University of Massachusetts Amherst

ScholarWorks@UMass Amherst

Masters Theses   Dissertations and Theses

November 2015

Generating Best Management Practices for Avian Conservation in a Land-Sparing Agriculture System, and the Habitat-Specific Survival of a Priority Migrant

Jeffrey D. Ritterson
University of Massachusetts Amherst

Follow this and additional works at: https://scholarworks.umass.edu/masters_theses_2

Part of the Other Ecology and Evolutionary Biology Commons, and the Other Forestry and Forest Sciences Commons

GENERATING BEST MANAGEMENT PRACTICES FOR AVIAN CONSERVATION
IN A LAND-SPARING AGRICULTURE SYSTEM, AND THE HABITAT-SPECIFIC
SURVIVAL OF A PRIORITY MIGRANT

A Thesis Presented

By

JEFFREY D. RITTERSON

Submitted to the Graduate School of the
University of Massachusetts in Partial Fulfillment of

MASTER OF SCIENCE

September 2015

Wildlife, Fish and Conservation Biology

GENERATING BEST MANAGEMENT PRACTICES FOR AVIAN CONSERVATION
IN A LAND-SPARING AGRICULTURE SYSTEM, AND THE HABITAT-SPECIFIC
SURVIVAL OF A PRIORITY MIGRANT

A Thesis Presented

By

JEFFREY D. RITTERSON

Approved as to style and content by:

_____
David I. King, Chair

_____
Stephen DeStefano, Member

_____
Peter W. Houlihan, Member

_____
Richard B. Chandler, Consultant

_____
Curtice R. Griffin, Department Head
Environmental Conservation

ABSTRACT

GENERATING BEST MANAGEMENT PRACTICES FOR AVIAN CONSERVATION
IN A LAND-SPARING AGRICULTURE SYSTEM, AND THE HABITAT-SPECIFIC
SURVIVAL OF A PRIORITY MIGRANT

SEPTEMBER 2015

JEFFREY D. RITTERSON, B.S., UNIVERSITY OF DELAWARE

M.S., UNIVERSITY OF MASSACHUSETTS AMHERST

Directed by: Dr. David I. King

A large amount of the world's biodiversity is located in a disproportionately small

amount of area, namely the tropics. Many of these areas are experiencing rapid

landscape changes, mainly in the form of deforestation for agricultural practices. Current

conservation efforts are focused on agricultural areas and their ability to provide habitat.

The conservation value of a novel land-sparing agroforestry system, known as Integrated

Open Canopy (IOC), was recently demonstrated on the study site when applied to coffee.

IOC coffee supports forest species that are uncommon or absent in shade grown coffee. I

generated best management practices for IOC farms relative to the conservation of forest-

dependent birds by examining what features support the highest richness of species. The

goal was to help develop guidelines for the implementation of IOC grown coffee.

The Golden-winged warbler (*Vermivora chrysoptera*) is a Nearctic-Neotropical

migrant of high conservation priority which has been documented using a range of

nonbreeding habitat types, including IOC coffee farms. However, as is the case with

many migrant species, little is known about whether survival differs among habitats.

Though generally forest dependent, previous work found Golden-winged warblers select

for habitat features other than categorical forest types, such as canopy height and

microhabitat features. In an attempt to identify quality nonbreeding habitat, I estimated

Golden-winged survival rates specific to an array of habitat features.

TABLE OF CONTENTS

LIST OF TABLES

LIST OF FIGURES

CHAPTER 1

INTRODUCTION

1.1 Background

Tropical forests provide a wide range of ecosystem goods and services at both local and global scales. Examples include maintaining the stability of watersheds and soils, influencing regional climates, providing resources for local communities, and retaining unexplored yet potentially important pharmaceutical compounds (Laurance 1999). Tropical forests have also been identified as important terrestrial carbon sinks, where deforestation and regeneration dynamics influence global climate change (Foody et al. 1996).

Tropical forests are estimated to cover only 2.3% of the Earth, yet they harbor at least half of its biodiversity (Wilson 1992). These organisms provide additional goods and services. Birds have been documented as being important predators, scavengers, pollinators, seed dispersers, cavity constructors, and regulators of insect populations in tropical systems (Sekercioglu 2006). Forest-dependent insects play important economic roles when pollinating crops (Ricketts 2004, Ricketts et al. 2004). The entire complement of forest-dwelling species provides a complex and varying range of ecosystem goods and services, some of which remain unidentified.

Tropical forests are being cleared at a rate of 16 million ha per year (Achard et al. 2002). A major contributor to deforestation is the clearing of land for agricultural practices, which ultimately drives the loss of biodiversity and associated ecosystem goods and services (Giest and Lambin 2001, Jenkins 2003). Between the years 1980 and 2000, an estimated 55% of agricultural expansion in the tropics resulted in the clearing of

primary forest, and an additional 28% replaced degraded forest (Gibbs et al. 2010), a trend likely to continue in the future (Laurance et al. 2014).

While the establishment of reserves is an important mechanism for protecting biodiversity, they often fail to adequately represent regional biodiversity and do not address local societal needs (Rodrigues et al. 2004, Gaston et al. 2008, Agrawal and Redford 2009, Chazdon et al. 2009). In the face of a growing human population and per capita consumption, conservationist have focused on the potential of agricultural landscapes to provide habitat and retain biodiversity (Pimentel et al. 1992, Tilman et al. 2002, Foley et al. 2005).

Much of this focus has centered on coffee farms and the conservation of bird species (Komar 2006). Chandler et al. (2013) demonstrated the conservation value of a novel coffee cultivation system, called Integrated Open Canopy (IOC), on my study site. In this research, I continue to develop the IOC system by generating best management practices with respect to the conservation of forest-dependent birds.

Neotropical-Neartic migrants, defined as species which migrate from the Neotropics to breed in North America, are a group of particular conservation concern as many have undergone severe population declines (King et al. 2006, Sauer et al. 2014). Over 200 of these species spend 6 to 8 months per year on their nonbreeding grounds (Rappole 1995), yet the vast majority of research focuses on the breeding season. Although it has been shown that events on the nonbreeding grounds may limit migrant populations (Rappole et al. 1989, 2003, Sherry and Holmes 1996, Strong and Sherry 2000, Studds and Marra 2005, Holmes 2007, Calvert et al. 2009), studies on the basic ecology during this period are non-existent for most species (Faaborg et al. 2010). With

this in mind, conservationists have begun to emphasize a holistic annual cycle approach to the management of migratory species.

One such migrant species is the Golden-winged warbler (*Vermivora chrysoptera*). Breeding Bird Survey data show an annual population decline of 2.6% over the past 45 years, resulting in extirpation through parts of the historic breeding range (Sauer et al. 2014). Many studies suggest that breeding ground factors are contributing to this decline (Buehler et al. 2007), with the two main hypotheses being the reduction of effective population size due to hybridization with Blue-winged warblers (*Vermivora cyanoptera*), and the loss of early-successional breeding habitat due to the maturation of forests (Litvaitis 1993, Gill 1997, Vallender et al. 2007). While these may contribute to population declines, information about the full annual cycle is crucial to a complete conservation approach (Rappole et al. 2003b). Chandler and King (2011) conducted the first empirical study of Golden-winged warbler ecology during the stationary nonbreeding period, providing estimates of habitat-specific abundance and selection of habitat features within home-ranges (second and third order selection, respectively; Johnson 1980). In this research, I provide habitat-specific survival estimates to complement Chandler and King's (2011) abundance estimates, furthering the collective knowledge of Golden-winged warbler ecology, and working toward the identification of high quality habitat.

The outline of my thesis is as follows. The following section of this chapter will describe the study area. Chapter 2 will give best management practices for IOC systems, including the identification of thresholds along habitat gradients corresponding to a response in the richness of forest-dependent bird species. Chapter 3 will provide habitat-

3

specific survival estimates of Golden-winged warblers. A novel adaptive resight

methodology used to elucidate the occupied habitat of cryptic species with large

territories will also be presented. The scientific and common names of bird species will

follow seventh edition of the Check-list of North American Birds, including the fifty-fourth

supplement, created by the American Ornithologists' Union (Chesser et al. 2013).

1.2 Study Area

Most of this study was conducted January to April of 2011 and 2012, with

encounter histories of Golden-winged warblers spanning seasons from 2006 to 2013.

The study area is a mosaic of forest, agriculture, and human settlements on the Pacific

slope of the Tilarán mountain range in Costa Rica N10°13' W84°39' (Figure 1.1). It is

located in the Puntarenas and Montes de Oro counties within the province of Puntarenas,

encompassing an area of about 50 km^2. This area is within the Río Aranjuez watershed,

and includes the towns of Cedral, Palmital, San Francisco, Corazón de Jesus, Ojo de Agua,

and San Martín. On the other side of the continental divide, which wraps around the area, is

the large protected area of Monteverde Reserve Complex (MRC, 28000 ha). Although not

part of the study area, the MRC includes the Alberto Manuel Brenes Biological Reserve,

the Monteverde Cloud Forest Preserve, and Children's Eternal Rainforest.

Forest types of the study area can be classified as montane wet forest (often

referred to as cloud forest) above 1200m, and a premontane moist forest below 1000m,

with a transition zone in between (Holdridge 1947). The montane wet forest is

characterized by an abundance of epiphytes and moss, and trees of a shorter stature than

those at lower elevations on either side of the continental divide. The premontane moist forest has fewer epiphytes, and some deciduous trees that drop their leaves in the dry season. Much of the study site is within the transitional area of these two life zones.

The Tilarán Mountains experience three distinct seasons within the year. The wet season extends from May through October, and is characterized by days which may begin sunny, but generally give way to a daily rain storm. Following this is the transitional season which lasts until January. Rainfall of 400 mm/month and winds of 100 km/hour are not uncommon during this period, and storms can last longer than a week (Chandler 2010). February through April is the dry season, with generally clear skies and only 0-200 mm/month rain. The dry season is much more pronounced at the lower elevations due to a rain shadow caused by the loss of precipitation as the northeast trade winds force clouds over the continental divide. The mean annual temperature ranges from 18-24C depending upon elevation, and is not particularly variable throughout the year.

Mostly families in the area practice at least one form of agriculture. Land use is dominated by cattle pastures, where famers produce either beef or dairy, resulting in a mosaic of mostly pasture and forest patches (Figure 1.1). There are also small family-operated coffee farms (2-5 ha). Other practices include the raising of pigs, chickens, or other crops such chayote (*Sechium edule*).

Figure 1.1 The study area is represented by the yellow pushpin on the map of Costa Rica, followed by a typical view of the area, showing a mosaic of forest patches and pastures.

CHAPTER 2

GENTERATING BEST MANAGEMENT PRACTICES FOR AVIAN
CONSERVATION IN A LAND-SPARING AGRICULTURAL SYSTEM

2.1 Introduction

Conservationists have widely acknowledged the importance of agricultural

systems for conservation, however they argue over the application of agroforestry

techniques. The crux of the argument is centered on intensification, with two major

strategies debated: wildlife-friendly farming (Green et al. 2005) and land-sparing

(Balmford et al. 2005). Those in favor of the wildlife-friendly approach argue that

biodiversity is negatively affected by agricultural intensification (Perfecto et al. 2003,

Schulze et al. 2004, Philpott et al. 2008), and emphasize incorporating ecosystem

elements (e.g., native shade trees) directly into the system. Critics argue that such

techniques only protect select components of a habitat, and often result in lower yields

(Swantz 1996, O'Brien and Kinnaird 2003). Land-sparing agriculture intensifies

production to maximize yield, availing other land for conservation. Advocates of land-

sparing emphasize the importance of protecting entire ecosystems (Rappole et al. 2003,

Haslem and Bennett 2008), and note that intensification will be necessary to

accommodate future food demands (Hazell and Wood 2008). Critics argue that native

habitat is not explicitly conserved, and destruction may be further driven by

intensification (Chappell et al. 2009).

Coffee (*Coffea arabica*) has been at the heart of the agroforestry debate. In Latin

America, coffee is the second largest international commodity, after oil exports, the

7

production of which generates $10 billion annually (Rice and Ward 1996). Covering

about 3.6 million ha in northern Latin America (Food and Agriculture Organization

2002), most coffee is grown under full sun, effectively creating a monoculture (Moguel

and Toledo 1999). In recent years, shade coffee production has been highly celebrated

for providing wildlife habitat, and is considered a wildlife-friendly farming technique as

coffee is incorporated directly into the ecosystem under a canopy of trees. However,

there are important limitations to its conservation potential (O'Brien and Kinnaird 2003,

2004, Komar 2006). By replacing native understory with coffee, these systems fail to

conserve entire ecosystems (Tejada-Cruz et al. 2010), and while they perhaps host similar

species richness (Greenberg et al. 1997, 1997b, Perfecto et al. 2003, Philpott et al. 2008),

community composition often varies from that of primary forest, with undesirable levels

of forest-dependent species (Roberts et al. 2000, Tejada-Cruz and Sutherland 2004).

