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Avian Ecology and Conservation in Tropical Agricultural Landscapes with Emphasis on Vermivora Chrysoptera

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AVIAN ECOLOGY AND CONSERVATION IN TROPICAL AGRICULTURAL LANDSCAPES WITH EMPHASIS ON *VERMIVORA CHRYSOPTERA*

A Dissertation Presented

by

RICHARD B. CHANDLER

Submitted to the Graduate School of the
University of Massachusetts Amherst in partial fulfillment
of the requirements for the degree of

DOCTOR OF PHILOSOPHY

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Wildlife and Fisheries Conservation

AVIAN ECOLOGY AND CONSERVATION IN TROPICAL AGRICULTURAL LANDSCAPES WITH EMPHASIS ON *VERMIVORA CHRYSOPTERA*

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DEDICATION

To Carly for your steadfast love throughout these years.

ACKNOWLEDGMENTS

My deepest gratitude goes to my advisor David King for his guidance and friendship. This research greatly expanded my knowledge of tropical ecology and conservation, and my time spent in Costa Rica has been one of the great joys of my life. None of these experiences would have been possible had he not given me this opportunity.

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Special thanks also go to Cooperativa Montes de Oro, whose members assisted with site selection, lodging, and transportation in the early phases of the project. Victor Julio Arce Chavez lent his expertise as an agronomist throughout the course of the study. He gave us free access to lodging in his home and at the Cooperative’s facilities. He also acted as our first tour guide of the area along with Santos Muñez and Luis Carlos. Arley Morales graciously helped us navigate the nuances of working in a foreign country. His

help with banking, car repair, car inspections, taxes, and accommodations saved us countless hours of work. More importantly, his friendship made the research more enjoyable.

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No one worked harder in the field than my wife Carly Chandler, even when she was three months pregnant, and her help with the study design and implementation were invaluable. Finally, I want to thank my son Orrin for enjoying the adventure as much as we did.

ABSTRACT

AVIAN ECOLOGY AND CONSERVATION IN TROPICAL AGRICULTURAL LANDSCAPES WITH EMPHASIS ON *VERMIVORA CHRYSOPTERA*

FEBRUARY 2011

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The world's biodiversity is concentrated in tropical ecosystems, yet tropical forests are being converted for agriculture at a rapid rate. I evaluated the potential of an alternative coffee production system known as Integrated Open Canopy (IOC) to contribute to avian conservation. This study was conducted from 2005-2010 in the Cordillera de Tilarán, Costa Rica. My results indicate that species richness of forest-dependent birds was significantly higher in IOC farms than in shade coffee farms, and was comparable to secondary forest sites. There was no difference in species richness of Neotropical-Nearctic migrants between IOC and shade coffee farms. Overall similarity was higher between IOC farms and primary forest than between shade coffee farms and primary forest.

The golden-winged warbler (*Vermivora chrysoptera*) is a declining Neotropical-Nearctic migrant bird, yet little is known about its non-breeding season ecology and demographics. I found that golden-winged warbler abundance was highest at intermediate precipitation levels found at middle elevations (1000-1200 m) of the Pacific slope, but they were absent from the dry forests at lower elevations on the Pacific slope.

Abundance peaked in forests with canopy heights of 22 m, and was positively related to the quantity of hanging dead leaves. Radio-telemetry data indicated that golden-winged warblers used microhabitat features characteristic of disturbance more frequently than expected by chance. Selection of these microhabitat features was related to their highly specialized dead-leaf foraging behavior, which may also have contributed to their high degrees of site fidelity, mixed-species flock attendance, and territoriality. These behaviors have important conservation implications because they constrain density, and thus could affect carrying capacity. Population dynamics were characterized by estimating plot-level and individual-level apparent survival and recruitment rates within and among non-breeding seasons. Both levels of analysis suggested that recruitment was too low to offset mortalities within this study area.

This study indicates that increasing forest cover in tropical agricultural landscapes may be the most effective way of providing habitat for bird species of high conservation concern, including the golden-winged warbler. Integrated open canopy coffee production is one option for achieving this goal because it provides a financial incentive to protect or restore forest.

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CHAPTER 1

INTRODUCTION

1.1 Background

Tropical forests cover only 2.3% of the Earth's land surface yet they contain at least half of the Earth's biodiversity (Wilson 1992). In spite of their global significance, these forests are being cleared at a rate of 16 million ha per year, largely due to expanding agriculture (Achard et al. 2002). Three hundred million hectares have already been lost and approximately 500 million hectares have been degraded (ITTO 2002). Increasing pressure is being placed upon remaining native ecosystems because the human population continues to grow at a rate of 75-85 million people per year, due primarily to high birth rates in tropical countries. Tropical deforestation has resulted in the extinction of numerous species (Myers 1994), and can influence local precipitation patterns as well as global climate (Salati and Nobre 1991, Bala et al. 2007, Fearnside and Laurance 2008).

Protected areas alone cannot successfully protect tropical ecosystems (Woodroffe and Ginsberg 1998, Gaston et al. 2008) because of their limited extent, uneven representation of ecosystem diversity, and the difficulties of enforcing regulations (Dirzo and Raven 2003, Schroth et al. 2004). Furthermore, the vast majority of arable lands are already under cultivation. These limitations do not undermine the importance of protected areas, but suggest that bird conservation in the tropics will depend in large part on habitat availability and quality in agricultural landscapes. It is therefore widely agreed that conserving tropical ecosystems while maintaining or increasing agricultural production and distribution is one of the most important challenges of the 21st century (McNeely and Scherr 2002, Foley et al. 2005).

Unfortunately, tropical agricultural landscapes have only recently received attention from conservation biologists, and little is known regarding how species respond to land use practices (Norris 2008). Thus, one major aspect of my research was to assess how alternative agricultural practices can be used to retain biodiversity. I chose birds as a study taxon for a variety of reasons. Birds represent an important component of biodiversity because of the number of species (>9000) and the important services they perform in virtually all ecosystems (Sibley and Monroe 1990, Sekercioglu 2006). In tropical ecosystems, birds are important pollinators, seed dispersers, predators, scavengers, cavity constructors, and regulators of insect populations (Sekercioglu 2006). They are also sensitive to environmental changes and can be effectively surveyed to allow for comparisons among habitat types and farming systems (Schulze et al. 2004). Their ecological importance and imperiled status are particularly evident in the tropics, where > 70% of all species and 93% of threatened species occur (Sodhi et al. 2004). The scientific and English common names of birds used in this dissertation follow the seventh edition of the Check-list of North American Birds and its supplements created by the American Ornithologists' Union.

Migratory bird species that breed in North America constitute an important component of the Neotropical avifauna. Throughout this dissertation I will refer to these species as Neotropical-Nearctic migrants. Well over 200 species spend six to eight months of the year in the Neotropics, and occur in most habitat types (Rappole 1995). Many of these species are declining rapidly, though the vast majority of research on these species has been conducted during the breeding season. The golden-winged warbler (*Vermivora chrysoptera*) is among the most imperiled of these species. Breeding Bird Survey data suggest that the population has declined at an annual rate of 2.2% over the past 50 years, and it is largely extirpated from much of its historic breeding range (Sauer et al. 2008). Despite this situation, no detailed studies of this species' non-breeding ecology have been conducted.

This study was designed to accomplish two broad objectives related to conservation in tropical agricultural landscapes: 1) evaluate the potential of an alternative coffee production system to contribute to avian conservation, and 2) describe aspects of the golden-winged warbler (*Vermivora chrysoptera*) non-breeding ecology to inform conservation efforts. The outline of my dissertation is as follows. The remaining sections of this chapter describe the study area. Chapter 2 provides an evaluation of a novel coffee production system in terms of avian species richness, composition, morphometrics, and ectoparasite prevalence. Chapter 3 describes patterns of golden-winged warbler habitat selection and population dynamics. Chapter 4 focuses on the behavioral ecology of golden-winged warblers, and Chapter 5 presents seasonal and annual survival estimates.

1.2 Study area

1.2.1 Geography and administrative boundaries

This study was conducted from 2004-2010 between 800 m and 1600 m on both slopes of the continental divide in the Cordillera de Tilarán, Costa Rica N10°13' W84°39' (Fig. 1.1). The study area lies within the watersheds of the Río Jamaical on the Caribbean slope and the Río Aranjuez on the Pacific slope and encompasses an area of approximately 100 km^2. The Pacific slope portion of the study area is located within Puntarenas Province, and is subdivided into the Montes de Oro and Puntarenas cantones (counties). On the Caribbean slope, the study area lies within the Alajuela Province and the San Ramon County. The towns within the study area are all situated on the Pacific slope and include Palmital, Ventanas, Cedral, Pueblo Nuevo, San Francisco, Corazón de Jesus, San Raphael, Ojo de Agua, Bajo Caliente, San Martín Sur, and San Martín Norte. These communities are surrounded by the Monteverde Reserve Complex (MRC), which includes the Monteverde Cloud Forest Preserve, the Children's Eternal Rainforest, and Alberto Manuel Brenes Biological Reserve (Powell et al. 2002). This protected area is > 28,000 ha in extent, and the Monteverde Cloud Forest Preserve is one of the most visited reserves in the tropics. By straddling equal areas of the agricultural landscape and the large protected area, this study area provided an ideal setting to assess the effects of agriculture on avian populations and communities.

1.2.2 Climate

The climate of the Tilarán Mountains varies seasonally and along elevational and physiographic gradients (Clark et al. 2000). Three seasons are recognized. The dry season lasts from February to April, the wet season spans from May to October, and November to January is the transitional season. Neotropical-Nearctic migrants generally arrive at the end of the wet season and the beginning of the transitional season when precipitation and wind can be at their highest. Over 400 mm of rain can fall during these months (Fig 1.3), and strong northeasterly trade winds can reach sustained speeds of over 100 km/hr (Nadkarni et al. 2000). Storms during the transitional season can last over two weeks and breaks between storms, when the rains cease, can be as short as two days (personal observation). The subsequent dry season is typically characterized by 0-200 mm of precipitation per month and low cloud cover. However, the dry season is much more extreme at lower elevations on the Pacific side of the continental divide because the northeasterly trade winds lose most of their precipitation as they rise and cool over the Caribbean slope. This rain shadow has a profound effect on the vegetation as discussed below. Heavy rains return in May, but the wet season is characterized by clear morning skies and increasing cumulus cloud formation resulting in convective precipitation in the afternoons.

Temperature is less variable seasonally than precipitation, and is instead influenced mainly by elevation and cloud cover (Clark et al. 2000). Mean annual temperature ranges from approximately 18°C at high elevations (1500 m) to 24°C at lower elevations (700 m). At a given elevation, mean annual temperature typically fluctuates by less than 5°C over the year, peaking in June or July and reaching the lowest levels in December and January.

1.2.3 Geology and soils

The landmass now known as Costa Rica was submerged beneath the ocean only 10 million years ago. The subduction of the Cocos plate beneath the Caribbean plate led to increased volcanic activity and the rise of southern Central America, which formed a land-bridge between the two continents 3.5 million years ago (Clark et al. 2000). The Cordillera de Tilarán is composed primarily of volcanic rock, which has weathered to form moderately fertile Andisols. Rich organic matter comprises the upper soil horizons because rates of litter decomposition are relatively low compared to lower elevations.

Erosion is severe in many areas following deforestation due to the region's steep topography. However, fertility typically remains high enough to support natural regeneration following pasture abandonment, which contrasts with other areas with lateritic soils that lose their fertility after deforestation.

1.2.4 Vegetation and life zones

The vegetation of the Cordillera de Tilarán has been summarized by Haber (2000), on which the following description is based. The forests that once dominated this landscape have been classified into six Holdridge life zones, although three predominate. Below 1000 m on the Caribbean slope is premontane wet forest, characterized by trees often exceeding 30 m in height. Common genera of trees include *Cercropia* (Cercropiaceae), *Cedrela* (Meliaceae), *Elaegia* (Rubiaceae), *Ficus* (Moraceae), *Guarea* (Meliaceae), *Inga* (Fabaceae), *Meliosma* (Sabiaceae), *Ocotea* (Lauraceae), *Quararibea* (Malvaceae), *Sapium* (Euphorbiaceae), and *Trichilia* (Meliaceae). Lianas and vines are also common. Understory and canopy palms are common in this life zone as are epiphytic orchids, mosses, and lichens. Above 1200 m on both slopes is montane wet forest, often referred to as cloud forest, which is characterized by an abundance of epiphytes and trees of shorter stature. Common genera of trees in this life zone include *Ardisia* (Myrsinaceae), *Beilschmiedia* (Lauraceae), *Cojoba* (Fabaceae), *Eugenia* (Myrtaceae), *Ficus* (Moraceae), *Guarea* (Meliaceae), *Ocotea* (Lauraceae), *Persea* (Lauraceae), *Pouteria* (Sapotaceae), *Sapium* (Euphorbiaceae), and *Weinmannia* (Cunoniaceae). Precipitation on the upper Caribbean slope is nearly twice as high as the lower Pacific slope (Young et al. 1998). The lower Pacific slope is classified as premontane moist forest. Epiphytes and lianas are rare in these dry forests, and many trees are deciduous, losing their leaves during the dry season. Common genera of trees in the dry forest include *Billia* (Hippocastanaceae), *Cedrela* (Meliaceae), *Clethra* (Clethraceae), *Cordia* (Boraginaceae), *Croton* (Euphorbiaceae), *Ficus* (Moraceae), and *Zanthoxylum* (Rutaceae). Several tree species in the Lauraceae and Meliaceae families that were formally common are now rare due to selective logging for lumber. Tree species that regularly colonize abandoned cattle pastures include *Myrsine coriacea*, *Psidium guajava*, and *Conostegia sp.*,

1.2.5 Habitat classification

Throughout this dissertation, I will use the following definitions, based upon Chokkalingam and de Jong (2001), to characterize the major habitat types within the study area. “Primary forest” is forest which has never been cleared for agriculture or timber extraction. Some of the primary forest included in my research could be considered degraded primary forests because one or two trees per hectare had been removed. “Secondary forest” refers to the “post-extraction” and “post-abandonment” subclasses of Chokkalingam and de Jong (2001). These are forests that naturally regenerated following timber extraction or agricultural abandonment. Most of the secondary forest in the study area existed as part of a governmental program that pays farmers to abandon degraded pastures to enhance water quality (Pagiola 2008). I use the phrase “naturally disturbed forest” to refer to the post-catastrophic secondary forest of Chokkalingam and de Jong (2001). These are regenerating forests following natural disturbances such as major wind storms, landslides, or floods. In my study area these were found on steep slopes, along large rivers, and in areas hit most directly by the northeasterly trade winds. The final habitat type frequently referenced is agroforestry systems, or “agroforests”. These are farms that integrate trees and other woody perennials through the conservation of existing trees, active planting and tending, or via natural regeneration (Schroth et al. 2004b p. 2).

1.2.6 Human demography and settlement

The first people of European decent to colonize the study area arrived from San Ramón, passing through what is now the town of Zapotal during the early 20th century. Several of the children of these first inhabitants are still living. The following information was provided them. Many of the first settlers fled San Ramon because they did not want to fight in the revolution of 1917 when the dictator Federico Tinoco Granados was overthrown. The entire region was forested when they arrived, and there were few or no indigenous inhabitants. The first settlement was on the Caribbean slope in an area referred to as Bajo Jamaical, now located in the Manuel Brenes Biological Reserve. Although the soils are fertile, this area receives much more rain than the Pacific slope and has high abundances of venomous snakes. For these reasons, the early settlers moved to what is now the town of Cedral. Bajo Jamaical remains a private farm in the middle of the reserve, but no permanent inhabitants live there.

Cedral had suitable climate and soils for sugar cane and coffee production, which were carried by foot or on horseback down the Pacific slope to market in the town of Miramar. Only later during the middle of the 20th century did farmers attempt to raise cattle. The forests were cut and repeatedly burned to suppress woody plant encroachment. The use of fire has decreased in recent years due to negative social and environmental impacts and new environmental policies. As a result, numerous forest fragments have regenerated across the landscape, but cattle pasture remains the dominant land use type in the region (Fig. 1.4) outside of the protected areas (Fig 1.5).

1.2.7 Biological diversity

Costa Rica harbors > 4% of the Earth's biodiversity, yet is one of the smallest countries on the planet. The Cordillera de Tilarán is renowned for its diverse flora and fauna, which are among the reasons why the Monteverde Cloud Forest Preserve is one of the most visited tropical tourist destinations in the world. More than 3000 vascular plants have been identified in the Monteverde region alone (Haber 2000). Over 500 species of birds, 100 species of mammals, and 100 species of amphibians and reptiles occur in the Monteverde region as well (Janzen 1983). This area is also known for the rapid rate of extirpations over recent years, notably the disappearance of many amphibian species (Pounds et al. 1999).

Slud (1964) categorized the birds of Costa Rica into the following four avifaunal zones: north Pacific lowlands, south Pacific lowlands, Caribbean lowlands, and the Costa Rica-Chirquí highlands. He based his classification upon the distinctness of the avifauna in these zones, which also have distinct climates and geological histories. The north Pacific lowland avifauna corresponds to the "Tropical Dry Forest" life zone, which reaches its southern extreme in Costa Rica and extends north to Mexico. Representative species in this zone are members of groups with Central American rather than South American evolutionary origins. The southern Pacific lowlands receive much more precipitation than the northern Pacific, and the region has an avifauna composed of species and genera most abundant in lowland rainforests of northwestern South America. The avifauna of the Caribbean lowlands is also dominated by species with evolutionary origins in South American, but due to its isolation from the south Pacific lowlands, the species composition is relatively distinct. Slud, however, acknowledges that these two avifaunas could be treated as one. The Costa Rica-Chiriquí highlands have the highest level of endemism of the four avifaunas. A small number of the species' evolutionary origins can be traced to northern Central America though most have stronger ties to South American lineages. Numerous authors have noted that the avifauna could be classified into more groups and many treat middle-elevation species distinct from highland species. Furthermore, it is always problematic to categorize avian communities or avifaunas because numerous species occur in multiple categories and each species has its own unique distribution. Nonetheless, Slud's avifaunas are useful in describing general patterns arising from Costa Rica's complex climate and geological history.

Bird species within my study area have affinities to three of the four avifaunal zones. Only the south Pacific lowland avifauna is not represented. This convergence of avifaunas results in high species richness and I have observed >300 species in the 10x10 km area (Appendix 1). Species representative of the dry northern Pacific avifauna include white-fronted parrot (scientific names in Appendix 1), steely-vented hummingbird, Hoffman's woodpecker, long-tailed manakin, and white-throated magpie-jay. These are all species that I primarily encountered below 1100 m on the Pacific slope. Affiliates of the Caribbean lowlands (and foothills) include broad-billed motmot, yellow-eared toucanet, gray-throated leaftosser, red-headed barbet, white-collared manakin, bare-necked umbrellabird, black-headed nightingale-thrush, Audubon's Warbler, black-cowled oriole, blue-and-gold tanager, crimson-collared tanager, white-lined tanager, and orange-billed sparrow. These species are primarily restricted to the Caribbean slope below 1200 m, though vagrants occasionally cross the continental divide. Species associated with the highlands include black guan, black-breasted wood-quail, Chiriquí quail dove, striped-tailed hummingbird, purple-throated mountain-gem, orange-bellied trogon, resplendent quetzal, prong-billed barbet, spotted barbtail, the silvery-fronted tapaculo, three-wattled bellbird, tawny-throated leaftosser, azure-hooded jay, three-striped warbler, collared redstart, blue-hooded euphonia, chestnut-capped brush-finch, and slaty flowerpiercer. I encountered these species above 1200 m on both sides of the continental divide.

To my knowledge no one has published studies of birds from this study area. An incomplete inventory of the birds of the Pacific slope of the study area was made at the request of the local coffee cooperative, but this study was not published. A farmer I worked with recalled a visit by Alexander Skutch back in the 1970s, though he says he did not stay for very long. The study area is probably understudied because Monteverde Cloud Forest Reserve is relatively close and most birdwatchers and scientists conduct their work from there. However, there is no low pass there, and it is much harder to access the Caribbean slope.

