although there was a female bias in small fragments (Table 2), Fisher's Exact test statistic of

P= 0.3150 suggests that the frequencies observed were not significantly different from what

would be expected from chance alone, at *a=0.05*. However, a greater proportion of females

in small fragments could have biological significance, if small fragments provide suboptimal

habitat (Roberts et al, unpublished manuscript) or are less likely to be protected.

POPULATION MODELING

La Selva

Wood Thrush population estimates for La Selva's primary forest differed depending on the

model approach. Playback Survey GIS Extrapolation model results estimated 1104

individual Wood Thrush were wintering in La Selva's 850 ha of primary forest area for an

estimated density of 1.3 birds / ha. In contrast, the Primary Forest Area / Mean Home Range

Model estimated 834 Wood Thrush wintering within La Selva's primary forest, for an

estimated density of 0.98 Wood Thrush / ha. This latter estimate was used in the regional

model, as it is similar to what was obtained from telemetry data from birds wintering in

forest fragments (Roberts et al. in review).

Regional Modeling

Within the extent of the 2001 land use classification, a total of 59,274 ha of natural forest and

late successional forests were available within a landscape of 143,333 ha. Of this total, 9 811

ha were within protected forest reserves, La Selva Biological Reserve and Braulio Carrillo

National Park land occurring below 600 m. Assuming equal average home range and even

densities across both continuous forest and fragmented forests, my model predicted that 83 percent of the Wood Thrush population winters outside of reserves, with 17 percent wintering inside reserves. This coarse estimate predicts 49,463 Wood Thrushes within the study extent outside of protected forest reserves. This is likely conservative, as Wood Thrushes may use other forested habitat, such as riparian forests or forest plantations, but these habitats were not surveyed for this study.

DISCUSSION

The presence of Wood Thrush in all fragments >= 1 ha, coupled with the fact that the majority of available forest is outside of protected reserves, provides strong evidence that forest fragments outside of protected reserves provide critical habitat for wintering Wood Thrushes. Forest fragments as small as 1 ha provided habitat for wintering Wood Thrushes. This minimum size is several orders of magnitude smaller than the minimum size requirements for maintaining breeding Wood Thrush (Trine 1998, Rosenberg et al. 2003), which in Midwestern agricultural landscapes with low forest cover may need to be > 2,500 ha.

Wood Thrush densities were highest within the large, continuous forests of La Selva, as would be predicted (Rappole et al. 1992, Blake and Loiselle 2001). Outside of La Selva in the fragmented landscapes, the highest densities observed were in the smallest fragments. Why might densities be higher in these small fragments? The high density of Wood Thrush in small fragments, even in highly deforested landscapes, suggests that the highest quality habitats, large primary forest tracts, are saturated. I conjecture that birds arriving later on the

winter grounds get pushed into fragmented landscapes by social dominance behavior, but this has yet to be tested. Once in these isolated fragments surrounded by varying intensities of agricultural land uses, territorial behavior may inhibit larger movements to search for more suitable habitat. If amount of overall forest is limiting for wintering Wood Thrushes, one would expect to observe certain ecological, demographic or behavioral responses during this period (Sherry and Holmes 1995). Suggested factors include strong territoriality, habitat saturation, differing densities, and differences in body condition and evidence for varying sex ratios between habitat types. Based on results from additional research on Wood Thrush in this same landscape, Roberts et al. (in review), reported lower site fidelity and poorer body condition for some birds in small fragments; the findings of this research strongly suggests that all remaining forest fragments may be critical for Wood Thrush populations, as even small fragments may be saturated.

The densities I observed in Costa Rica were lower in all habitats than those reported by studies of Wood Thrushes within intact forests of Las Tuxlas, Mexico, which reported densities from 2.41 thrushes/ha to as high as 8.2 birds/ha (Winker et al. 1990, Rappole et al. 1992). The higher estimate was thought to reflect the high proportion of the population classified as floaters that arrived periodically at lowland study sites during harsh weather events from higher elevations, but the authors suggest that 2.41 thrushes/ha is closer to the actual density (Winker et al. 1990, Rappole et al. 1992). The lower densities observed in this study may reflect the difference in proximity from the breeding grounds. Costa Rica lies at the southern end of the winter distribution of Wood Thrushes (Mexico to Panama), and thus fewer birds may migrate to these latitudes.

Population Protection Status

The results that a majority of the population was estimated to winter outside of protected reserves further demonstrates the importance of forest fragments on private lands to the long-term conservation of wintering Wood Thrush. These populations estimates were likely conservative, as other habitat types, such as riparian forests and tree plantations may provide winter habitat, but were not surveyed during this study.

The population estimates for La Selva's primary forest and at the regional scale provide critical baseline data that could serve as a starting point for monitoring land use change on Neotropical-Nearctic migrant songbirds in this dynamic tropical landscape. Land use change will continue to be the main driver of change across tropical regions (Sala et al. 2000), and understanding how change impacts wildlife could inform current and future forest management practices.

Using playback surveys to detect the presence or assess relative densities of vocal, but cryptic Wood Thrushes across habitats is a feasible and relatively simple method, but little-utilized to study this species on its wintering grounds. Future research could also assess Wood Thrush use across other forested habitats, such as riparian forests and forest plantations, as other land cover types with tree cover have been shown to be important for biodiversity in other parts of the tropics (Harvey et al. 2006).

Sex ratios and fragmentation

Female-biased sex ratios across a habitat gradient have not been previously demonstrated for wintering Wood Thrushes. Sexual habitat segregation has been shown to

occur for two species of Neotropical-Nearctic warbler (Marra 1998, Wunderle, Jr. and Latta 2000, Marra and Holmes 2006) and for European Robins wintering in southern Europe (Catry et al. 2004). Breaking apart the number of samples from Wood Thrush using different fragment sizes may have affected the statistical power of our results; however, there appears to be a threshold of fragment size where sex ratio switches, but more sampling across a greater number of fragments and with more Wood Thrush is necessary to confirm my results.

Conservation Implications

The results of this research suggest that the conservation of small forest patches within agricultural landscapes is important for the long-term conservation of Wood Thrush and that even patches ca. 1 ha in area merit inclusion in conservation strategies. This does not suggest that large reserves aren't important, indeed, the positive value of large forest reserves and parks in many tropical regions for conserving global biodiversity and ecosystem services has been theoretically debated and empirically shown (Laurance et al. 2002, Rodrigues et al. 2004). For a species such as the Wood Thrush, which winters below 1000 m in elevation, reserves provide habitat for only a small proportion of the wintering population in Costa Rica. Moreover, Costa Rica's forest protection laws do not apply to forest patches less than 2 ha in size (Costa Rica 1996 Forestry Law No. 7575), thus these small patches are not protected.

Payments for environmental services that reward farmers for conserving forests could help prevent the loss of small forest fragments. Rural farmers and landowners with private forest patches near remaining large parks and reserves often receive priority from governmental- and NGO-sponsored conservation initiatives seeking to protect biodiversity

and environmental services on private land outside of reserves (Watson et al. 1998; Pagiola 2005). However, recent research into participation by farmers in environmental service schemes suggests that small landowners are not participating due to low economic incentives (W. Morse, *personal communication*). There is therefore an urgent need to develop additional incentives and mechanisms to protect existing small forest fragments before these are lost from the landscape. Building relationships with landowners and farmers that manage small and medium fragments will also be critical to developing forest management practices and conservation strategies that benefit both rural livelihoods and wildlife that depend on remaining natural habitats embedded in agricultural landscapes.

conducted with permission from MINAE (Permit No. 30851), and USFWS (subpermit No.

0982-CL), and an ACUC permit from UI to Dr. E.O. Garton.

LITERATURE CITED

Bell, K. E., and M. A. Donnelly. 2006. Influence of forest fragmentation on community structure of frogs and lizards in Northeastern Costa Rica. Conservation Biology 20:1750-1760.

Blake, J. G. 1992. Temporal variation in point counts of birds in lowland wet forest in Costa Rica. The Condor 94:265-275.

Blake, J. G., and B. A. Loiselle. 1992. Habitat use by Neotropical migrants at La Selva Biological Station and Braulio Carrillo National Park, Costa Rica, p. 257-272. *In* J. M. I. Hagan, and D. W. Johnston [eds.], Manomet Symposium. Smithsonian Institution Press, Washington.

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

Blake, J. G., and B. A. Loiselle. 2001. Bird assemblages in second-growth and old-growth forest, Costa Rica: perspectives from mist nets and point counts. The Auk 118:304-326.

Boza, M. A. 1993. Conservation in action: past, present, and future of the National Park System in Costa Rica. Conservation Biology 7:239-247.

Brenes, J. 2003. Land cover map of Rio Frio based on Quickbird imagery. CATIE GIS lab.

Catry, P., A. Campos, V. Almada, and W. Cresswell. 2004. Winter segregation of migrant European robins *Erithacus rubecula* in relation to sex, age and size. Journal of Avian Biology 35:204-209.

Chomitz, K. M., E. Brenes, and L. Constantino. 1999. Financing environmental services: the Costa Rican experience and its implications. The Science of the Total Environment 240:157-169.

Donovan, T. M., and C. H. Flather. 2002. Relationships among North American songbird trends, habitat fragmentation, and landscape occupancy. Ecological Applications 12:364-374.

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

ESRI. 2005. ArcGIS. 9.1 Redlands, California.

Fauth, P. T. 2001. Wood Thrush populations are not all sinks in the agricultural Midwestern United States. Conservation Biology 15:523-527.

Harcourt, C. S., and J. A. Sayer. 1996. The Conservation Atlas of Tropical Forests: The Americas. IUCN, New York.

Harvey, C.A., A. Medina, D. Sanchez Merlo, S. Vilchez, B. Hernandez, J. Saenz, J. Maes, F. Cassanoves, and F.L. Sinclair. 2006. Patterns of animal diversity associated with different forms of tree cover retained in agricultural landscapes. Ecological Applications 16: 1986-1999.

Holdridge, L.R. 1947. Determination of world plant formations from simple climatic data. Science 105: 367-368.

Kahn, N. W., J. St.John, and T. W. Quinn. 1998. Chromosome-specific Intron size differences in the avian CHD gene provide an efficient method for sex identification in birds. The Auk 115:1074-1078.

Langholz, J. and J. Lassoie. 2001. Combining conservation and development on private lands: lessons from Costa Rica. Environment, Development, and Sustainability 3:309-322.

Laurance, W., T. E. Lovejoy, H. L. Vasconcelos, E. M. Bruna, R. K. Didham, P. C. Stouffer, C. Gascon, R. Bierregaard, S. Laurance, and E. Sampaio. 2002. Ecosystem decay of Amazonian forest fragments: a 22-year investigation. Conservation Biology 16:605-618.

Loiselle, B. A., and J. G. Blake. 1999. Dispersal of melastome seeds by fruit-eating birds of tropical forest understory. Ecology 80:330-336.

Marra, P. P. 1998. Causes and consequences of sexual habitat segregation in a migrant bird population during the non-breeding season. Dartmouth College, Hanover, New Hampshire.

Marra, P. P., and R. T. Holmes. 2006. Consequences of dominance-mediated habitat segregation in American Redstarts during the nonbreeding season. The Auk 118:92-104.

McDade, L.A. and G.S. Hartshorn. 1994. La Selva Biological Station, p. 6-14 in L.A. Dade [ed.], La Selva: ecology and natural history of a Neotropical rainforest. The University of Chicago Press, Chicago.

Mills, A. M. 2006. Winter range compression of migrants in Central America. Journal of Avian Biology 37:41-51.

Pagiola, S., P. Agostini, J. Gobbi, C. de Haan, M. Ibrahim, E. Murgueitio, E. Ramirez, M. Rosales, and J.P. Ruiz. 2005. Paying for biodiversity conservation services: experiences in Colombia, Costa Rica, and Nicaragua. Mountain Research and Development 25: 206-211.