There are also economic shortcomings of shade coffee. Because shade conditions cannot

be managed to maximize productivity nor control diseases, yields are regularly lower

than sun grown coffee (Beer et al. 1998, Perfecto et al. 2005, Avelino et al. 2006, 2007,

Philpott et al. 2007). Also, market premiums for shade coffee could create incentives for

converting native forest to shade (Rappole et al. 2003). Finally, conversion from sun to

certifiable shade coffee requires the lengthy process of growing trees.

Despite debate over wildlife-friendly and land-sparing approaches, direct

comparisons are lacking, primarily because very few land-sparing systems have been

proposed (Norris 2008). In fact, Chandler et al. (2013) conducted the first empirical,

field-based study comparing the conservation values of each strategy. The proposed

land-sparing system, titled Integrated Open Canopy (IOC), allows farmers to freely

manage shade conditions to maximize yield. In return, farmers must conserve an adjacent patch of forest, typically at a 1:1 ratio, and not cut any additional forest for coffee production. Although not considered a formal cultivation system, many farmers naturally practice IOC farming due to the benefits of having a forest patch adjacent to coffee. Specifically, the forest provides an effective wind break, deposits organic material, fights erosion, and can be used for fuel wood or timber extraction (Arce et al. 2010). Chandler et al. (2013) found that IOC supported over twice as many forest-dependent species than shade coffee, and was most similar to secondary forest, which has been shown to be important for maintaining biodiversity (Chokkalingam and De Jong 2001).

Especially when coupled with innovative solar biomass coffee driers (as employed by the Mesoamerican Development Institute), IOC cultivation provides a market-based mechanism to conserve and possibly regenerate native forests (Arce et al. 2010), while also working to address local societal needs. Regenerating forests may qualify for carbon credit under the Kyoto Protocol, further adding economic value to IOC farms. This market-based aspect of IOC, founded on increased yields and decreased costs, offers advantages over certification schemes such as those used for shade coffee. Described as a non-governmental and market-driven tool to effectively self-govern natural resources (Cashore 2002), certification systems connect consumers of responsibly produced goods with generally small-scale producers. Products are certified by a third party, ensuring production standards are met. In turn, the producer receives a higher price premium than what a free market would dictate. The difference in price is made up by either a consumer's willingness to pay for responsibly produced products or,

9

increasingly more often, by corporations being pressured to stock such products. The corporation's motivation is to remain criticism-free and appear environmentally conscious (Conroy 2007).

The predominant organization certifying shade coffee with a primary focus on bird (and general biodiversity) conservation is the Smithsonian Migratory Bird Center and their brand Bird Friendly Coffee. They have been moderately successful with 1181 growers in 10 countries, representing 5739 ha of shade-grown coffee (Smithsonian Migratory Bird Center 2015). However, certain aspects of the certification scheme may limit enrollment. For example, farmers have to pay for the certification processes and often require external funding (Dietsch et al. 2004). Also, certification requirements are numerous and daunting. For example, criteria considered includes canopy height, shade cover, diversity of woody species, structural diversity, leaf litter, herbs or forbs in the ground layer, live fences, vegetative buffer zones along waterways, and organic certification. A certification system should be economically and logistically attainable for farmers (Conroy 2007).

Furthermore, when establishing certification criteria, socio-economic considerations can result in a compromise between management for biodiversity and management for yield and profit. For example, Bird Friendly's required minimum of 40% shade, as stated on their website, is a compromise because biodiversity likely increases with shade cover, yet farmers generally want to manage for lesser amounts of shade. Because shade coffee imposes costs to farmers in terms of yields and the certification itself, and ultimately does not provide actual forest habitat for some sensitive

species, it is clear that a supplementary strategy less subjective to these shortcomings would be a valuable contribution.

By definition, IOC coffee systems incorporate patches of forests with various characteristics affecting suitability for forest-dependent species. These occur on at least three different scales: landscape level, patch level, and internal patch attributes. On a landscape scale, the surrounding land use matrix, patch isolation, and the distance from large protected areas can affect the composition of species in a metapopulation context (MacArthur and Wilson 1967, Levins 1969, Ferraz et al. 2007). At the patch level, the amount of forest edge has been found to influence forest-dependent bird species in tropical systems (Graham and Blake 2001). Also, island biogeography theory states that species richness of a forest patch should be positively associated with area, and has been found to largely hold true in tropical systems (MacArthur and Wilson 1967, Bayard and Elphick 2010). Finally, internal patch characteristics such as structural complexity and microhabitat features can also affect the bird assemblage (MacArthur and MacArthur 1961, Graham and Blake 2001).

The objective of this study was to compare the richness of forest-dependent bird species among coffee farms practicing IOC to determine what conditions create the highest conservation value. A further objective was to examine those variables for points where richness exhibited a threshold, or drastic change in response, giving a conservation target. Biologists generally consider species-based targets such as the effective number of breeders, or a desired level of richness. These metrics are useful in judging the effectiveness of conservation actions. On the other hand, setting targets based on habitat attributes (e.g., area of protected forest, number of nesting sites) provides something

more tangible to other interest groups such as land owners and managers, environmentalists, and politicians, helping to focus and coordinate on the ground action. For example, Guenette and Villard (2005) demonstrated that 70% canopy closure and a density of 80 stems/ha (trees >30 cm dbh) should be maintained to provide habitat for the entire assemblage of late-seral bird species on their site in New Brunswick, Canada. Homan et al. (2004) found critical thresholds in occurrence for two amphibians in relation to the cover of upland forest habitat surrounding vernal pools in which they breed. Quantities such as these can be directly strived for in a managed landscape, and in this case, be used to develop guidelines for the implementation of IOC coffee production.

Use of quantitative targets is not without pitfalls. Methods must be based on sound biology and scientific procedures to avoid a waste of time and energy, and the disengagement of stakeholders. Even after taking such precautions, it must be conceded that target setting methods are still in development, and basic tenets have yet to be established. For example, it is unclear whether thresholds in occurrence correspond to demographic parameters such as survival and reproduction (Lampila et al. 2005). While using a 'snapshot' approach is logistically attractive, the viability of populations over time is not considered. Furthermore, favoring sites with minimum threshold levels, which host small populations, may actually increase local extinction. Thus, targets should not be set at the thresholds themselves, and should not be set in stone, but instead provide the basis for an adaptive management approach (Villard and Jonsson 2009).

I hypothesized that an increased forest patch area and width, and a low amount of edge relative to area would support more forest-dependent species due to decreased area and edge effects. Also, a larger amount of microhabitat features such as vines,

bromeliads and epiphytes would create more complexity and habitat niches, and thus be positively associated with richness.

2.2 Methods

2.2.1 Field Methods

To estimate the richness of forest-dependent species, I conducted 100-meter fixed radius point count surveys in IOC (Figure 2.1). A total of 9 farms were identified as practicing IOC (with at least as much forest as coffee under cultivation). To increase sample size, an additional 6 farms were added, featuring a forest patch surrounded by pasture rather than coffee. I maximized the number of points in each patch, while keeping them spaced 200 meters apart to minimize the occurrence of individuals at multiple points. This resulted in 25 points conducted on 15 farms, with 15 points on farms practicing IOC. Each point was surveyed three times, during which all detected individuals were be recorded by species during a 10 minute interval. The following variables, believed *a priori* to affect the richness of forest-dependent bird species, were recorded at each point: the extent of each habitat category within 100 meters (primary forest, secondary forest, pasture, or coffee), the average canopy height, percent canopy cover, and elevation. Within 50 meters I recorded a complexity index for vines (none, some vines but no tangles, 1-2 tangles, >2 tangles), dead hanging leaves (0, <100, 100-1000, >1000), and epiphytes (none, moss <2cm thick and few bromeliads, moss 2-5cm and few bromeliads, moss >5cm and many bromeliads). Finally, I measured the diameter at breast height of all trees as selected by a 10-factor cruising prism to estimate basal

area. Due to past difficulty finding usable remotely-sensed spatial data, I walked around the edge of each forest patch with a hand held global positioning system (GPS) unit. From this I calculated the area of each patch, the edge/area ratio, and the distance from each patch to the edge of the large protected area of the Monteverde Reserve Complex (MRC) using a geographic information system (GIS).

2.2.2 Statistical Methods

The classification of forest-dependent species was based on Stiles (1985), where species which score ≤ 2 on a scale of 1-5 are considered forest-dependent. I used an adjusted richness of forest-dependent bird species as the response variable. Observed richness is sensitive to the number of individuals sampled. Therefore, I adjusted for different sample sizes by performing rarefaction on the raw species counts using the function rarefy from package vegan in program R (Oksanen et al. 2013, R Core Team 2013). The rarefied values were then standardized by the amount of forest in each 100-m point count. From here forward, this adjusted response variable will be referred to as "richness". Explanatory variables were also standardized by the amount of forest when appropriate.

Despite some points being in the same forest patch, I treated each as an independent sample. I screened for possible spatial dependence among points by examining variograms and by plotting the standardized residuals from GLM models versus their spatial coordinates, and found no evidence of high spatial correlation.

I examined the variables described above for breakpoints or threshold values, where the richness of forest-dependent bird species shows a drastic change in response. I

used a smoother (e.g., loess) on each univariate relationship and if a breakpoint was suggested, I continued with piecewise regression using the following model:

$$y_i = \begin{cases} \beta_0 + \beta_1 x_i + e_i & for \ x_i \leq \alpha \\ \beta_0 + \beta_1 x_i + \beta_2(x_i - \alpha) + e_i & for \ x_i > \alpha \end{cases}$$

where is y_i is the value for the ith observation, x_i is the value of the independent variable, α is the breakpoint, and e_i are assumed to be independent with homogeneous variance (Toms and Lesperance 2003). I found the optimal breakpoint location by calculating the model deviance along a range of the independent variable. The value minimizing the deviance indicates the breakpoint location. Finally, I generated confidence intervals for the breakpoint location with a bootstrap technique, nonparametric resampling of the errors (Davison and Hinkley 1997, Toms and Lesperance 2003). The errors are sampled with replacement and added to the fitted values to create a new set of "observations" from which the breakpoint is estimated. After repeating this many times, the 2.5[th] and 97.5[th] percentiles of the breakpoint distribution give a 95% confidence interval for the point estimate.

Richness of forest-dependent bird species was also modeled as a function of the explanatory variables described above using multiple linear regression. I began by examining the distribution of each variable and decided to log transform Area, Width, and Distance to MRC, giving them a normal distribution. I then screened for collinearity among variables with correlations >0.6 (or < -0.6) being unacceptable. I continued by examining variance inflation factors among variables, with an acceptable value being ≤ 3 (Zuur et al. 2009).

The variables of Log_{10} Width, Edge and Log_{10} Area are highly collinear. However, these variables describe the shape of the forest patch and are important for making management recommendations. I therefore ran the proceeding analysis three times, rotating which shape variable was included. The variables comprising the full multiple regression model are presented in Table 2.1. After assessing the full model for heterogeneity of variance, I took two model selection approaches, both yielding similar results. I first performed a manual backwards selection by conducting likelihood ratio tests on nested models, successively removing terms until all were significant. In the second approach, I examined all subsets of models nested within the full model and ranked them according to AICc.

2.3 Results

I detected 113 species during three repetitions of 25 point counts, 48 of which are considered forest-dependent species. Of the forest-dependent species, 14 were detected at just one site, and an additional 8 were detected at only two sites. A full list of forest-dependent species detected is presented in Table 2.2.

A loess smoother suggested that the variables Log_{10} Area and Basal Area have a nonlinear relationship with Richness. A breakpoint at the value of Log_{10} Area = 4.42, 95% CI [4.16, 4.87] was identified, corresponding to back-transformed value of 2.6 ha (Figure 2.2). For Basal Area, a value of 25.15 m^2/ha, 95% CI [5.51, 45.03] was identified as the breakpoint.

According to AICc, the top multiple regression model included either Log_{10} Area, Log_{10} Width, or Edge (whichever shape variable was in the model). Also included were Basal Area, Vine, and for the model with Log_{10} Area, Canopy Height was included (Table 2.3). The models predict that the richness of forest-dependent species will increase with (i) an increase in forest patch area, (ii) an increase in patch width, (iii) a decrease in the amount of edge, (iv) an increase in vine complexity, (v) and an increase in the basal area of trees. Each model, containing either Log_{10} Area, Log_{10} Width, or Edge, explained of 80.4%, 80.5%, and 78.1% of the variation, respectively.