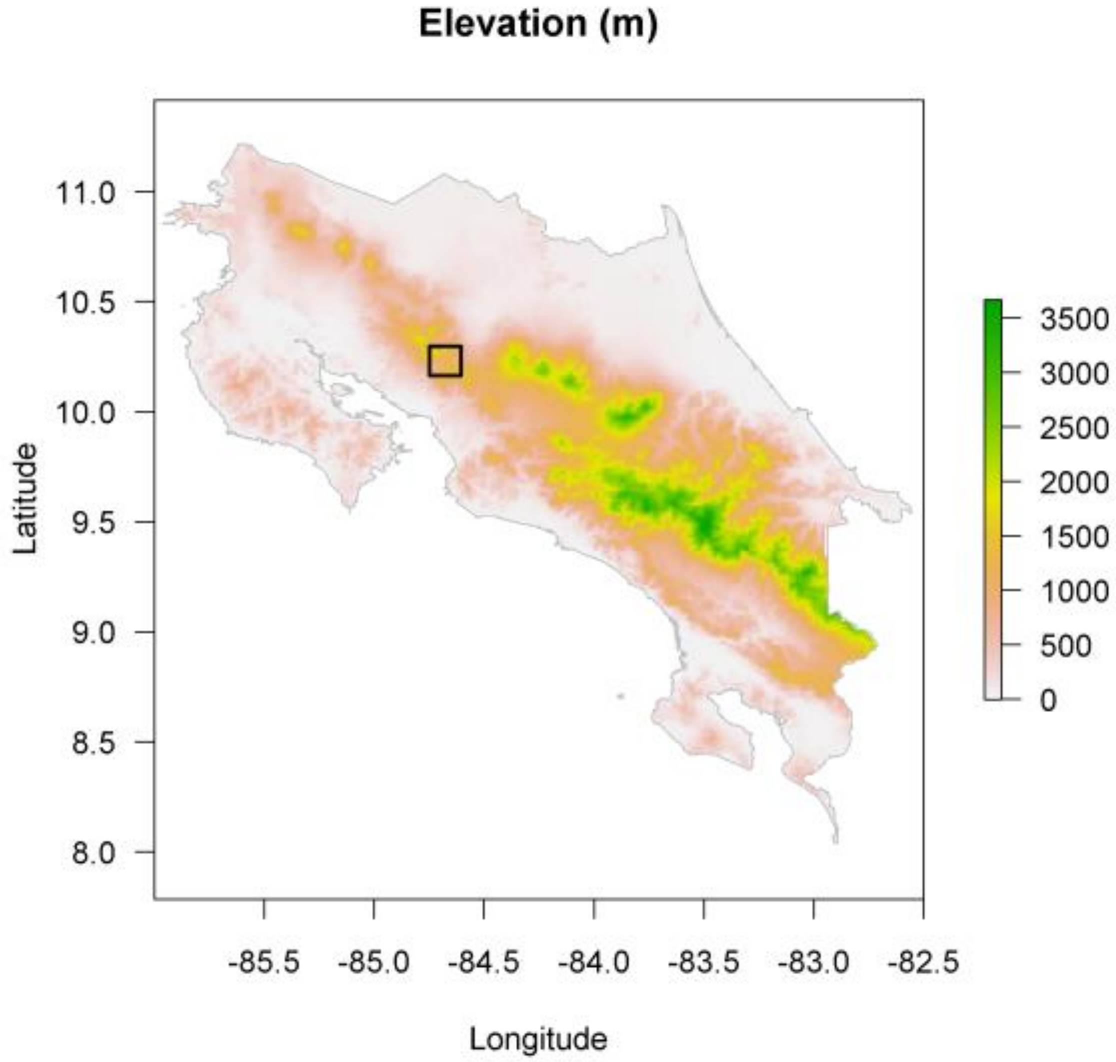

Figure 1.1. Costa Rica topography and study area location (black box).

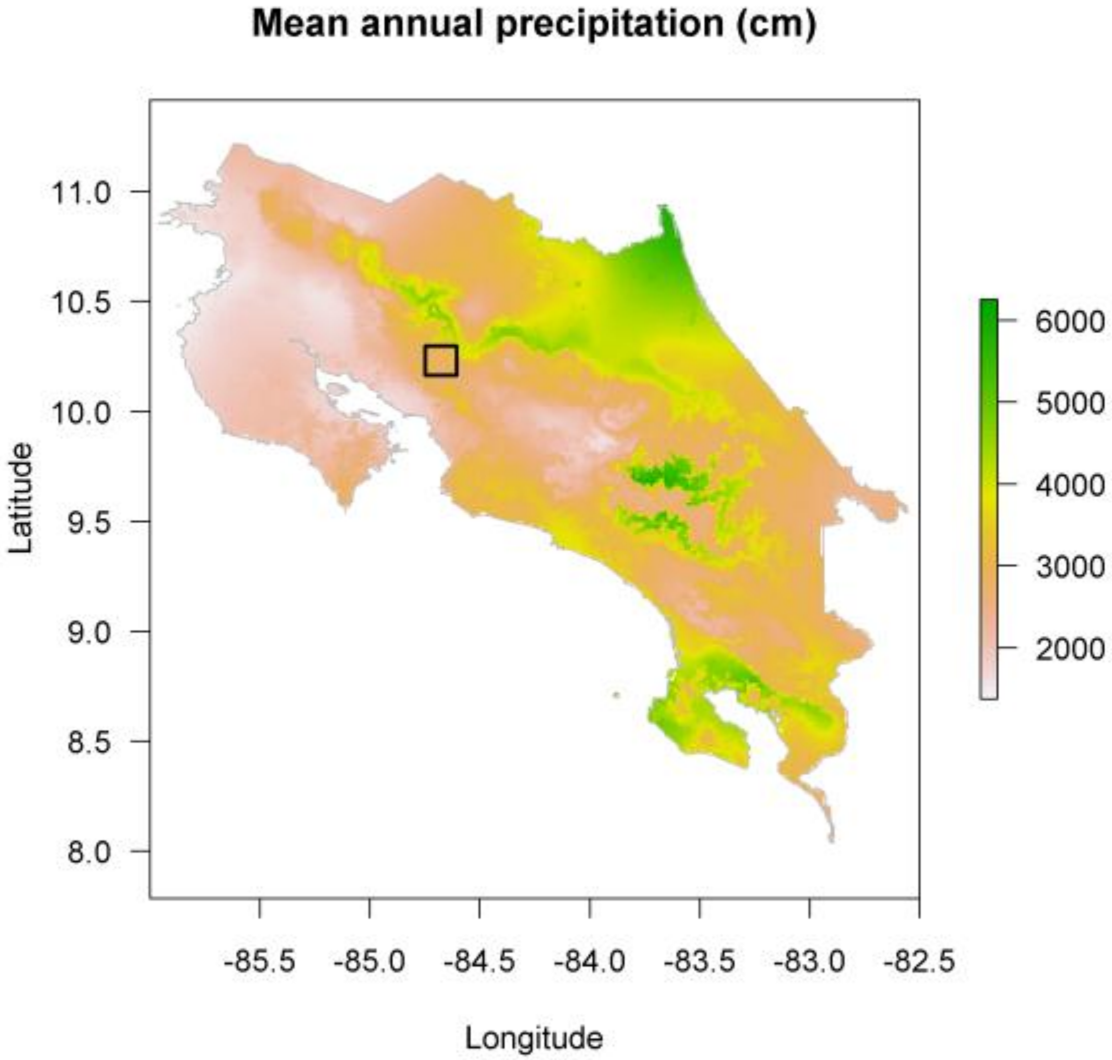

Figure 1.2. Mean annual precipitation in Costa Rica and study area (black box).

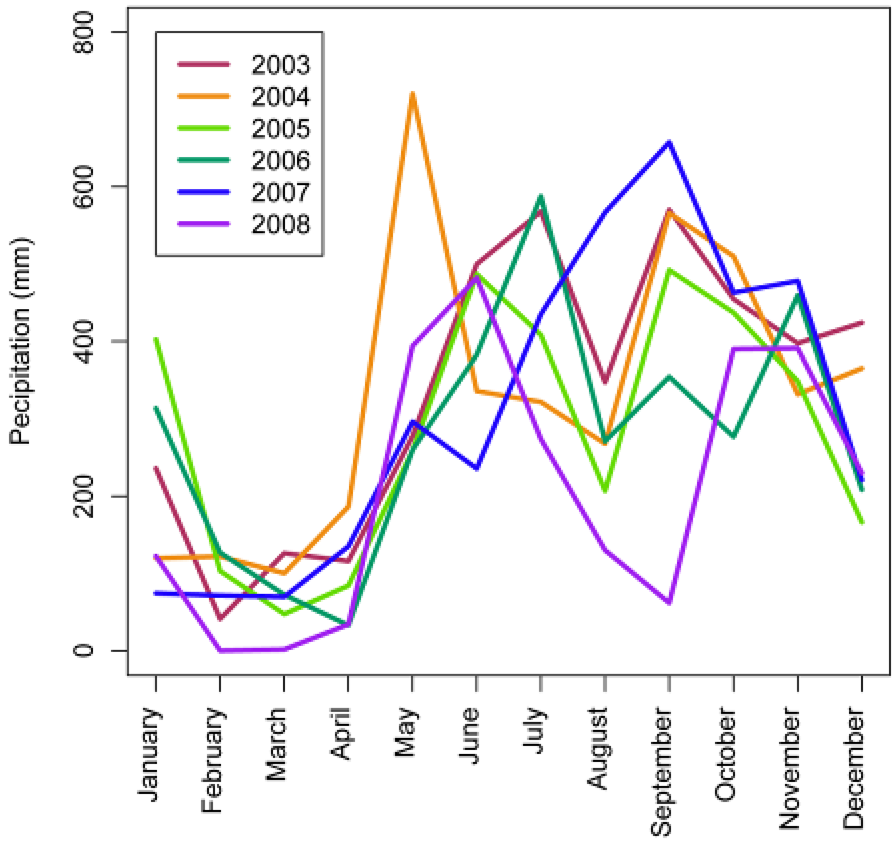

Figure 1.3. Seasonal precipitation data for study area from weather station in Cedral, Puntarenas Province, Costa Rica.

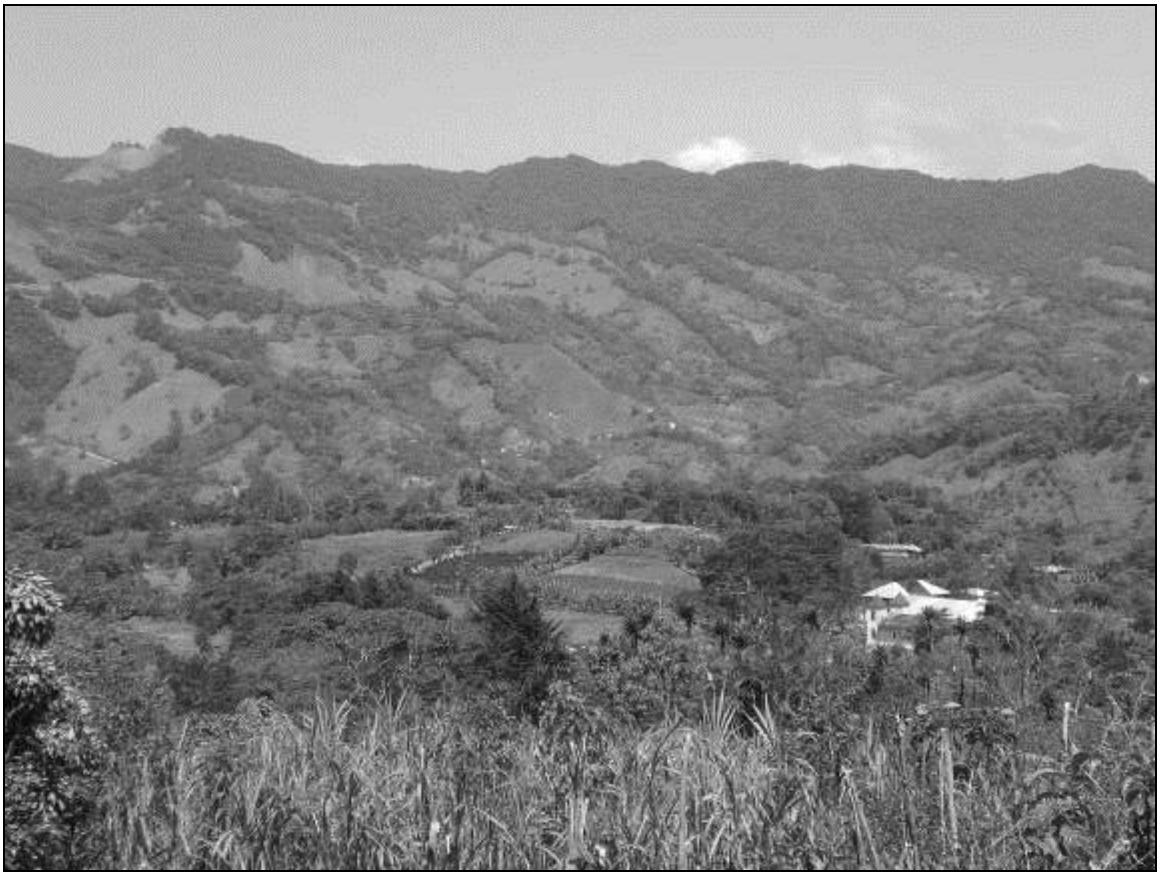

Figure 1.4. Looking northwest from Cedral (Puntarenas Province, Costa Rica) over the Pacific slope of the Cordillera de Tilarán. Forested ridge is part of the Monteverde Reserve Complex. Photograph by author.

Figure 1.5. Alberto Manuel Brenes Biological Reserve on the Caribbean slope side of the Cordillera de Tilarán. Photograph by author, Alajuela Province, Costa Rica.

CHAPTER 2

BIRD SPECIES RICHNESS AND COMPOSITION IN A LAND-SPARING COFFEE PRODUCTION SYSTEM

2.1 Introduction

Tropical agricultural landscapes have become focal points of global conservation efforts due to the rapid conversion of natural ecosystems for agriculture and the inability to conserve biodiversity in protected areas (Pimentel et al. 1992, Rodrigues et al. 2004, Foley et al. 2005). In Central America alone, more than 1.2 million km^2 of land are used for agriculture, which represents over fifty percent of the total land area (FAO 2007). In contrast, protected areas comprise only 2.2% of this area, do not represent ecosystem diversity, and are not always compatible with local societal needs (WDPA 2006, Gaston et al. 2008, Agrawal and Redford 2009). The disparity between protected and unprotected land is especially important in tropical regions, which contain a disproportionately large share of the Earth's biodiversity (Dirzo and Raven 2003).

Although the importance of tropical agricultural landscapes for conserving global biodiversity is widely recognized, conservationists disagree about the strategies for applying agroforestry to achieve these goals (Schroth et al. 2004b, Green et al. 2005, Vandermeer et al. 2005, Fischer et al. 2008). A fundamental disagreement hinges on the role of agricultural intensification (Tilman et al. 2002), and two diametrically opposed model systems have been proposed. The first strategy, referred to as "wildlife-friendly farming" (Green et al. 2005), involves integrating components of native ecosystems (e.g. shade trees) into the cultivation system. This agroforestry system is based upon research indicating that biodiversity is negatively affected by agricultural intensification at local scales (Perfecto et al. 2003, Schulze et al. 2004, Philpott et al. 2008). Critics note that such agroforestry practices do not explicitly protect native habitats, and can be economically prohibitive due to the often-associated low yields (Swantz 1996, O'Brien and Kinnaird 2003, Rappole et al. 2003b).

The second approach, known as land-sparing, involves maximizing yields in order to make other lands available for conservation (Balmford et al. 2005, Green et al. 2005). Supporters of this approach point contend that food demands over the past half-century would not have been met without yield increases, and future food demands are projected to outpace production unless further yield increases are achieved (Hazell and Wood 2008). They further emphasize that protecting native ecosystems is a higher conservation priority than protecting elements of native habitats (Rappole et al. 2003b, Haslem and Bennett 2008). Finally, it is often reported that more land must be cultivated to support low yielding agricultural practices relative to high yielding methods (Brown and Pearce 1994, Evenson and Gollin 2003). Critics of the land-sparing approach argue that increasing yields does not ensure conservation and may stimulate further agriculture-driven deforestation (Chappell et al. 2009). Intensification is typically associated with increased inputs of chemical fertilizers and pesticides, which contaminate local food chains and water supplies (Pimentel et al. 2005). Furthermore, this approach is characterized as treating human and biodiversity needs as inherently opposed, and could encourage large monocultures at the expense of small farmers and their traditional livelihoods (Perfecto and Vandermeer 2010).

Coffee (*Coffea arabica*) production systems have been at the center of this research and debate. Coffee is the second largest globally-traded commodity, and coffee production and processing methods can strongly affect local and regional environments via habitat loss, erosion, water pollution, and energy consumption (Rice and Ward 1996, Arce et al. 2010). Traditionally, coffee was cultivated under a canopy of native trees, but as part of efforts to increase yields, many of these "shade coffee" farms were converted to "sun coffee" farms that resemble other non-shaded monocultures (Moguel and Toledo 1999). Numerous studies demonstrate that species richness and composition of various taxa are more similar to native forest in shade coffee farms than in sun coffee farms (Greenberg et al. 1997a, 1997b, Perfecto et al. 2003, Philpott et al. 2008). Furthermore habitat quality can be high for some species that use shade coffee (Johnson et al. 2006, Bakermans et al. 2009). For these reasons, shade coffee is considered an example of a "wildlife farming" system (Fischer et al. 2008).

Although clearly preferable to sun coffee, there are important limitations to the conservation value of shade coffee (O'Brien and Kinnaird 2003, Rappole et al. 2003b, Komar 2006). Most importantly, shade-coffee certification programs do not conserve native ecosystems and can lead to deforestation (Tejeda-Cruz et al. 2010, Rappole et al. 2003b). Although species richness is often reported to be similar between shade coffee farms and primary forest, community composition often differs, with generalist species being more prevalent than forest-dependent species (Tejeda-Cruz and Sutherland 2004). This is especially important because many threatened species rarely use degraded habitats (Sodhi et al. 2008, Stouffer and Bierregaard 1995). For example, in the Neotropics, understory insectivores are one of the most threatened guilds of birds, and shade coffee production involves removing most understory vegetation (Sekercioglu et al. 2002). Furthermore, recent studies have demonstrated that the degree to which forest-dependent species will use shade coffee farms depends strongly on landscape context. Specifically, the presences of adjacent forest can exert stronger influence on community structure than local farm-level attributes such as tree density or structure (Roberts et al. 2000, Naidoo 2004, Anand et al. 2008).

Economic factors also constrain the utility of shade-coffee cultivation. Yield is known to decrease above forty percent canopy cover, which is the minimum recommended value of some shade-coffee certification programs (Perfecto et al. 2005, Philpott et al. 2007). Second, and less appreciated, farmers use shade to manage diseases such as Central American leaf spot disease (*Mycena citricolor*) and leaf rust (*Hemileia vastatrix*), and the effects of shade on disease, and hence production, depend upon local climatic conditions (Beer et al. 1998, Avelino et al. 2006, 2007). Specifically, high shade cover can increase disease prevalence in growing conditions with limited sunlight and high precipitation. Shade-coffee also has limited geographic relevance because it is not a suitable production method for lowland *robusta* varieties that dominate production in Africa and Asia (O'Brien and Kinnaird 2004). In addition, the value of shade-coffee as an effective restoration practice is limited because external investments are needed to support farmers during the lengthy process of growing trees to qualify for certification (Dietsch et al. 2004).

Although the debate between land-sparing and wildlife-friendly farming practices is nearly 10 years old, no empirical studies have been conducted to compare the conservation value of these production systems. This lack is partially due to the fact that few land-sparing systems have been proposed (Norris 2008). To address this limitation and improve upon methods of conserving biodiversity in agricultural landscapes, I conducted a study of a land-sparing coffee production system that involves forest conservation. The system, referred to as integrated open canopy (IOC) coffee, has only two requirements: forest must be protected on the farm at a minimum ratio of 1:1, and no new forest can be cut to plant coffee. Though not currently recognized by certification schemes, variations of this system have been implemented throughout the coffee growing world due to its economic benefits. Specifically, the forest adjacent to planted coffee can serve as an effective wind-break, contribute organic material, reduce erosion, and can be used for fuelwood and timber extraction (Arce et al. 2010). Recent research also demonstrates that coffee yield is substantially higher when forest is near because many bee species that pollinate coffee are forest-dependent (Ricketts et al. 2004a).