Powell, G. V. N., J. Barborak, and S. M. Rodriquez. 2000. Assessing representativeness of protected natural areas in Costa Rica for conserving biodiversity: a preliminary gap analysis. Biological Conservation 93:35-41.

Powell, G. V. N., J. H. Rappole, and S. A. Sader. 1992. Neotropical migrant landbird use of lowland Atlantic habitats in Costa Rica: A test of remote sensing for identification of habitat, *In* J. M. I. Hagan, and D. W. Johnston [eds.], Ecology and conservation of Neotropical migrant landbirds. Smithsonian Institution Press, Washington.

Rappole, J. H., E. S. Morton, and M. A. Ramos. 1992. Density, philopatry, and population estimates for songbird migrants wintering in Veracruz, p. 337-344. *In* J. M. I. Hagan, and D. W. Johnston [eds.], Ecology and conservation of Neotropical migrant landbirds. Smithsonian Institution Press, Washington D.C.

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

Rodrigues, A.S.L., S.J. Andelman, M.I. Bakarr, L. Botiani, T. Brooks, R.M. Cowling, L.D.C. Fishpool, G.A.B. da Fonseca, K.J. Gaston, M. Hoffman, J.S. Long, P.A. Marquet, J.D. Pilgrim, R.L. Pressy, J. Schipper, W. Sechrest, S.N. Stuart, L.G. Underhill, R.W. Waller, M.E.J. Watts, and X. Yan. 2004. Effectiveness of the global protected area network in representing species diversity. Nature 428: 640-643.

Rosenberg, K. V., R. S. Hames, R. W. Rohrbaugh, Jr., S. B. Swarthout, J. D. Lowe, and A. A. Dhondt. 2003. A land manager's guide to improving habitat for forest thrushes. Cornell Lab of Ornithology, Cornell University, Ithaca, NY.

Ross, R. F., H. B. Quigley, M. G. Hornocker, T. Merrill, and P. C. Paquet. 1996. Conservation biology and carnivore conservation in the Rocky Mountains. Conservation Biology 10:949-963.

Roth, R. R., M. S. Johnson, and T. J. Underwood. 1996. Wood Thrush (*Hylocichla mustelina*), *In* A. Poole, and F. Gill [eds.], Birds of North America. The Academy of Natural Sciences and The American Ornithologists' Union, Philadelphia, PA and Washington, D.C.

Rudel, T., and J. Roper. 1997. Forest fragmentation in the humid tropics: a cross-national analysis. Singapore Journal of Tropical Geography 18:99-109.

Sala, O. E., F. S. Chapin, J. J. Armesto, E. Berlow, J. Bloomfield, R. Dirzo, E. Huber-Sanwald, L. F. Huennekke, R. B. Jackson, A. Kinzig, R. Leemans, D. M. Lodge, H. A. Mooney, M. Oesterheld, M. L. Poff, M. T. Sykes, B. H. Walker, M. Walker, and D. H. Wall. 2000. Global biodiversity scenarios for the year 2100. Science 287:1770-1774.

Sanchez-Azofeifa, G. A., C. Quesada-Mateo, P. Gonzalez-Quesada, S. Dayanandan, and K. S. Bawa. 1999. Protected areas and conservation of biodiversity in the tropics. Conservation Biology 13:407-411.

Sauer, J. R., J. E. Hines, and J. Fallon. 2004. The North American breeding bird survey. Results and Analysis. 1966-2003. 2004.1. U.S. Geological Survey, Patuxent Wildlife Research Center, Laurel, Maryland.

Sesnie, S. E. 2006. Integrating Landsat TM and SRTM-DEM derived varaibles with decision trees for habitat classification in complex neotropical environments. University of Idaho, Moscow, Idaho.

Sherry, T. W., and R. T. Holmes. 1995. Summer versus winter limitation of populations: what are the issues and what is the evidence, p. 85-120. *In* T. E. Martin, and D. M. Finch [eds.], Ecology and management of Neotropical migratory birds. Oxford University Press, New York.

Thomas, L., J. L. Laake, S. Strindberg, F. F. C. Marques, S. T. Buckland, D. L. Borchers, D. R. Anderson, K. P. Burnham, S. L. Hedley, J. H. Pollard, and J. R. B. Bishop. 2004. Distance 4.1. Release 2. Research Unit for Wildlife Population Assessment, University of St.Andrews, UK .

Trine, C. L. 1998. Wood Thrush population sinks and implications for the scale of regional conservation strategies. Conservation Biology 12:576-585.

Turner, I. M. 1996. Species loss in fragments of tropical rain forest: a review of the evidence. Journal of Applied Ecology 33:200-299.

Watson, V., S. Cervantes, C. Castro, L. Mora, M. Solis, I.T. Porras, B. Cornejo. 1998. Making space for better forestry. Policy that works for forests and people no. 6. Centro Cientifico Tropical and International Institute for Environment and Development, San Jose and London.

Webster, M. S. 2005. Behavioral Ecology: Overview, p. 305-306. *In* R. S. Greenberg, and P. P. Marra [eds.], Birds of Two Worlds. The Smithsonian Institution and John Hopkins University Press, Baltimore.

White, P. S., and L. D. Densmore. 1992. Mitochondrial DNA isolation, p. 29-58. *In* A. R. Hoelzel [ed.], Molecular Genetic Analysis of Populations. Oxford University Press, Oxford.

Winker, K., J. H. Rappole, and M. A. Ramos. 1990. Population dynamics of the Wood Thrush in Southern Veracruz, Mexico. The Condor 92:444-460.

Wunderle, J. M., Jr., and S. C. Latta. 2000. Winter site fidelity of Nearctic migrants in shade coffee plantations of different sizes in the Dominican Republic. Auk 117:596-614.
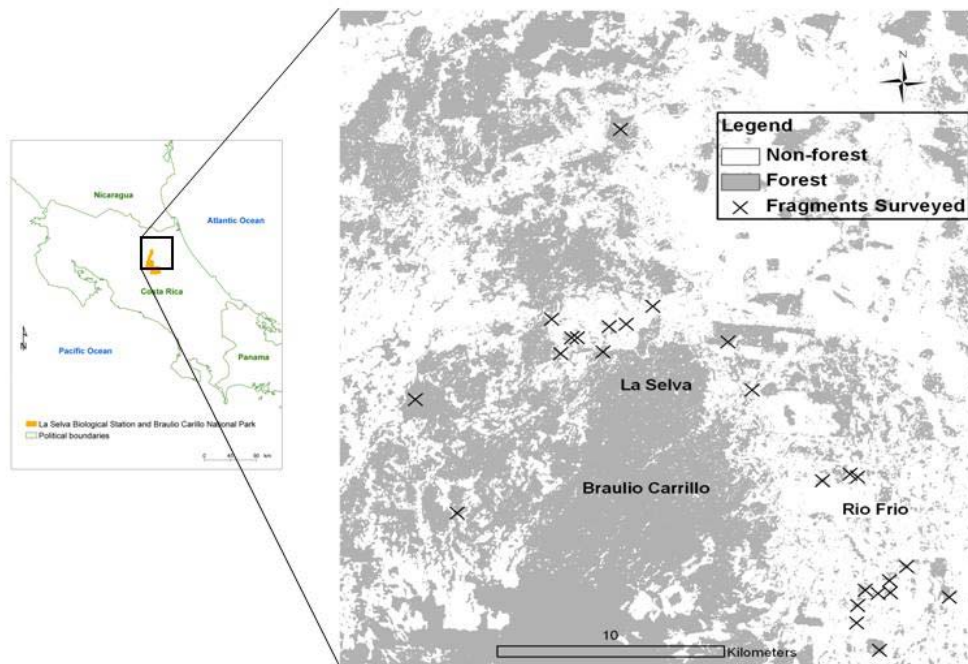
Figure 1. Study area, northeastern Costa Rica, Central America. Location of La Selva

Biological Reserve (continuous forest) and 25 forest fragments (X) surveyed for Wood