2.4 Discussion

The debate over whether agricultural practices should locally intensify to spare other lands for conservation, or decrease intensity to create a more wildlife friendly landscape has largely remained in a theoretical context. This is in part due to a lack of empirical studies comparing both strategies. Chandler et al. (2013) presented the first well-defined land-sparing system, IOC coffee, and demonstrated important advantages when compared with wildlife friendly shade coffee. The identification of habitat thresholds for IOC coffee cultivation given here represents a key advancement in the implementation of land-sparing agriculture for biodiversity conservation. It should be noted that threshold values are where the richness of forest-dependent species shows a change in response, and are not an actual management recommendations.

Area-related increases in the richness and abundance of species is a cornerstone concept in the discipline of conservation biology (MacArthur and Wilson 1967). This has been extended to include effects of local extinction and colonization events in the

17

context of metapopulation theory (Levins 1969, Hanksi 1989). However, this model, originally developed to explain patterns of diversity on oceanic islands, may not entirely explain patterns observed on terrestrial habitat "islands", which are also influenced by biotic or abiotic effects of surrounding habitat. For example, forest edges are prone to different microclimates, and abundance of generalist open-area species that either compete with or prey on adults or nests of forest-dependent birds (Murcia 1995). The potential for edge-related effects as additional drivers of forest species richness in these patches is further suggested by the negative relationship of their abundance with forest patch width, because narrower patches have less core habitat that appears to be required by forest species in our system.

Since the analyses included patches that were irregularly shaped, the area threshold value is probably conservative, because rounder and less complex patches of the same area would probably support more species. This is supported by the multiple regression models including forest patch width and edge (Table 2.3). Thus, it would not satisfy the objectives of IOC if practitioners conserved >2.6 ha in a narrow elongated or highly linear strip of forest. I was unable to unambiguously partition the effects of area, width, and edge amount of forest patches, and therefore recommend that a 2.6 ha IOC forest patch be no narrower than the average width (131 m) in the dataset, and contain no more than the average edge density (398 m/m^2). In addition to area, width and edge, richness of forest birds was also influenced by internal characteristics, such as increased basal area and vine growth. Increased richness with these variables is expected because they represent conditions associated with stand maturity (Clark 1996, Guarigauta and Ostertag 2001, Nadkarni et al. 2004). Unlike patch area and width, however, it is less

18

clear how these variables can be related to best management practices for IOC coffee

farms. In the case of basal area, the conservation of even young forest is valuable, since

forests develop rapidly in the tropics and soon provide at least some of the ecosystem

function of mature forests (Letcher and Chazdon 2009). Thus, it might be advantageous

to allow farmers with young forest to claim them as part of their IOC farms, and because

the value of the carbon is a direct function of basal area, farmers conserving more

biologically desirable mature forest as IOC will receive more benefit. An alternative

would be to permit farmers with forest with basal area values of at least 5.51 m^2/ha

(corresponding at my site to a forest approximately 15-20 years old), which would strike

a balance between making IOC applicable to farms even with little or highly degraded

forests and ensuring that it in fact conserves the desired forest values. Vine tangles could

be more problematic, since it is not really feasible to mandate that farmers manipulate

vine levels, or even clear whether it would be possible to do so. Mandating values for

these vegetative characteristics represent one of the key impediments to shade coffee

certification.

A principal advantage of IOC from the standpoint of the farmer is that it increases

yields relative to shade coffee. Nevertheless, farmers could further increase their income

by converting forested portions of farms to coffee as well. Identifying strategies for

increasing the value of the forested portions of IOC farms will be important to the

widespread adoption of this strategy. One potential idea would be to allow farmers to

extract resources from an IOC forest patch. As long as trees were harvested while still

remaining above the threshold level of basal area it is likely the value for forest-

dependent species would be maintained. The value of the carbon from the IOC forest

19

would be undermined, however, both because of the direct reduction in basal area that comprises the carbon and because it could devalue the carbon itself. Thus, it seems like even restricted exploitation of IOC forests would be counterproductive.

IOC is practiced on farms with small areas under cultivation, resulting in small patches of forest which may exclude forest-dependent species that are highly sensitive to area. IOC could be practiced in conjunction with a larger reserve to accommodate those species, perhaps even facilitating the persistence of metapopulations (Falcy and Estades 2007). Chandler and King (2011) did find an effect of distance from the MRC on the richness of forest-dependent species. This of course will vary by species due to different area requirements, perception of scale, dispersal abilities, and tolerance to the surrounding landscape matrix (Phalan et al 2011). Though the needs of more wide-ranging species such as raptors would not be met within IOC farms themselves, it is hard to conceive how the permanent protection of even small forest patches would not make these landscapes more permeable to these species. Several species listed by the International Union of Concerned Scientists as near threatened or vulnerable have been recorded on the study site (Table 2.4).

IOC coffee has important advantages over shade coffee, favoring a land-sparing over wildlife friendly approach. However, as pointed out by Chandler et al (2013), the adoption of either system may depend on the existing land use pattern. For example, where there is not land available for restoration, and shade coffee farms already exist, it may be best to maintain the status quo, as shade coffee is clearly preferable to a sun grown monoculture. That said, IOC could be widely adopted because many farms

already have an IOC-like patch of forest, and if not, degraded lands can be allowed to regenerate.

The threshold values I calculated for IOC forest patches represent an important step in implementing this land-sparing agricultural practice within a market-based framework to support the conservation of habitat for priority species that cannot persist in shade coffee farms. Additional work is planned to establish the voluntary standard for marketing carbon from IOC farms, which will include the quantification of carbon stocks and their relationship to forest patch characteristics. Furthermore, modeling exercises to explicitly contrast development scenarios for shade-coffee versus IOC in terms of coffee yields, carbon yields and biodiversity conservation at landscape-scales will help further illustrate the value of this approach and guide its implementation.

Table 2.1 Summary statistics of variables included in multiple regression models. Note: only one of the first three variables were in a given model due to high colinearity. A dummy variable indicating whether the forest edge was bordered by coffee (n = 14) or pasture (n = 11) was also included.

Variable	Mean ± s.d.	Min – Max
Area (ha)	5.4 ± 6.1	1.4 – 26.1
Width (m)	131 ± 88.8	44.1 – 331.9
Edge (m/m^2)	397.5 ± 171.32	103.6 – 682.3
Dist mrc (m)[a]	1559 ± 1588	320 – 6172
Extent primary forest (%)	43.84 ± 26.5	0 – 90
Canopy height (m)	13.82 ± 4.62	5 – 24
Canopy cover (%)	70.7 ± 10.08	40 – 82
Basal area (m^2/ha)	14.79 ± 12.55	0 – 53.7
Epiphyte index (1-4)	1.92 ± 0.64	1 – 3
Vine index (1-4)	2.8 ± 0.82	1 – 4
Leaf index (1-4)	3.32 ± 0.56	2 – 4
Elevation (m)	1114 ± 97.61	928 – 1262

[a]Distance from the Monteverde Reserve Complex

Table 2.2 List of forest-dependent species detected on point counts

Common Name	Species	Family
Black Guan	*Chamaepetes unicolor*	Cracidae
Green Hermit	*Phaethornis guy*	Trochilidae
Violet Sabrewing	*Campylopterus hemileucurus*	Trochilidae
Purple-throated Mountain-gem	*Lampornis calolaemus*	Trochilidae
Coppery-headed Emerald	*Elvira cupreiceps*	Trochilidae
Stripe-tailed Hummingbird	*Eupherusa eximia*	Trochilidae
Orange-bellied Trogon	*Trogon aurantiiventris*	Trogonidae
Keel-billed Toucan	*Ramphastos sulfuratus*	Ramphastidae
Emerald Toucanet	*Aulacorhynchus prasinus*	Ramphastidae
Rufous-tailed Jacamar	*Galbula ruficauda*	Galbulidae
Golden-olive Woodpecker	*Colaptes rubiginosus*	Picidae
Pale-billed Woodpecker	*Campephilus guatemalensis*	Picidae
White-fronted Parrot	*Amazona albifrons*	Psittacidae
Zelodon's Antbird	*Myrmeciza zeledoni*	Thamnophilidae

Plain Antvireo	*Dysithamnus mentalis*	Thamnophilidae
Spotted Barbtail	*Premnoplex brunnescens*	Furnariidae
Spotted Woodcreeper	*Xiphorhynchus erythropygius*	Furnariidae
Olivaceous Woodcreeper	*Sittasomus griseicapillus*	Furnariidae
Bright-rumped Attila	*Attila spadiceus*	Tyrannidae
Scale-crested Pygmy-Tyrant	*Lophotriccus pileatus*	Tyrannidae
Paltry Tyrannulet	*Zimmerius vilissimus*	Tyrannidae
Yellowish Flycatcher	*Empidonax flavescens*	Tyrannidae
White-throated Spadebill	*Platyrinchus mystaceus*	Tyrannidae
Three-wattled Bellbird	*Procnias tricarunculatus*	Cotingidae
Long-tailed Manakin	*Chiroxiphia linearis*	Pipridae
Lesser Greenlet	*Hylophilus decurtatus*	Vireonidae
Rufous-and-white Wren	*Thryophilus rufalbus*	Troglodytidae
Gray-breasted Wood-Wren	*Henicorhina leucophrys*	Troglodytidae
Long-billed Gnatwren	*Ramphocaenus melanurus*	Pilioptilidae
Slaty-backed Nightingale-Thrush	*Catharus fuscater*	Turdidae
Swainson's Thrush	*Catharus ustulatus*	Turdidae
White-throated Thrush	*Turdus assimilis*	Turdidae
Wood Thrush	*Hylocichla mustelina*	Turdidae
Golden-crowned Warbler	*Basileuterus culicivorus*	Parulidae
Slate-throated Redstart	*Myioborus miniatus*	Parulidae
Tropical Parula	*Setophaga pitiayumi*	Parulidae
Rufous-capped Warbler	*Basileuterus rufifrons*	Parulidae
Black-and-white Warbler	*Mniotilta varia*	Parulidae
Black-throated Green Warbler	*Setophaga virens*	Parulidae
Common Bush-tanager	*Chlorospingus flavopectus*	Thraupidae
Silver-throated Tanager	*Tangara icterocephala*	Thraupidae
Scarlet-thighed Dacnis	*Dacnis venusta*	Thraupidae
Chestnut-capped Brush-Finch	*Arremon brunneinucha*	Emberiziae
Chestnut-headed Oropendola	*Psarocolius wagleri*	Icteridae
Golden-browed Chlorophonia	*Chlorophonia callophrys*	Fringillidae

Table 2.3 Best multiple linear regression models for richness of forest-dependent species including either Log_{10} Area, Log_{10} Width, or Edge

Shape variable	Parameter	Estimate	s.e.	t	p
Log_{10} Area	Constant	-3.327	1.078	-3.087	0.006
	Log10 Area	0.923	0.206	4.482	<0.001
	Vine	0.202	0.086	2.341	0.030
	Basal	0.383	0.006	6.497	<0.001
	Canopy				
	Height	-0.035	0.017	-2.001	0.059
Log_{10} Width	Constant	-2.965	0.601	-4.931	<0.001
	Log10 Width	1.676	0.266	6.300	<0.001
	Vine	0.234	0.084	2.782	0.011
	Basal	0.028	0.006	4.981	<0.001
Edge	Constant	1.494	0.322	4.635	<.0001
	Edge	-0.003	0.0004	-5.748	<0.001
	Vine	0.222	0.089	2.500	0.021
	Basal	0.027	0.006	4.505	<0.001

Table 2.4 Species which occur on the study site and listed by the IUCN as near threatened or vulnerable. Forest-dependent species, who could benefit from IOC cultivation, are shown in bold.

Common Name	Species	Family	IUCN Status	Trend
Black Guan	*Penelope purpurascens*	Cracidae	Near threatened	Decreasing
Solitary Eagle	*Harpyhaliaetus solitarius*	Accipitridae	Near threatened	Decreasing
Ornate Hawk-eagle	Spizaetus ornatus	Accipitridae	Near threatened	Decreasing
Ruddy Pigeon	*Patagioenas subvinacea*	Columbidae	Vulnerable	Decreasing
Resplendent Quetzal	*Pharomachrus mocinno*	Trogonidae	Near threatened	Decreasing
Red-fronted Parrotlet	*Toit costaricensis*	Psittacidae	Near threatened	Decreasing
Ochre-breasted Antpitta	*Grallaricula flavirostris*	Grallariidae	Near threatened	Decreasing
Gray-throated Leaftosser	*Sclerurus albigularis*	Furnariidae	Near threatened	Stable
Olive-sided Flycatcher	*Contopus cooperi*	Tyrannidae	Near threatened	Decreasing
Three-wattled Bellbird	Procnias triarunculatus	Cotingidae	Vulnerable	Decreasing
Golden-winged Warbler	*Vermivora chrysoptera*	Parulidae	Near threatened	Decreasing
Painted Bunting	*Passerina ciris*	Cardinalidae	Near threatened	Decreasing

Figure 2.1 Spatial configuration of forests with point count locations indicated by the red dots.