The objectives of this study were to compare avian species richness and composition among coffee farm and forest types. Specifically, I tested for differences in species richness of all species, forest-dependent species, and Neotropical-Nearctic migrants among primary forest, secondary forest, IOC farms, and shade coffee farms. I hypothesized that by protecting actual forest rather than just canopy trees, more forest-dependent species would occur in IOC farms than in shade coffee farms. An additional objective was to compare habitat quality among farm and forest types; however, direct estimates of habitat quality require species-specific survival estimates, which I could not obtain. I therefore compared morphometrics and ectoparasite loads among individuals in each habitat type because some studies have found correlations between these metrics and measures of apparent survival (Thompson et al. 1997, Latta 2003, Johnson et al. 2006).

2.2 Methods

2.2.1 Field methods

I quantified bird species richness, species composition, mass adjusted for length, subcutaneous fat, and ectoparasite loads in eight replicates of IOC coffee, shade coffee, secondary forest, and primary forest sites during November – March, 2006 – 2008. All sites were located between 800 and 1400 m elevation on the Pacific slope (Table 2.1). Secondary forest sites were 10-30 year-old stands formed from natural regeneration following pasture abandonment. Shade coffee sites were considered if they had at least 40% shade cover and 10 species of native trees because these are the primary requirements of most certification schemes (Philpott et al. 2007). Under the classification system of Moguel and Toledo (1999), these farms would be considered commercial polyculture systems, which is the only commonly used coffee agroforestry system in Costa Rica (Somarriba et al. 2004). Rustic shade coffee farms, which are farms with the original forest canopy partially intact, did not occur in the study area because previous experience led farmers to intensify production to achieve higher yields. The coffee portion of the IOC sites had few or no shade trees, and could have been classified as either un-shaded monocultures or shaded monocultures (Moguel and Toledo 1999). Only sites that had an amount of forest adjacent to the farm greater or equal to the area of the cultivated portion were used as IOC farms in this study. Sites were ≥ 0.5 km apart to maintain statistical independence. I observed no movement of banded individuals among sites.

To sample bird communities, I established grids of 10 mist nets (12 x 2.5 m, 32 and 36 mm mesh sizes) spaced 25 m apart in each site. In IOC sites, five nets were placed in the coffee portion of the farm and five in the adjacent forest. Thus, the IOC sample unit included both the coffee and forest portion of the farm. This sampling design effectively standardized the area of the net array, and reflected that IOC farms are comprised of both coffee plantation and forest. Sampling was conducted for seven hours per day over three consecutive days at each site. I recorded the following data for each bird captured: species, weight, sex, subcutaneous fat score (scale 0-7), wing chord, and the number of flight feathers (primaries, secondaries, and tertials) with at least one mite (family Analgesidae). Captures from ground mist-nets are biased towards species that use the lower strata of the forest, so I compensated for this bias by statistically accounting for heterogeneous capture probabilities among species as described below.

Field crews measured the following environmental variables in 20 x 20 m plots centered on each net location: diameter at breast height (dbh) of all stems > 2 cm, canopy height, and canopy cover. Extremely dense vegetation made the use of canopy densitometers and range finders to estimate canopy height and closure impractical. Therefore, to standardize our estimation of these variables we practiced estimating canopy height and closure in open conditions where actual values could be accurately estimated.

2.2.2 Statistical methods

I modeled variation in species richness for three species groups: all species, Neotropical-Nearctic migrants, and forest-dependent species. Neotropical-Nearctic migrants were treated separately because they are the target of specific conservation efforts (Rich et al. 2004). Forest-dependent species, which included some Neotropical-Nearctic migrants, were defined based upon the classification scheme of Stiles (1985). Specifically, species with dependency scores ≤ 2 on a scale of 1 to 5 were considered to be forest-dependent (Stiles 1985; Table 1.2). Recent work indicates that far more species are actually dependent upon forest than recognized by this classification scheme (Ruiz-Gutiérrez et al. 2010). Therefore, this is a conservative classification method that identifies species that rarely leave forest habitats.

My modeling strategy involved two steps. First, I used the model of Chao (1987) to estimate species richness for each site and each habitat type. This model accounts for species present but not detected, so long as they have non-zero detection probabilities. Because I used ground mist-nets, it is likely that some canopy species were not available for detection, and thus my inferences extend only to species that can be captured from the ground. This analysis was performed using the estimateR function in the R package vegan (Oksanen et al. 2010, R Development Core Team 2010). I then used weighted linear regression with an ANCOVA model structure to test for differences among habitat types. I used the inverse of the standard errors as weights to reduce the influence of estimates with low precision. These models also accounted for variation in effort due to small differences in net-hours among sites (Table 2.1). For 11 sites with few forest-dependent species, asymptotic standard errors could not be computed, and so I resampled the data 1000 times using a non-parametric bootstrap method to generate standard errors for those sites. Because the proximity to large forest reserves is known to influence bird species composition in more isolated sites (Anand et al. 2008), I included distance from the Monteverde Reserve Complex (MRC) to account for its influence in the analyses. The ANCOVA models were fit using the lm function and the R statistical software (R Development Core Team 2010).

Species composition was addressed using two techniques. First, I used multi-dimensional scaling to ordinate sites in relation to community structure. This multivariate technique allows for visualization of the gradients in species-level and site-level differences (Minchin 1987), which was performed using the metaMDS function in the R package vegan (Oksanen et al. 2010). The second technique I used to compare species composition was similar to the species richness models. I used the program EstimateS (Colwell 2010) to generate site-level similarity indices between non-primary forest sites and primary forest sites using the Chao-Jaccard similarity index (Chao et al. 2006). Similarity indices are computed as site-to-site pairs, and thus to compare a single site to all primary forest sites I used the mean of the eight values for each non-forest site. These values represent the average similarity between each non-forest site to the primary forest bird community. I used the inverse of the standard deviation of these scores as weights in the ANCOVA model. The response variable was the similarity scores for each non-forest site and the predictor variables were habitat type and distance from the MRC.

To test for differences in morphometrics and ectoparasite loads on individuals among habitat types I used linear mixed-effects models (Pinheiro and Bates 2000). I ran models with the following metrics as response variables: residuals from mass regressed on wing length, subcutaneous fat, and flight-feather parasite loads (feather mites in the family Analgesidae). These three variables have been found to correlate with individual fitness or habitat quality; however, it is important to note that these relationships have not been determined for the species studied here. Nonetheless, some evidence exists that mass-length residuals can be positively related to physiological condition and apparent survival (Schulte-Hostedde et al. 2005, Johnson et al. 2006). Fat reserves can reflect habitat quality because individuals of some species store less fat in habitats with more predictable food resources (Rappole and Warner 1980, Holberton and Able 2000). Ecto-parasite prevalence is reported to be negatively correlated with individual fitness as it can affect sexually-selected traits such as plumage coloration, and may influence return rates (Thompson et al. 1997, Latta 2003). Habitat type was treated as both a fixed and random effect, and bird species was treated as a random effect. Treating species and habitat type as random effects accounts for variation among species in their response to habitat and allows for inferences to be made for individual species or for average differences among species. I used a Gaussian distribution for the mass-length residual model, and a Poisson distribution for the fat-score and parasite models. I selected models using Akaike's Information Criterion (AIC). These analyzes were conducted in R-2.11.0 using the lme4 package (Bates and Maechler 2010).

2.3 Results

2.3.1 Species richness

I captured 2,298 individuals representing 148 species during 6,629 net-hours (Table 2.1). Twenty-five of these species were Neotropical-Nearctic migrants and 36 were forest-dependent species. Estimates of species richness at the habitat level, ignoring site-specific covariates showed there was no difference in species richness among primary forest, secondary forest and IOC, or shade coffee, as indicated by overlapping 95% confidence intervals (Table 2.2). Similarly, there was no difference in species richness of forest dependent species among primary forest, secondary forest and IOC, however richness of forest dependent species was significantly lower in shade coffee than all other habitats.

Similarly, modeling species richness of all species at the site level showed there was no difference in species richness between farm and forest types, and species richness was not related to distance from the Monteverde reserve complex (Table 2.3). When analyzing forest-dependent species separately, however, I found a strong effect of both habitat type and distance from the protected area (Table 2.3). This model indicated that forest-dependent species richness was highest in primary forest and IOC farms followed by secondary forest and lowest in shade coffee farms. In all habitat types, species richness of this guild declined with distance from the reserve complex (Figure 2.1).

Neotropical-Nearctic migrant species richness significantly differed among habitat types but was not affected by distance from the MRC (Table 2.4). Species richness of this guild was lowest in primary forest, followed by secondary forest, and highest in IOC and shade-coffee farms, which had equivalent numbers of species (Figure 2.2).

2.3.2 Species composition

The multidimensional scaling ordination revealed clear separation of the primary forest sites from the other habitat types (Figure 2.3). Shade coffee sites had the least similarity in community composition to the primary forest as demonstrated by its position on dimension one. The second dimension partially separated IOC sites from secondary forest sites, though some overlap existed between all three non-primary forest sites.

The ANCOVA model of community similarity between non-primary forest sites and primary forest indicated that similarity declined with distance from the MRC and was lowest in shade-coffee farms (Figure 2.4), although the latter finding was only marginally significant (Table 2.5). Species level occurrence data provided additional evidence that bird communities were more similar between IOC farms and forest, than shade farms and forest. Seven species were found in all habitat types except for shade coffee farms, all of which are forest-dependent species: *Basileuterus culicivorus*, *Lampornis hemileucus*, *Myrmotherula schisticolor*, *Platyrinchus mystaceus*, *Premnoplex brunnescens*, *Sclerurus mexicanus*, and *Turdus obsoletus*. In contrast only two species occurred in all habitats other than IOC farms, and neither of these two species are considered forest-dependent: *Aulacorhynchus prasinus*, *Turdus plebejus*. These species-level results should be considered suggestive, however, because, owing to the large number of species, I did not conduct detailed occurrence analyses that accounted for detection probability.

2.3.3 Morphometrics and ectoparasites

I found no differences in mass-length residuals or fat scores among farm and forest types, but flight feather parasite levels did differ (Tables 2.5-2.8). Birds in secondary forests had higher numbers of feather mites than individuals in the other habitat types (Table 2.6). Although there was evidence of differences in parasite loads among species, the habitat effect was consistent among species as demonstrated by the lack of support for a random habitat effect.

2.3.4 Habitat characteristics

The four habitat types differed with respect to most environmental variables as intended by the study design (Table 2.7). Basal area in shade-coffee farms was more than seven times as high as in the coffee portion of IOC farms. Similarly, the number of trees, canopy cover and canopy height were much higher in shade farms than in the coffee portion of IOC farms. Total dbh was similar between shade coffee farms and secondary forest sites. Although the forest in the IOC farms was second growth, it was structurally intermediate between the even-aged secondary forest sites and the primary forest sites in terms of tree basal area and canopy height. This finding was probably because these forest patches were used for wind breaks and timber and thus trees were allowed to grow tall albeit at lower tree densities than primary forest sites.

2.4 Discussion

Conserving biodiversity in tropical agricultural landscapes is an integral component of global conservation efforts (Foley et al. 2005, Norris 2008). Conservationists disagree on the best strategies to accomplish this goal; however, few empirical data exist to compare alternatives. This study is the first to evaluate a land-sparing agricultural production system that can be used as a market-based conservation tool to incentivize forest protection and restoration.

My results indicate that the Integrated Open Canopy coffee production system improves upon alternative agroforestry systems from the standpoint of biodiversity conservation by accommodating forest-dependent species that are of high conservation concern. Numerous studies have found forest-dependent species to be uncommon in shade coffee farms (Roberts et al. 2000, Tejeda-Cruz and Sutherland 2004, Raman 2006, Anand et al. 2008) as well as other agroforestry systems (King et al. 2006a). My finding that approximately twice as many forest-dependent species occurred in IOC farms as in shade coffee farms shows that this system is more effective at providing habitat for these threatened bird species. In addition, Neotropical-Nearctic migrants, whose occurrence in shade coffee farms has been used to justify its environmental certification (Sherry 2000), were abundant in IOC farms even though the coffee plantation portion of the farms had few or no shade trees. Other groups also benefited as demonstrated by higher community similarity between IOC farms primary forest sites than between shade coffee farms and primary forest. Species composition in IOC farms was most similar to secondary forest sites. This result is important because numerous studies have demonstrated the importance of secondary forest to maintaining biodiversity, but few economically feasible strategies have been put forward to protect secondary forests (Chokkalingam and De Jong 2001, Chazdon et al. 2009).

I found no evidence of differences between morphometrics or ecotparasite prevalence among individuals in IOC farms and primary forest, suggesting that habitat quality is comparable for species that use both habitats. However, this assertion is based upon the assumption that these metrics correlate with survival, which has not been demonstrated. Therefore, studies comparing vital rates such as survivorship are needed for a more definitive assessment of the habitat quality of IOC farms because previous research has indicated that survival can be lower in disturbed habitats than in primary forest (Rappole et al. 1989).

My finding that the many forest-dependent species can occur in the forested portion of IOC farms contributes to a growing body of research demonstrating the importance of conserving remnant forest patches in tropical agricultural landscapes (Luck and Daily 2003, Haslem and Bennett 2008, Ruiz-Gutiérrez et al. 2010), but unlike past studies, I found that forest-dependent species richness declined by more than 50% in all habitat types over the range of distances from a large protected area. Working in a tropical agricultural landscape abutting the 30,000 ha Monteverde Reserve Complex enabled me to detect this effect, which is likely missed in regions where protected areas do not occur. These results emphasize the importance of conserving large areas of protected forest to serve as a source population for maintaining populations of forest-dependent species in isolated parks and preserves (Barlow et al. 2007a, Brooks et al. 2009). My results also suggest that future studies of habitat use of forest dependent birds in tropical landscapes should include proximity to large protected areas in their analyses to avoid potential confounding between distance to forest with habitat type. This procedure would also reduce the risk of mistakenly concluding that a population in a given isolated forest is stable, when it could be being maintained by individuals from nearby large preserves.

Integrated open canopy coffee production demonstrates that many of the criticisms of land-sparing techniques are not necessarily valid. For instance, critics maintain that the higher yields require increased chemical inputs on large-scale monocultures that impinge upon traditional rural lifestyles (Evenson and Gollin 2003). However, IOC coffee cultivation is currently being practiced by small farmers in Costa Rica due to its inherent agro-economic advantages. Specifically, the system can increase yield without added chemical inputs by allowing farmers to manage shade to control disease and sun exposure (Avelino et al. 2007, Arce et al. 2010). In contrast, certification programs that mandate high levels of shade cover and tree densities restrict farmers' abilities to maximize yield and adapt to local conditions. Yield increases are also likely due to higher pollination rates associated with forest-dependent bees (Ricketts et al. 2004b, Arce et al. 2010). Wind damage can also reduce coffee yield in many growing regions, and the forest components of IOC farms can mitigate this problem. A second argument against land-sparing is that increasing yield does not ensure that freed land will be spared for conservation. IOC overcomes this limitation by requiring a 1:1 farm to forest ratio and requiring that no new forest is cleared to establish new farms. Furthermore, the IOC model could be applicable to shade intolerant crops. Numerous researchers have called for improving the habitat quality of farmland, yet few have explained how the production of crops such as corn, sugarcane, or oil palm could be made sustainable (Perfecto and Vandermeer 2010). The IOC model offers a possible solution because virtually any crop could be complemented with forest offsets.

Integrated open canopy coffee production offers numerous economic benefits over alternative conservation strategies for agricultural landscapes. Most "payment for biodiversity protection" strategies are hampered by two problems (Pagiola et al. 2004). First, initial investments are often required to plant trees or purchase land. Second, most plans require top-down approaches to enforce regulation. The viability of these programs depends on political commitments or economic resources that may change with changes in government policies or economic conditions, and this increased uncertainty can present another impediment to farmer participation in these programs. The IOC system avoids both of these problems because market-driven economic incentives would motivate farmers to handle implementation and regulation without requiring support from external government entities or NGOs.

Although these inherent benefits are sufficient to make this system economically viable, a formal certification system could increase the economic incentives for protecting forest because “environmentally friendly” coffee commands a higher market price (Philpott et al. 2007). Many aspects of the certification system could be similar to that used by shade-grown coffee, such as procedures for verification and chain of custody; however, the certification of the agricultural practices themselves could be far simpler. Rather than certifying the amount and types of shade trees on a farm, an IOC certification would simply require verifying that spared lands are protected. Thus, a farmer could gain coffee price premiums by simply removing cattle from degraded pasture. This premium requires a consumer demand for environmentally certified coffee. Such specialty markets are currently growing at rate of 20% per year compared to negligible growth in conventional markets, indicating that consumer demand does exist (Wollni and Zeller 2007). The simplicity of the system would make inspection easy in comparison to other programs in which trained field biologists must measure numerous structural characteristics of the farm. A second, non-mutually exclusive, option would be to pay farmers for the carbon credits earned by regenerating forest (Goldstein et al. 2006). Carbon credit programs are growing rapidly in response to concerns over global climate change (Laurance 2008). Conceivably, no separate certification would be needed to qualify a farm as IOC other than that carried out in the course of verifying the qualifications of the farm for carbon credits, reducing the cost and complexity of the certification process even further.

One limitation of this study was that I was unable to directly compare IOC to rustic shade coffee production systems, which are considered to have the highest conservation value among shade coffee systems (Moguel and Toledo 1999), and thus, would have compared more favorably to primary forest than the commercial polycultures in my study. However, the lack of rustic farms in my study area is typical of coffee growing regions (Philpott et al. 2007) because these farms, as depicted by Moguel and Toledo (1999), have very low yields. As a result, rustic coffee cultivation is not practiced at a scale large enough to affect a significant amount of bird habitat (Somarriba et al. 2004), and its inclusion in this study would not have been informative. Furthermore, the shade-coffee farms I worked in met many of the requirements of current certification programs (Philpott et al. 2007). An additional limitation of my study was that many of the shade coffee farms were adjacent to forest remnants, and thus some species captured in these farms probably would not have occurred there if the farms were truly isolated (Cohen and Lindell 2005, Sekercioglu et al. 2007).

Integrated open canopy coffee production can complement current coffee certification systems by providing an incentive to increase forest cover in tropical agricultural landscapes, and thereby provide habitat for forest-dependent birds that do not use shade coffee. Widespread adoption of this production system could have a transformative effect in tropical agricultural landscapes where agriculture continues to expand at the expense of forest cover. Future research should investigate the effect of forest patch size and shape on forest-dependent species with the goal of developing best management practices for the application of IOC coffee, which could provide the basis of a formal certification system.

Table 2.1. Captures per 100 net-hours. Forest dependence score is from Stiles (1985). Neotropical-Nearctic migrants are in bold. N is the number of individuals captured. Data are from 32 sites surveyed in the Cordillera de Tilarán, Costa Rica, 2006-2008.