Thrushes during winter 2005.
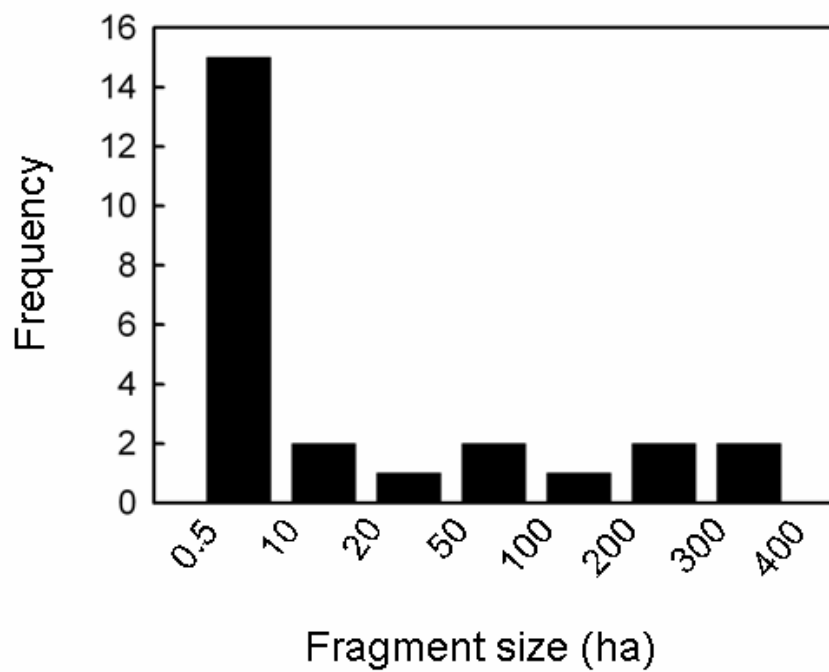
Figure 2. Size distribution of forest fragments surveyed for Wood Thrush.
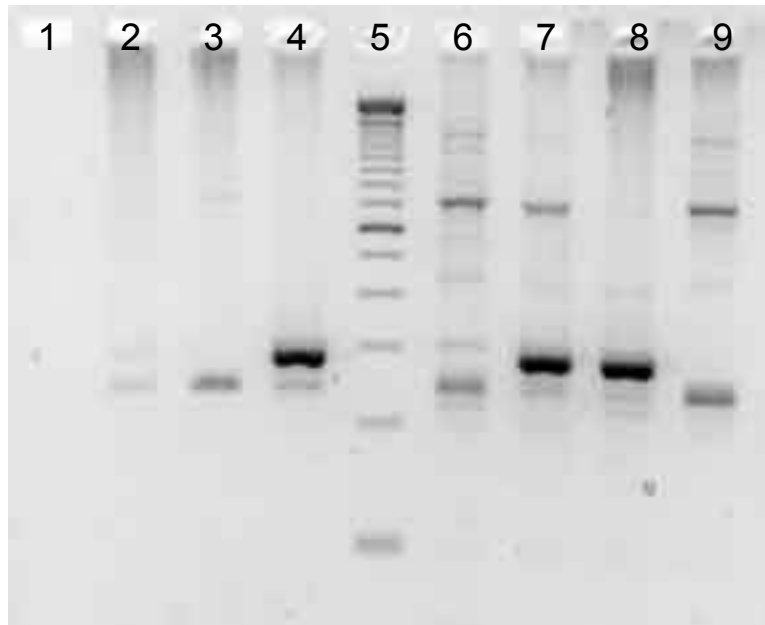
Figure 3. Photo of electrophoresed PCR gender determination method. Female Wood Thrushes were determined by the bold dark band above lighter band (Lanes 4, 7, & 8). Male Wood Thrush lack this signature (Lanes 2, 3, 6, 9). Lane 1 was a control test for contamination and lane 5 was the ladder to indicate marker band sizes (amplification products differ over a range of 210 to 285 bp).
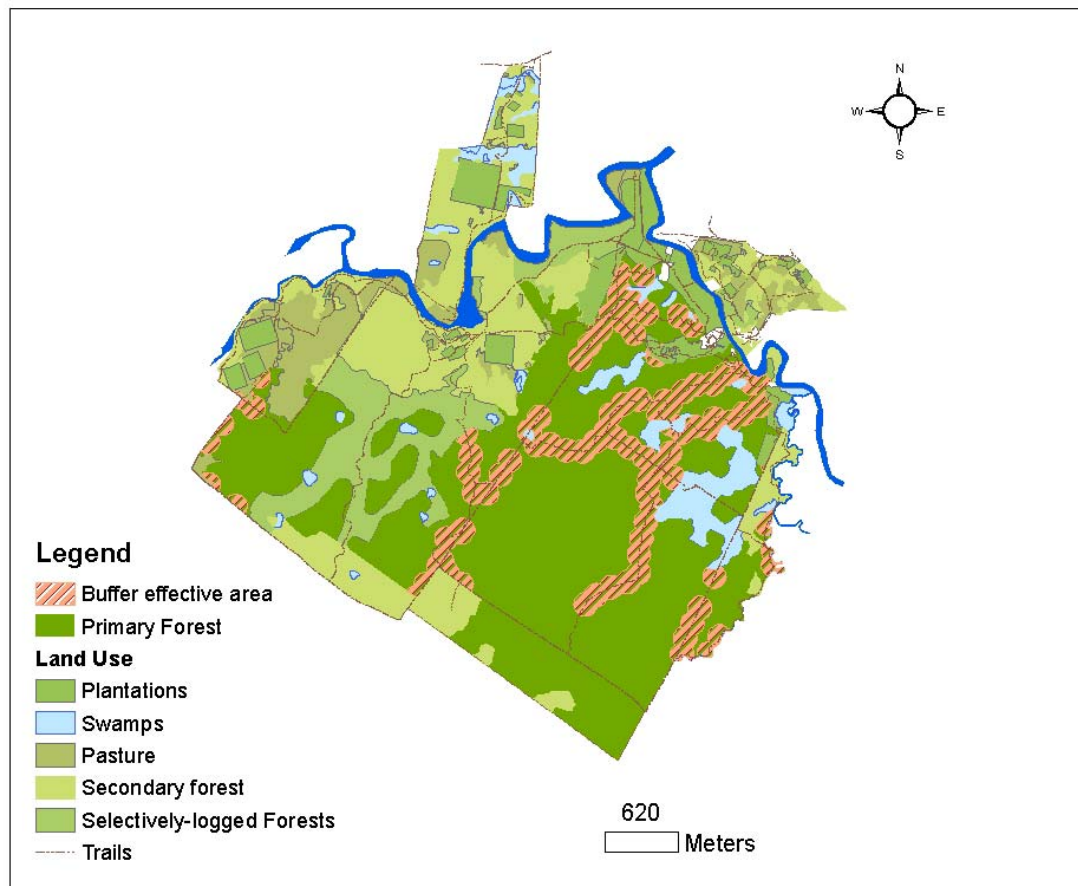
Figure 4. La Selva Reserve with Wood Thrush survey locations buffered (Buffer effective area) of 60-m radius circle, except at the reserve boundaries. Wood Thrush population size for La Selva GIS Model was estimated for the primary forest area (~ 850 ha).
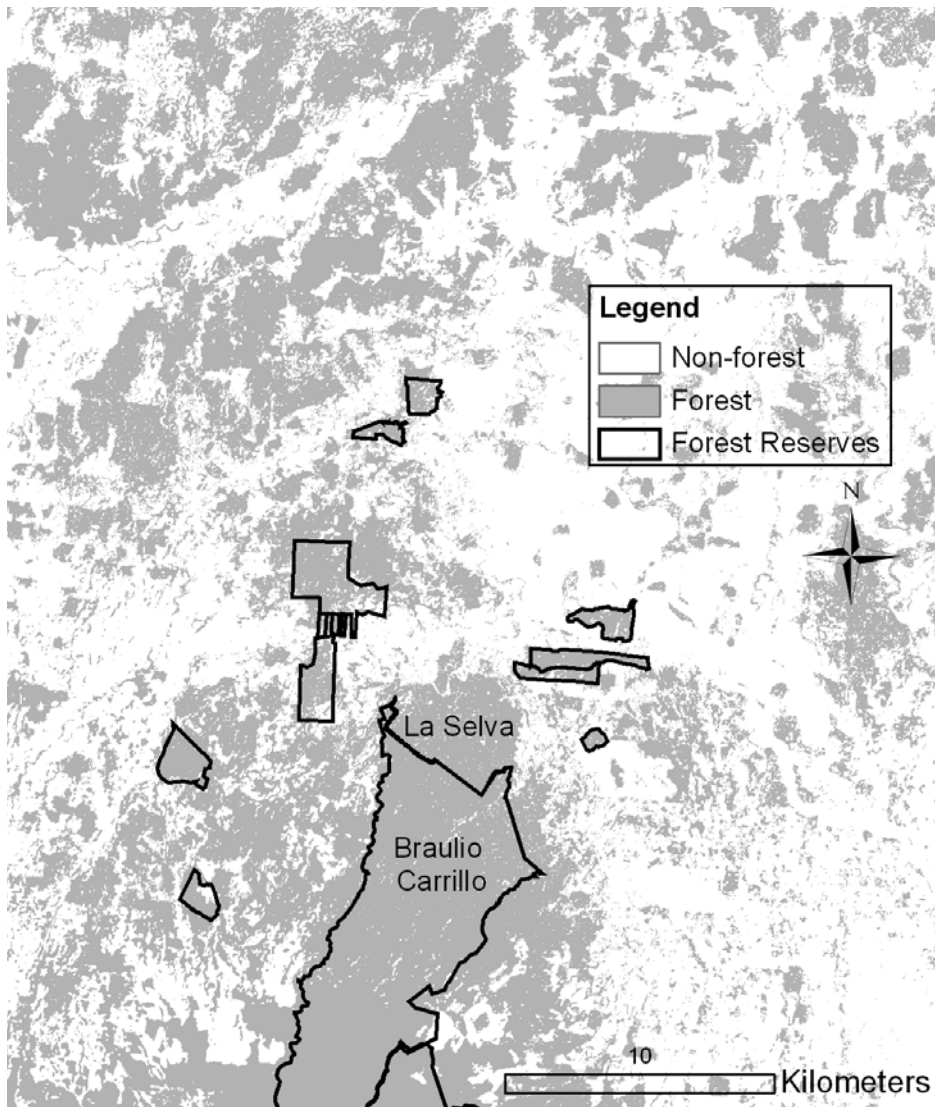
Figure 5. Map of forest cover within the study area in northeastern Costa Rica.

Forests refer to late-successional forests; forest reserves are areas in some formal

protection status; non-forest lands refer to pasture and agricultural land uses. The

amount of forest within protected status was compared to that outside reserves.
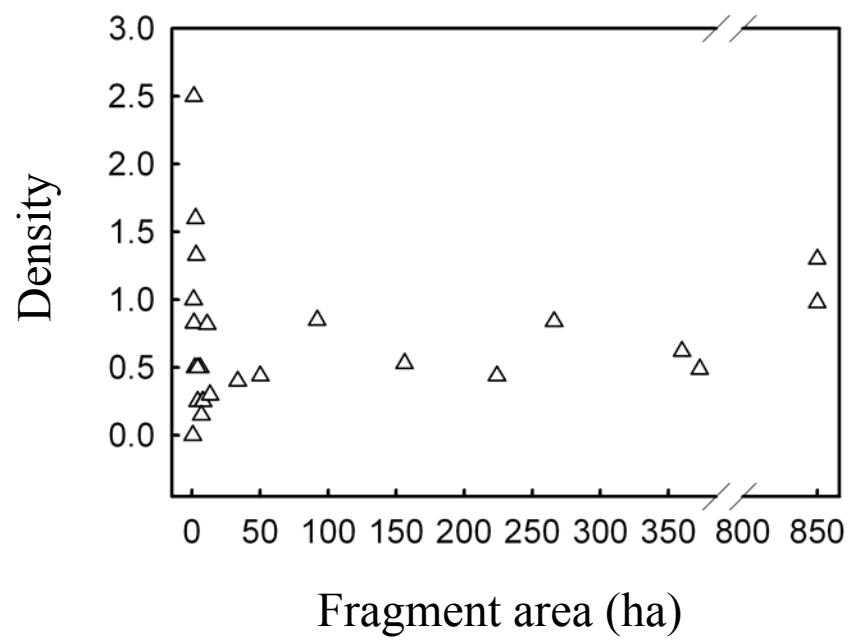
Figure 6. Wood Thrush densities plotted against fragment size obtained by using playback surveys across forest fragments and continuous forests (850 ha +) in lowland Costa Rica during January and February 2005.

Table 1. Results of Wood Thrush playback surveys conducted in Sarapiquí, Costa Rica across forest fragments of different classes.

Fragment Size (no. survey points)	Percentage of Points w/ Wood Thrush	Estimated Density ($\bar{x}$)	Absolute Density ($\bar{x}$)
Large (>200 ha) (n=80)	68	0.60 Wood Thrush / ha	--
Medium (33 to 156 ha) (n=55)	64	0.57 Wood Thrush / ha	--
Small (0.5 to 20 ha) (n=75)	55	0.71 Wood Thrush / ha	

Table 2. Sex ratios (percent) for Wood Thrushes wintering across a gradient of fragment size classes in Costa Rica. Large fragments were those > 200 ha and small fragments were < 20 ha in size.

	Continuous forest	Habitat Large fragments	Small fragments
Females/Males *(percent)*	35/65	25/75	60/40
n=	20	8	10

n = number of individual birds in each habitat from which blood was collected for gender determination

CHAPTER 3

What guilds don't tell us: modeling species-specific responses of rainforest birds to forest fragmentation and land use change in lowland Costa Rica

Dina L. Roberts[1], Stephen E. Sesnie[2], Edward O. Garton[1], and Celia A. Harvey[3]

[1] Department of Fish and Wildlife Resources, College of Natural Resources, University of Idaho, Moscow, ID 83844

[2] Department of Forest Resources and Rangeland Ecology, College of Natural Resources, University of Idaho, Moscow, ID 83844

[3] Department of Agriculture and Agroforestry, CATIE, Turrialba, Costa Rica

ABSTRACT

Generalizations about vulnerability of certain avian foraging guilds to tropical forest

fragmentation and degradation have been reported widely in the literature. Guilds are often

used to simplify the complexity of species-rich tropical community studies for elucidating

patterns of response to habitat change. Few studies have sought to understand how

individual species within guilds respond at broader spatial scales. To assess the impacts of

fragmentation and land use change patterns on lowland rainforest avifauna, we studied

abundance and occupancy patterns of eight rainforest bird species at a semi-regional scale in

northeastern Costa Rica, at elevations between 50 m and 450 m. We chose eight bird species

from across three foraging guilds, two of which are reported to be particularly susceptible to

declines and local extinctions as patch sizes decrease or distances to source areas increase.

We predicted that species within the understory frugivore and understory insectivore guilds

would decline across a gradient from large to small forest fragments, in those fragments with

lower forest cover and at increasing distances from a source. We conducted fixed-radius

point counts across 30 forest fragments of various sizes, distances from a large, potential

source area, and embedded within a continuum of forest cover levels. Abundances of two

species, *Pipra mentalis*, a frugivorous manakin, and *Thamnophilis atrinucha*, an

insectivorous antshrike, declined or the species disappeared entirely in fragments with

decreasing patch size, isolation from a source, and low surrounding percent forest cover,

following our predictions. However, the two most abundant species were also understory

insectivores, a wren, *Henicorhina leucosticta*, which was observed in all 30 fragments, and

an antbird, *Myrmeciza exsul*. The third most common species, *Mionectes oleaginous*, is an

understory frugivore that also occurred in a majority of fragments surveyed. *Ramphastos swainsonii*, an omnivorous toucan, was absent from a majority of the largest fragments, although its highest abundances were significantly explained by greater percent forest cover. Despite our predictions that species within the same foraging guild, or those with other shared life history strategies, would respond similarly to fragmentation, we found that species responded individualistically. Organizing species-rich tropical avifaunas within guilds is a useful construct for describing patterns of change at the community level or comparing sites. However, our results suggest that at semi-regional scales or for assessing impacts on abundances or patch occupancy, studying individual species and population responses of those species may provide more pertinent information for conserving important species in fragmented tropical landscapes.