Figure 2.2 Scatterplot of Richness and Log_{10} Area. The center vertical line indicates the estimated breakpoint at 4.42, corresponding to an area of about 2.6 ha. The outer lines indicate a 95% confidence interval (4.164, 4.870).
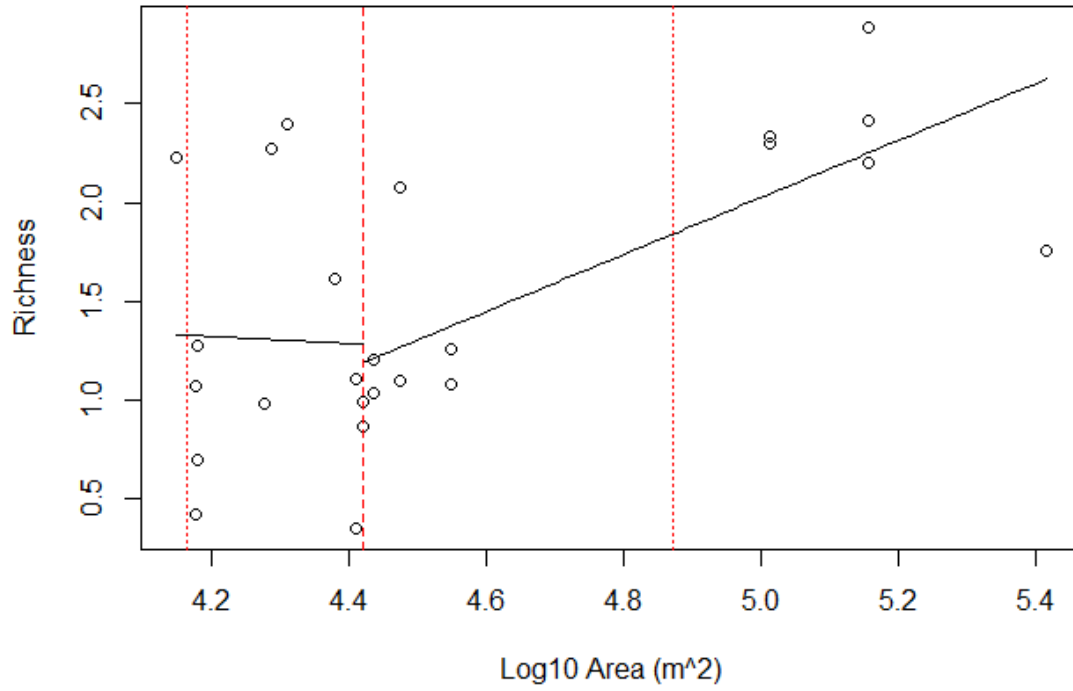
Figure 2.3 Scatterplot of Richness and Basal Area. Thick dashed vertical line indicates the estimated breakpoint at 25.15 m^2/ha, while the outer lines indicate a 95% confidence interval (5.51, 45.03).
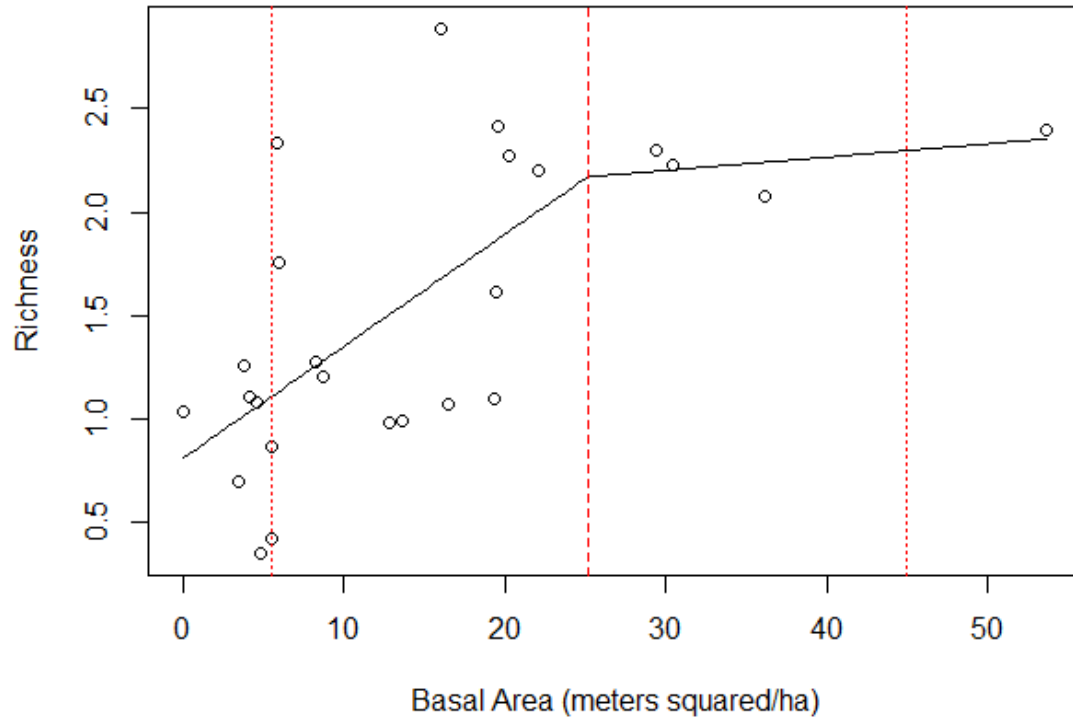
CHAPTER 3

THE HABITAT-SPECIFIC SURVIVAL OF A PRIOIRY MIGRANT

3.1 Introduction

Although it is widely recognized that migrant populations can be limited in the

nonbreeding season (Rappole et al. 2003b, Norris et al. 2004), there exists few detailed

studies of Golden-winged warbler (*Vermivora chrysoptera*) nonbreeding ecology in the

literature. Chandler and King (2011) conducted the first intensive study in which they

quantified habitat selection patterns and estimated habitat-specific abundances. They

found that Golden-winged warblers are forest-dependent species that appear to select for

moderate canopy heights and patchily distributed microhabitat features. Such a high

degree of specialization has been found to increase extinction risk (Clavel et al. 2010).

They maintain large, non-overlapping home ranges resulting in low densities, and

increased rarity. For these reasons, this population of Golden-winged warblers in this

study appears especially vulnerable to habitat loss, and may require large areas of forest

to persist.

Estimates of abundance and density can be misleading indicators of habitat

quality (Van Horne 1983). High densities can occur in habitats with low survival rates

due to social factors such as the territorial defense of quality habitat (Rappole et al.

1989). It is therefore important to consider multiple indicators of habitat quality when

logistically feasible (Johnson 2007). Habitat quality is often determined through a

measurement of performance, such as reproductive success or fitness (i.e., per capita

population change, Fretwell and Lucas 1969). The most obvious performance parameter

on nonbreeding grounds is survival (Stearns 1992), and estimates of habitat-specific survival can effectively be used as an indicator of nonbreeding habitat quality (Johnson et al. 2006). Also, if general survival is highest during the breeding season, or between nonbreeding seasons, nonbreeding ground factors may limit migrant populations (Rappole and McDonald 1994), stressing the importance of management during all phases of the annual cycle. I complemented Chandler and King's (2011) estimates of Golden-winged warbler habitat-specific abundances with measures of habitat-specific survival.

3.2 Methods

3.2.1 Field Methods

I identified quality Golden-winged warbler habitat through estimates of habitat-specific survival by recording encounters of marked individuals through time. Other studies using this approach revisiting locations where individuals were originally banded, sometimes standardizing the number and duration of these resighting visits (Holmes et al. 1989, Sillett and Holmes 2002, Johnson et al. 2006). The species for which this approach has been employed (e.g. *Setophaga caerulescens, Setophaga ruticilla, Seiurus aurocapilla*) are relatively conspicuous and occupy small territories (<1 ha), so this approach can be feasibly employed. In contrast, Golden-winged warblers can occupy large home ranges (3-15 ha, average 9 ha, Chandler 2010) which may feature multiple habitat categories, and are very inconspicuous on the nonbreeding grounds, making it difficult to determine what area their territories encompass. Therefore, habitat was

quantified with the use of an intensive playback/resight survey protocol which takes an adaptive approach at identifying what areas the individual frequents or defends (Figure 3.1). Individuals were located by traversing the ~30 km^2 area surrounding our headquarters in Cedral, Puntarenas Provence and searching all habitats in which Golden-winged warblers had been located during a prior, systematic survey by Chandler (2010). These habitats included primary and secondary forests, forested ravines, scrub areas of abandoned pastures, orchards, and coffee farms near forest. Searches consisted of visually scanning habitat for individual birds or more often the mixed-species flocks that Golden-winged warblers associate with, and using playback periodically to confirm the absence of birds from searched areas. As indicated by the values of habitat measurements, a broad range of habitat conditions were encompassed. Once located, birds were captured using a decoy placed between nets, and broadcasting the species song. From the central capture location, resight attempts were made 50 meters away on a randomly selected bearing of 0, 120, or 240 degrees. If the individual was detected, then location and habitat variables were measured as described below. If the individual was not detected an attempt was made at a second randomly chosen bearing, and if still not detected, at the original capture location. Visits to each point were 10 minutes long during which a recording of Golden-winged warbler vocalizations was played at a standard volume of 100 dB at a distance of 1 meter from the speaker during the entire period, as recommended by Chandler (2010). Each survey of 1-3 points comprised a single resight attempt, which were conducted biweekly. Subsequent resight attempts used the location where the individual was last detected as the central location, with radiating points expanding into potentially new areas. This allowed the establishment of

points within the birds' home range without the prior knowledge of territory extent typically available to researchers working on conspicuous species with small, well defined home ranges. Points were only conducted in habitat types used by Golden-winged warblers as indicated above and reported by Chandler (2010). If two resight attempts passed without detection, a 30 minute search of the area was undertaken using playback within the vicinity of the initial capture location. The following variables were recorded at each point: geographic coordinates, elevation, habitat category, canopy height, percent canopy cover, and the basal area of trees as estimated with a cruising prism. The following microhabitat features were recorded within 8 meters: dead hanging leaf index (0-10 low, 11-100 med, >100 high), bromeliad index (0-10 low, 11-50 med, >50 high), the number of vine tangles greater than 1 meter in diameter, and the average thickness of the moss layer covering trees.

Because Golden-wings are difficult to find, let alone catch, all located individuals were targeted for tagging and inclusion in survival estimates. Individuals banded previously by Chandler (2010) were be searched for and, if found, also included. Upon subsequent field seasons, previously marked birds were searched for and, if located, the resight protocol described above was resumed. If not found, individuals were searched for 3 times.

3.2.2 Statistical Methods

Cormack-Jolly-Seber (CJS) models were used to estimate survival rates (Lebreton et al. 1992). CJS is a flexible class of models that account for detection probabilities alongside of apparent survival and can be extended to investigate differential survival

among individuals or groups, such as age class or sex, or environmental variables, such as habitat covariates.

I modeled apparent survival (ϕ) and resight probability (p) as using a hierarchical formulation of the CJS model (Royle 2008, Royle and Dorazio 2008), described as follows:

$$z(i,t) \mid z(i,t-1) \sim \text{Bernoulli}(z(i,t-1)\phi)$$

$$y(i,t) \mid z(i,t) \sim \text{Bernoulli}(z(i,t)p)$$

Where $z(i, t)$ is the underlying variable describing if individual i was alive at time t, and $y(i,t)$ is the observation process. Apparent survival is determined by the status of the individual in the proceeding time period (0 if dead, 1 if alive) multiplied by survival probability. This way, individuals considered dead (or emigrated) have a zero chance of being detected, as the observation process is conditional on the survival state. Otherwise, an individual is detected with a probability of p. In this formulation, covariates of both survival probability and detection probability can be easily accommodated. Bayesian analysis requires the specification of prior distributions for all estimated parameters. I used non-informative distributions as little previous information was known. Convergence was assessed using visual inspections and Ruben-Gelman diagnostics (Gelman and Ruben 1992).

Encounter histories were set up by day (versus week or month), which provides estimates of daily survival. This way, by explicitly defining the nonbreeding season (based on arrival and departure dates, Chandler 2010), survival can be estimated for the

entire 6.5 month stationary nonbreeding season, as well as among seasons. This is an improvement over many past studies where mark-resight efforts occur during a shorter period, and individuals who die within the stationary nonbreeding season, but outside the observation period, are treated by the CJS model as dying outside of the season entirely.