Species	Forest dependence score	Primary forest	Secondary Forest	IOC Coffee	Shade Coffee	N
Tiaris olivacea	5	0.06	6.10	0.68	4.18	182
Mionectes olivaceus	3	3.87	0.48	1.35	0.49	105
Phaethornis guy	3	2.34	1.38	0.99	0.98	95
Chiroxiphia linearis	3	0.12	2.57	1.23	0.92	80
Amazilia tzacatl	5	0.06	1.20	0.68	2.83	78
Vermivora peregrina	4	0.06	1.68	0.43	2.21	72
Basileuterus rufifrons	3	0.00	1.38	1.17	1.78	71
Eupherusa eximia	3	1.46	1.44	0.99	0.43	72
Campylopterus hemileucurus	3	0.88	0.66	0.62	2.03	69
Lampornis calolaemus	3	3.22	0.18	0.31	0.12	65
Saltator maximus	5	0.06	1.14	0.43	2.03	60
Catharus aurantiirostris	4	0.18	0.72	1.60	0.68	52
Myioborus miniatus	3	0.88	0.66	1.05	0.18	46
Turdus grayi	5	0.00	0.60	0.68	1.48	45
Melozone leucotis	4	0.00	1.02	0.25	1.29	42
Wilsonia pusilla	4	0.00	0.96	0.55	0.98	41
Myadestes melanops	2	2.23	0.06	0.06	0.12	41
Thryothorus rufalbus	2	0.06	0.84	0.49	0.98	39
Chlorospingus ophthalmicus	3	1.41	0.00	0.86	0.00	38
Phaethornis striigularis	4	0.41	0.90	0.31	0.61	37
Myiarchus tuberculifer	4	0.00	0.60	0.49	0.86	32
Zimmerius vilissimus	3	0.00	0.72	0.18	1.04	32
Amazilia saucerrottei	4	0.00	0.42	0.68	0.74	30
Buarremon brunneinucha	1	1.23	0.18	0.18	0.12	29
Premnoplex brunnescens	2	1.41	0.12	0.18	0.00	29
Turdus obsoletus	2	0.47	0.06	1.17	0.00	28
Euphonia hirundinacea	4	0.00	0.48	0.62	0.55	27
Catharus fuscater	1	1.46	0.00	0.12	0.00	27
Thryothorus modestus	5	0.00	0.24	0.92	0.37	25

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Dendrocincla homochroa	2	0.35	0.42	0.49	0.25	25
Chlorostilbon canivetii	5	0.00	0.36	0.12	0.92	23
Glyphorhynchus spirurus	3	0.47	0.42	0.37	0.12	23
Catharus ustulatus	3	0.06	0.36	0.86	0.06	22
Turdus plebejus	3	0.06	0.00	0.43	0.80	21
Basileuterus culicivorus	2	0.76	0.24	0.25	0.00	21
Dendroica pensylvanica	4	0.00	0.60	0.00	0.61	20
Seiurus aurocapillus	3	0.00	0.06	0.68	0.43	19
Pheucticus ludovicianus	5	0.00	0.06	0.00	1.04	18
Momotus momota	4	0.00	0.30	0.43	0.37	18
Hylocichla mustelina	2	0.06	0.30	0.37	0.37	18
Troglodytes aedon	5	0.00	0.36	0.18	0.49	17
Platyrinchus mystaceus	1	0.64	0.06	0.31	0.00	17
Elaenia frantzii	4	0.00	0.06	0.86	0.06	16
Thraupis episcopus	5	0.00	0.18	0.00	0.80	16
Empidonax flaviventris	3	0.00	0.30	0.12	0.55	16
Heliodoxa jacula	3	0.70	0.00	0.25	0.00	16
Leptotila verreauxi	4	0.00	0.30	0.12	0.49	15
Atlapetes albinucha	4	0.00	0.30	0.25	0.31	14
Mniotilta varia	3	0.06	0.12	0.12	0.49	13
Myrmotherula schisticolor	2	0.29	0.06	0.43	0.00	13
Vireo philadelphicus	3	0.00	0.00	0.37	0.37	12
Henicorhina leucophrys	1	0.53	0.00	0.18	0.00	12
Euphonia anneae	3	0.64	0.00	0.06	0.00	12
Elvira cupreiceps	2	0.06	0.12	0.43	0.06	11
Myiozetetes similis	5	0.00	0.00	0.00	0.55	9
Sporophila americana	5	0.00	0.24	0.00	0.31	9
Ramphocelus passerinii	5	0.00	0.30	0.00	0.25	9
Phlogothraupis sanguinolenta	5	0.12	0.24	0.00	0.18	9
Archilochus colubris	5	0.00	0.06	0.12	0.31	8
Hylophilus decurtatus	3	0.00	0.18	0.06	0.25	8
Sittasomus griseicapillus	3	0.06	0.24	0.12	0.06	8

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Dysithamnus mentalis	2	0.41	0.00	0.06	0.00	8
Basileuterus tristriatus	1	0.47	0.00	0.00	0.00	8
Cyanerpes cyaneus	3	0.00	0.00	0.00	0.37	6
Mionectes oleagineus	3	0.00	0.24	0.06	0.06	6
Attila spadiceus	3	0.12	0.06	0.12	0.06	6
Vermivora chrysoptera	3	0.12	0.12	0.06	0.06	6
Xiphorhynchus erythropygius	2	0.29	0.00	0.06	0.00	6
Piranga rubra	4	0.00	0.06	0.06	0.18	5
Aulacorhynchus prasinus	3	0.06	0.00	0.12	0.12	5
Passerina cyanea	5	0.00	0.18	0.00	0.12	5
Lampornis hemileucus	2	0.06	0.12	0.12	0.00	5
Zonotrichia capensis	5	0.00	0.30	0.00	0.00	5
Dendroica virens	3	0.12	0.12	0.06	0.00	5
Empidonax flavescens	3	0.29	0.00	0.00	0.00	5
Sporophila torqueola	5	0.00	0.00	0.00	0.25	4
Melanerpes hoffmannii	4	0.00	0.06	0.06	0.12	4
Rhynchocyclus brevirostris	2	0.06	0.00	0.18	0.00	4
Cyanocorax morio	5	0.00	0.12	0.06	0.06	4
Carduelis psaltria	5	0.00	0.12	0.00	0.12	4
Lepidocolaptes souleyetii	4	0.00	0.12	0.00	0.12	4
Coereba flaveola	4	0.12	0.00	0.12	0.00	4
Sclerurus mexicanus	1	0.18	0.06	0.00	0.00	4
Eutoxeres aquila	2	0.23	0.00	0.00	0.00	4
Semnornis frantzii	3	0.23	0.00	0.00	0.00	4
Arremonops rufivivgatus	2	0.00	0.00	0.18	0.00	3
Tangara dowii	3	0.00	0.00	0.18	0.00	3
Tangara icterocephala	3	0.00	0.00	0.18	0.00	3
Passerina ciris	5	0.00	0.00	0.12	0.06	3
Oporornis philadelphia	5	0.00	0.00	0.06	0.12	3
Myiodynastes luteiventris	4	0.00	0.00	0.00	0.18	3
Stelgidopteryx serripennis	5	0.00	0.00	0.00	0.18	3
Lophotriccus pileatus	3	0.00	0.06	0.12	0.00	3
Thamnophilus doliatus	4	0.00	0.06	0.12	0.00	3
Heliomaster constantii	4	0.00	0.06	0.00	0.12	3

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Vireo flavifrons	3	0.00	0.06	0.00	0.12	3
Seiurus motacilla	5	0.18	0.00	0.00	0.00	3
Myiarchus nuttingi	3	0.00	0.00	0.12	0.00	2
Elaenia flavogaster	5	0.00	0.00	0.00	0.12	2
Megarhynchus pitangua	4	0.00	0.00	0.00	0.12	2
Psarocolius montezuma	4	0.00	0.00	0.00	0.12	2
Tachyphonus rufus	5	0.00	0.00	0.00	0.12	2
Tolmomyias sulphurescens	5	0.00	0.00	0.00	0.12	2
Dendrocolaptes sanctithomae	3	0.00	0.06	0.06	0.00	2
Henicorhina leucosticta	2	0.00	0.06	0.06	0.00	2
Hylocharis eliciae	3	0.00	0.06	0.00	0.06	2
Volantinia jacarina	5	0.00	0.06	0.00	0.06	2
Lysurus crassirostris	1	0.06	0.00	0.06	0.00	2
Trogon aurantiiventris	3	0.00	0.12	0.00	0.00	2
Cyanolyca cucullata	1	0.12	0.00	0.00	0.00	2
Amaurospiza concolor	4	0.00	0.00	0.06	0.00	1
Colibri thalassinus	4	0.00	0.00	0.06	0.00	1
Cranioleuca erythrops	2	0.00	0.00	0.06	0.00	1
Empidonax minimus	4	0.00	0.00	0.06	0.00	1
Galbula ruficauda	3	0.00	0.00	0.06	0.00	1
Leptopogon superciliaris	3	0.00	0.00	0.06	0.00	1
Manacus candei	3	0.00	0.00	0.06	0.00	1
Myiarchus crinitus	3	0.00	0.00	0.06	0.00	1
Piaya cayana	4	0.00	0.00	0.06	0.00	1
Xiphorhynchus susurrans	3	0.00	0.00	0.06	0.00	1
Amblycercus holosericeus	5	0.00	0.00	0.00	0.06	1
Dives dives	5	0.00	0.00	0.00	0.06	1
Icterus galbula	4	0.00	0.00	0.00	0.06	1
Oporornis tolmiei	5	0.00	0.00	0.00	0.06	1
Saltator coerulescens	5	0.00	0.00	0.00	0.06	1
Tityra semifasciata	4	0.00	0.00	0.00	0.06	1
Todirostrum cinereum	4	0.00	0.00	0.00	0.06	1
Tolmomyias assimilis	2	0.00	0.00	0.00	0.06	1
Cyclarhis gujanensis	4	0.00	0.06	0.00	0.00	1

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Dendroica petechia	5	0.00	0.06	0.00	0.00	1
Eucometis penicillata	2	0.00	0.06	0.00	0.00	1
Oporornis formosus	1	0.00	0.06	0.00	0.00	1
Pachyramphus aglaiae	4	0.00	0.06	0.00	0.00	1
Piculus rubiginosus	3	0.00	0.06	0.00	0.00	1
Ramphastes sulfuratus	3	0.00	0.06	0.00	0.00	1
Sclerurus albigularis	1	0.00	0.06	0.00	0.00	1
Tangara gyrola	3	0.00	0.06	0.00	0.00	1
Thryothorus rutilus	5	0.00	0.06	0.00	0.00	1
Turdus assimilis	1	0.00	0.06	0.00	0.00	1
Anabacerthia ochrolaemus	2	0.06	0.00	0.00	0.00	1
Campylorhamphus pusillus	1	0.06	0.00	0.00	0.00	1
Corapipo altera	3	0.06	0.00	0.00	0.00	1
Micrastur semitorquatus	2	0.06	0.00	0.00	0.00	1
Myrmeciza immaculata	1	0.06	0.00	0.00	0.00	1
Oryzoborus funereus	5	0.06	0.00	0.00	0.00	1
Scytalopus argentifrons	2	0.06	0.00	0.00	0.00	1
Syndactyla subalaris	1	0.06	0.00	0.00	0.00	1
Veniliornis fumigatus	3	0.06	0.00	0.00	0.00	1

Table 2.2. Species richness by species group and habitat type. Estimates and 95% confidence intervals are from the abundance-based model of Chao (1987). Data are from mist-net captures in 32 sites in the Cordillera de Tilarán, Costa Rica, 2006-2008.

Species group	Habitat	Observed	Estimate	Lower CI	Upper CI
All	Primary forest	61	96	73	163
	Secondary forest	88	107	95	133
	IOC coffee	86	128	104	197
	Shade coffee	84	94	87	107
Forest-dependent	Primary forest	28	61	37	164
	Secondary forest	21	26	21	49
	IOC coffee	18	29	20	84
	Shade coffee	7	7	7	13
Nearctic migrants	Primary forest	7	9	7	22
	Secondary forest	16	19	16	34
	IOC coffee	17	22	18	45
	Shade coffee	19	22	19	37

Table 2.3. Parameter estimates and significance tests from ANCOVA models of species richness. The reference level (ß0) is primary forest. SF, IOC, and Shade are differences from ß0 for secondary forest, integrated open canopy coffee, and shade coffee sites respectively. DistMRC is the slope parameter for distance from Monteverde Reserve Complex. Data are from mist-net captures in 32 sites in the Cordillera de Tilarán, Costa Rica, 2006-2008.

Response	Parameter	Estimate	SE	*t*	*P* (>|*t*|)	$F_{4, 27}$	*P*(>*F*)
All species	ß0	26.74	4.70	5.69	<0.001	1.201	0.333
	SF	6.93	6.02	1.15	0.260		
	IOC	12.83	7.27	1.77	0.089		
	Shade	14.21	7.02	2.02	0.053		
	DistMRC	-2.89	2.83	-1.02	0.317		
Forest-dependents (log transformed)	ß0	2.13	0.23	9.11	<0.001	20.77	<0.001
	SF	-0.52	0.29	-1.82	0.080		
	IOC	-0.60	0.31	-1.91	0.067		
	Shade	-1.20	0.29	-4.19	<0.001		
	DistMRC	-0.43	0.09	-4.81	<0.001		
Nearctic migrants (log transformed)	ß0	0.74	0.23	3.21	0.003	7.742	<0.001
	SF	0.89	0.27	3.32	0.003		
	IOC	1.20	0.33	3.60	0.001		
	Shade	1.17	0.34	3.44	0.002		
	DistMRC	0.17	0.11	1.49	0.147		

Table 2.4. Parameter estimates and significance tests from ANCOVA models of species composition. The reference level (*ß*0) is similarity between secondary forest and primary forest. IOC and Shade are differences in the similarity to primary forest from *ß*0 for integrated open canopy coffee and shade coffee sites respectively. DistMRC is the slope parameter for distance from Monteverde Reserve Complex. Data are from mist-net captures in 32 sites in the Cordillera de Tilarán, Costa Rica, 2006-2008.

Response	Parameter	Estimate	SE	t	P (>|t|)	$F_{3, 20}$	$P(>F)$
All species (square-root transformed)	*ß*0	0.04	0.05	0.89	0.384	12.54	<0.001
	IOC	-0.04	0.07	-0.55	0.589		
	Shade	-0.13	0.07	-1.86	0.078		
	DistMRC	-0.14	0.03	-4.94	<0.001		

Table 2.5. Mean ± SD of mass-wing chord residuals for species captured in all four farm and forest types. Sample size is shown in parentheses. Data are from mist-net captures in 32 sites in the Cordillera de Tilarán, Costa Rica, 2006-2008.

Species	Primary forest	Secondary forest	IOC coffee	Shade coffee
Black-and-White Warbler	0 ± NA (1)	1 ± 1 (2)	1 ± NA (1)	0 ± 1 (7)
Black-faced Solitare	0 ± 2 (34)	-3 ± NA (1)	-2 ± NA (1)	-1 ± NA (1)
Buff-throated Saltator	-2 ± NA (1)	-1 ± 2 (7)	1 ± 4 (16)	0 ± 4 (30)
Chestnut-capped Brush-Finch	0 ± 3 (16)	-2 ± 1 (3)	2 ± NA (1)	-1 ± 2 (2)
Golden-winged Warbler	0 ± 0 (2)	-1 ± NA (1)	0 ± 1 (2)	1 ± NA (1)
Long-tailed Manakin	1 ± 0 (2)	0 ± 1 (20)	0 ± 1 (40)	0 ± 1 (14)
Olivaceous Woodcreeper	0 ± NA (1)	0 ± 0 (2)	0 ± 1 (2)	0 ± NA (1)
Olive-striped Flycatcher	0 ± 1 (64)	0 ± 1 (20)	0 ± 1 (6)	1 ± 2 (7)
Orange-billed Nightingale-Thrush	2 ± 3 (3)	0 ± 2 (25)	0 ± 2 (11)	0 ± 2 (11)
Ruddy Woodcreeper	0 ± 3 (6)	-1 ± 1 (7)	1 ± 2 (7)	1 ± 5 (4)
Rufous-and-white Wren	-4 ± NA (1)	1 ± 1 (6)	-1 ± 3 (9)	1 ± 1 (8)
Slate-throated Redstart	0 ± 0 (12)	0 ± 0 (14)	0 ± 0 (10)	0 ± 0 (3)
Swainson's Thrush	0 ± NA (1)	0 ± 2 (14)	0 ± 1 (4)	2 ± NA (1)
Wedge-billed Woodcreeper	-1 ± 1 (7)	0 ± 1 (6)	1 ± 3 (6)	-1 ± 1 (2)
Wood Thrush	9 ± NA (1)	-1 ± 4 (6)	-1 ± 1 (5)	0 ± 4 (4)

Table 2.6. Mean ± SD of number of flight feather with parasitic mites. Sample size is shown in parentheses. Data are from mist-net captures in 32 sites in the Cordillera de Tilarán, Costa Rica, 2006-2008.

Species	Primary forest	Secondary forest	IOC coffee	Shade coffee
Black-and-white warbler	12 ± NA (1)	5 ± 6 (2)	9 ± 6 (2)	5 ± 4 (7)
Black-faced solitare	8 ± 4 (37)	9 ± NA (1)	17 ± NA (1)	3 ± NA (1)
Bright-rumped attila	2 ± 2 (2)	4 ± 0 (2)	2 ± NA (1)	0 ± NA (1)
Buff-throated saltator	7 ± NA (1)	17 ± 0 (7)	12 ± 4 (19)	13 ± 4 (31)
Chestnut-capped brush-finch	8 ± 5 (19)	8 ± 7 (3)	1 ± 1 (2)	5 ± 6 (2)
Golden-winged warbler	5 ± 6 (2)	0 ± NA (1)	3 ± 1 (2)	5 ± NA (1)
Long-tailed manakin	6 ± 0 (2)	9 ± 5 (19)	8 ± 5 (41)	4 ± 5 (15)
Olivaceous woodcreeper	7 ± NA (1)	9 ± 8 (2)	4 ± 3 (3)	15 ± NA (1)
Olive-striped flycatcher	3 ± 3 (65)	3 ± 3 (21)	4 ± 4 (5)	0 ± 1 (8)
Orange-billed nightingale-thrush	1 ± 2 (3)	5 ± 4 (25)	5 ± 4 (12)	4 ± 5 (11)
Ruddy woodcreeper	4 ± 4 (6)	11 ± 6 (7)	9 ± 7 (7)	12 ± 6 (3)
Rufous-and-white wren	11 ± NA (1)	6 ± 7 (8)	4 ± 6 (13)	4 ± 5 (11)
Slate-throated redstart	12 ± 4 (14)	13 ± 3 (15)	12 ± 5 (10)	11 ± 1 (3)
Swainson's thrush	6 ± NA (1)	8 ± 5 (13)	8 ± 7 (6)	7 ± NA (1)
Tennessee warbler	4 ± NA (1)	5 ± 3 (7)	5 ± 5 (27)	3 ± 4 (31)
Wedge-billed woodcreeper	10 ± 6 (6)	14 ± 6 (6)	10 ± 6 (7)	6 ± 8 (2)
Wood thrush	0 ± NA (1)	10 ± 5 (6)	11 ± 6 (5)	13 ± 4 (6)
Yellow-faced grassquit	0 ± NA (1)	0 ± 1 (10)	1 ± 2 (87)	1 ± 2 (50)

Table 2.7. Mean ± SD of fat scores for species captured in all four farm and forest types. Sample size is shown in parentheses. Data are from mist-net captures in 32 sites in the Cordillera de Tilarán, Costa Rica, 2006-2008.

Species	Primary forest	Secondary forest	IOC coffee	Shade coffee
Black-and-White Warbler	2 ± NA (1)	2 ± 2 (2)	3 ± 3 (2)	1 ± 2 (7)
Bright-rumped Attila	0 ± 0 (2)	0 ± 0 (2)	0 ± NA (1)	1 ± NA (1)
Buff-throated Saltator	0 ± NA (1)	0 ± 1 (7)	0 ± 0 (19)	1 ± 1 (31)
Chestnut-capped Brush-Finch	0 ± 1 (20)	0 ± 0 (3)	0 ± 0 (2)	0 ± 0 (2)
Golden-winged Warbler	0 ± 0 (2)	1 ± NA (1)	1 ± 1 (2)	0 ± NA (1)
Long-tailed Manakin	1 ± 1 (2)	1 ± 1 (20)	1 ± 1 (42)	1 ± 1 (15)
Olivaceous Woodcreeper	0 ± NA (1)	1 ± 1 (2)	1 ± 1 (3)	0 ± NA (1)
Olive-striped Flycatcher	1 ± 1 (66)	1 ± 1 (22)	1 ± 1 (6)	2 ± 2 (8)
Orange-billed Nightingale-Thrush	0 ± 0 (3)	0 ± 1 (25)	0 ± 1 (12)	1 ± 1 (11)
Ruddy Woodcreeper	0 ± 0 (6)	0 ± 0 (7)	0 ± 0 (7)	0 ± 1 (4)
Rufous-and-white Wren	1 ± NA (1)	0 ± 0 (8)	0 ± 1 (14)	0 ± 1 (13)
Slate-throated Redstart	0 ± 1 (14)	0 ± 0 (17)	0 ± 1 (10)	0 ± 1 (3)
Swainson's Thrush	0 ± NA (1)	1 ± 1 (14)	0 ± 0 (5)	1 ± NA (1)
Tennessee Warbler	0 ± NA (1)	1 ± 1 (7)	1 ± 1 (28)	1 ± 1 (34)
Wedge-billed Woodcreeper	2 ± 2 (7)	0 ± 0 (5)	2 ± 2 (7)	0 ± 0 (2)
Wood Thrush	1 ± NA (1)	1 ± 1 (6)	1 ± 0 (5)	1 ± 1 (6)
Yellow-faced Grassquit	3 ± NA (1)	0 ± 1 (9)	1 ± 1 (91)	0 ± 0 (55)

Table 2.8. Mixed-effects models of mass-wing chord residuals (M-L resids), flight feather parasites (Parasites), and subcutaneous fat scores (Fat) ranked by AIC. Data are from mist-net captures in 32 sites in the Cordillera de Tilarán, Costa Rica, 2006-2008.