INTRODUCTION

An estimated one-fifth of the world's bird species are threatened or near threatened with extinction (Birdlife International 2004). High rates of deforestation in tropical regions, where a majority of species exist, contributes substantially to biodiversity loss and increasing bird extinction rates (Balmford and Long 1994, Pimm et al. 2006). Globally, land use change will continue to be the main driver in the loss of terrestrial biodiversity in coming decades (Sala et al. 2000), followed by climate change. Understanding patterns of species richness and threats to protection are necessary for providing information on which to base management and conservation decisions (Raven and Wilson 1992, Scott et al. 1993, Pimm et al. 2001, Olson and Dinerstein 2002). Assessing impacts of human-driven land change,

however, requires more than just determining extinction risks (Hobbs and Mooney 1998).

Estimated rates of loss of populations in tropical areas due to land use changes are much

higher than species extinction rates but have received relatively little research and

conservation attention (Hughes et al. 1997).

Conserving tropical avifauna will require a greater understanding of population losses

of species that persist in fragmented landscapes. Recent evidence suggests that for species

that tolerate intermediate levels of habitat modification, natural forest patches and native tree

cover can provide important refuges for native avifauna in human-dominated landscapes

(Petit and Petit 2003, Harvey et al. 2006). Effects of tropical forest loss and fragmentation

on avifauna have been driven by information from relatively few sites and from studies

conducted at small spatial scales (Newmark 1991, Turner 1996, Laurance et al. 2002, Sigel et

al. 2006). Historically, natural resource management efforts in tropical regions have been

hampered by a lack of money, often difficult logistics, and lack of expertise to initiate

research and conservation efforts (Norris and Pain 2002). Moreover, sampling species-rich

avifaunal communities in wet tropical forests requires multiple sampling methods (Terborgh

et al. 1990, Blake and Loiselle 2001), often over long time periods, which has contributed to

the limited spatial extent of many studies to a single protected forest area or a small number

of forest fragments of different sizes (Kattan et al. 1994, Turner 1996, Sodhi et al. 2005b,

Sigel et al. 2006).

Generalizations about responses of tropical bird community composition to

fragmentation are often documented by assessing species' associations with particular

habitats and foraging guilds. Guilds are often used to simplify the complexity of species-rich

tropical community studies for elucidating patterns of response to habitat change. Few

studies have sought to understand how individual species within guilds respond at broader

spatial scales. We chose species from across foraging guilds as declines in the species

richness of particular guilds, including understory insectivorous birds (Canaday 1996,

Laurance et al. 2002, Sekercioglu et al. 2002, Sigel et al. 2006, Aratrakorn et al. 2006), and

frugivorous birds (Leck 1979, Kattan et al. 1994, Aratrakorn et al. 2006) have been well

documented. Despite the generalizations, little research has addressed the impacts of forest

fragmentation on abundance patterns of individual species.

　　　　Currently, synthesis of broader patterns about species richness or population

abundances and fragmentation effects from broader spatial scales across tropical regions is

lacking.

　　　　Our research addressed the question of how tropical bird species populations are

impacted by tropical forest fragmentation in lowland Atlantic forests of northeastern Costa

Rica. We quantified changes in bird species abundance and patch occupancy for eight focal

species in forest fragments that exist across a continuum of fragmentation, distances from the

largest source population and remaining percent forest cover. All eight species are resident

birds that breed in Costa Rica's wet lowland forest. Two species were classified as

understory frugivorous, three species as understory insectivorous, and three species were

selected that possess omnivorous dietary habits (Stiles et al. 1989). By focusing on a subset

of the tropical forest avian community, we were able to conduct a relatively rapid assessment

across a larger number of fragments at a semi-regional scale. There is a need to balance the

information gathered to understand ecological processes at the community level with that of

comprehending the habitat requirements and space use of individual species (Marzluff et al. 2004) across broader spatial scales. Individual species or foraging guild responses to critical thresholds of forest loss and subsequent fragmentation may vary and it is critical to gain understanding of patterns and processes before further habitat degradation or land use changes occur. In Costa Rica, White-throated Thrushes (*Turdus assimilis*) persist in fragmented landscapes where coffee plantations juxtapose forest patches; however, there is evidence that local extirpation is occurring where no large forest patches remain (Cohen and Lindell 2004).

A greater understanding of how fragmentation impacts important members of the avifaunal community could inform local resource management decisions. At least half of the eight species we chose are partially or wholly frugivorous, and play an important role in plant dispersal. In wet tropical forests, 80% of trees and shrubs produce fruit ingested by birds and mammals (mainly bats) that later regurgitate or defecate the seeds away from the parent plant (Levey et al. 1994). At a community level, avian and bat dispersal are thought to maintain local plant diversity and population level processes (i.e., genetic dispersal, increased survival) (Howe and Smallwood 1982, Janzen and Vasquez-Yanes 1991, Loiselle and Blake 1999, Westcott 2002). Moreover, avian seed dispersers often play a critical role in jump-starting restoration in degraded tropical landscapes (Wunderle, Jr. 1997, Holl et al. 2000, Holl 2002).

We tested the null hypothesis that there is no difference in species abundance of eight resident bird species across forest fragments due to size, distance and forest cover. Based on the results of past research, reporting largely size, isolation and tree cover effects on species

richness, we predicted that overall, species' abundances would decrease from larger to smaller fragments, from less isolated to more isolated fragments and in fragments imbedded within areas of lower forest cover. Moreover, species with specialist foraging strategies (understory frugivores and understory insectivores) and low dispersal abilities would decline across a gradient from large, near to small, far and at farther distances and at lower percent forest cover. Conversely, we predicted that birds with omnivorous diets, also the largest species in terms of size, would likely persist, at least where adequate forest and tree cover remained within the fragmented landscape.

We present data on the occupancy and abundance of eight species of resident wet forest birds from forest fragments at a semi-regional scale in northeastern Costa Rica. We also assess land use change patterns across the region from 1986 to 2001 to create a scenario on which to base projections about probable trends and generate ideas for future research on tropical avian ecology and conservation that could be used by local managers to assess impacts of forest management decisions.

STUDY SITE

The Sarapiquí study area is located in the northeastern Atlantic zone of Costa Rica, where remaining natural forests are characterized by species-rich, multilayered, tropical wet forest supported by annual rainfall averaging ~ 4000 mm. Forests throughout the region, including forest fragments surveyed for this study, are dominated in terms of abundance by one tree species, *Pentaclethra macroloba* (Hartshorn and Hammel 1994). Patterns of land use change in Costa Rica include a decrease in the number of large, undisturbed forest tracts,

coinciding with greater isolation and smaller size of remaining patches (Sanchez-Azofeifa et

al. 2001). Since the 1950's, clearing of once expansive forests have been driven largely by

expansion of agricultural and pastoral production systems (Butterfield 1994). Major land

uses include cattle and dairy farming, banana, pineapple and

tree farm production, as well as an emerging forest management and environmental service

payments sector (Leclerc and Chacon 1998).

This research was conducted near the towns of Puerto Viejo de Sarapiquí, Rio Frio,

and La Virgen, within privately owned forest fragments. Access to forest fragments was

arranged with the assistance of Fundacion para el Dessarollo Sostenible de la Cordillera

Volcánica Central (FUNDECOR) a non-governmental organization working with

landowners in the region, thru cooperation with Centro Agronómico Tropical de

Investigación y Enseñanza (CATIE) FRAGMENTS project working in the Rio Frio area just

east of Puerto Viejo, and from personal contact by D. Roberts with other field researchers

with access to sites, as well as finding sites on GIS maps and asking local farmers about

contact information.

STUDY ORGANISMS

Eight resident bird species were chosen from across a range of life history strategies:

two frugivores, the Red-Capped Manakin (*Pipra mentalis* - PIPMEN) (Pipridae) and the

Ochre-bellied Flycatcher (*Mionectes oleaginous* - MIOOLE) (Tyrannidae); three

insectivores, the White-breasted Wood Wren (*Henicorhina leucosticte* - HENLES)

(Troglodytidae), and two members of the antbird family (Thamnophilidae), the Western

Slaty-Antshrike (*Thamnophilis atrinucha* – THAATR) and the Chestnut-backed Antbird (*Myrmeciza exculs* - MYREXS); and three omnivores, although the two toucans (Ramphastidae), the Chestnut-mandibled Toucan (*Ramphastos swainsonii*- RAMSWA) and the Keel-billed Toucan (*Ramphastos sulfuratus* - RAMSUL) are largely frugivorous, they also opportunistically feed on insects and small vertebrates. The Bright-rumped Attila (*Attila spadiceus* - ATTSPA) (Tyrannidae), feeds on insects, lizards, frogs, and small berries and seeds.

These eight species were chosen as they represent variation in not only tropical avifauna foraging strategies, but in mating systems they exhibit and in ecological niches they occupy in tropical wet forests. *P. mentalis* and *M. oleagineus*, inhabit wide geographic ranges linked to the distribution of tropical wet forest, from southern Mexico to northern South America. Specific life-history characteristics of both *P. mentalis* and *M. oleagineus* include specialized mating behavior, where several males gather in close proximity to attract mates, otherwise known as leks (Westcott and Smith 1994, Stutchbury and Morton 2001). The three insectivorous species inhabit the lower strata of wet forests, but are also known to use advanced second growth and edge habitats. The omnivorous species depend on forests and areas with moderate to high tree cover, but have greater dispersal abilities than understory birds, based on size and use of upper strata (Stiles et al. 1989, Graham 2001, Short and Horne 2001). All eight species breed at different intervals between January and September, depending on the species, the breeding season lasts between 4-5 months to upwards of 6-9 months (Stiles et al. 1989). Further justification for choosing these eight species, in addition to traits listed above, was that each species is still common within the

largest old-growth tract in the region, La Selva Biological Reserve. D. Roberts (unpublished

data) conducted point counts in 2005 to assess occurrence within La Selva and

found that these species were readily observed. Additionally, a recent study (Sigel et al.

2006) compared current abundances of all birds recorded during surveys within La Selva

with data collected since 1960. While this paper reported observed declines by 50 % of the

insectivorous species within La Selva during the last forty years, the species we chose

remained abundant, with the exception of *M. exsul*, whose population appeared to have

declined in overall abundance but not in frequency of detection.

METHODS

SELECTION OF FOREST FRAGMENTS

We selected 30 forest fragments (Table 1) that ranged in area from 4 to 550 ha and were

located at varying distances from large, source forests of La Selva and Braulio Carrillo

(Figure 1). As small fragments were more common in areas with lower forest cover, we

worked to find a similar number of small patches that were close to La Selva and parts of the

landscape that were characterized by higher forest cover. Forest fragments were

characterized by late successional forest, for the most part, with a closed canopy (on average

> 75 %), and a generally open understory. Forest throughout the region have been

selectively logged to some degree during the last forty years, but we did not survey sites that

had evidence of recent logging. All patches were privately owned, with 6 being protected

forest reserves.

SURVEY METHODS

Surveys were completed between late March and June, 2005. We conducted 15, 50m fixed-radius point counts in each of the 30 fragments for a total of 240 point count stations. Equal effort was accomplished in small fragments by repeated surveys to obtain 15 points. Each point count was conducted for 8 minutes and all individuals of focal species detected visually or aurally within the 50 m circle were recorded. Start points were located at randomly chosen distances, at least 150 m from the fragment edge, and from an access point that was located using GPS units programmed with UTM coordinates for each fragment. Trails were used if available. Each surveyor then paced the 100 m distance to the next point, until 15 points were completed. All point counts were completed in the morning from sunrise to 9:00 a.m.