I conducted these analyses using Bayesian Markov-chain Monte Carlo methods to estimate model parameters implemented in the program JAGS (Plummer 2003). I was unable to model survival as a function of individual random effects – that is, as a continuous covariate – due to a low sample size resulting in convergence issues. Instead, I modeled survival as a fixed group effect, where individuals were placed into one of three groups, each representing a range of the explanatory variable. Three groups allowed for enough resolution to detect either a quadratic or linear relationship with survival, while keeping the number of estimated parameters low to avoid convergence issues. Groups were defined based on the number of individuals divided into groups of equal numbers as well as the values of the covariates divided into equal intervals. The two approaches yielded qualitatively similar results. However, comparisons were made based on groups of equal sample sizes, because that yielded a more comparable precision per group. I considered two habitat variables shown to be important in habitat-specific abundance estimates of Golden-winged warblers (Chandler and King 2011): canopy height, and the number of dead hanging leaves. Dividing canopy height into equal numbers of individuals gave ranges of 5.15 – 8.75, 8.75 – 13.4, and 13.4 – 22 meters. Leaf numbers were recorded as an index (1 = low, 2 = med, 3 = high) at each point, and then averaged for the territory value. Dividing leaf numbers into groups resulted in ranges of 1.1 – 1.82, 1.82 – 2.12, and 2.12 – 2.86.

I modeled survival among habitat groups with an additive effect of age, accounting for the fact the survival is generally lower for juvenile songbirds. Individuals in their first winter, or second calendar year, represented the juvenile age class, whereas all other individuals, being after second year birds, were of the adult class. Initial modeling efforts found no differences in among season survival between age classes, and therefore was not included in subsequent models. Detection probability was allowed to vary among habitat groups.

To ensure that differential survival in canopy height or dead hanging leaves was not being driven by another variable, I conducted a principle components analysis (PCA) on all recorded variables believed to be potentially important for Golden-winged survival: canopy height, canopy cover, basal area, leaf index, bromeliad index, moss thickness, number of vine tangles, and elevation.

3.3 Results

I banded 45 Golden-winged warblers in the 2011 and 2012 seasons, 42 males and 3 females. I was able to locate 3 males and 1 female previously banded by Chandler (2010). I also included 1 individual monitored by Chandler (2010), but not encountered during my study. Habitat data for this individual were collected post hoc. I excluded 6 individuals from analysis that were banded in thin riparian strips of forest, or in brushy areas far from a forest patch, habitats not typically defended by Golden-winged warblers. I searched the closest forest patches likely to be occupied by a Golden-winged warbler, and never relocated these individuals. Some were captured after March 15 and were thus likely passage migrants. The others were possibly floaters, on off-territory forays, or

moving between areas of forest. This procedure resulted in 397 resight attempts for 44 individuals (40 males, 4 females).

The areas identified by the adaptive resight approach resulted in an average of 9.9 points (min 6; max 20) per territory, covering an average minimum convex polygon (MCP) of 1.07 ha (min 0.28; max 3.93; Figure 3.2).

Apparent monthly survival was 0.945 (SD 0.02), equivalent to a 0.692 probability of surviving the entire 6.5 month stationary nonbreeding season. Detection probability was estimated at 0.545 (SD 0.03). Eighteen individuals were encountered in multiple seasons. Two individuals survived for at least four seasons, four for three seasons, and twelve for two seasons. Among season apparent survival was estimated at 0.728 (SD 0.08). This rate includes survival during the breeding season as well as both migratory periods. Annual survival was derived by multiplying the within season probability by among season, yielding an apparent survival probability of 0.504.

I marked a total of 17 juveniles and 27 adults, and was therefore able to estimate age-specific survival rates. Juvenile monthly survival (0.827, SD 0.06) was less than adult monthly survival (0.942, SD 0.02, $p = 0.067$). This equates to probabilities of 0.292 and 0.682 respectively for surviving the 6.5 month stationary nonbreeding season.

The tallest canopy height grouping had a lower monthly survival (0.886, SD 0.04) when contrasted against the middle (0.981, SD 0.02) and lower (0.963, SD 0.03) heights ($p = 0.045$, Figure 3.3). I found no significant difference in monthly survival among sites with a low amount of dead hanging leaves (0.980, SD 0.02), a moderate amount of leaves (0.923, SD 0.04), or with many dead hanging leaves (0.916, SD 0.05, $p = 0.272$, Figure 3.3).

The summary statistics of posterior distributions for all estimated parameters are presented in Table 3.1.

The latent root and scree plot criterion agreed that the first three principle components should be retained for interpretation. These components explained 38.8, 21.3 and 12.6% of the variation, respectively, for a cumulative of 72.7 %. Principle component loadings are given in Table 3.2. I interpreted the first component as primarily describing a gradient from forests with a high basal area and tall canopy to lower basal area and shorter canopy heights. Monthly survival estimates along the first component were similar to the original canopy height model, with survival lowest for the group associated with a tall canopy. I interpreted the second component as primarily describing a gradient of dead hanging leaf numbers, as that variable was loaded with a high level of significance. There was no significant difference found among groups.

3.4 Discussion

Many species of Neotropical migrant birds have undergone declines (King et al. 2006, Sauer et al. 2014), yet the causes remain unclear, partially due to the lack of information on key vital rates throughout the year (Faaborg et al. 2010b). The winter period is particularly understudied despite evidence that this period of the annual cycle could be critical (Rappole and McDonald 1994, Studds and Marra 2005, Calvert et al. 2009), and that habitat alteration from anthropogenic influences could severely degrade habitat needed for some species. The difficulty of obtaining reliable vital rates is one impediment to progress in this area. Conspicuous species with small territories can be reliably tracked to obtain decent survival estimates, however for cryptic species with

large home ranges a different approach is indicated. Radio telemetry is useful, but battery life is limited and transmitter weight might actually alter survival rates (Chandler and King 2011). For this reason, the adaptive resight methodology I developed represents an important advancement in generating standardized, robust survival estimates for cryptic species in intractable habitats.

It must be conceded that mark-resight analyses yield only 'apparent survival' because mortality cannot be separated from permanent emigration, however, anecdotal evidence from our study area suggests very high site fidelity of individuals within a season, regardless of age, and individuals have been observed occupying the same territory in subsequent seasons, making it less likely that survival estimates are confounded by emigration. Furthermore, permanent emigration still indicates lower persistence, and since persistence is also widely used as a correlate of survival (Johnson et al. 2006), it still is useful for yielding information on the influence of habitat on demographic rates during the nonbreeding season.

The annual survival rate for Golden-winged warblers of 0.504 reported here is within the range $(0.41 - 0.64)$ of estimates for other Nearctic-Neotropical songbird migrants (Stutchbury et al. 2009, Calvert et al. 2010, Faaborg et al. 2010b, Wolfe et al. 2013). Differences in monthly survival rates among periods of the annual cycle can determine when mortality is highest. For example, Jones et al. (2004), found that male Cerulean warblers *Setophaga cerulea* had a higher breeding season monthly survival (0.98) than among season (0.93), indicating that most mortality occurs during migration or the overwinter period. By examining both stationary breeding and nonbreeding

monthly survival rates, Sillett and Holmes (2002) concluded that mortality during migration is extremely high for the Black-throated blue warbler *Setophaga caerulescens*.

For Golden-winged warblers, I found the monthly rate of surviving the nonbreeding season (0.945) to be the same as the monthly among season survival rate (0.944). The among season period encompasses both migrations and the breeding season, which cannot be separated in my data. However, it is hypothesized that migratory species may experience high mortality during migratory periods (Sillett and Holmes 2002, Newton 2006, Calvert et al. 2009, Klaassen et al. 2012). If this holds true for Golden-winged warblers, then the monthly survival estimate for the breeding season is biased low. Season-specific survival rates for other parts of the annual cycle, and other areas of the range are needed. This is true for all species, as most studies only give annual survival estimates.

My estimates of age-specific survival are consistent with the general finding that juvenile survival is less than adults (Gardali et al. 2003). Lower within season juvenile survival could be caused by juveniles being disproportionately displaced into suboptimal habitat. I was unable to estimate habitat-specific differences in survival between ages, however analyses of contingency tables indicated no segregation by habitat for any of the measured variables. Lower juvenile survival may also be caused by less experience in general, greater predation rates, or driven by a habitat variable that I did not consider.

Initial exploratory modeling showed no difference in among season survival between ages. That is, after surviving their first stationary nonbreeding season, juveniles are estimated to have the same survival as adults. This is supported by similar return

rates among seasons (~41%). An estimate of annual juvenile survival was not possible as my data do not include the post-fledgling period nor the first migration.

Estimates of juvenile survival rates for different phases of the annual cycle remain uncommon, despite the fact that differences may be important. For example, Gruebler et al. (2014) found that lower annual survival in juvenile Barn swallows *Hirundo rustica* can be attributed to low survival during the post fledgling period, after which they have similar survival to adults.

Canopy height and dead hanging leaves were included in the habitat-specific survival models because they have been shown to be associated with Golden-winged warbler abundance (Chandler and King 2011). Contrary to my expectations, the canopy height at which Golden-winged warblers experience the lowest survival rates (~13-22m) corresponds to the canopy height at which Golden-winged warblers reach their highest abundance (Chandler and King 2011). Similarly, I found no significant difference in survival among areas varying in the amount of dead hanging leaves, despite prior findings that Golden-winged warbler abundance is positively associated with dead leaf abundance (Chandler and King 2011).

It seems there are several different hypotheses to explain the observation that the abundance of Golden-winged warblers at my sites was associated with habitat conditions in which survival was lowest. First, Golden-winged warblers might be actually selecting habitats in which they experience lower survival. This seems unlikely, as the conditions under which this occurs tends to be characterized by high density populations, despotic interactions or recent large-scale habitat perturbations. Although Golden-winged warblers are fiercely territorial during the winter period, they occur at low densities, and

40

our study area still encompasses extensive, although diminishing, natural habitat. Alternatively, our estimates of survival or analyses in relation to covariates might be flawed. This too seems unlikely, since the procedures we used to establish resight histories and calculate apparent survival are standard and relatively straightforward. Alternative groupings for subjects into habitat categories yielded similar results, suggesting these estimates are robust. Finally, because birds were drawn to survey points in my study using playback, habitat measurements may not necessarily reflect the habitat they selected. This is also unlikely as I was concerned with the placement of territories within the species range (second order selection, Johnson 1980), and habitat was measured at points following a protocol, ensuring unbiased placement within a defended territory. However, playback may have drawn individuals outside of their territory. It is possible that Golden-winged warblers avoid tall canopy heights within whatever forests they occupy, and the tall height range at which they reach their lowest survival in my study represents less preferred habitat. Shorter canopy heights are characteristic of disturbed forests, which may provide greater foraging opportunities and better protection from predators than taller, undisturbed forest.

Bulluck et al. (2013) report high elasticity in adult annual survival for both the northern and southern breeding populations they studied, and suggest focusing conservation efforts on maximizing this parameter. However, management on the breeding grounds may not affect annual survival, as rates of migratory passerines are generally high during this period (Sillett and Holmes 2002, Jones et al. 2004). Managing for quality habitat on the nonbreeding grounds may increase annual survival and help to recover Golden-wing populations.

It is important to note that the study area is in a human-dominated landscape with many degraded forests embedded within an agricultural matrix. This may have affected the seasonal survival rate reported here. Range wide conservation efforts should focus on protecting what remains of intact forests. While disturbance features that Golden-winged warblers seem to prefer may be less common in contiguous mature forests, survival could be higher in these areas (e.g., steep hillsides, riparian areas, tree fall gaps).

In agricultural landscapes, regenerating and secondary forests could provide necessary habitat features. Although not specifically tested, Golden-winged warblers may also be able to persist in the regenerating forest patches of IOC coffee farms, and possibly in patches of mature forest because there are typically disturbance features at the edge of the forests. IOC forests may also contain features such as streams, which cause natural disturbances. However, negative edge effects may need to be considered.

It has been suggested that Golden-winged warbler populations can persist in shade-grown coffee farms (Confer et al. 2011). While individuals do occur on such farms in my study area (Chandler and King 2011), telemetry results indicated that these individuals like used the farm to move among forest patches (Chandler unpublished data). It should be noted that these farms were not quite certifiable following the criteria of most programs. Rustic shade coffee farms with plenty of microhabitat features, such as vine tangles and dead hanging leaves, may be able to provide suitable habitat, however many farms only satisfy the bare minimum to gain certification and low yields seem to make rustic shade unpalatable to most farmers. Ideally, habitat suitability should be determined through more than just occurrence, and the surrounding landscape should be considered, as proximity to forest may influence occurrence of on farm species (Anand et

al. 2008). The protection and regeneration of forest should be given precedence over improving on-farm conditions.

I was unable to estimate among season survival by habitat type, due to an already low sample of returning warblers being distributed among habitat types. Future researchers could attempt to band more individuals for a larger sample size, though this is difficult. It would also be valuable to get habitat-specific survival estimates in contiguous undisturbed forests and other areas of the stationary nonbreeding range. For example, Bennett (2012) found that Golden-winged warblers have different habitat associations in Honduras, including pine-oak forests. Differential survival between temporal periods within a season could be examined. For example, on my study site, it is possible that individuals have a lower survival probability during the *temporales* – a period of high wind and rain from October to January. Finally, we should continue working on the migratory connectivity of this species and examine possible carry over effects. Hobson et al. (in press) made a significant contribution to this using stable isotope analysis, including samples of individuals on my site (Figure 3.4).