Response	Fixed	Random	Individuals	Species	Parameters	AIC
M-L resids	.	Species	503	15	3	2096.8
	Habitat	Species	503	15	6	2098.0
	.	Species, Habitat	503	15	12	2114.8
	Habitat	Species, Habitat	503	15	15	2116.0
Parasites	Habitat	Species, Habitat	754	18	5	2675.9
	.	Species, Habitat	754	18	14	2676.4
	Habitat	Species	754	18	2	2744.1
	.	Species	754	18	11	2772.2
Fat	.	Species, Habitat	778	18	11	937.9
	Habitat	Species	778	18	5	942.4
	Habitat	Species, Habitat	778	18	14	959.5
	.	Species	778	18	2	964.0

Table 2.9. Parameter estimates from most supported mixed-effects model of flight feather parasite load. Estimates are fixed effects coefficients except for the random effect of “Species”, which is the standard deviation of the differences among species. The reference level (*ß*0) is primary forest. SF, IOC, and Shade are differences from *ß*0 for secondary forest, integrated open canopy coffee, and shade-coffee sites respectively.

Parameter	Estimate	SE	*z*	Pr(>|*z*|)
*ß*0	1.71	0.16	10.82	0.00
SF	0.17	0.05	3.22	0.00
IOC	0.04	0.06	0.80	0.43
Shade	-0.10	0.06	-1.61	0.11
Species	0.64	-	-	-

Table 2.10 Summary statistics of environmental, geographical, and survey effort variables. For net-level variables, values are shown for coffee nets and forest nets within IOC sites. Data are from 32 sites surveyed in the Cordillera de Tilarán, Costa Rica, 2006-2008.

Variable	Habitat[a]	Mean	SD	Min	Median	Max
Elevation (m)	PF	1289	93	1120	1280	1401
	SF	1105	127	863	1151	1240
	Shade	1080	87	912	1080	1180
	IOC	1073	107	923	1076	1196
Distance from Monteverde Reserve Complex (m)	PF	1261	797	226	1129	2893
	SF	2145	1678	155	1867	4465
	Shade	2821	941	1680	2750	4263
	IOC	2512	1542	997	2126	5398
Total dbh[b] (cm)	PF	857	391	566	712	1429
	SF	363	278	137	307	819
	Shade	319	313	169	332	422
	IOC	312	381	80	311	618
	IOC coffee	97	242	0	32	767
	IOC forest	678	353	160	633	1583
Mean dbh (cm)	PF	17	3	14	17	20
	SF	10	6	7	9	18
	Shade	13	5	9	13	18
	IOC	13	5	8	12	19
	IOC coffee	11	4	6	11	18
	IOC forest	16	6	7	16	27
Trees	PF	51	22	33	45	85
	SF	38	32	18	28	96
	Shade	24	14	19	24	30
	IOC	23	23	10	22	42
	IOC coffee	9	17	0	4	57
	IOC forest	44	18	9	45	91
Canopy height (m)	PF	25	6	18	25	31
	SF	7	4	4	6	15
	Shade	7	11	4	7	11
	IOC	8	9	0	9	17
	IOC coffee	4	6	0	3	15
	IOC forest	18	9	8	16	35
Canopy cover (%)	PF	93	11	80	94	100
	SF	79	29	43	88	96

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	Shade	56	18	43	50	75
	IOC	49	43	38	45	73
	IOC coffee	14	34	0	5	70
	IOC forest	94	25	65	95	100
Net-hours	PF	1289	93	1120	1280	1401
	SF	1105	127	863	1151	1240
	Shade	1080	87	912	1080	1180
	IOC	1073	107	923	1076	1196

[a] PF = primary forest, SF = secondary forest, Shade = shade coffee, IOC = integrated open canopy coffee, IOC coffee = coffee portion of IOC farm, IOC forest = forest portion of IOC farm.

[b] dbh = diameter at breast height

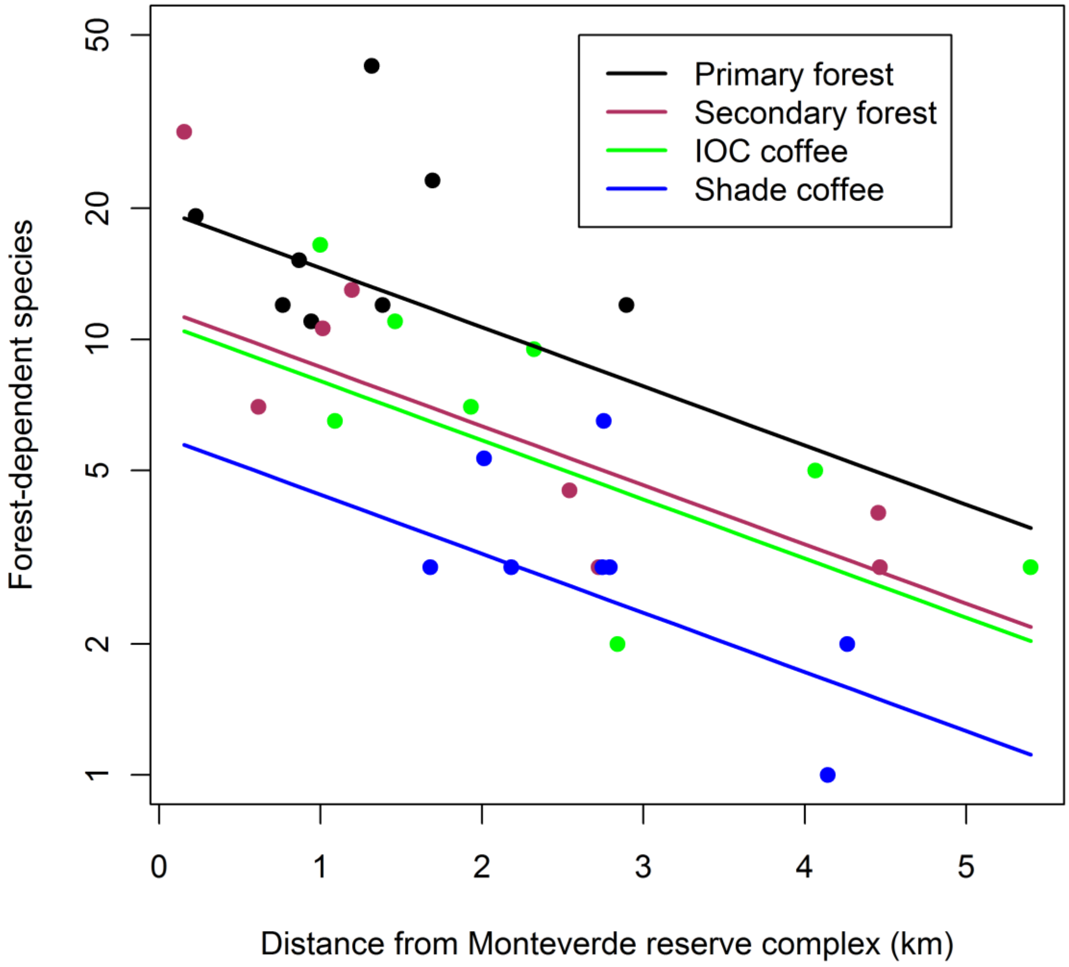

Figure 2.1. Species richness of forest-dependent species in relation to farm and forest types and distance from protected area. Fitted lines are from ANCOVA model of forest-dependent species. Data are from mist-net captures in 32 sites in the Cordillera de Tilarán, Costa Rica, 2006-2008.

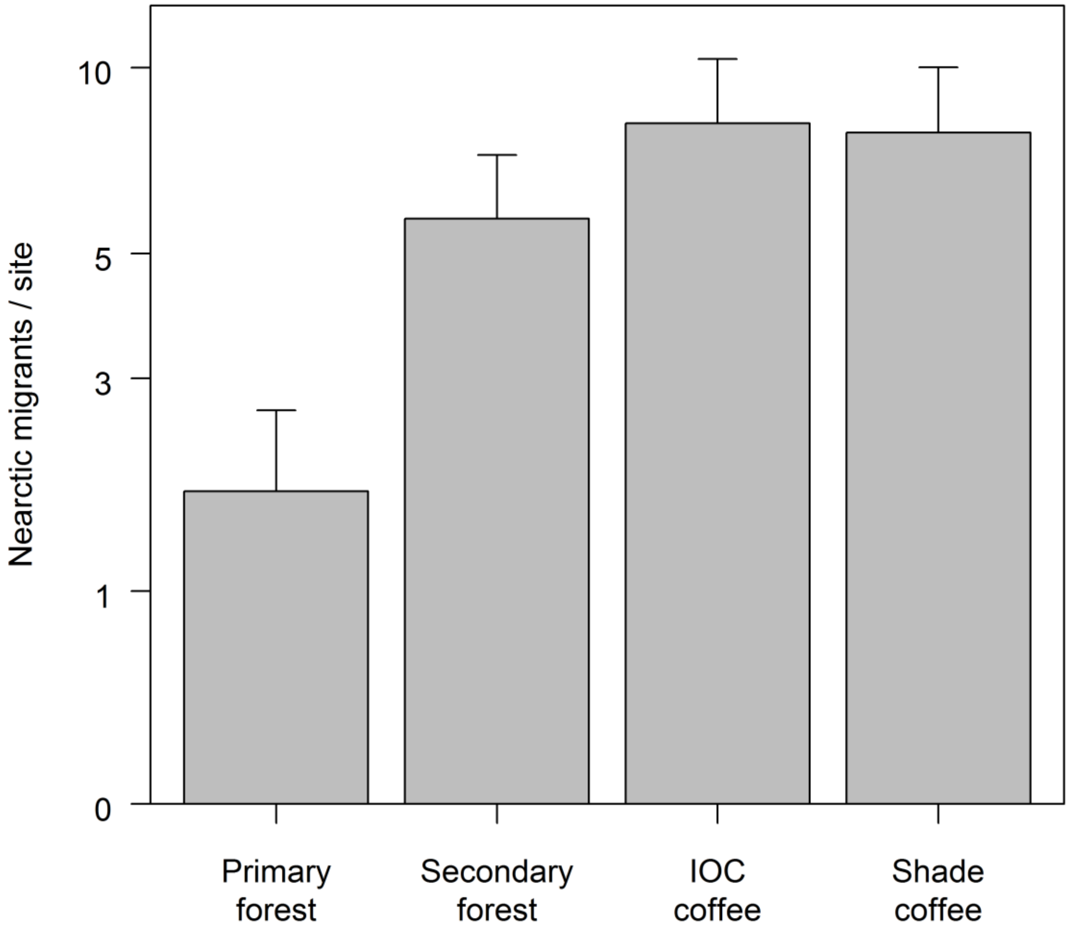

Figure 2.2. Site-level species richness estimates from ANCOVA model of Neotropical-Nearctic migrants. y-axis is on log-scale. Data are from mist-net captures in 32 sites in the Cordillera de Tilarán, Costa Rica, 2006-2008.

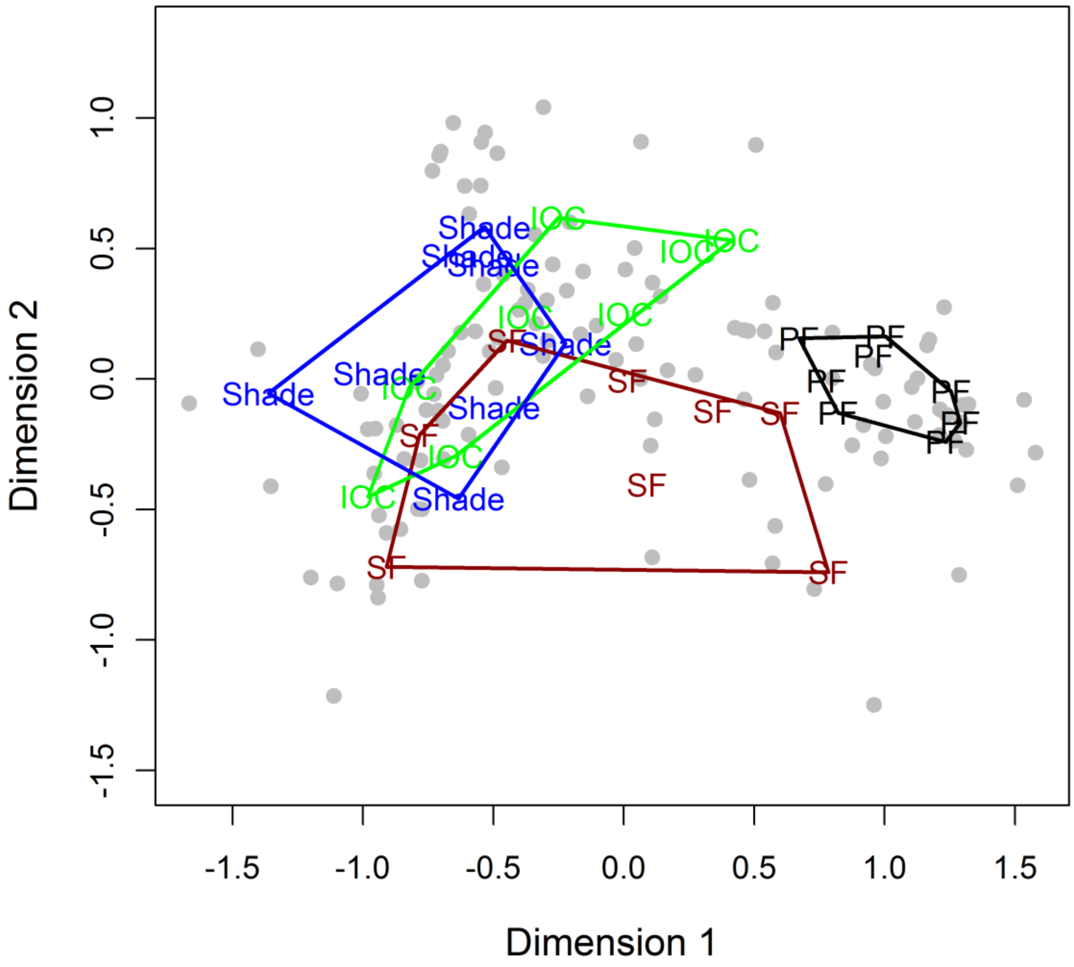

Figure 2.3. Non-metric multidimensional scaling plot representing community similarity of all species among sample plots. Gray points are species scores. PF is primary forest, SF is secondary forest, IOC is integrated open canopy coffee, and Shade is shade coffee. Data are from mist-net captures in 32 sites in the Cordillera de Tilarán, Costa Rica, 2006-2008.

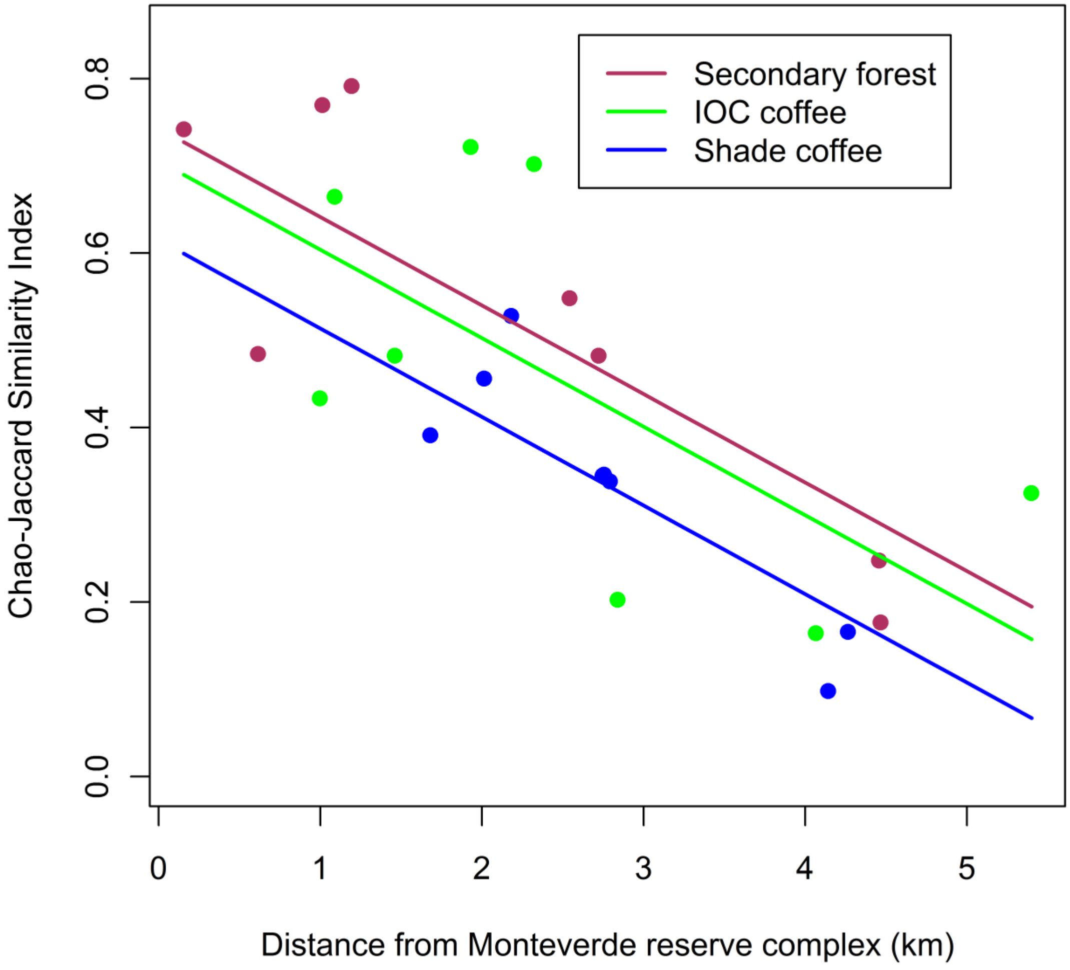

Figure 2.4. Similarity indicies (square-root transformed) between each site and primary forest sites. Fitted lines are from ANCOVA model for all species. Data are from mist-net captures in 32 sites in the Cordillera de Tilarán, Costa Rica, 2006-2008.

CHAPTER 3

GOLDEN-WINGED WARBLER HABITAT SELECTION AND POPULATION DYNAMICS DURING THE STATIONARY NON-BREEDING SEASON

3.1 Introduction

The annual cycle of Neotropical-Nearctic migratory passerines is dominated by the non-breeding season, yet compared to the voluminous amount of information available on their breeding ecology (Nolan 1978, DeGraaf and Yamasaki 2001, Askins and Zickefoose 2002, Sauer et al. 2008) relatively little is known about the ecology of these species during this period. This absence of information is concerning because many species of Neotropical-Nearctic migrants are experiencing population declines (King et al. 2006b, Sauer et al. 2008), and non-breeding season events can profoundly affect Neotropical-Nearctic migrant population dynamics (Rappole et al. 1989, 2003a, Sherry and Holmes 1996, Strong and Sherry 2000, Studds and Marra 2005, Calvert et al. 2009). Unfortunately, for most species we do not have basic information on habitat-specific abundance, habitat selection, and habitat quality during the non-breeding season, which are critical to conservation efforts (Faaborg et al. 2010).