STATISTICAL ANALYSIS

Summary statistics were calculated using SAS (SAS Institute Inc. 2000) as well as exploratory analysis of data. Occupancy of forest patches was tallied using MS Excel.

Modeling approaches

We related either abundance or presence/absence data for eight focal bird species to the important predictor variables of patch size, degree of patch isolation, and percent forest cover for each site surveyed. We tested for effects of forest fragment area, isolation and percent forest cover (all continuous predictors) on species' abundances using generalized additive models (GAMs), a modern non-parametric regression technique (Lehmann et al. 2002, Guisan et al. 2002). Using the Poisson model, as abundances were counts of individuals, we

first tested for interaction effects, but if interactions were not significant, we pooled the interaction terms into the error term to gain power.

During an exploratory phase of data analysis, we observed possible thresholds for a few species with regard to occupancy, especially those that were likely more susceptible to forest fragmentation and were not observed in several of the fragments. We ran classification and regression tree (Cart) models for three species with low abundances (<50 individuals detected across the 30 fragments) to assess threshold levels for significant predictor variables corresponding with occupancy patterns (Presense/Absence((Table 2). While there are limitations to using Cart models for detecting interactions among predictor variables, we assessed that aspect using GAMs. Both GAMs and Cart models were run in R Stats package (http://cran.r-project.org/).

Values of continuous variables were obtained with ArcGIS 9.1 Spatial Analyst and Hawth's Tools extensions (Beyer 2004, ESRI 2005). A one-kilometer buffer was placed around each forest site where surveys were conducted and percent forest cover was assessed. We chose a one-kilometer buffer based a compromise between assessing coverage around this continuum of fragment sizes and to minimize overlap of buffers at fragments situated in close proximity to one another (S. Cushman, personal communication). Forest fragment area was obtained from high-resolution imagery when available from La Selva Biological Station GIS Laboratory manager (Marcia Snyder, La Selva 2005) and the fragment project (Brenes 2003). If forest fragments were outside of the extent of the high-resolution imagery, the land use classification (Landsat TM data, 2001) (Sesnie 2006) was used; forest cover percentages were also derived from this classification.

LANDSCAPE STRUCTURE ANALYSIS

To assess land use change trends at the semi-regional scale, we used three-land use

classifications derived from Landsat TM data (Sesnie 2006). The original classification had

22 land use types, but for these analyses we aggregated those 22 types into the following

classes analyzed in FRAGSTATS 3.3 (McGarigal et al. 2002): 1) Natural forests, defined as

late successional forests; 2) Riparian forests and tree cover, such as tree plantations;

3) Pasture; 4) Early successional forest, those forests < 10 years old; 5) Agriculture of

moderate intensity (e.g., heart of palm and fruit trees); 6) Agriculture of high intensity (e.g.,

banana, pineapple and sugar cane production); and 7) Non-forest, such as urban, water. We

report results of 12 class-level, landscape-structure metrics (Neel et al. 2004) across three

time periods (1986, 1996. 2001) for the first 6 categories listed above. From this trend

analysis, we propose probable future scenarios for focal bird species population responses to

continued land use change. We also propose suggestions for future research to address

impacts of land use trajectories on rainforest bird species in this landscape.

RESULTS

We counted a total of 742 individual birds of all eight species across 30 fragments. A large

amount of variation in the abundances of different species was observed (Table 2). The most

abundant species across all fragments was *H. leucosticta* and the rarest species with the

lowest abundances were *P. mentalis* and *R. swainsonii*.

The high proportion of occupancy (species presence in a fragment) across the range of size classes (Figure 2) was an unexpected result, especially for the small fragments that were embedded within pastoral and agricultural systems.

GAM Modeling

A common result was the importance of forest cover, acting alone or interacting with area or distance to predict species abundances (Table 3). Area, or fragment size, in conjunction with forest cover were important variables predicting abundance of all understory insectivorous species, but the effects on each species were not necessarily the same. In general, species within the same guild did not respond to the effects of fragmentation in patterns related to guild or shared life history traits as predicted.

For both frugivorous, understory species, we had predicted a similar response to forest fragmentation, but these two species responded individually to effects of forest fragmentation. The results for *P. mentalis* followed our predictions, but only partly for the response of *M. oleaginous*. *P. mentalis* abundance declined across the continuum from large to small and with greater distances, but the significant predictor variables were an interaction between distance and percent forest cover (Table 3). With no significant interactions, the highest *M. oleaginous* abundances were observed in small and medium-sized fragments, and in fragments closer to source populations (Table 4).

For the insectivorous species, *H. leucosticta* and *M. exsul* abundance patterns were both significantly influenced by the interactions of fragment area and percent forest cover. *T. atrinucha* was the only species with abundance significantly influenced by a three-way interaction between area, distance, and forest cover (Table 3).

Two of the omnivorous species, *R. sulfuratus*, the smaller of the toucan species in our study area, and *A. spadiceus*, were detected across the landscape in a large proportion of the fragments surveyed. For *A. spadiceus,* the highest abundances were significantly associated with higher percent forest cover (Table 4). *R. sulfuratus* abundance was not significantly associated with any of the predictor variables. However, 4 of 6, or 67 % of the fragments lacking this species were < 25 ha. For *R. swansonii*, the largest toucan in the study region, highest abundances were associated with fragments embedded within areas of higher percent forest cover (Table 4). An unexpected result for *R. swansonii* was that several of the larger fragments had no detections, the opposite of *R. sulfuratus* (Figure 2).

Classification and regression tree

For the three species with low abundances, we used occupancy of fragment (present or absent) as a binary response to examine the same three predictor variables used in GAM models (fragment area, distance from source, and percent forest cover). Both *P. mentalis* and *T. atrinucha* exhibited thresholds of occupancy predicted from percent forest cover by the Cart models (Figures 3 and 4, respectively). *R. swainsonii* abundance was best predicted from forest cover in the GAM models, but looking only at presence/absence in the cart model, fragment area best predicted whether or not this species was present. Individuals of this species were absent from 7 of 9 fragments that were >100 ha in size.

Landscape structure analysis

Fragmentation analyses suggest that the landscape has changed dramatically over the last twenty years. The spatial extent of our study area was 1433 km^2, but the trends observed were similar to land change studies conducted at broader scales (Sesnie 2006). In general,

forest patch size decreased, from a mean of 12.6 ha in 1986 to 6.6 ha in 2001, in concert with

overall amount of forest decreasing during the period from 1986 to 2001 (Table 5).

Agricultural expansion continued within the region, particularly the growth of intensive

agricultural, such as banana and pineapple production.

DISCUSSION

Widespread presence of rainforest birds across a range of fragment sizes, distances from a

source, and percent forest cover strongly implies that forest fragments, even those embedded

within agricultural matrices, provide important habitat complementing bird populations

protected within larger reserves in lowland Costa Rica. While abundances varied by species,

three species in particular, *M. oleaginous*, *M. exsul*, and *R. sulfuratus*, belonging to reported

vulnerable guilds (i.e., frugivorous and insectivorous) (Gray et al. 2007), were detected

across all fragment sizes, even within highly degraded areas of the study extent. These

results are encouraging and suggest that efforts to protect forest fragments of all sizes are

very important for long-term conservation of rainforest avifauna within human-modified

landscapes.

As percent forest cover of greater than 50-60 % was significantly associated with

higher abundance patterns for 5 of the eight species (Table 4), forest fragments embedded

within higher amounts of remaining forest cover may be associated with higher quality

habitat for a greater variety of species. Additionally, distance to source was important in

predicting greater abundances for two species, and one would predict this would allow for

greater immigration and/or recolonization of individuals into fragments.

While there were patterns within the data, the lack of similar response by species within guilds or with shared life history traits, and instead largely species-specific responses, provide an alternative approach to assessing land change impacts on rainforest avifauna beyond the community studies. What specific ecological traits or adaptations may predispose some members of the rainforest community to persist, at least in response to moderate levels of habitat perturbations, while others vanish?

Species that persisted widely

Frugivorous species

M. oleaginous – As one of the few species within the family Tyrannidae to possess a largely frugivorous diet (Traylor and Fitzpatrick 1982), the widespread persistence of this species, even in small fragments, may be partially explained by characteristics of this species' ecology. Territory size requirements are relatively small, with a reported average of 763 m^2 for this 11-12 g bird (Westcott and Smith 1994). Also, a large percentage of individual males move widely within intact forests, and this predisposition to move may provide a mechanism for dispersal across the fragmented landscape (Westcott and Graham 2000).

Fruit resource availability in this region within forest fragments or across the landscape, such as along living fencerows or in abandoned pastures may be sufficient to both facilitate movement across the landscape (Harvey et al. 2006) and sustain populations of *M. oleaginous* within forest fragments. Many species of the genus *Miconia* sp, a common understory shrub or treelet in wet forests, were readily observed fruiting along the edges of fragments. Increased light penetration due to increased edge characteristic of small

fragments may increase fruit production of fruiting species and this may offset the effects of fewer plant species associated with smaller fragment area. Individuals within fragments may have to maintain larger territories and therefore fewer individuals may occupy suitable areas as compared to large, continuous forests, but this has not been documented for most resident birds in this landscape.

R. sulfuratus – The persistence of this toucan species within this semi-regional area is not an unexpected result. *R. sulfuratus* has been shown previously to use forest fragments as small as 5 to 10 ha (Graham 2001). The abundance of remaining forest fragments and riparian forests provide important habitat for this species in agricultural matrices. This species is also known to use very disturbed habitats, such as pastures, for movement and feeding, especially if sufficient tree cover occurs, such as isolated trees or living fencerows (Graham 2001). Moreover, if *R. swainsonii*, the dominant species where the two co-occur (Short and Horne 2001), is less common in the fragmented landscape, *R. sulfuratus* may increase due to lack of competition for food resources or nesting sites.

Insectivorous species

H. leucosticta – This species is a generalist insectivore with presumably small territory size requirements, as this bird weighs just 16 g, suggesting that even small patches can provide sufficient resources. Relatively high abundances of H. leucosticta in small fragments may suggest that ecological release has occurred. Other insectivorous bird species, such as ground-foraging, ant-following birds and small, flocking antwrens have been shown to decline and go extinct in lowland wet forest fragments (Willis 1974, Sigel et al. 2006). This may allow this generalist species to dominate this understory niche.

M. exsul - Habitat use and lack of competition from other insectivorous antbirds may also allow *M. exsul* to sustain populations in a fragmented landscape. This species uses the understory layer of wet forests and has been regularly observed within tree-fall gaps and edge habitats (Willis and Oniki 1972, Marcotullio and Gill 1985). Ecological release may also occur for this species with local extirpation of ant-following birds (highly vulnerable to disappearance in small forest fragments). In lowland Panama, where Spotted Antbirds (*Hylophalax naevoides*) co-occur with *M. exsul*, aggressive behavior by *M. exsul* has been suggested as evidence for competition for critical resources (Willis and Oniki 1972). If ant-following birds go extinct in forest fragments, or decline in even larger, continuous forest, small insectivorous birds may persist and thrive, but no studies have documented mechanisms as far as we are aware.

A. spadiceus – This omnivorous species appears to have adaptations to feeding in edge habitats and opportunistic dietary habits may enable this species to persist in fragmented landscapes. The third largest species at 40 g, *A. spadiceus'* ability to disperse and fly across habitats with sufficient tree cover may also help explain its widespread abundance in this region.