Table 3.1 Summary statistics of posterior distributions for all parameters of Golden-winged Warbler apparent survival estimated by Cormack Jolly Seber models.

Parameter	Mean	SD	95% CI Lower	95% CI Upper
Within Season Monthly	0.945	0.020	0.906	0.979
Among Season	0.728	0.080	0.567	0.843
Adult Within Season Monthly	0.942	0.020	0.895	0.978
Juvenile Within Season Monthly	0.827	0.060	0.641	0.973
Canopy Low Within Season Monthly	0.963	0.030	0.885	0.998
Canopy Med Within Season Monthly	0.981	0.020	0.912	0.999
Canopy High Within Season Monthly	0.886	0.040	0.773	0.982
Leaf Low Within Season Monthly	0.980	0.020	0.934	0.999
Leaf Med Within Season Monthly	0.923	0.040	0.828	0.990
Leaf High Within Season Monthly	0.916	0.050	0.805	0.991
Component 1 Low Within Season Monthly	0.971	0.020	0.912	0.999
Component 1 Med Within Season Monthly	0.973	0.020	0.916	0.999
Component 1 High Within Season Monthly	0.822	0.060	0.690	0.935
Component 2 Low Within Season Monthly	0.975	0.020	0.921	0.999
Component 2 Med Within Season Monthly	0.874	0.060	0.751	0.975
Component 2 High Within Season Monthly	0.953	0.030	0.884	0.997

Table 3.2 Principle component loadings from PCA on all variables thought to potentially influence the survival of Golden-winged warblers. Absolute values above 0.32 are considered slightly significant and are shown in gray. Those above 4.0 are considered more significant and are shown in yellow. Anything above 5.0 is considered highly significant.

	Comp 1	Comp 2	Comp 3
Basal Area	-0.42446	0.083072	0.392211
Elevation	-0.28458	0.425467	0.289907
Log_{10} Canopy Height	-0.48732	-0.01739	0.107726
Canopy Cover	-0.32879	-0.4004	0.369798
Log_{10} Vine	-0.31451	-0.29698	-0.63393
Rank Transformed Moss	-0.34535	0.361366	-0.39093
Bromeliad	-0.28508	0.396706	-0.23149
Leaf	-0.3063	-0.52469	-0.07405

Figure 3.1 Conceptual model of the resight protocol. The capture location is represented by the red circle labeled 'C'. Box A represents the first resight occasion after banding. One attempt was made at Point 1 with no detection. A second attempt was then made at Point 2, and the individual was resighted. The subsequent occasion, Box B, is centered on Point 2, with an unsuccessful attempt made at Point 3, followed by a successful resighting at Point 4. In Box C, the selected resight locations are now centered on Point 4, with an unsuccessful attempt made at Point 5, followed by a successful resighting at point 6.
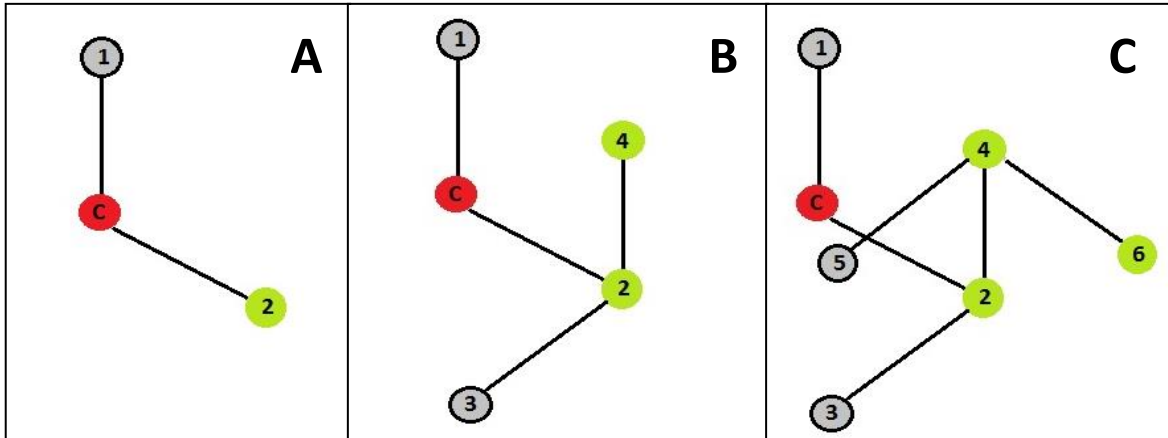
Figure 3.2 Minimum convex polygons around points used in the adaptive resight methodology to identify Golden-winged warbler territories (N=44). Areas range from 0.28 – 3.93 ha, with a mean of 1.07 ha.
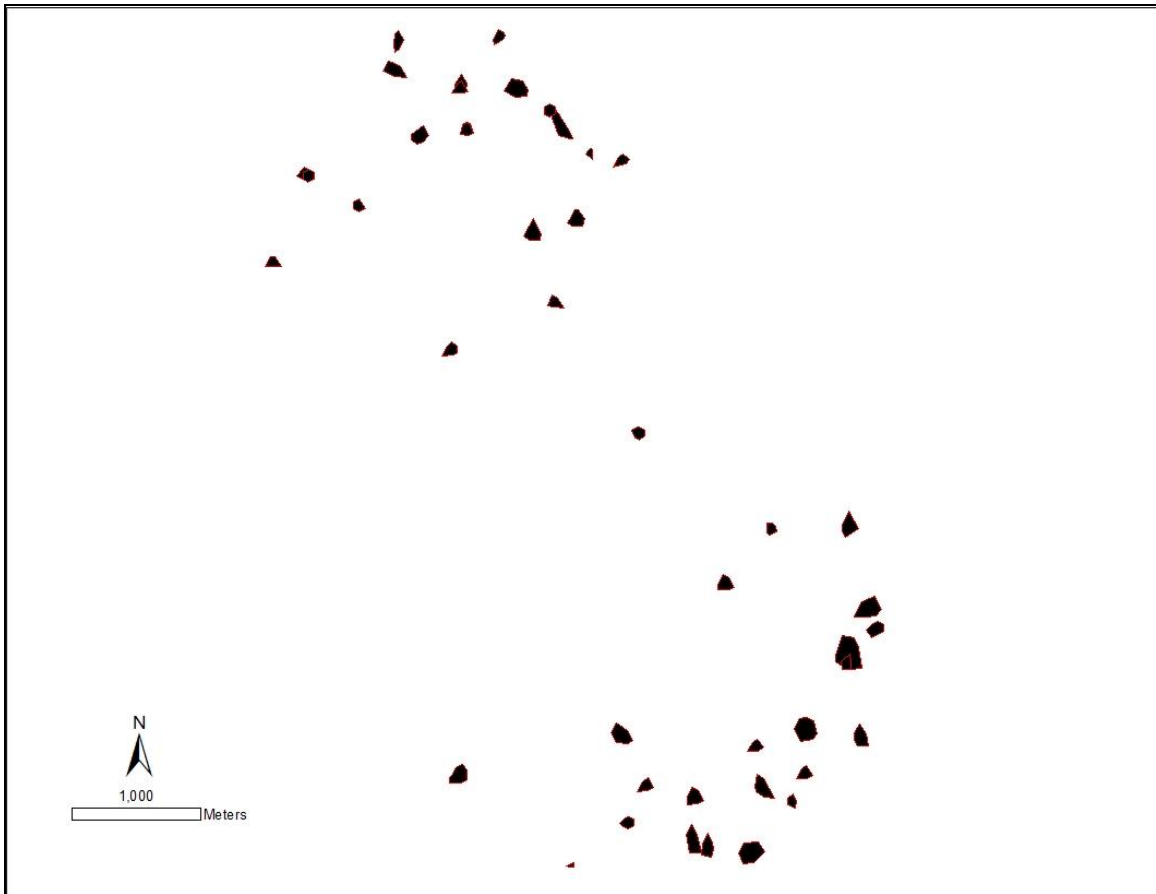
Figure 3.3 Within season monthly survival estimates as a function of canopy height, dead hanging leaves, and their associated eigenvectors. The top row shows models representing canopy height. Survival was lower at tall canopy heights in each model. The bottom row shows the models representing dead hanging leaf quantity. No significant effect was found.
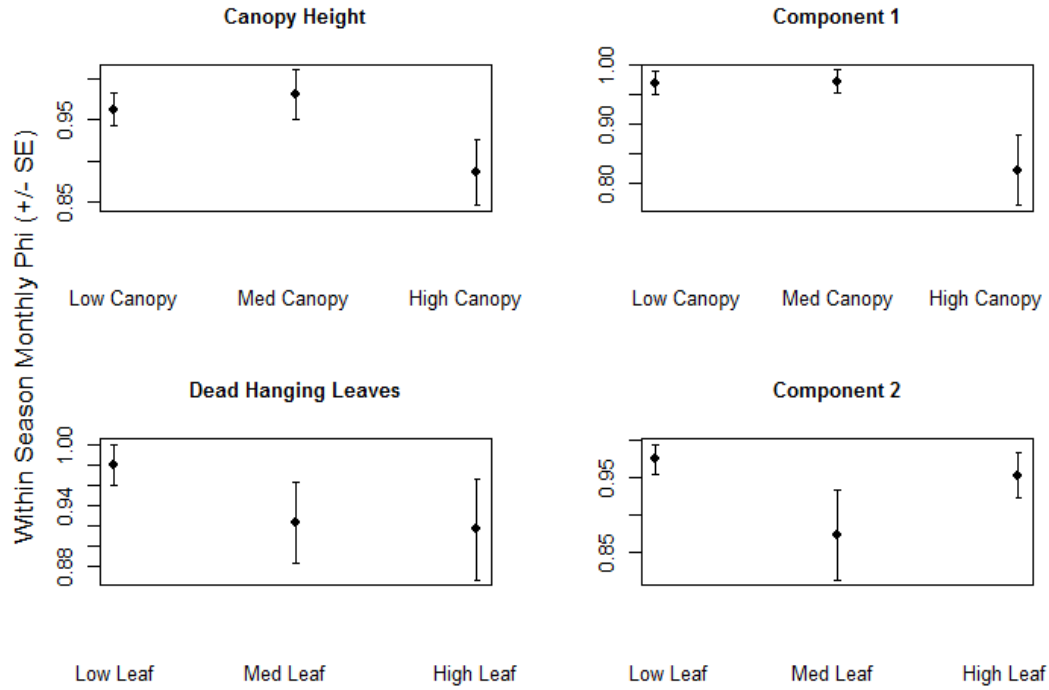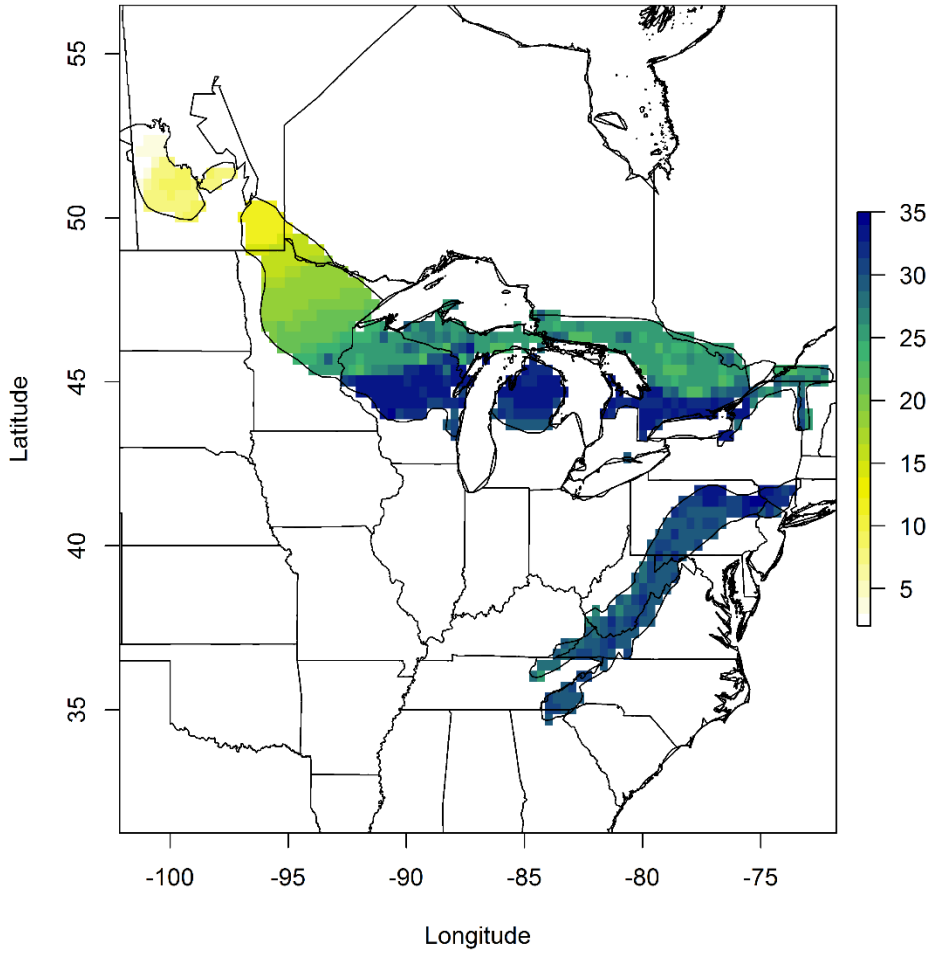
Figure 3.4 Geographic distribution of assigned origins for Golden-winged warblers sampled in Costa Rica (N=65). Numbers on legend indicate the number of individuals in the sample that were isotopically consistent with similarly colored portions of the map. Figure and results are from Hobson et al. (in press).