The golden-winged warbler (*Vermivora chrysoptera*) is a Neotropical-Nearctic migrant that breeds in southern Manitoba and Ontario, the Great Lakes states, and in the central and southern Appalachian Mountains (Confer 1992). The stationary non-breeding range has not been adequately delimited, but it is believed to extend from extreme southern Mexico south to the northern Andes of Venezuela, Colombia, and Ecuador (DeGraaf and Rappole 1995). Within this area golden-winged warblers are reported to inhabit wet evergreen forests below 2500 m in elevation and to be most abundant at intermediate elevations (Bent 1963, Johnson 1980, Tramer and Kemp 1982, Blake and Loiselle 2000).

Between 1966 and 2007 the golden-winged warbler declined at a rate of 2.8% per year, and is now listed as near-threatened by the IUCN and considered as one of the most threatened Neotropical-Nearctic migrants (Sauer et al. 2008, North American Bird Conservation Initiative 2009). Numerous studies suggest that breeding season factors may contribute to this population decline (Buehler et al. 2007). Effective population size has been reduced by hybridization with blue-winged warblers (*V. pinus*), and habitat extent has declined following the maturation of forests in eastern North America (Litvaitis 1993, Gill 1997, Vallender et al. 2007a). Although these two factors pose clear threats to this species, several lines of evidence suggest that non-breeding season factors may be important as well. Golden-winged warblers are nearly extirpated from New England, but much early-successional habitat with few to no blue-winged warblers still exists (Trani et al. 2001, King et al. 2001, Chandler et al. 2009). In addition, recent analyses demonstrate that genetic introgression is reciprocal, and thus hybridization should not necessarily favor one species over the other (Shapiro et al. 2004, Dabrowski et al. 2005). Golden-winged warblers have disappeared from several areas following the arrival of blue-winged warblers, but there also exist regions of sympatry where the two species have coexisted for over a century (Gill 1980, Confer and Tupper 2000).

To fully understand what factors contribute to the decline of golden-winged warblers, information is needed regarding carrying capacity and habitat quality during the non-breeding season (Rappole et al. 2003a). Carrying capacity is influenced by habitat extent and population density, yet no efforts have been made to estimate either of these important parameters for golden-winged warblers. Habitat quality is also related to carrying capacity because the critical factor is the number of individuals that survive to migrate back to the breeding grounds. Although no detailed studies of golden-winged warblers have been conducted during the non-breeding season, anecdotal observations and incidental reports from community-level studies indicate that golden-winged warblers are specialized in their habitat use, which would increase their potential susceptibility to destruction or alteration of non-breeding habitat. For example, this species appears to be restricted to lower and middle-elevation tropical wet forests, which have experienced high levels of deforestation over the past 50 years (Powell et al. 1992, Robbins et al. 1992, Blake and Loiselle 2000). Evidence also exists that golden-winged warblers are specialized dead leaf foragers, which could further limit the extent of usable habitat since this habitat feature is patchily distributed (Tramer and Kemp 1980, Gradwohl and Greenberg 1982).

Assessing habitat extent and habitat quality for Neotropical-Nearctic migrants during the non-breeding season is difficult because they may occur at low densities over large areas, and are often cryptic relative to the breeding season when they vocalize more frequently. In addition, these species can occur in similar or even greater numbers in poor quality habitat as the result of despotic interactions between age classes or sexes (Rappole et al. 1989). This problem highlights the importance of supplementing estimates of habitat-specific density with estimates of demographic rates such as survival and recruitment (Johnson et al. 2006). Although these more detailed measures of habitat quality are typically assessed by studying individually marked populations, the consequences of mortality can be assessed without marking individuals by measuring differential declines in habitat-specific abundance within a season (Greenberg 1992). Although these patterns can be confounded by floaters replacing vacated territories, abundance should nonetheless decline faster in suboptimal habitats because floaters should be more likely to colonize higher quality territories (Rappole and McDonald 1994).

Given the dearth of information on golden-winged warbler ecology during the stationary non-breeding season, I designed a study to quantify habitat selection patterns and to estimate habitat-specific abundance and habitat quality.

3.2 Methods

3.2.1 Field methods

Habitat selection is a hierarchical process (Johnson 1980, Thomas and Taylor 2006), and human impacts on the environment can affect habitat selection and habitat use patterns at any of these hierarchical scales. Thus, I conducted this study at both the second order scale, which describes where an individual locates its home range, and third order scale, which describes habitat features selected within home ranges (Johnson 1980).

For the second order habitat selection component of the study, I surveyed golden-winged warblers at 94 points visited three times each during the 2008-09 and 2009-10 non-breeding seasons using a 20-minute point count methodology. To avoid the possibility of including transients, surveys were conducted between 1 January and 15 March each season. These surveys could have begun earlier in the season because golden-winged warblers appear to establish territories by late October; however, a pilot study during Oct-Dec 2006 failed to obtain sufficient detections during those months (4 of 84 survey points) due to the extreme rain typical of that period. The end date was determined based upon radio-telemetry and resight data, which indicate that migratory movements do not begin until late March. Each survey was divided into an initial 10-minute passive period and a subsequent 10-minute period during which golden-winged warbler songs and chips were broadcast from handheld speakers. Vocalizations were acquired from the Cornell Lab of Ornithology's Macauly Lab, and were played at a volume of 100 dB at distance of 1 meter from the speakers. For each individual detected, I recorded the sex and the 10-minute time intervals in which it was observed.

The 94 points were stratified among four habitat types: closed-canopy primary forest (*n*=25), naturally disturbed primary forest near rivers and landslides (*n*=25), secondary forest resulting from pasture abandonment (*n*=23), and agroforestry systems. (*n*=24). Agroforestry systems were mostly coffee plantations, but other crops were often integrated in these farms. These habitat types are defined in Chapter 1, and represent the major categories present in the study area, with the exception of cattle pastures, which pilot data as well as published information indicated are not used by golden-winged warblers. All survey points were located at least 500 m apart to ensure that no individual was detected at more than one point.

To quantify habitat characteristics selected by golden-winged warblers, I also established 50-m radius plots centered on each point, and measured the following variables: elevation, canopy height, percent canopy cover, slope, aspect, and dbh of trees selected using a 10-factor cruising prism. Each plot was partitioned into quarters and the following microhabitat variables, which behavioral observations suggested were used by golden-winged warblers (Chapter 4), were measured within each: hanging dead leaf index (0, 1-100, 101-1000, >1000), vine tangle index (none, vines but no tangles > 1m diameter, vines and 1-2 tangles, vines and >2 tangles), and epiphyte index (no moss or bromeliads, moss < 2cm thick and few bromeliads, moss 2-5cm thick with numerous bromeliads, moss > 5cm thick).

To quantify third order (within home range) level habitat selection, I used radio-telemetry. I captured individuals using broadcast vocalizations and a clay decoy placed between two nets. Each individual was fitted with a 0.43g Holohil BD-2N transmitter using an elastic backpack harness design (Rappole and Tipton 1991). The weight of these units was approximately 6% of the total body weight and was thus higher than the recommended level of 3%. This was justified because of the importance of obtaining reliable behavioral observations which would not have otherwise been possible given the cryptic nature of this species. The transmitters did not appear to substantially affect movement or behavior within seasons, although return rates were lower for birds that departed with transmitters (Chapter 5). Several birds occasionally picked at the harness during the first two to three days after radios were deployed. Only one individual appeared to be bothered by the transmitter for the duration of the tracking period, and this individual was not included in the analysis.

Tracking began one day after the transmitter was attached, and continued until battery failure or mortality. Each day I located the bird and followed it for two hours, recording locations every 30 minutes using a handheld global positioning system (GPS) unit. I made an effort to visually locate the bird at each point because otherwise it was not possible to record certain habitat variables (see below). This process resulted in approximately five relocations per day. Relocation data were spaced evenly to minimize observer bias (Fieberg 2007). GPS measurement error was typically less than 10 m. At each relocation point I recorded the habitat type as primary forest, secondary forest, naturally disturbed forest, or agroforestry system. Agroforestry systems were mostly coffee farms, but included “silvopastures”, which were pastures with dense or scattered trees. I also measured canopy height, and diameter at breast height (dbh) of all trees selected by 10-factor cruising prism. For locations where I saw the bird I established 2-m radius plots and measured the dbh of all stems > 2 cm, dead leaves (0-10, 11-50, >50), vine tangles > 1 m in diameter (yes/no), number of bromeliads, and epiphytic moss thickness. The 2-m plot variables were only recorded during the second and third seasons of the study, and of these, bromeliads and moss were only recorded in the final season. Upon battery failure or mortality, I used kernel density estimators to delimit the 95% home range boundaries. Within these boundaries I took habitat measurements on a 20 meter grid. At each grid intersection I measured the same habitat variables as were measured at points where marked birds had been located.

3.2.2 Statistical methods

To analyze second-order patterns of golden-winged warbler abundance in relation to habitat variables from point count data, I used the binomial mixture model of Dail and Madsen (2010). This model is very well suited to non-breeding season data because it assumes that abundance patterns are determined by an initial territory establishment process followed by gains and losses due to mortality and movements. It also accounts for imperfect detection probability. The model requires both spatial and temporal replication and can be described as follows:

$$N_{i1} \sim \text{Poisson}(\lambda)$$

$$G_{it} \sim \text{Poisson}(\gamma)$$

$$S_{it} \sim \text{Binomial}(N_{it-1}, \omega)$$

$$N_{it+1} = G_{it} + S_{it}$$

$$y_{it} \sim \text{Binomial}(N_{it}, p)$$

where N_{it} is the number of individuals at site i on survey occasion t, G_{it} is the number of gains (recruits) between seasons, S_{it} is the number of survivors, and y_{it} is the observed count at site i on survey occasion t. M in the number of plots and T is the number of survey occasions. The four model parameters are initial abundance (λ), recruitment rate (γ), apparent survival (ω), and detection probability (p). Because this is a model of data from unmarked individuals, it is not possible to distinguish between losses due to mortality and those due to permanent emigration; therefore, I use the term phrase apparent survival, which can be defined as one minus the probability of losing an individual at a given plot.

All four parameters can be modeled in relation to covariates. I used a step-wise selection process based upon AIC to find the best combination of covariates that I had *a priori* reason to believe were important (Venables and Ripley 2002). These included all variables listed previously as well as a precipitation proxy (distance from continental divide). I used distance from the continental divide as a proxy for precipitation because detailed precipitation data do not exist for my study area, whereas the relationship between distance from the continental divide and precipitation has been clearly established (Young et al. 1998, Clark et al. 2000). I also considered three subcategories of diameter at breast height (dbh) size classes (<20, 20-50, > 50 cm). I evaluated quadratic terms for precipitation, average canopy height, elevation, and epiphytes because field observations led me to believe that golden-winged warbler abundance might peak at intermediate levels of these variables. I modeled recruitment and apparent survival using these same predictor variables, and I included season in each model to estimate within- and among-season rates separately. In the detection probability component of the model I considered wind, observer skill, precipitation, time of day, date, canopy height, and basal area. Wind and precipitation were measured on a 1-5 scale. Observer skill was defined as follows: 1=limited point count experience, 2=extensive point count experience on breeding grounds, 3=some point count experience with golden-winged warblers during the non-breeding season, 4=extensive experience surveying golden-winged warblers during non-breeding season. Summary statistics for all predictor variables are presented in Table 3.1. The precipitation gradient in the study area can be seen in Fig. 3.1b by the decrease in epiphytes with the distance from the continental divide on the Pacific slope. Covariates that were included in models with ΔAIC values < 2 and whose 95% confidence intervals did not include zero were considered to be important predictor variables.

I used a mixed-effects logistic regression model to analyze home range level (second order) habitat selection. When using logistic regression to analyze use vs. availability data it is important to recognize that an unknown fraction of the availability data includes points that were used. Thus, the logistic regression model is not predicting the probability of use relative to the probability of no use; rather, it is the probability of use relative to availability (Keating and Cherry 2004). The null hypothesis is that individuals use habitat in proportion to availability. Treating variation among individuals as a random process made it possible to make inference at both the individual and population (individual average) levels. For this analysis, I used the same AIC-based model selection process as described for the landscape level analysis. A summary of the distributions of these predictor variables is shown in Table 3.2.

3.3 Results

3.3.1 Second order habitat selection

I detected 59 golden-winged warblers during 546 surveys over two seasons. Only 4 of these detections (6.8%) occurred during the first 10 minutes of the survey, highlighting the importance of using broadcast vocalizations for surveying non-breeding golden-winged warblers. In 2009, I detected golden-wings at 25 of 94 plots (26.6%). In 2010, I did not resurvey four plots that were very difficult to access, and I added three new plots. Golden-winged warblers were not detected at any of the four plots dropped in 2009. In 2010, I detected golden-wings at 17 of 93 plots (18.3%). In both years, virtually all detections (95%) were of single individuals; however, at one plot a female and a male were detected on different occasions in 2009. Two males were detected simultaneously at one plot during two consecutive survey occasions in 2010. Only three females were detected, and thus I was not able to model the sexes separately.

In addition to these 59 observations on point counts, I observed 89 other individuals (69 males and 20 females) incidentally while carrying out other duties associated with the project (Fig. 3.1d). The spatial locations of point count detections were closely aligned with incidental observations of golden-winged warblers (Fig 3.1d), the one exception being that several golden-winged warblers were incidentally detected along large rivers within the Manuel Brenes biological reserve but were never detected in this habitat during point counts.

Abundance adjusted for detection probability, but ignoring covariate effects, was less than 0.5 birds per plot (Table 3.3). However, substantial variation in abundance existed among plots as demonstrated by the inclusion of covariates in all supported models. The importance of four covariates was clear, although there was considerable uncertainty regarding the best combination of these variables. A quadratic effect of distance from the continental divide was present in all supported models (Table 3.3) and indicates that abundance peaked at a distance of 1.45 kilometers on the Pacific slope, which is an area that receives approximately 2.5 meters of annual rainfall. (Fig. 3.1b). This amount corresponds to climatic conditions favoring intermediate levels of microhabitat variables such as epiphytes (Fig. 3.2b). The second most supported effect was a quadratic relationship with canopy height, indicating that abundance peaked in forests with canopy heights of 21 meters. Habitat type and hanging dead leaves were included in the list of supported models, and indicated that golden-winged warblers were most abundant in naturally disturbed secondary forest, and their abundance was positively associated with dead leaves.

Golden-winged warblers were detected at seven plots in 2010 where they had not been detected in 2009, and they were not detected at 15 plots in 2010 that had been occupied in 2009. After accounting for detection probability, the models indicated that the seven plots that appeared to be colonized were most likely used by golden-winged warblers in 2009 but those individuals were not detected , and thus, the recruitment rate was close to zero (Table 3.3). This near-zero recruitment rate made it unnecessary to account for seasonal differences as there was no variation to model. Once detection probability was accounted for, the models indicated that the 15 plots where birds were present in 2009 but not in 2010 represented actual losses, consistent with other evidence that that this population is declining. Apparent survival was not related to any of the habitat covariates I considered, but I included a season effect in all models to allow for differences in among vs. within season differences. The point estimate for within-season monthly apparent survival was 0.870, although the confidence interval was large (Table 3.3). The six month estimate of non-breeding season apparent survival probability was 0.434. This value contrasts with a relatively high among-season monthly apparent survival probability of 0.958. Detection probability after three surveys was 0.62. Detection probability was negatively related to wind and positively related to the observer skill index, indicating the importance of controlling them in the study design to the extent possible (e.g. training observers and rotating them among survey points), as well as accounting for them statistically.

3.3.2 Second order (home-range level) habitat selection

I radio-tracked 24 golden-winged warblers during three non-breeding seasons, but only 11 individuals had sufficient relocations (> 5) and home-range habitat data (> 20 measurements) to model habitat selection. Only two of these individuals were females and thus I was not able to assess differences between the sexes. I was not able to include habitat type (primary forest, secondary forest, or agroforestry system) in these models because very few home ranges included sufficient proportions of multiple habitat types to assess selection. Canopy height was strongly correlated with tree dbh ($r > 0.7$), and thus I only considered canopy height in these models.

Analyses of home range level use vs. availability data indicated a consistently supported quadratic relationship between the probability of use by golden-winged warblers and canopy height, with a maximum probability at a canopy height of 12 m (Fig 3.5). Golden-winged warblers also preferred areas within their home ranges that had high basal area in 2-m plots, and where vine tangles were present.

3.4 Discussion

Concerns about population declines of Nearctic-Neotropical migratory birds were raised over 40 years ago (Aldrich and Robbins 1970), and although habitat loss during the stationary non-breeding season has been suggested as a cause of these declines, we still know very little about the habitat requirements of many of these species during this period, which accounts for more than half of the of the annual cycle (Monroe 1970, Terborgh 1989, Rappole 1995). This dearth of knowledge applies even to the most rapidly declining species, including the golden-winged warbler. In fact, prior to this study, no detailed studies of this species had been undertaken outside the breeding grounds. Because the degree to which a species exhibits habitat specialization is an indicator of its sensitivity to habitat alteration or destruction (Devictor et al. 2008), the lack of this basic information represents a serious deficiency in our ability to conserve this species.

Golden-winged warblers exhibited high degrees of specialization, both in terms of the habitats they selected to establish their home ranges (second order habitat selection), as well as within home ranges (third order habitat selection). My analyses of point count data showed golden-winged warblers were most abundant close to the continental divide on the Pacific slope, which is dryer than the Caribbean slope and wetter than the lower Pacific (Young et al. 1998). They were never detected in the dry forests far from the continental divide on the Pacific slope, which is consistent with previous qualitative findings (Bent 1963). Although I detected few golden-winged warblers far from the divide on the Caribbean slope during point count surveys, my incidental observations and records from other researchers demonstrate that they do occur in these lower elevation wet forests (Powell et al. 1992). These findings along with the lack of support for elevation in the abundance models indicate that precipitation and not elevation drive second-order habitat selection. Elevation, however, may play a role outside of the range I studied. For example, golden-winged warblers are rarely reported above 2500 m. There also exist few records of this species in forests near sea level (Restall et al. 2007, eBird 2010).

Within their preferred precipitation band, golden-winged warblers were most abundant in conditions characterized by intermediate disturbance. Specifically, abundance was highest in forests with canopies 22 m tall and high levels of hanging dead leaves. The association with hanging dead leaves is probably due to their specialized foraging behavior, which involves probing and prying open dead leaves to extract insects (Chapter 4). Model selection results provided some evidence that golden-winged warblers were less abundant in undisturbed primary forest than in other habitat types, but this effect was relatively weak. These second-order habitat selection results suggest that golden-winged warblers are microhabitat specialists rather than habitat specialists; i.e., their preferred microhabitat conditions can be found in primary forest as well as secondary forest and occasionally agroforestry systems, but the appropriate combination of these microhabitat variables is rare, which is probably one reason why this species appears to be patchily distributed at low densities throughout its non-breeding range (Bent 1963).

Although I regularly encountered golden-winged warblers along the large rivers within the Manuel Brenes Biological Reserve, I never detected them at these locations during point count surveys. This finding, I believe, is due to a near zero detection probability in that habitat type. Ambient noise caused by these rivers was extremely loud, and on several occasions, golden-winged warblers did not respond to broadcast vocalizations even when they were as close as 25 m. Typically golden-winged warblers chip loudly in response to the broadcast vocalizations, and approach the observer aggressively (Chapter 4). Away from rivers, I was able to hear broadcast vocalizations at distances of 100 m, even in primary forest, whereas near rivers observers could not hear recorded calls at one quarter of that distance, suggesting that detection probability in riverside habitats was very low. Therefore, my abundance estimates in these riverine habitats were probably negatively biased. Many other species of migratory birds were also seen in that habitat type, but assessing its conservation value for these species will require specialized survey methods because the vegetation is extremely dense, the topography is steep, and the noise of the river is very loud.