Species that declined:

P. mentalis – This species was detected in just 12 of the 30 fragments. *P. mentalis* was absent from all 8 of the smallest fragments (< 15 ha). Small fragments may lack sufficient fruit resources or lek sites for this species. It has been shown that fruit resources are patchily distributed and asynchronous in tropical wet forests and despite the fact that this species has been reported to forage on over 100 different plant species across 40 tropical

plant families (Graham 1996, Loiselle and Blake 1999), decreasing forest patch size and isolation likely impact the ability of understory frugivorous birds to find important resources during breeding or for maintenance during the non-breeding season. However, *M. oleagineus* persists in the landscape despite its largely frugivorous diet. Taxonomic constraints are different for these two species, as all members of the Pipridae family are frugivorous, whereas *M. oleagineus* is unique as one of the few, predominately frugivorous flycatchers (Tyrannidae). Another difference between these two frugivorous species is nest architecture. Open-cup nests are often considered more susceptible to the large number of potential predators in tropical lowland forests than more concealed pendant nests (Styrsky 2005). *P. mentalis* is an open-cup nesting passerine, whereas *M. oleaginous* constructs a hanging, closed nest that may provide better protection from certain avian or ground-dwelling mammalian predators.

T. atrinucha – This species was also absent from a majority of small and medium sized fragments. *T. atrinucha* also constructs an open-cup nest and may be vulnerable to nest predation in forest fragments. If immigration rates, via low dispersal capabilities are coupled with high reproductive failure, then populations in forest fragments may be susceptible to local extinctions. Understory insectivorous birds have been repeatedly shown to avoid sharp edge boundaries or large openings due to a natural inhibition to cross open habitats (Harris and Reed 2002, Laurance et al 2004).

R. swainsonii – This is the largest of the species studied, at > 600 g for male *R. swainsonii*, the larger of the sexes. Kattan (1992) found that larger body size combined with frugivorous dietary habits increased the vulnerability of species to forest loss and

fragmentation. While this species was observed in a large proportion of the fragments < 50 ha, it was not detected in several of the largest fragments. Logging activities and human hunting activities within privately owned forest fragments might also affect this species disappearance within fragments. Anecdotal evidence that hunting pressures do exist for many of the larger forest bird species was documented during the field season, but no local studies have quantified this fact. Alternatively, this large toucan would be more easily detected in small fragments, and detection probabilities may be higher in small fragments due to survey methodology. Additional research may be necessary to confirm or further elucidate our observed patterns.

CONCLUSIONS

All eight species of rainforest birds studied were detected within either all or a subset of the fragments surveyed during this study. Forest fragments across the spectrum of size classes, as small as 5 ha, provided habitat for a majority of the focal species. Species within the same foraging guild or with shared ecologies did not respond similarly to land use change.

Overall, it is possible that perceptions about rainforest avifauna have been formed from too narrow a focus on species richness and not enough from community ecology studies. We understand little about mechanisms that drive species to extinction in tropical regions, instead focusing on the patterns observed at the community level. Assumptions about landscape -level processes are often extrapolated from too few studies.

Land use trends and tropical bird populations

Widespread deforestation has occurred in northeastern Costa Rica, outside of protected areas, over the last fifty years (Butterfield 1994). Within our study extent, between 1986 and 2001, overall natural forest area declined by ~ 8,000 ha. Deforestation reduced the mean size of natural forest patches by half (Table 5). Increased isolation and reduction in patch size could negatively affect many species of forest birds requiring year-round access patchy fruit resources. Moreover, a reduction fragment size could lessen availability to specialized habitats readily available in larger, continuous forest areas. Greater isolation could impede movement between remaining fragments and minimize genetic isolation processes that can have deleterious impacts on reproduction and long-term species survival.

Future land use change scenarios may be difficult to predict, but one can surmise, based on past trends, that one thing is certain, and that is that the landscape will continue to change. There are reasons to be both optimistic and pessimistic about future bird population trends of species that are dependent on forests in this dynamic region. Positive scenarios are that forest fragments will persist, due to continued civil obedience in relation to the 1996 Forestry Protection Law (No. 7575), which prohibits removal or conversion of forests greater than 2 ha. Another positive trend will be increased participation in environmental service payment program by landowners and farmers throughout the region, which places a value on retaining forest cover in the region. The need for increased wood production and the development of native tree plantations throughout the northeastern zone of Costa Rica could provide important habitats for movement between remaining forest fragments.

Negative trends that are likely to continue are the lack of recruitment of secondary forests into the landscape. Secondary forests might provide important fruit resources and movement corridors, but if other land uses are considered more desirable, this habitat type will remain limited in distribution. One of the most alarming trends observed during field work and apparent within the analyses of land change (Table 5), is the increase in area of intensive agriculture. The conversion of moderate agricultural practices, such as heart of palm production to ever-expanding pineapple fields creates a hard edge around forest fragments that will likely increase isolation due to impeding movement of forest birds out of fragments. Increased isolation of bird populations in small fragments could facilitate rapid genetic drift characteristic of small populations, which could impact demographic traits of bird species negatively.

Conservation Implications

Roberts (2007) found that a large proportion of forest was located outside of protected reserves in lowland Costa Rica. The remaining natural forests of northeastern Costa Rica are one of three large aggregations of private forestlands remaining in the country (Watson et al. 1998). Environmental service payment programs currently provide willing landowners and farmers within the Sarapiquí region with financial incentives to retain forest cover. One of the stated environmental services is the protection of forest biodiversity, along with carbon storage and hydrological and watershed protection. However, little research has assessed what the payments are protecting. Our research suggests that forest fragments are currently protecting a diverse assemblage of rainforest birds and deserve continued

protection and study as land use change continues within the region. Of particular importance for the widest assemblage of our eight focal species are fragments of all sizes embedded within landscapes that have > 50 percent forest cover, and those that are within 5 km of the continuous forest. However, clusters of remaining forest fragments could also be important for maintaining populations of species within more highly degraded landscapes, but our research did not assess this directly.

Future research efforts should focus on the impacts of land use practices in the matrix habitat adjacent to fragments and between neighboring fragments on the organisms within the fragments. A paucity of research into the effects of chemicals used during intensive agricultural production on the landscape and natural habitats in particular hinders sound conservation decisions. It is also largely unclear how intensification of agriculture will impact movement of organisms within the landscape.

LITERATURE CITED

Aratrakorn, S., S. Thunhikorn, and P. F. Donald. 2006. Changes in bird communities following conversion of lowland forest to oil palm and rubber plantations in southern Thailand. Bird Conservation International 16:71-82.

Balmford, A., and A. Long. 1994. Avian endemism and forest loss. Nature 372:623-624.

Beyer, H. L. Hawth's analysis tools for ArcGIS. 2004. Available at the following web site: www.spatialecology.com/htools.

Blake, J. G., and B. A. Loiselle. 2001. Bird assemblages in second-growth and old-growth forest, Costa Rica: perspectives from mist nets and point counts. The Auk 118:304-326.

Butterfield, R. P. 1994. The regional context: land colonization and conservation in Sarapiqui, p. 299-306. *In* L. A. McDade, K. S. Bawa, H. Hespenheide, and G. S.

Hartshorn [EDS.], La Selva: ecology and natural history of a Neotropical rain forest. University of Chicago Press, Chicago and London.

Canaday, C. 1996. Loss of insectivorous birds along a gradient of human impact in Amazonia. Biological Conservation 77:63-77.

ESRI. 2005. ArcGIS 9.1. Redlands, California.

Graham, C. H. 2001. Factors influencing movement patterns of Keel-billed Toucans in a fragmented tropical landscape in southern Mexico. Conservation Biology 15:1789-1798.

Graham, D. L. 1996. Interactions of understory plants and frugivorous birds in a lowland Costa Rican forest. PhD Thesis, University of Miami, Coral Gables, Fla.

Gray, M. A., S. L. Baldauf, P. J. Mayhew, J. K. Hill. 2006. The response of avian feeding guilds to tropical forest disturbance. Conservation Biology 21: 133-141.

Guisan, A., T. C. Edwards, and T. Hastie. 2002. Generalized linear and generalized additive models in studies of species distributions: setting the scene. Ecological Modeling 157:89-100.

Hartshorn, G. S., and B. E. Hammel. 1994. Vegetation types and floristic patterns, p. 73-89. *In* L. A. McDade, K. S. Bawa, H. Hespenheide, and G. S. Hartshorn [eds.], La Selva Ecology and natural history of a neotropical rain forest. University of Chicago Press, Chicago and London.

Harvey, C. A., A. Medina, D. M. Sanchez, S. Vilchez, B. Hernandez, J. C. Saenz, J. M. Maes, F. Casanoves, and F. L. Sinclair. 2006. Patterns of animal diversity in different forms of tree cover in agricultural landscapes. Ecological Applications 16:1986-1999.

Hobbs, R. J., and H. A. Mooney. 1998. Broadening the extinction debate: population deletions and additions in California and Western Australia. Conservation Biology 12:271-283.

Holl, K. D. 2002. Effect of shrubs on tree seedling establishment in an abandoned tropical pasture. Journal of Ecology 90:179-187.

Holl, K. D., M. E. Loik, E. H. V. Lin, and I. A. Samuels. 2000. Tropical montane forest restoration in Costa Rica: overcoming barriers to dispersal and establishment. Restoration Ecology 8:339-349.

Hughes, J., G. C. Daily, and P. R. Ehrlich. 1997. Population diversity: its extent and extinction. Science 278:689-692.

Kattan, G. H. 1992. Rarity and vulnerability: the birds of the Cordillera Central of Colombia. Conservation Biology 6:64-70.

Kattan, G. H., H. Alvarez-Lopez, and M. Giraldo. 1994. Forest fragmentation and bird extinctions: San Antonio eighty years later. Conservation Biology 8:138-146.

Laurance, S. G. W., P. C. Stouffer, 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., T. E. Lovejoy, H. L. Vasconcelos, E. M. Bruna, R. K. Didham, P. C. Stouffer, C. Gascon, R. Bierregaard, S. Laurance, and E. Sampaio. 2002. Ecosystem decay of

Amazonian forest fragments: a 22-year investigation. Conservation Biology 16:605-618.

Leck, C. F. 1979. Avian extinctions in an isolated tropical wet-forest reserve, Ecuador. The Auk 96:343-352.

Leclerc, G., and J. R. Chacon. 1998. Using a GIS to determine critical areas in the Central Volcanic Cordillera Conservation Area, p. 108-126. *In* B. G. Savitsky, and T. E. Lacher, Jr. [eds.], GIS methodologies for developing conservation strategies. Columbia University Press, New York.

Lehmann, A., J. McC.-Overton, and J. R. Leathwick. 2002. GRASP: generalized regression analysis and spatial prediction. Ecological Modeling 157:189-207.

Levey, D. J., T. C. Moermond, and J. S. Denslow. 1994. Frugivory: an overview, p. 282-294. *In* L. A. McDade, K. S. Bawa, H. Hespenheide, and G. S. Hartshorn [eds.], La Selva Ecology and natural history of a neotropical rain forest. University of Chicago Press, Chicago and London.

Loiselle, B. A. and J.G. Blake. 1999. Dispersal of melastome seeds by fruit-eating birds of tropical forest understory. Ecology 80: 330-336.

McGarigal, K., S.A. Cushman, M.C. Neel, and E. Ene. 2002. FRAGSTATS: Spatial pattern analysis program for categorical maps. Computer software program produced by the authors at the University of Massachusetts, Amherst, Massachusetts, USA. Available at the following web site: www.umass.edu/landeco/research/fragstats/fragstats.html.

Montagnini, F. 1994. Agricultural systems in the La Selva region, p. 307-316. *In* L. A. McDade, K. S. Bawa, H. Hespenheide, and G. S. Hartshorn [eds.], La Selva Ecology and natural history of a neotropical rain forest. University of Chicago Press, Chicago and London.

Naidoo, R. 2004. Species richness and community composition of songbirds in a tropical forest-agricultural landscape. Animal Conservation 7:93-105.

Neel, M.C., K. McGarigal, and S.A. Cushman. 2004. Behavior of class-level landscape metrics across gradients of class aggregation and area. Landscape Ecology 19:435-455.