LITERATURE CITED

Achard, F., H. D. Eva, H. J. Stibig, P. Mayaux, J. Gallego, T. Richards, and J. P. Malingreau. 2002. Determination of deforestation rates of the world's humid tropical forests. Science 297:999-1002.

Agrawal, A., and K. Redford. 2009. Conservation and displacement: An overview. Conservation and Society 7:1-10.

Anand, M. O., J. Krishnaswamy, and A. Das. 2008. Proximity to forest drives bird conservation value of coffee plantations: implications for certification. Ecological Applications 18: 1754-1763.

Arce, V. C., R. Raudales, R. Trubey, D. I. King, R. B. Chandler, and C. C. Chandler. 2010. Measuring and Managing the Environmental Cost of Coffee Production in Latin America. Conservation and Society 7:141-144.

Avelino, J., H. Zelaya, A. Merlo, A. Pineda, M. Ordoñez, and S. Savary. 2006. The intensity of a coffee rust epidemic is dependent on production situations. Ecological Modelling 197:431-447.

Avelino, J., S. Cabut, B. Barboza, M. Barquero, R. Alfaro, C. Esquivel, J. Durand, and C. Cilas. 2007. Topography and crop management are key factors for the development of American leaf spot epidemics on coffee in Costa Rica. Phytopathology 97:1532-1542.

Balmford, A., R. E. Green, and J. P. W. Scharlemann. 2005. Sparing land for nature: exploring the potential impact of changes in agricultural yield on the area needed for crop production. Global Change Biology 11:1594-1605.

Bayard, T. S., and C. S. Elphick. 2010. How area sensitivity in birds is studied. Conservation Biology 24: 938-947.

Beer, J., R. Muschler, D. Kass, and E. Somarriba. 1998. Shade management in coffee and cacao plantations. Agroforestry Systems 38:139-164.

Bennett, R. E. 2012. Habitat associations of the Golden-winged warbler in Honduras. Master's Thesis, Michigan Technological University.

Buehler, D. A., A. M. Roth, R. Vallender, T. C. Will, J. L. Confer, R. A. Canterbury, S. B. Swarthout, K. V. Rosenberg, and L. P. Bulluck. 2007. Status and conservation priorities of Golden-winged Warbler (Vermivora chrysoptera) in North America. The Auk 124:1439–1445.

Bulluck, L., D. Buehler, R. Vallender, and R. J. Robertson. 2013. Demographic comparison of golden-winged warbler (*Vermivora chrysoptera*) populations in

northern and southern extremes of their breeding range. The Wilson Journal of Ornithology 125:479-490.

Calvert, A. M., S. J. Walde, and P. D. Taylor. 2009. Nonbreeding-season drivers of population dynamics in seasonal migrants: conservation parallels across taxa. Avian Conservation and Ecology 4:5-31.

Calvert, A. M., J. Woodcock, and J. D. McCracken. 2010. Contrasting seasonal survivorship of two migratory songbirds wintering in threatened mangrove forests. Avian Conservation and Ecology 5(1):2

Cashore, B. 2002. Legitimacy and the privatization of environmental governance: how non-state market driven (NSMD) governance systems gain rule-making authority. Governance: An International Journal of Policy, Administrations and Institutions 15, 503-529.

Chappell, M. J., J. Vandermeer, C. Badgley, and I. Perfecto. 2009. Wildlife-friendly farming vs land sparing. Frontiers in Ecology and the Environment 7:183-184.

Chandler, R. B., D. I. King, R. Raudales, R. Trubey and V. J. Arce. 2013. A Small-Scale Land-Sparing Approach to Conserving Biological Diversity in Tropical Agricultural Landscapes. Conservation Biology 27:785–795.

Chandler, R. 2010. Avian Ecology and Conservation in Tropical Agricultural Landscapes with Emphasis on *Vermivora chrysoptera*. Ph.D. dissertation, University of Massachusetts, Amherst, MA.

Chandler, R. B, and D. I. King. 2011. Habitat quality and habitat selection of golden-winged warblers in Costa Rica: an application of hierarchical models for open populations. Journal of Applied Ecology 48, 1038-1047.

Chazdon, R. L., C. A. Harvey, O. Komar, D. M. Griffith, B. G. Ferguson, M. Martínez- Ramos, H. Morales, R. Nigh, L. Soto-Pinto, M. V. Breugel, and S. M. Philpott. 2009. Beyond reserves: a research agenda for conserving biodiversity in human- modified tropical landscapes. Biotropica 41:142-153.

Chesser, T. R., R. C. Banks, F. K. Barker, C. Cicero, J. L. Dunn, A. W. Kratter, I. J. Lovette, P. C. Rasmussen, J. V. Remsen, Jr., J. D. Rising, D. F. Stotz, and K. Winker. 2013. Fifty-fourth supplement to the American Ornithologists' Union Check-list of North American Birds. The Auk 130:558-571.

Chokkalingam, U., and W. De Jong. 2001. Secondary forest: a working definition and typology. International forestry review 3:19–26.

Clark, D. B. 1996. Abolishing virginity. Journal of Tropical Ecology 12:735-739.

Clavel, J., R. Julliard, and V. Devictor. 2010. Worldwide decline of specialist species: toward a global functional homogenization? Frontiers in Ecology and the Environment (e-View) doi:10.1890/080216

Confer, J. L., P. Hartman, and A. Roth. 2011. Golden-winged Warbler (*Vermivora chrysoptera*), The Birds of North America Online (A. Poole, Ed.). Ithaca, Cornel Lab of Ornithology; Retrieve from the the Birds of North America Online: http://bna.birds.cornell.edu/bna/species/020doi:10.2173/bna.20

Conroy, M. 2007. Certification systems as tools for natural asset building. IN Boyce, J. K., S. Narain, E. A. Stanton, eds., Reclaiming nature: environmental justice and ecological restoration. Anthem Press, London and Chicago.

Davison, A., and D. Hinkley. 1997. Bootstrap methods and their application. Cambridge University Press, New York, New York, USA.

Dietsch, T. V., S. M. Philpott, R. A. Rice, R. Greenberg, P. Bichier, T. G. O'Brien, and M. F. Kinnaird. 2004. Conservation policy in coffee landscapes. Science 303:625–626.

Faaborg, J., R. T. Holmes, A. D. Anders, K. L. Bildstein, K. M. Dugger, S. A. Gauthreaux, P. Heglund, K. A. Hobson, A. E. Jahn, D. H. Johnson, S. C. Latta, D. J. Levey, P. P. Marra, C. L. Merkord, E. Nol, S. I. Rothstein, T. W. Sherry, T. S. Sillett, F. R. Thompson, and N. Warnock. 2010. Conserving migratory land birds in the New World: Do we know enough? Ecological Applications 20:398-418.

Faaborg, J., R. T. Holmes, A. D. Anders, K. L. Bildstein, K. M. Dugger, S. A. Gauthreaux Jr., P. Heglund, K. A. Hobson, A. E. Jahn, D. H. Johnson, S. C. Latta, D. J. Levey, P. P. Marra, C. L. Merkord, E. Nol, S. I. Rothstein, T. W. Sherry, T. S. Sillett, F. R. Thompson, and N. Warnock. 2010b. Recent advances in understanding migration systems of New World land birds. Ecological Monographs 80:3-48.

Falcy, M. R., and C. F. Estades. 2007. Effectiveness of corridors relative to enlargement of habitat patches. Conservation Biology 21:1341-1346.

Ferraz, G., J. D. Nichols, J. E. Hines, P. C. Stouffer, R. O. Bierregaard Jr., T. Lovejoy. 2007. A large-scale deforestation experiment: effects of patch area and isolation on Amazon birds. Science 315:238-241.

Foley, J. A., R. DeFries, G. P. Asner, C. Barford, G. Bonan, S. R. Carpenter, F. S. Chapin, M. T. Coe, G. C. Daily, H. K. Gibbs, J. H. Helkowski, T. Holloway, E. A. Howard, C. J. Kucharik, C. Monfreda, J. A. Patz, I. C. Prentice, N.

Ramankutty, and P. K. Snyder. 2005. Global Consequences of Land Use. Science 309:570-574.

Foody, G. M., G. Palubinskas, R. M. Lucas, P. J. Curran, and M. Honzak. 1996. Identifying terrestrial carbon sinks: classification of successional stages in regeneration tropical forest from Landsat TM data. Remote sensing of environment 55, 205-216.

Fretwell, S. D., and H. L. Lucas Jr. 1969. On territorial behavior and other factors influencing habitat distribution in birds. Acta Biotheoretica 19:16-36.

Gardali, T. D., D. C. Barton, J. D. White, and G. R. Geupel. 2003. Juvenile and adult survival of Swainson's Thrush (*Catharus ustulatus*) in coastal California: annual estimates using capture-recapture analysis. Auk 120:1188-1194.

Gaston, K. J., S. F. Jackson, L. Cantú-Salazar, and G. Cruz-Pinón. 2008. The ecological performance of protected areas. Annual review of ecology, evolution, and systematics 39:93–113.

Gelman, A., and D. B. Rubin. 1992. Inference from iterative simulation using multiple sequences. Statistical Science 7:457-472.

Gibbs, H. K., A. S. Ruesch, F. Achard, M. K. Clayton, P. Holmgren, N. Ramankutty, and J. A. Foley. 2010. Tropical forests were the primary sources of new agricultural land in the 1080s and 1990s. Proceedings of the National Academy of Sciences of the United States of America 107:16732-16737.

Giest, H. J., and E. F. Lamdin. 2001. What drives tropical deforestation? Louvain University, Louvain-Da-Neuve, Belgium.

Gill, F. B. 1997. Local cytonuclear extinction of the Golden-winged Warbler. Evolution 51:519–525.

Graham, C. H., and J. G. Blake. 2001. Influence of patch- and landscape-level factors on bird assemblages in a fragmented tropical landscapre. Ecological Applications 11:1709-1721.

Green, R. E., S. J. Cornell, J. P. W. Scharlemann, and A. Balmford. 2005. Farming and the fate of wild nature. Science 307:550-555.

Greenberg, R., P. Bichier, A. C. Angon, and R. Reitsma. 1997. Bird populations in shade and sun coffee plantations in central Guatemala. Conservation Biology 11:448- 459.

Greenberg, R., P. Bichier, and J. Sterling. 1997b. Bird populations in rustic and planted shade coffee plantations of eastern Chiapas, Mexico. Biotropica 29:501-514.

Gruebler, M. U., F. Korner-Nievergelt, and B. Naef-Daenzer. 2014. Equal nonbreeding period survival in adults and juveniles of a long-distant migrant bird. Ecology and Evolution 4:756-765.

Guariguata, M. R., and R. Ostertag. 2001. Neotropical secondary forest succession: changes in structural and functional characteristics. Forest Ecology and Management 148:185-206.

Guenette, J-S, and M-A Villard. 2005. Thresholds in forest bird response to habitat alteration as quantitative targets for conservation. Conservation Biology 19:1168-1180.

Hair, J. F., R. E. Anderson, and R. L. Tatham. 1987. Multivariate Data Analysis, 2nd Edition. Macmillan. New York, NY.

Hanksi, I. 1989. Metapopulation dynamics; does it help to have more of the same? Trends in Ecology & Evolution 4:113-114.

Haslem, A., and A. F. Bennett. 2008. Birds in agricultural mosaics: the influence of landscape pattern and countryside heterogeneity. Ecological Applications 18:185- 196.

Hazell, P. and S. Wood. 2008. Drivers of change in global agriculture. Philosophical Transactions of the Royal Society B-Biological Sciences 363: 495-515.