I found a high degree of congruence between second and third order habitat selection patterns. At the home range level, I found a similar quadratic relationship with canopy height as was evident in the second-order analyses, although the maximum probability of use peaked at a lower value for canopy height (12 m). My analyses of second-order habitat selection indicated that golden-winged warblers selected home ranges with high numbers of hanging dead leaves, and within home ranges, golden-winged warblers preferentially used areas where vine tangles were present. Golden-winged warblers were often observed foraging in dead leaves hanging in vine tangles (Chapter 4), thus it appears as though they were selecting areas within their home ranges where foraging opportunities are greatest. This observation is consistent with previous research indicating that Neotropical-Nearctic species select habitat during the non-breeding season to optimize foraging opportunities (Rappole et al. 1999, Johnson and Sherry 2001). These microhabitat conditions were often found in large canopy gaps, along rivers, on steep slopes, and in advanced secondary forests; thus it appears that golden-winged warblers prefer disturbance features within disturbed forests. Golden-winged warblers also occurred in agroforestry systems such as shade-grown coffee, but telemetry results indicate that individuals detected on point count surveys in shade coffee were in transit between adjacent patches of forest. It seems unlikely that shade coffee certification programs could effectively mandate the retention of habitat features such as vine tangles and hanging dead leaves that would potentially make shade coffee suitable for golden-winged warblers, and thus forest protection and regeneration should therefore be given higher priority than efforts to improve on-farm habitat conditions.

Although too few females were encountered on point counts or radio-marked to analyze their habitat selection, we did resight 22 females incidentally while traversing the study area engaged in other activities. Females were observed in similar locations throughout the study area corresponding to the point count survey results (Figure 3.1d), and were observed in the same habitat types as males and did not appear to occur at different elevations or in different life zones. Although these incidental observations were not standardized, they did not indicate any geographical-segregation of the sexes. The reasons why golden-winged warblers were seldom encountered in my study area are not clear. It is possible that females have different detection probabilities than males, however I observed females responding aggressively to playback on multiple occasions suggesting that the observed sex ratio bias was real. Male dominance behaviors, which are reported as a possible mechanism for sexual habitat segregation in other species (Rappole 1988, Marra 2000), were not observed in my study (Chapter 4). In fact, on several occasions males and females were seen foraging within 5 m of each other without any signs of aggression, but two males were rarely seen together and male-male aggression was evident from the strong response to broadcast vocalizations and decoys.

Although golden-winged warblers appear to have specialized microhabitat requirements, their utilization of advanced secondary forests suggests that habitat restoration is possible in deforested areas. It does not, however, indicate that this species will persist without active conservation efforts. Some researchers have suggested that species utilizing secondary forest are immune to the effects of deforestation (Hutto 1988). However, it is important to note that deforestation often results in cattle pastures or monocultures that do not provide habitat for these species. Furthermore, disturbance-dependent species recently became the focus of major conservation efforts on the breeding grounds (Hunter et al. 2001). Although secondary forests are becoming more common in some tropical agricultural landscapes as people migrate from rural to urban locations (Grau and Aide 2008, Chazdon et al. 2009), net primary and secondary forest cover continues to decline, and golden-winged warblers only used advanced stages of regeneration. This net loss results from forest being cleared for permanent agriculture and human settlements (García-Barrios et al. 2009). Secondary forest is still rare in the Neotropics relative to more degraded land cover types (Asner et al. 2009). In Costa Rica, financial incentives and conservation regulations are the only reasons why most secondary forests exist (Pagiola 2008).

The conservation value of secondary forests and agroecosystems depends upon the survival rates and body conditions of the individuals in these habitat types. Evidence exists that human-modified habitats can serve as ecological traps, resulting in high densities of birds in habitats where survival rates are low (Rappole et al. 1989). I found no evidence of differences in apparent survival among habitats, though low local abundance and few repeated visits per season limited my ability to separate detection probability from mortality or permanent emigration. Future surveys conducted over the entire course of the non-breeding season, perhaps combined with mark-resight studies, could provide better estimates of habitat-specific apparent survival and thus habitat quality.

One limitation of my study was that I was unable to directly estimate density, although I was able to model abundance. The use of playback was necessary to obtain sufficient detections for my analysis, but it excluded the possibility of directly computing density because it violated the assumptions of density models such as distance sampling (e.g., birds were attracted to playback). However, because I estimated abundance, density can be calculated for various assumed plot sizes. For example, assuming that golden-winged warblers within a 100 m radius were available for detection, which is a conservative assumption given than home range size averaged 8.7 ha (Chapter 4), density would be 0.159 individuals per hectare. This is a low non-breeding season density estimate relative to other Neotropical-Nearctic migrants (Bakermans et al. 2009). In addition, I believe this density estimate represents an upper threshold because I did not survey cattle pastures, which now cover much of the non-breeding ground range and are not used by golden-winged warblers unless they have numerous trees and are adjacent to forest (personal obs.). Furthermore, non-breeding season records of golden-winged warbler locations, though not standardized, indicate that my study area was located in a region where non-breeding density may be highest (eBird 2010). This evidence supports the view that golden-winged warbler carrying capacity may be extremely low during the non-breeding season.

Thirty years ago, tropical deforestation led researchers to predict that the rate of Neotropical-Nearctic migrant bird population declines would correlate with the degree of forest dependence (Terborgh 1980). This hypothesis has been supported (Robbins et al. 1989, Rappole et al. 2003a, King et al. 2006b), and many of these species continue to decline in spite of concomitant increases in habitat extent in North America (Stutchbury 2007, Sauer et al. 2008). Furthermore, habitat specialization has also been demonstrated to increase extinction risk (Clavel et al. 2010). My results indicate that golden-winged warblers are both forest-dependent species and disturbance-dependent microhabitat specialists during the non-breeding season. Furthermore, they are highly territorial and occupy large non-overlapping home ranges resulting in low densities. Large areas of forest are therefore necessary to maintain this population. Unfortunately less than half of the forests in their non-breeding ground range still remain, and these forests continue to be cleared at an alarming rate (Sader and Joyce 1988, Myers et al. 2000). Conservation actions should be directed towards protecting what remains of lower and middle elevation tropical wet forests while encouraging efforts to regenerate forests on degraded lands. Future research should strive to determine carrying capacity on the breeding and non-breeding grounds and estimate habitat-specific survival rates.

Table 3.1. Summary statistics of variables considered in abundance models for golden-winged warblers surveyed with point counts in the Cordillera de Tilarán, Costa Rica, 2007-2009. See text for description of indices.

Variable	Mean	SD	Min	Median	Max
Elevation (m)	1119	181	716	1123	1591
Distance from Divide (m)	2135	1297	23	2032	5482
Slope	17	11	1	14	55
Aspect	148	103	5	113	355
Dead leaves index	11	2	5	12	16
Vine tangle index	11	3	4	12	16
Epiphyte index	11	3	4	12	16
Canopy height (m)	17	7	4	16	34
Canopy cover (%)	59	17	24	61	90
Prism tree dbh sum	432	343	16	362	1587
Prism trees	13	7	2	13	30
Prism trees (<20cm)	5	3	0	4	14
Prism trees (20-50cm)	6	4	0	5	17
Prism trees (>50cm)	2	3	0	1	13
Time of day	10	2	6	10	16
Julian date	46	20	7	48	79
Wind index	2	1	0	2	4
Observer skill index	3	1	1	4	4

Table 3.2. Summary statistics of home range habitat availability variables for 17 radio-tracked Golden-winged Warblers surveyed at 97 point count station counts in the Cordillera de Tilarán, Costa Rica, 2007-2009.

Variable	Mean	SD	Min	Median	Max
Canopy height (m)	13.1	5.7	6.7	12.2	27.4
Prism trees	10.0	3.2	3.7	10.5	14.3
2m plot trees	8.4	6.7	0.0	8.5	20.2
DBH sum prism trees	301.8	183.2	88.8	255.4	683.1
DBH sum 2m trees	31.0	22.9	0.0	42.6	68.3
Bromeliads	2.1	1.3	0.0	2.2	4.2
Moss	1.1	0.6	0.1	1.2	2.0
Dead leaves	2.1	0.1	1.9	2.1	2.4
Vine tangles	0.3	0.3	0.0	0.2	0.8
Aspect	163.8	58.3	55.1	154.3	258.4
Slope	16.8	7.6	6.4	16.5	37.0

Table 3.3. Parameter estimates and 95% confidence intervals from the most general dynamic abundance model considered for golden-winged warblers surveyed at 97 point count stations counts in the Cordillera de Tilarán, Costa Rica, 2007-2009.

Parameter	Estimate	SE	lower	upper
Initial abundance[a] (λ – individuals/plot)	0.498	0.153	0.272	0.911
Recruitment (γ – gains/month)	0.006	0.008	0.001	0.076
Within-season apparent survival (ω_w – monthly rate)	0.870	0.153	0.322	0.990
Among-season apparent survival (ω_a – monthly rate)	0.958	0.035	0.805	0.992
Detection probability (p – per survey)	0.274	0.075	0.152	0.442

[a] Corresponds to January 1.

Table 3.4. Model selection results for golden-winged warbler abundance. λ is initial abundance, γ is recruitment, ω is apparent survival, and p is detection probability. Squared terms indicate quadratic effects. A dot signifies no covariate effect. Data are from 97 point count surveys counts in the Cordillera de Tilarán, Costa Rica, 2007-2009.

λ	γ	ω	p	ΔAIC	R^2
Precip^2 + CanHt^2	.	Season	Wind + Obs	0.00	0.30
Precip^2 + CanHt^2 + Habitat	.	Season	Wind + Obs	0.13	0.34
Precip^2 + Habitat	.	Season	Wind + Obs	0.13	0.32
Precip^2 + CanHt^2	.	Season	Obs	0.30	0.28
Precip^2 + Leaves	.	Season	Obs	0.30	0.27
Precip^2 + CanHt^2	.	Season	Obs	0.30	0.33
Precip^2 + Habitat	.	Season	Obs	0.34	0.30
Precip^2 + CanHt2 + Habitat	.	Season	.	0.41	0.31
Precip^2 + CanHt^2	.	Season	Wind	0.53	0.33
Precip^2 + CanHt^2	.	Season	Wind	0.53	0.28
Precip^2 + CanHt^2	.	Season	.	0.59	0.27
Precip^2 + Leaves	.	Season	.	0.65	0.25
Precip^2 + Leaves	.	Season	Wind + Obs	0.66	0.28
Precip^2 + Habitat	.	Season	.	0.69	0.28
Precip^2	.	Season	Obs	0.90	0.25
Precip^2	.	Season	Wind	1.29	0.24
Precip^2	.	Season	.	1.43	0.23
Precip^2 + CanHt^2 + Habitat + Leaves	.	Season	Wind	1.65	0.33
Precip^2 + CanHt^2 + Leaves	.	Season	.	1.65	0.27
Precip^2 + CanHt^2 Leaves	.	Season	Wind + Obs	1.65	0.30
Precip^2	.	Season	Time	1.79	0.24

Table 3.5. Model selection results for use versus availability logistic regression models for data from 11 radio-marked golden-winged warblers counts tracked in the Cordillera de Tilarán, Costa Rica, 2007-2009. An intercept was included in all models as was a random effect term for variation among individuals.

Fixed	Random	AIC
CanopyHt^2 + BasalArea + Vines	CanopyHt	939.70
CanopyHt^2 + BasalArea + Vines	Intercept only	940.13
CanopyHt^2 + BA	CanopyHt	940.19
CanopyHt^2 + Vines	CanopyHt	940.90
CanopyHt^2 + BA	Intercept only	941.42
CanopyHt^2	CanopyHt	941.61

Table 3.6. Parameter estimates from the most supported logistic regression model of golden-winged warbler use versus availability. Random effects are reported as standard deviations and can be interpreted as the among individual variation in corresponding fixed effects. Data are from 11 radio-marked Golden-winged Warblers counts tracked in the Cordillera de Tilarán, Costa Rica, 2007-2009.

Parameter	Type	Estimate	SE	*z*	*P*
*ß*0	Fixed	-2.741	0.307	-8.914	<0.001
Canopy height	Fixed	0.178	0.043	4.155	<0.001
Canopy height^2	Fixed	-0.007	0.001	-5.096	<0.001
Basal area (2-m plot)	Fixed	0.055	0.030	1.837	0.066
Vines	Fixed	0.341	0.211	1.615	0.106
*ß*0	Random	0.581			
Canopy height	Random	0.039			

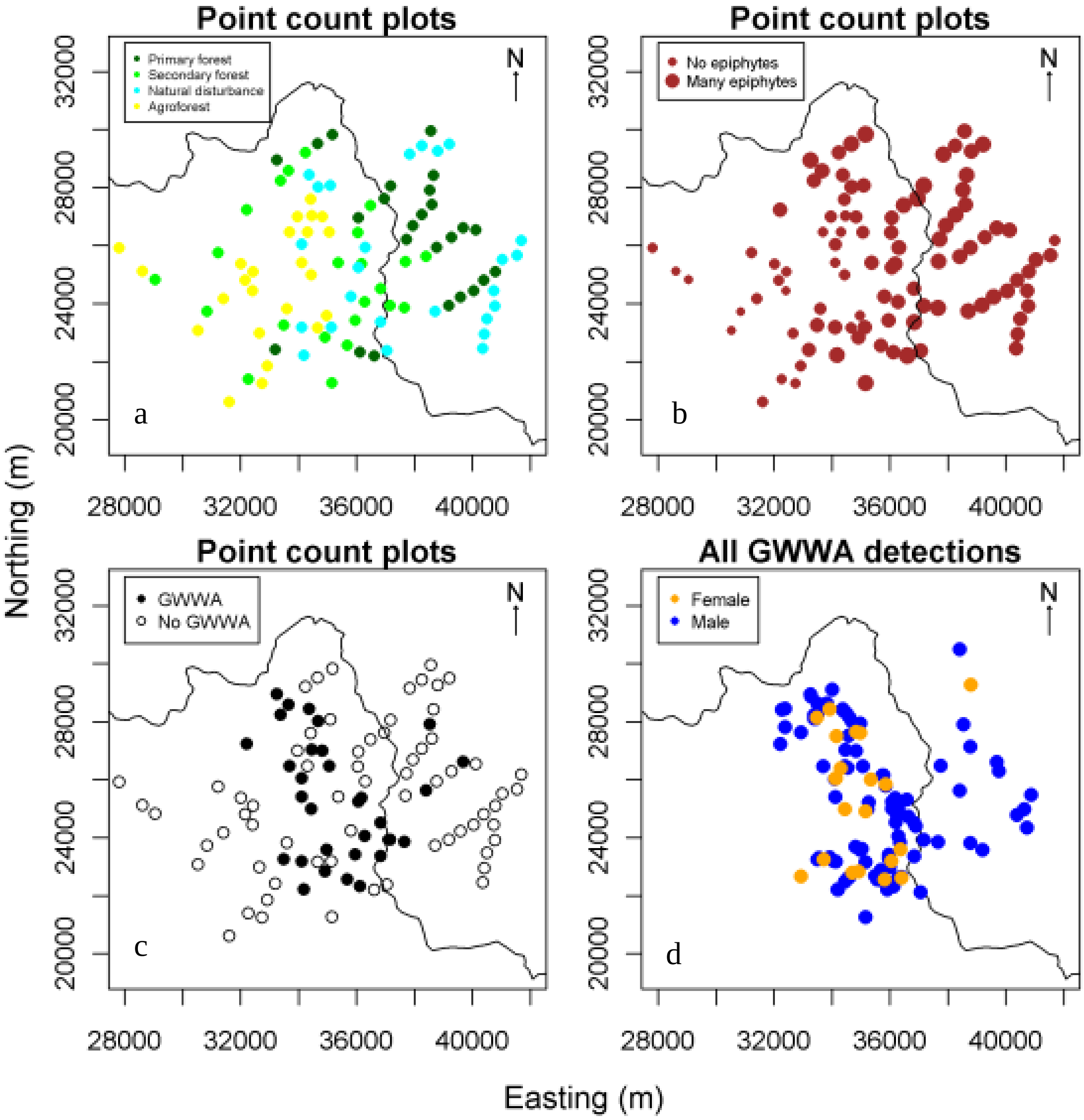

Figure 3.1. Maps of habitat type distribution and golden-winged warbler locations in the Cordillera de Tilarán, Costa Rica, 2007-2009. The points in plots a-c are point count locations. Solid line is the continental divide.

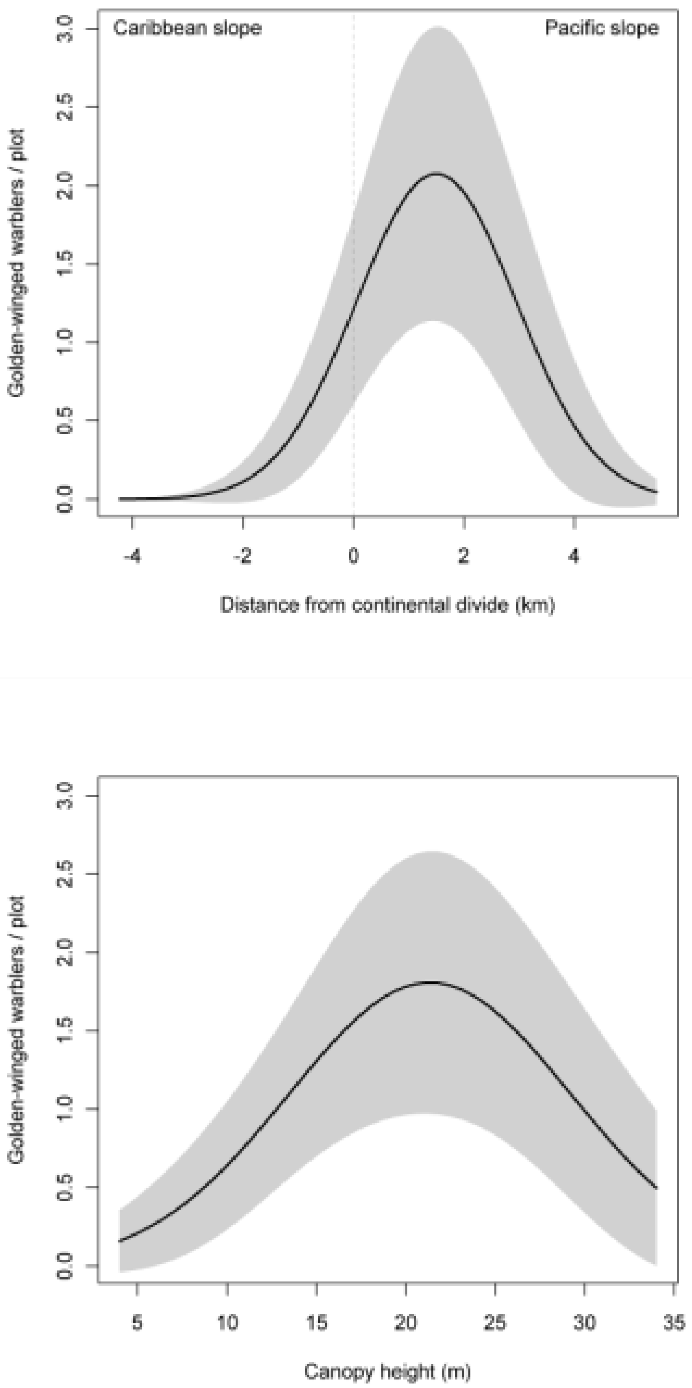

Figure 3.2. Golden-winged warbler abundance in relation to distance from continental divide (top) and canopy height (bottom) in the Cordillera de Tilarán, Costa Rica, 2007-2009. Error band is 95% confidence interval.