Newmark, W. D. 1991. Tropical forest fragmentation and the local extinction of understory birds in the Eastern Usambara Mountains, Tanzania. Conservation Biology 5:67-78.

Norris, K., and D. Pain. 2002. Conserving bird biodiversity. Cambridge University Press, Cambridge.

Olson, D. M., and E. Dinerstein. 2002. The global 200: priority ecoregions for global conservation. Annals of the Missouri Botanical Garden 89:199-224.

Petit, L. J., and D. R. Petit. 2003. Evaluating the importance of human-modified lands for Neotropical bird conservation. Conservation Biology 17:687-694.

Pimm, S. L., M. Ayres, A. Balmford, G. Branch, K. Brandon, T. Brooks, R. Bustamante, R. Costanza, R. C. L. Cowling, A. Dobson, Farber.S., G. A. B. Fonseca, C. Gascon, R. Kitching, J. McNeely, T. Lovejoy, R. Mittenmeier, N. Myers, J. A. Patz, B. Raffle, D. Rapport, P. Raven, C. Roberts, J. P. Rodriquez, A. B. Rylands, C. Tucker, C. Safina, C. Samper, M. L. J. Staissny, Supriatna.J., D. H. Wall, and D. Wilcove. 2001. Can we defy nature's end? Science 293:2207-2208.

Pimm, S. L., P. Raven, A. Peterson, C. H. Sekercioglu, and P. R. Ehrlich. 2006. Human impacts on the rates of recent, present and future bird extinctions. Proceedings of the National Academy of Science 103:10941-10946.

Raven, P. H., and E. O. Wilson. 1992. A fifty-year plan for biodiversity surveys. Science 258:1099-1100.

Sala, O. E., F. S. Chapin, J. J. Armesto, E. Berlow, J. Bloomfield, R. Dirzo, E. Huber-Sanwald, L. F. Huennekke, R. B. Jackson, A. Kinzig, R. Leemans, D. M. Lodge, H. A. Mooney, M. Oesterheld, M. L. Poff, M. T. Sykes, B. H. Walker, M. Walker, and

D. H. Wall. 2000. Global biodiversity scenarios for the year 2100. Science 287:1770-1774.

Sanchez-Azofeifa, G. A., R. C. Harriss, and D. L. Skole. 2001. Deforestation in Costa Rica: a quantitative analysis using remote sensing imagery. Biotropica 33:378-384.

SAS Institute Inc. SAS 9.1.3. 2000. Cary, N.C., SAS Institute Inc. (GENERIC)
Ref Type: Computer Program

Scott, M. J., F. Davis, B. Csuti, B. Butterfield, R. Noss, S. Caicco, C. Groves, J. Ulliman, R. D'erchia, H. Anderson, and R. G. Wright. 1993. Gap analysis: a geographic approach to protection of biological diversity. Wildlife Monograph 123:1-41.

Sekercioglu, C. H., P. R. Ehrlich, G. C. Daily, D. Aygen, D. Goehring, and R. F. Sandi. 2002. Disappearance of insectivorous birds from tropical foerst fragments. Proceedings of the National Academy of Science 99:263-267.

Sesnie, S. E. 2006. Integrating Landsat TM and SRTM-DEM derived variables with decision trees for habitat classification in complex neotropical environments. Dissertation. University of Idaho.

Short, L. L., and J. F. M. Horne. 2001. Toucans, barbets and honeyguides. Oxford University Press, New York.

Sigel, B. J., T. W. Sherry, and B. 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.

Sodhi, N. S., L. P. Koh, D. M. Prawiradilaga, Darjono, I. Tinulele, D. D. Putra, and T. H. Tong Tan. 2005a. Land use and conservation value for forest birds in Central Sulawesi (Indonesia). Biological Conservation 122:547-558.

Sodhi, N. S., Lee T.M., L. P. Koh, and J. B. Dunning. 2005b. A century of avifaunal turnover in a small tropical rainforest fragment. Animal Conservation 8:217-222.

Stiles, F. G., A. Skutch, and D. Gardner. 1989. A guide to the birds of Costa Rica. Cornell University Press, Ithaca, NY.

Styrsky, J. N. 2005. Influence of predation on nest-site reuse by an open-cup nesting Neotropical passerine. The Condor 107:133-137.

Terborgh, J., 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.

Traylor, M. A. and J. W. Fitzpatrick. 1982. A survey of the tyrant flycatchers. Living Bird 19: 7-50.

Turner, I. M. 1996. Species loss in fragments of tropical rain forest: a review of the evidence. Journal of Applied Ecology 33:200-299.

van Dorp, D., and P. F. M. Opdam. 1987. Effects of patch size, isolation and regional abundance on forest bird communities. Landscape Ecology 1:59-73.

Westcott, D.A. and J.N.M. Smith. 1994. Behavioral and social organization during the breeding season in *Mionectes oleagineus*, a lekking flycatcher. The Condor 96:672-683.

Westcott, D. A. and D. L. Graham. 2000. Patterns of movement and seed dispersal of a tropical frugivore. Oecologia 122:249-257.

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

Willis, E. O. and Y. Oniki. 1972. Ecology and nesting behavior of the Chestnut-backed Antbird. The condor 74: 87-98.

Wunderle, J. M., Jr. 1997. The role of animal seed dispersal in accelerating native forest regeneration on degraded tropical lands. Forest Ecology and Management 99:22235.
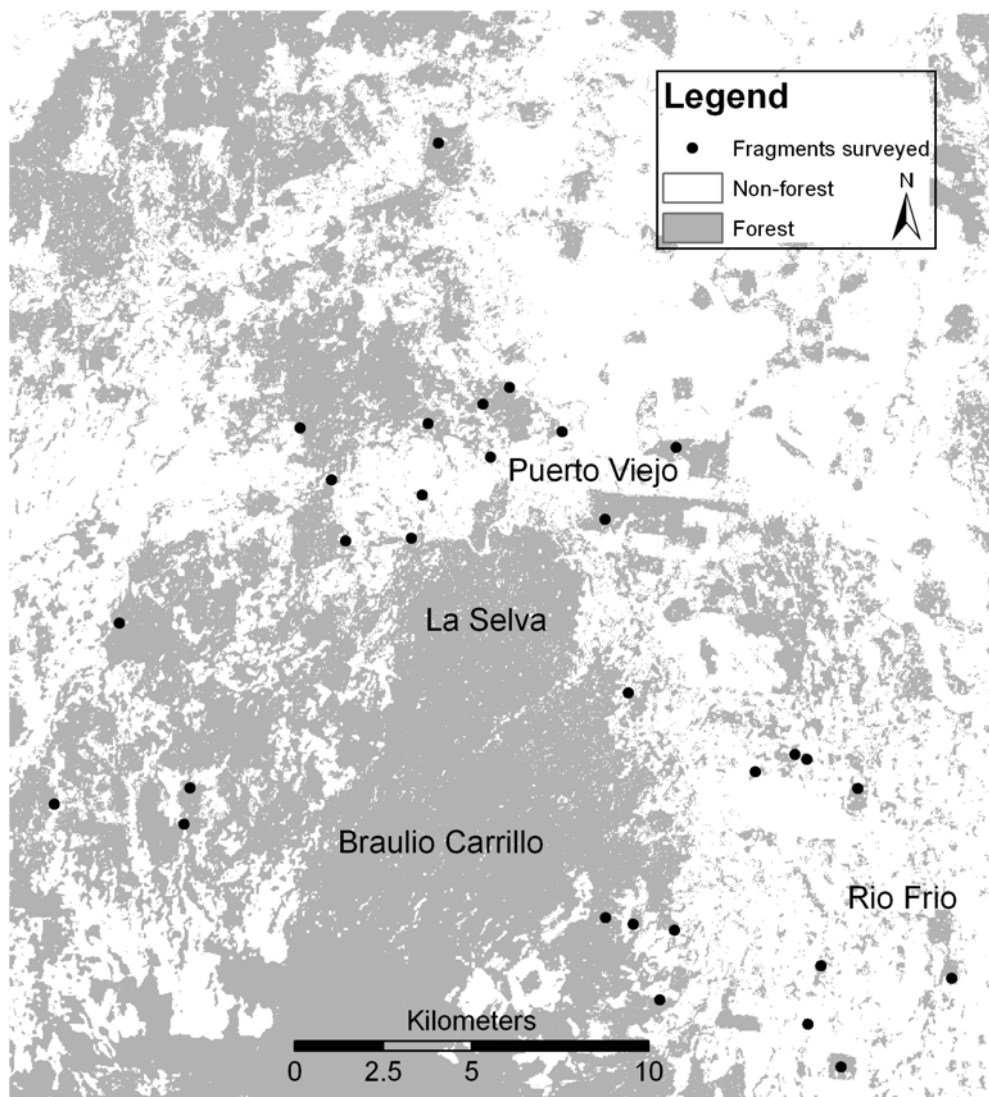
Figure 1. Distribution of the thirty fragments surveyed for eight species of resident birds in lowland Costa Rica.
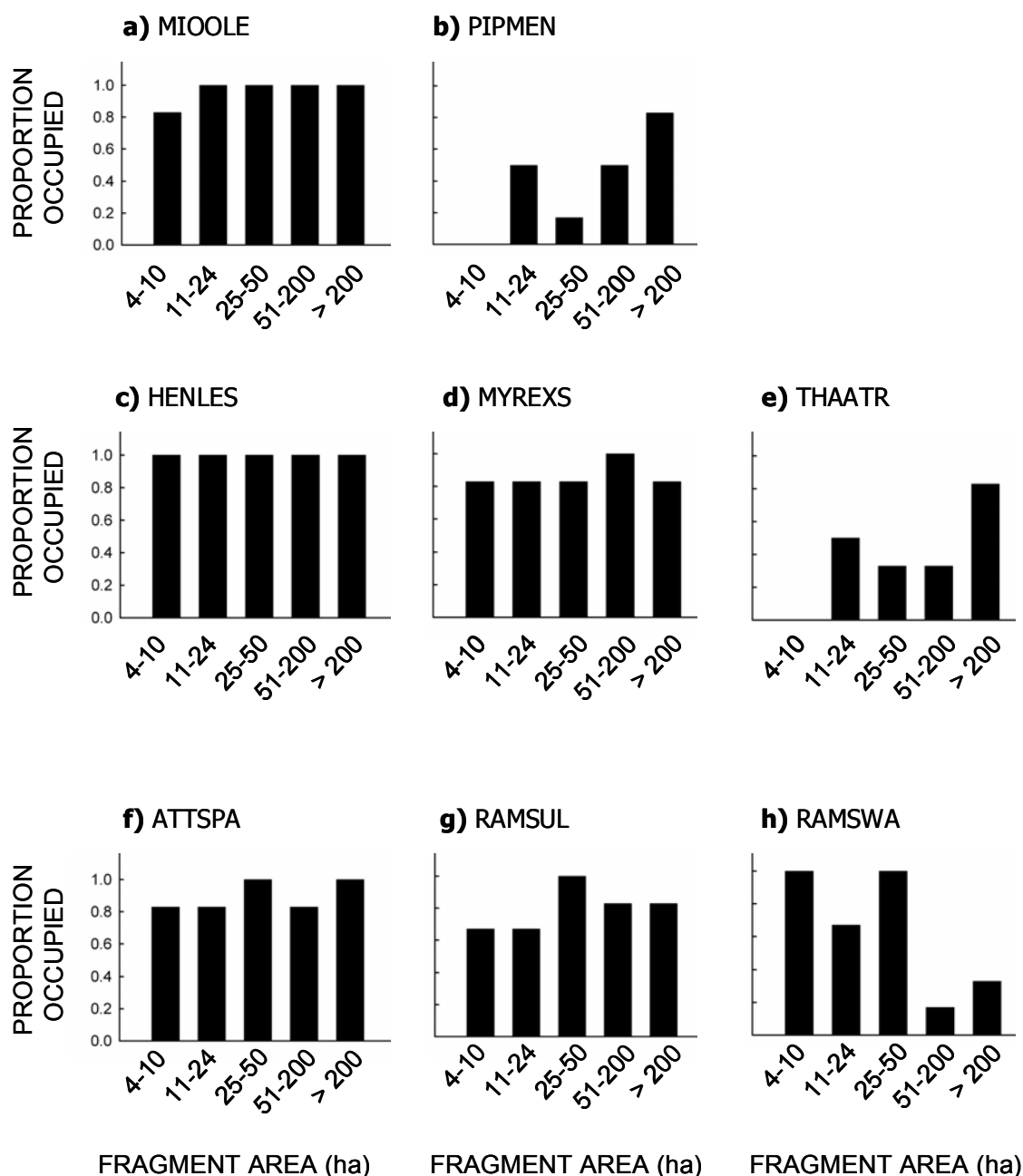
Figure 2. Occurrence of resident bird species across all forest fragments surveyed, within five size classes of equal divisions (n=6). Rows correspond with foraging guilds a) MIOOLE (*M. oleagineus*) and b) PIPMEN (*P. mentalis*) are understory frugivores; c) HENLES (*H. leucosticta*), d) MYREXS (*M. exsul*), and e) THAATR (*T. atrinucha*) are understory insectivores; f) ATTSPA (*A. spadiceus*), g) RAMSUL (*R. sulfuratus*), h) RAMSWA (*R. swainsonii*) are omnivores.