Hobson, K. A., S. L. Van Wilgenburg, A. M. Roth, and R. E. Bennett. In Press. Golden-winged warbler (Vermivora chrysoptera) migratory connectivity derived from stable isotopes IN Golden-winged Warbler Ecology, Conservation and Habitat Management. H. M. Streby, D. Buehler, and D. E. Anderson, editors. Studies in Avian Biology.

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

Holmes, R. T., T. W. Sherry, and L. Reitsma. 1989. Population structure, territoriality, and overwinter survival of two migrant warbler species in Jamaica. Condor 91:545-561.

Holmes, R. T. 2007. Understanding population change in migratory songbirds: long-term and experimental studies of Neotropical migrants in breeding and wintering areas. Ibis 149:2-13.

Homan, R. N., Bryan S. W., and J. M. Reed. 2004. Critical thresholds associated with habitat loss for two vernal pool-breeding amphibians. Ecological Applications 14:1547-1553.

Jenkins, M. 2003. Prospects for biodiversity. Science 302:1175.

Johnson, D. H. 1980. The comparison of usage and availability measurements for evaluations resource preference. Ecology 61:65-71.

Johnson, M. D., T. W. Sherry, R. T. Holmes, and P. P. Marra. 2006. Assessing habitat quality for a migratory songbird wintering in natural and agricultural habitats. Conservation Biology 20:1433-1444.

Johnson, M. D. 2007. Measuring habitat quality: a review. The Condor 109:489-504

Jones, J., J. J. Barg, T. S. Sillett, M. L. Veit, and R. J. Robertson. 2004. Minimum estimates of survival and population growth for cerulean warblers (*Dendroica cerulea*) breeding in Ontario, Canada. The Auk 121:15-22.

King, D. I., J. H. Rappole, and J. P. Buonaccorsi. 2006. Long-term population trends of forest-dwelling Nearctic-Neotropical migrant birds: a question of temporal scale. Bird Populations 7:1-9.

Klaassen, M., B. J. Hoye, B. A. Nolet, and W. A. Buttemer. 2012. Ecophysiology of avian migration in the face of current global hazards. Philosophical Transactions of the Royal Society of London B Biological Sciences 367:1719-1732.

Komar, O. 2006. Priority Contribution. Ecology and conservation of birds in coffee plantations: a critical review. Bird Conservation International 16:1-23.

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

Laurance, W. F. 1999. Reflections on the tropical deforestation crisis. Biological Conservation 91, 109-117.

Laurance, W. F., J. Sayer, K. G. Cassman. 2014. Agricultural expansion and its impacts on tropical nature. Trends in Ecology and Evolution 29:107-116.

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

Letcher, S. G., R. L. Chazdon. 2009. Rapid recovery of biomass, species richness, and species composition in a forest chronosequence in northeastern Costa Rica. Biotropica 41:608-617.

Levins, R. 1969. Some demographic and genetic consequences of environmental heterogeneity for biological control. Bulletin of the Entomological Society of America 15:237-240.

Litvaitis, J. A. 1993. Response of early successional vertebrates to historic changes in land use. Conservation Biology 7:866–873.

MacArthur, R., and J. MacArthur. 1961. On bird species diversity. Ecology 42:594-598.

MacArthur R. H. and E. O. Wilson. 1967. The theory of island biogeography. Evolution Princeton University Press, Princeton.

McGarigal, K., S. A. Cushman, and S. G. Stafford. 2000. Multivariate Statistics for Wildlife and Ecology Research. Spring-Verlag, New York.

Moguel, P., and V. M. Toledo. 1999. Biodiversity conservation in traditional coffee systems of Mexico. Conservation Biology 13:11-21.

Murcia, C. 1995. Edge effects in fragmented forests: implications for conservation. Trends in Ecology and Evolution 10:58-62.

Nadkarni, N. M., D. Schaefer, T. J. Matelson, and R. Solano. 2004. Biomass and nutrient pools of canopy and terrestrial components in a primary and a secondary montane cloud forest, Costa Rica. Forest Ecology and Management 198:223-236.

Newton, I. 2006. Can condition experiences during migration limit the population levels of birds? Journal of Ornithology 147:146-166.

Norris, D. R., P. P. Marra, K. T. Kyser, T. W. Sherry, and L. M. Ratcliffe. 2004. Tropical winter habitat limits reproductive success on the temperate breeding grounds in a migratory bird. Proceedings of the Royal Society of London Series B 271:59–64.

Norris, K. 2008. Agriculture and biodiversity conservation: opportunity knocks. Conservation Letters 1:2-11.

O'Brien, T. G., and M. F. Kinnaird. 2003. Conservation: caffeine and conservation. Science 300:587-587.

O'Brien, T. G., and M. F. Kinnaird. 2004. Conservation policy in coffee landscapes— response. Science 303:625–626.

Oksanen, J. F. G. Blanchet, R. Kindt, P. Legendre, P. R. Minchin, R. B. O'Hara, G. L. Simpson, P. Solymos, M. H. Stevens, and H. Wagner. 2013. Vegan: Community Ecology Package. R package version 2.0-10. URL http://cran.r-project.org/package=vegan.

Perfecto, I., A. Mas, T. Dietsch, and J. Vandermeer. 2003. Conservation of biodiversity in coffee agroecosystems: a tri-taxa comparison in southern Mexico. Biodiversity and Conservation 12:1239-1252.

Perfecto, I., J. Vandermeer, A. Mas, and L. S. Pinto. 2005. Biodiversity, yield, and shade coffee certification. Ecological Economics 54:435–446.

Phalan, B., A. Balmford, R. E. Green, and J. P.W. Scharlemann. 2011. Minimising the harm to biodiversity of production more food globally. Food Policy 36:S62-S71.

Philpott, S. M., P. Bichier, R. Rice, and R. Greenberg. 2007. Field-testing ecological and economic benefits of coffee certification programs. Conservation Biology 21:975–985.

Philpott, S., W. Arendt, I. Armbretch, P. Bichier, T. Dietsch, C. Gordon, R. Greenberg, I. Perfecto, R. Reynoso-Santos, and L. Soto-Pinto. 2008. Biodiversity loss in Latin American coffee landscapes: review of the evidence on ants, birds, and trees. Conservation Biology 22:1093-1105.

Pimentel, D., U. Stachow, D. A. Takacs, H. W. Brubaker, A. R. Dumas, J. J. Meaney, A. S. John, D. E. Onsi, and D. B. Corzilius. 1992. Conserving biological diversity in agricultural/forestry systems. BioScience 42:354–362.

Plummer, M. 2003. JAGS: a program for anlaysis of baysian graphical modesl using GIBS sampling.

R Core Team. 2013. R: a language and environment for statistical computing. R Foundation for Statistical Computing, Vienna, Austria. URL http://www.R-project.org/.

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

Rappole, J. H., and M. V. McDonald. 1994. Cause and effect in migratory bird population changes. Auk 111:652-660.

Rappole, J. H. 1995. The ecology migrant birds. A Neotropical perspective. Smithsonian Institution Press, Washington, D.C.

Rappole, J. H., D. I. King, and J. Diez. 2003. Winter- vs. breeding-habitat limitation for an endangered avian migrant. Ecological Applications 13:735-742.

Rappole, J. H., D. I. King, and J. H. Vega Rivera. 2003b. Coffee and conservation. Conservation Biology 17:334-336.

Rice, R. A., and J.R. Ward. 1996. Coffee, conservation, and commerce in the Western Hemisphere. Washington, DC: Smithsonian Migratory Bird Center and National Resources Defense Council

Ricketts, T. H. 2004. Tropical forest fragments enhance pollinator activity in nearby coffee crops. Conservation Biology 18, 1262.

Ricketts, T. H., G. C. Daily, P. R. Ehrlich, and C. D. Michener. 2004. Economic value of tropical forest to coffee production. Proceedings of the National Academy of Sciences 101, 12579-12582.

Roberts, D. L., R. J. Cooper, and L. J. Petit. 2000. Flock characteristics of ant-following birds in premontane moist forest and coffee agroecosystems. Ecological Applications 10:1414-1425.

Rodrigues, A. S., S. J. Andelman, M. I. Bakarr, L. Boitani, T. M. Brooks, R. M. Cowling, L. D. Fishpool, G. A. da Fonseca, K. J. Gaston, M. Hoffmann, and others. 2004. Effectiveness of the global protected area network in representing species diversity. Nature 428:640–643.

Royle, J. A. 2008. Modeling individual effects in the Cormack-Jolly-Sever model: a state-space formulation. Biometrics 64:364-370.

Royle, J. A., and R. M. Dorazio. 2008. Hierarchical Modeling and Inference in Ecology: The Analysis of Data from Populations, Metapopulations and Communities, 1st edition. Academic Press.

Sauer, J. R., J. E. Hines, J. E. Fallon, K. L. Pardieck, D. J. Ziolkowski, Jr., and W. A., Link. 2014. The North American Breeding Bird Survey, Results and Analysis 1966-2012. Version 02.19.2014. USGS Patuxent Wildlife Research Center, Laurerl, MD. Available at: www.mbr-pwrc.usgs.gov/

Schulze, C. H., M. Waltert, P. J. A. Kessler, R. Pitopang, D. Veddeler, M. Mühlenberg, S. R. Gradstein, C. Leuschner, I. Steffan-Dewenter, and T. Tscharntke. 2004. Biodiversity indicator groups of tropical land-use systems: comparing plants, birds, and insects. Ecological Applications 14:1321-1333.

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

Sekercioglu, C. H. 2006. Increasing awareness of avian ecological function. Trends in Ecology and Evolution 21:464-471.

Sillett, T. S., and R. T. Holmes. 2002. Variation in survivorship of a migratory songbird throughout its annual cycle. Journal of Animal Ecology 71:296-308.

Smithsonian Migratory Bird Center. Bird Friendly Coffee Farms. [online] http://nationalzoo.si.edu/scbi/migratorybirds/coffee/search_farms.cfm (accessed 23 March 2015).

Stiles, F. G. 1985. Conservation of forest birds in Costa Rica: problems and perspectives. Page 141 in Conservation of tropical forest birds: proceedings of a workshop and symposium held at the XVIII World Conference of the International Council for Bird Preservation, 7, 8, and 10 August 1982, Kings College, Cambridge, England.

Stearns, S. C. 1992. The evolution of life histories. Oxford University Press, London.

Strong, A. M., and T. W. Sherry. 2000. Habitat-specific effects of food abundance on the condition of ovenbirds wintering in Jamaica. Journal of Animal Ecology 69:883- 895.

Studds, C. E., and P. P. Marra. 2005. Nonbreeding habitat occupancy and population processes: an upgrade experiment with a migratory bird. Ecology 86:2380-2385.

Stutchbury, B. J. M., J. R. Hill III, P. M. Kramer, S. A. Rush, and S. A. Tarof. 2009. Sex and age-specific annual survival in a neotropical migratory songbird, the Purple Martin (*Progne subis*). Auk 126:278-287.

Swantz, S. 1996. Economic differences between shaded and full sun coffee cultivation in Costa Rica. in First Sustainable Coffee Congress. Smithsonian Migratory Bird Center.

Tejeda-Cruz, C., and W. J. Sutherland. 2004. Bird responses to shade coffee production. Animal Conservation 7:169-179.

Tejeda-Cruz, C., E. Silva-Rivera, J. R. Barton, and W. J. Sutherland. 2010. Why shade coffee does not guarantee biodiversity conservation. Ecology and Society 15:13-25.

Tilman, D., K. G. Cassman, P. A. Matson, R. Naylor, and S. Polasky. 2002. Agricultural sustainability and intensive production practices. Nature 418:671-677.

Toms, J. D., and M. L. Lesperance. 2003. Piecewise regression: a tool for identifying ecological thresholds. Ecology 84:2034-2041.

Vallender, R., R. J. Robertson, V. L. Friesen, and I. J. Lovette. 2007. Complex hybridization dynamics between golden-winged and blue-winged warblers (Vermivora chrysoptera and Vermivora pinus) revealed by AFLP, microsatellite, intron and mtDNA markers. Molecular Ecology 16:2017-2029.

Van Horne, B. 1983. Density as a misleading indicator of habitat quality. Journal of Wildlife Management 47:893-901.

Villard, M. and B. G. Jonsson. 2009. A plea for quantitative targets in biodiversity conservation. In Setting conservation targets for managed forest landscapes. 2009. Cambridge University Press. Cambridge, England.

Wilson, E. O. 1992. The Diversity of Life. Belknap Press of Harvard University Press, Cambridge, Mass.

Wolfe, J. D., M. D. Johnson, and C. J. Ralph. 2013. Greater mass increases annual survival of prothonotary warblers wintering in northeastern Costa Rica. The Condor 115:163-167.

Zuur, A. F., E. N. Ieno, N. J., Walker, A. A. Saveliev, G. M. Smith. 2009. Mixed Effects Models and Extensions in Ecology with R. Springer, New York, New York.