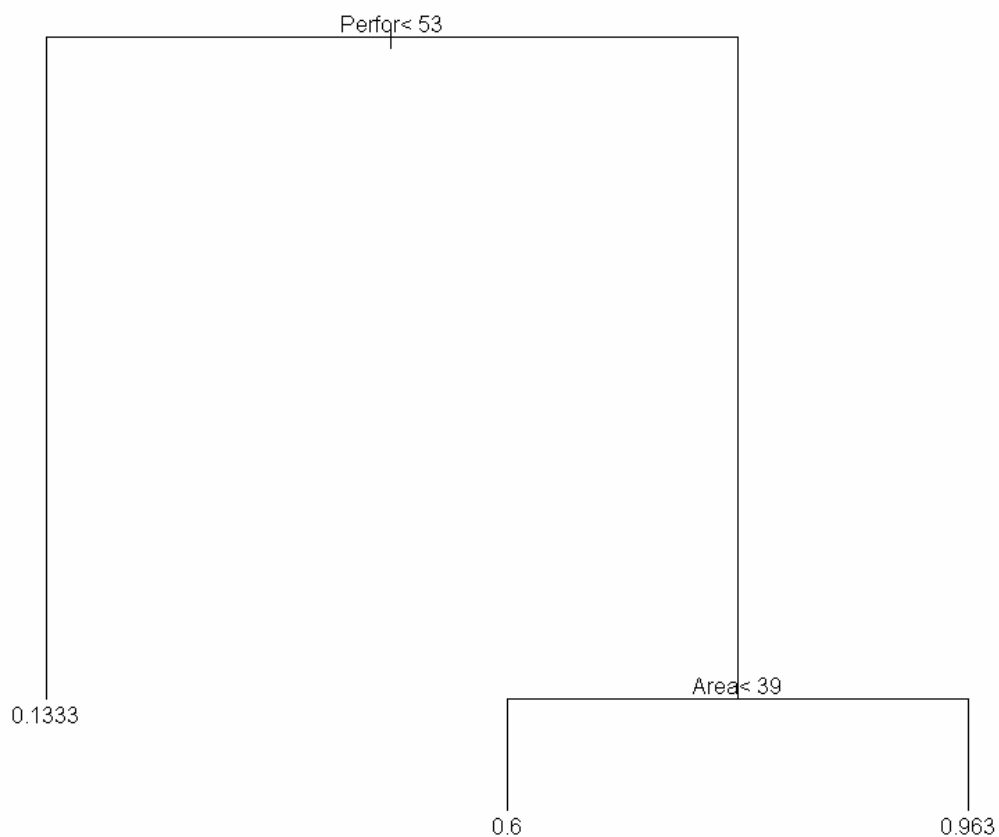Figure 3. Tree created for *P. mentalis* with classification and regression techniques in rpart (R Stats Package). The use of both GAM and CART models enables us to describe the interactions of predictor variables, but also determine thresholds evident during exploratory analysis. For this species, in 0.13 or 2 of 15 observations in fragments in landscapes with less than 53 percent forest cover was this species detected.
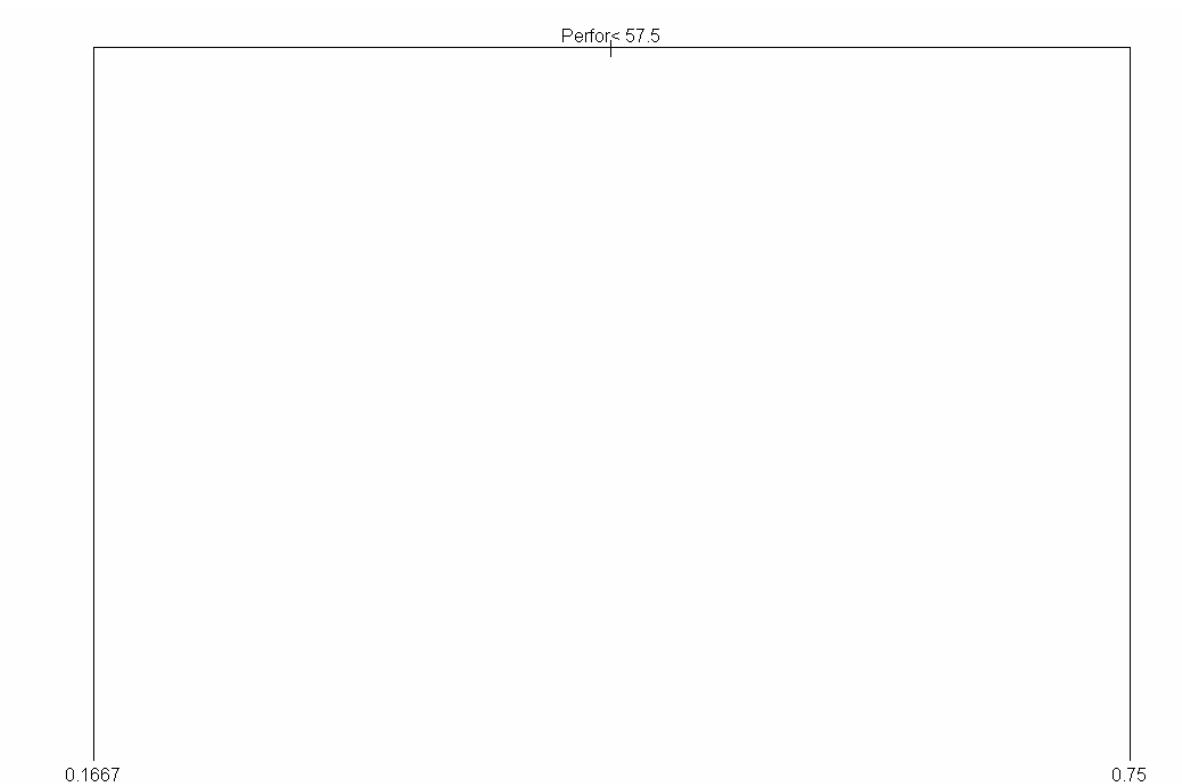
Figure 4. Tree created for *T. atrinucha* with classification and regression techniques (Cart) in R Stats Package. While GAM modeling results showed the interaction of the predictor variables, the Cart model enables us to determine threshold of approximately 57 percent for the most important predictor, forest cover. For this species, 0.75 of the observations with this species present were in landscapes with greater than 57 percent forest cover.

Table 1. Fragment size, distance from source and percent forest cover within 1 km buffer centered over resident bird survey plots in lowland Costa Rica.

Fragment No.	Area (ha)	Distance (km)	Forest Cover (%)
1	550	4.1	72
2	433	0.26	78
3	373	0.97	65
4	360	6.4	72
5	266	1.9	54
6	224	10.1	70
7	179	3.4	41
8	168	2.6	55
9	156	3.97	71
10	92	7.3	30
11	89	1.7	58
12	57	4.4	32
13	45	3.8	65
14	45	5.7	43
15	33	0.38	57
16	27	1.9	20
17	26	7.6	81
18	25	0.44	68
19	22	0.32	40
20	22	3.5	52
21	21	2.8	62
22	17	0.43	65
23	13	3.8	43
24	11	4.6	32
25	8	2.8	22
26	8	1.7	55
27	7	4.2	41
28	7	1.5	24
29	6	1.8	23
30	4	4.4	31

Table 2. Summary of bird counts for resident bird species conducted in 30 forest fragments in Sarapiquí, Costa Rica.

Scientific Name	Sum	Mean	SD	Range
Atilla spadiceus	83	2.8	1.7	(0-7)
Henicorhina leucosticte	231	7.7	4.4	(1-19)
Mionectes oleagineus	124	4.1	2.6	(0-11)
Myrmeciza exsul	145	4.8	4.0	(0-19)
Pipra mentalis	34	1.1	1.6	(0-6)
Ramphastos sulfuratus	53	1.8	1.6	(0-6)
Ramphastos swainsonii	31	1.0	1.1	(0-4)
Thamnophilis atrinucha	41	1.4	2.4	(0-9)

Table 3. GAM model results to predict **Abundance** from explanatory variables of **Area** (fragment), **Distance** (to source population), and **Percent Forest Cover** (within 1 km radius circle around plot).

Scientific Name	Variables with significant effect with trend (+ = positive) in abundance	*P*-value
Understory Frugivores:		
Mionectes oleagineus °	+ (Distance up to 5 km); + (Area up to 100 ha)	0.008; 0.028
Pipra mentalis *	+ (Distance up to 4 km); + (Forest Cover > 50%)	0.011
Understory Insectivores:		
Henicorhina leucosticte *	+ (< 50 ha, Area, >200 ha); + (increase in Forest Cover)	0.003
Myrmeciza exsul *	+ (Increase in Area); + (Increase in Percent Forest Cover)	0.007
Thamnophilis atrinucha *	+ (Increase in Area); (Varied Distance effects); + (Forest Cover > 57.5 %)	0.023
Omnivores:		
Atilla spadiceus °	(Forest Cover > 60 %)	0.008
Ramphastos sulfuratus	---	
Ramphastos swainsonii °	(Forest Cover > 50 %)	0.007

* Interactions were significant

° Interactions were not significant, so the interaction terms were pooled into the error term to gain power

--- No significant results

Table 4.   Landscape metrics in northeastern Costa Rica computed by habitat class using FRAGSTATS 3.3 for the semi-regional classifications from three dates (1986, 1996, 2001).

Land Use Type	Total area (ha)			Number of fragments			Mean area of fragments (ha) +/- (SD)		
Year:	1986	1996	2001	1986	1996	2001	1986	1996	2001
Natural forest	66,397	57,353	58,474	5,251	7,522	8,809	12.6 (287.5)	7.6 (217.4)	6.6 (246.9)
Early successional	12,546	10,628	7,343	19,045	17,190	17,263	0.7 (2.16)	0.6 (3.0)	0.4 (1.4)
Pasture	40,030	41,779	35,730	6,484	7,063	7,366	6.2 (76.2)	5.9 (98.2)	4.9 (54.3)
Agri – Intense	2,803	8,329	10,021	9,114	7,705	8,102	0.3 (3.5)	1.1 (34.7)	1.2 (43.2)
Agri - Moderate	2,090	2,527	4,297	8,217	7,739	11,557	0.3 (1.6)	0.3 (1.8)	0.4 (1.7)
Riparian	10,887	12,353	19,461	17,681	17,047	21,636	0.6 (3.0)	0.7 (5.1)	0.9 (5.2)