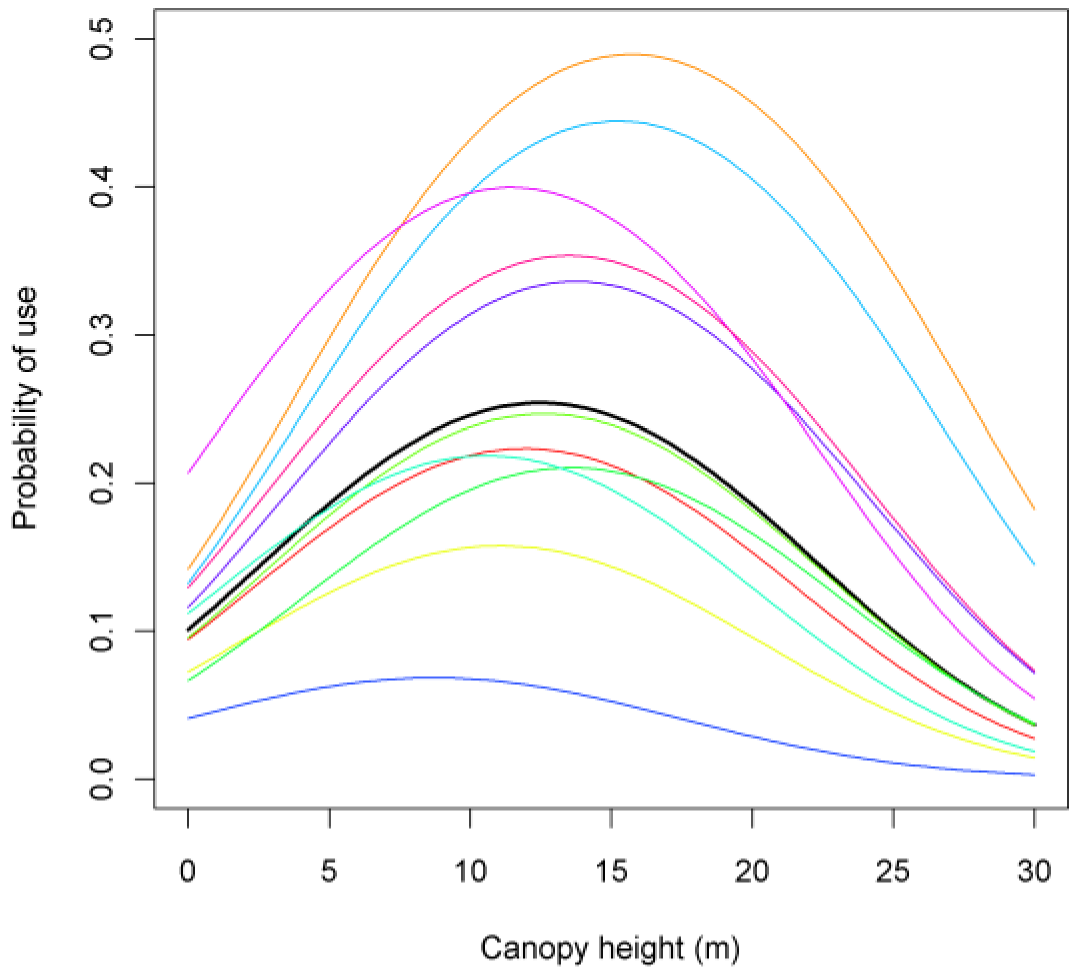

Figure 3.3. Probability of observed use versus random use for 11 radio-tracked golden-winged warbler. Thick black line is mean response among individuals. Data are from 11 radio-marked golden-winged warblers counts tracked in the Cordillera de Tilarán, Costa Rica, 2007-2009.

CHAPTER 4

CONSERVATION IMPLICATIONS OF GOLDEN-WINGED WARBLER SOCIAL AND FORAGING BEHAVIOR

4.1 Introduction

Birds exhibit a wide array of social systems during the non-breeding season when their behaviors are not constrained by breeding requirements such as mate guarding, nest maintenance, and provisioning young (Powell 1979, Pulliam and Millikan 1982). Although non-breeding season sociality has been extensively studied in birds (Zahavi 1971, Rappole and Warner 1980, Davies and Houston 1983, Heinrich 1988, Brown and Long 2007), the conservation implications of sociality have largely been ignored (Sutherland 1998, Greenberg and Salewski 2005). This is an important oversight because social systems influence space use, energy expenditure, and susceptibility to predation (Rappole and Morton 1985, Rappole et al. 2003a, Morton and Stutchbury 2005). Many species of Neotropical-Nearctic migrants are experiencing population declines, and some species may be limited by these factors during the non-breeding season (Terborgh 1974, Haney et al. 1998, Rappole et al. 2003a, 2005, 2007, Sherry et al. 2005, King et al. 2006b, Sauer et al. 2008, Calvert et al. 2009).

Greenberg and Salewski (2005) summarized the literature on Neotropical-Nearctic migrant social systems and identified five major components. The first two of these are regional movements and local tenacity. Some frugivorous migrants like Swainson’s thrushes (scientific names in Appendix A) and eastern kingbirds (*Tyrannus tyrannus*) form conspecific flocks and search for their preferred fruits over large areas.

Other species, such as the black-throated blue warbler (*Dendroica caerulescens*), exhibit extreme site fidelity during the non-breeding season (Sherry and Holmes 1996). Another component of migrant non-breeding social systems concerns territoriality, which is pronounced in some species (e.g. ovenbirds and wood thrushes; (Rappole and Warner 1980)), but not in others, such as prairie warblers (Nolan 1978). A related component is group size. Species such as the Tennessee warbler occur in large, monospecific flocks, while other species, including the black-and-white warbler, typically do not occur with conspecifics (Greenberg and Salewski 2005). Finally, some species, the like golden-cheeked warblers (*Dendroica chrysoparia*) occur almost exclusively as attendants of mixed species flocks (Rappole et al. 1999).

Each of these components of sociality can potentially have important conservation implications. For example, territoriality and group size can clearly affect population density, which is a primary determinant of carrying capacity (Brown 1969, Rappole and Morton 1985, Rappole et al. 2003a, Morton and Stutchbury 2005). Furthermore, dependence upon mixed-species foraging flocks may be a liability because forest fragmentation can disrupt flocks (Rappole and Morton 1985, Stouffer and Bierregaard 1995, Stratford and Stouffer 1999). Assessing the conservation implications of sociality also requires an understanding of foraging behavior, because resource availability and exploitation systems can be primary determinants of social behavior (Greenberg and Salewski 2005). Limited data on the social systems of Neotropical-Nearctic migrants has made it difficult to predict how these species are expected to respond to habitat loss and fragmentation.

The golden-winged warbler is one of the most rapidly declining Neotropical-Nearctic migrants, and although I have done extensive investigations of its winter habitat use (Chapter 3), no published quantitative studies of its social behavior exist. Anecdotal observations suggest that this species occurs as sedentary, solitary individuals in mixed-species flocks and forages in hanging dead leaves (Buskirk et al. 1972, Morton 1980, Tramer and Kemp 1980). These behaviors could make this species vulnerable to habitat loss and fragmentation, as described above, yet few quantitative data exist to assess this possibility.

The objectives of this study were to 1) describe the social and foraging behaviors of golden-winged warblers during the stationary non-breeding season, 2) assess the conservation implications of these behaviors by quantifying the impacts of these behaviors on energy expenditure (measured as home range size and movement rate), and 3) assess the degree to which social and foraging behaviors were related to habitat characteristics. These data should help conservationists predict how this species is likely to respond to future habitat change.

4.2 Methods

4.2.1 Field methods

I studied golden-winged warbler sociality during three nonbreeding seasons: December 2006 - March 2007, October 2007 - March 2008, and January-March 2009. I used radio-telemetry to collect data on site fidelity, home range size, and movement rates. Radio-telemetry was necessary because during the non-breeding season golden-winged warblers move rapidly, inhabit structurally complex habitats on steep terrain, forage high in the canopy, and are generally silent. I began tracking one day after attaching 0.43 g Holohil BD-2N transmitters to birds caught using mist-nets, broadcast vocalizations and decoys. The responses of birds to playback were noted as evidence of territoriality. Birds were relocated every 1-2 days, and tracking lasted approximately two hours per day. Handheld GPS units were used to record locations. Tracking continued until battery failure or mortality. During the first season, I only recorded GPS locations at points where I saw the bird because my primary interest was to record behavioral observations. This, however, did not adequately reflect space use because some birds were very difficult to see. Therefore, in the latter two seasons, I recorded locations every 30 min whether the bird was seen or not. Using regular time increments between location points allowed me to collect movement rate data in standardized fashion, and it provided a representative sample of space use. When birds were not seen, I was able to determine their approximate location based upon the strength of the signal, which I could calibrate from visual observations.

At the end of each season, I quantified home range habitat by evenly sampling points along 20-m grids within the 95% kernel home range boundaries. At each point, I measured habitat type (primary forest, secondary forest, riverside forest, or agroforest), canopy height, and basal area (using 10-factor cruising prism).

Data on group size and mixed-species flock participation were also recorded while radio-tracking. At each 30-min time period, I recorded the flocking status of golden-winged warblers as one of three categories. Following (Hutto 1987), I defined a flock as individuals of two or more species within 25 m of each other moving in the same direction. This definition suffices for the majority of flocks joined by golden-winged warblers; however, there are numerous types of mixed-species flocks with diverse social organizations and foraging guild representations (Munn 1985), and golden-winged warblers occasionally joined other types. For example, Tramer and Kemp (1980) describe loose flocks without coordinated movement patterns. In addition, flocks of frugivorous birds congregate when abundant resources are present, such as at fruiting *Ficus sp.*, and golden-winged warblers occasionally associated with such groups (although they were never observed eating fruit). I therefore categorized flocking status as either flocking, not flocking, or associating with other species that were not traveling in concert. This third category is often ignored, but is important because the predation risk hypothesis predicts that birds should associate with numerous individuals regardless of movement patterns and foraging guild status. Mixed species flock composition data were collected continuously during each tracking period. I compiled a list of all species encountered each day and classified each species as flocking, associating, or not flocking with the tracked golden-winged warbler. I did not color band other species so it was not possible to determine with accuracy the abundance of other species in the flocks.

I collected additional data on site fidelity by monitored color-banded individuals over multiple non-breeding seasons. For each color-banded individual, I made monthly visits to its territory and broadcast recorded golden-winged warbler songs and chip notes for 30 min or until the bird was encountered at three locations within the home range. Additional details on this protocol are described in Chapter 5.

Foraging observations were collected opportunistically while radio-tracking. An effort was made to standardize the collection process with respect to time by recording foraging behaviors at each 30-min location point, but this was often not possible due to limited visibility. Instead, I recorded data on the first foraging maneuver observed during each 30 minute interval. Foraging data included the height of the bird, the height of the tree, the distance from the central stem, the foraging maneuver (glean, probe, sally, hawk, flush), and the substrate (open live leaf, rolled live leaf, dead leaf, flower, bark, moss/lichen, bromeliad, or miscellaneous epiphyte). I was unable to adequately measure foraging rate because it was not often possible to watch the birds for prolonged periods due to their rapid movements within dense vegetation.

4.2.2 Statistical methods

Home range size was estimated using kernel density and minimum convex polygon (MCP) estimators (Worton 1989). Kernel density estimators yield utilization distributions (UD), which are the relative probability of an individual occurring at each location in its home range. Kernel density estimation requires specifying a distribution to fit over each location point. I used a bivariate normal kernel and considered two methods to select the smoothing parameters governing the kernel shape: the so-called *ad hoc* method and least-squares cross-validation (Worton 1989). Minimum convex polygons do not provide a probabilistic measure of space use, but do serve as a good reference for comparison with the kernel methods because they yield a minimum home range size. For each method, I characterized differences in space use by estimating 50, 75, and 95% intensity levels. As a measure of territoriality and social tolerance, I computed the overlap of 50% kernel home ranges using the volume intersection index described in Fieberg and Kochanny (2005). For 50% kernels, this index ranges from 0 (no overlap) to

0.5 (complete overlap). I used a one-tailed *t*-test to test the hypothesis female-male neighbors had higher degrees of overlap than male-male neighbors.

To measure movement rate, I restricted my analysis to days with at least four consecutive 30-min locations, and individuals with at least three such observation days. Standardized time intervals are necessary because net differences in movement over unequal time frames could result from multiple processes and thus have no biological significance. Home range size and movement analyses were conducted in R-2.11.1 (R Development Core Team 2010) using the adehabitat package (Calenge 2006).

I used multiple linear regression to model the effects of habitat and sex on space use and flocking parameters. Specifically, I regressed home range size, movement rate, and species richness of mixed-species flocks on sex, percent cover variables for each habitat type, the total number of habitat types per home range, basal area, and canopy height. For the movement rate data, I treated the individual as the sample unit and averaged movement rates over observation days. I used a step-wise model selection process based upon AIC to choose the best model (Hastie and Pregibon 1992). I assessed model fit and adherence to model assumptions by comparing residuals to fitted values and computing measures of leverage and influence. Model fitting, selection, and diagnosis were conducted in R-2.11.1 using the lm and step functions (R Development Core Team 2010).

To determine if foraging behavior differed between the sexes or between the flocking states, I used mixed-effects models. Specifically, I modeled foraging height, canopy position, and distance from stem as normally distributed response variables and treated variation among individuals as a random effect. These models are equivalent to two-way ANOVA models with an additional error term for random variation among individuals. Foraging maneuver is a categorical variable and since 99% of observations were probes or gleans, I used a binary response distribution. Because I only modeled two predictor variables, I did not use a variable selection process but instead evaluated the global model. These models were fit in R-2.11.1 using the lme4 package (Bates and Maechler 2010).

4.3 Results

4.3.1 Site fidelity, home range size, and movement patterns

I captured and radio-tracked 26 golden-winged warblers over three non-breeding seasons. Battery life varied greatly among individuals (median=12 days, range=2-26 days). Premature battery failure prevented me from acquiring enough data to calculate kernel-based utilization distributions for six individuals. Of the twenty individuals with sufficient location points, seventeen were males and three were females. All individuals were located on the Pacific slope side of the study area (Fig. 4.1). Both male and female golden-winged warblers maintained stable home ranges over the course of the non-breeding season (Fig. 4.2). Home ranges were characterized by one or two core areas where most activity was concentrated. In some instances, activity centers shifted slightly among days, but there was no temporal trend as demonstrated by extensive inter-day overlap (Fig 4.3).

Three golden-winged warblers exhibited movement patterns inconsistent with the general patterns described above. One individual, a male, was relocated the day following capture and then never seen again despite three days of searching the surrounding area using broadcast vocalizations. Since the probability of detection with playback is extremely high, it is unlikely that this individual remained within the study area but had a defective radio transmitter. If it moved to another location within the study area, the radio must have been defective, because I was able to detect transmitter signals at distances greater than 1 km and the entire study area is accessible at that range. Two individuals made off-territory forays. In each case, the birds moved from patches of secondary forest to points within contiguous forest < 2 km from their previous locations, and then returned to their home range within 24 hours. These locations were not included in home range size calculations.

Resighting data demonstrated that golden-winged warblers remained on their home ranges for longer durations than could be determined using radio-telemetry. Systematic visits to home ranges of color-marked birds throughout all three field seasons indicated that all relocated individuals remained on their home-ranges until the onset of migration. Furthermore, all five individuals that I was able to relocate in subsequent years were found within 200 m of their capture location, including three individuals that were observed during three consecutive seasons. This is clear evidence that at least some golden-winged warblers exhibit high within and among season site fidelity.

The method used to estimate home range size clearly affected the estimate. The median kernel density estimates were more than twice as high as MCP estimates for each of the three home range levels (Table 4.1). The smoothing parameter estimates for the bivariate normal distribution ranged from 17.0 – 52.8 m (mean = 36.5, SD = 9.3). This indicates that golden-winged warbler used areas within 75 m of each relocation point.

These smoothing parameter estimates were based upon the *ad hoc* method because the least-squares cross validation method returned values that did not seem biologically plausible (<10m) and yielded home ranges with numerous modes. Home range size was not related to either habitat variables or sex (Table 4.3).

Golden-winged warblers were highly active throughout the day. The mean movement speed was 142 m/hr (SD = 43) although there was substantial variation among individuals (Fig 4.4). Movement speed was positively related to basal area within the home range, and negatively related to canopy height ($F_{4,5} = 11.67$, $P = 0.009$; Table 4.2).

4.3.2 Territoriality, group size, and competition

Both female and male golden-winged warblers showed aggressive responses to broadcast vocalizations and clay decoys. Twenty-three of 26 birds captured for the radio-telemetry study were captured using these stimuli. In several instances, the decoy was attacked. One individual left a 4 mm deep puncture in the "neck" of the decoy. The other three individuals (2 males and 1 female) were caught while using constant effort mist-netting. These birds also maintained stable home ranges suggesting that my sample was not biased towards territorial individuals.

Home ranges of neighboring birds did not overlap extensively (Fig 4.5). The overlap of 50% core areas was higher for male-female pairs than for male-male pairs. Even with a sample of only three male-female pairs and two male-male pairs, this finding was significant ($t = -3.78$, df = 2, $P = 0.031$). For the male-male pair, the overlap occurred only in the outer extremes of the home range; there was no overlap of the core areas.

4.3.3 Mixed-species flock characteristics

I collected mixed-species flock data for 26 golden-winged warblers observed on 214 occasions totaling 562 hours. Golden-winged warblers spent an average of 59% of their time with cohesive mixed-species flocks, which were often centered around the nuclear species *Chlorospingus ophthalmicus* (Table 4.3). An additional 26% of their time was spent associating with other species in loose flocks without obvious movement cohesion or nuclear species. Thus, golden-winged warblers were only observed away from flocks 15% of the time, although individual variation was pronounced (Fig 4.6). Eighty-eight species were observed flocking with golden-winged warblers in cohesive flocks. No species was ubiquitously present with golden-winged warblers, and both resident and migratory species were common participants (Table 4.3).

Flock participation was not related to sex or habitat variables ($F_{6,2}$ = 8.29, P = 0.112). Species richness of flocks was positively related to canopy height, the number of tracking days, and the percent cover of primary forest ($F_{3,11}$ = 7.24, P = 0.006; Table 4.3). Neither flock participation nor flock size differed between the sexes, though only three females were included in the sample.

4.3.4 Foraging behavior

Of 293 foraging observations made on 24 color-banded golden-winged warblers, 72% were probes and 27% were gleans (Fig 4.7). Sallies, hawks, hover-gleans, and flush-dives constituted < 2% of observations. The most commonly probed substrate was hanging dead leaves (40%), though moss, bark, rolled leaves, bromeliads, and flowers were used to a lesser extent (Fig 4.7). Golden-winged warblers probe in a unique fashion that involves inserting the beak and opening it in order to pry open the leaf or flake off bark.

Most of the bark foraging observed occurred in *P. guajava*, which like many other members of the Myrtaceae has thin flaking bark. Golden-winged warblers were the only species observed utilizing this resource. The longest foraging maneuvers (>1 min) occurred on individual *Cercropia sp.* leaves. Although *Cercropia sp.* was never a dominant plant species in home ranges, the large leaves with hooked petioles are easily caught in the canopy. These leaves form tight curls upon desiccation and often host diverse arthropod assemblages (Rosenberg 1997). Finally, the one individual that regularly foraged above 20 m was observed almost exclusively in *Ocotea sp.* It was not possible to closely observe the foraging behavior of this individual due to its height.

Foraging behavior variables (bird height, tree height, distance from stem, and maneuver) varied greatly among individuals (Figs. 4.8, 4.9), but did not differ between the sexes nor between flocking states (Figs 4.10, 4.11, Table 4.4).

4.4 Discussion

I documented several aspects of golden-winged warbler behavior ecology that have important conservation implications because they are traits that could affect susceptibility to habitat destruction or degradation. Golden-winged warblers maintained large stable home ranges within seasons. The average 95% kernel home range size was 8.8 ha, much larger than values reported for other Neotropical-Nearctic migrant passerines. Brown and Sherry (2008) estimated ovenbird home range to be 0.78 ha, 9.6 times smaller than the average for golden-winged warblers. Rappole and Warner (1980) reported home range sizes < 1 ha for all 10 species they studied. None of these species, however, are regular participants of mixed-species foraging flocks, which may explain why they have substantially smaller home ranges.

In addition to their large area requirements, golden-winged warblers were rarely seen with conspecifics. Two hypotheses could explain why golden-winged warblers occurred as solitary individuals. First, golden-winged warblers may be so rare that chance alone would make it unlikely to observe two individuals in the same area. My data do not support this hypothesis. This hypothesis predicts that individuals should be randomly distribution throughout the study area. Golden-winged warblers, however, were most abundant within a narrow elevational band along the Pacific slope (Chapter 3), and neighboring home ranges had very little overlap. The alternative hypothesis is that golden-winged warblers are territorial, which is supported by my data. The aggressive response to playback and decoys is evidence that golden-winged warblers will attack intruders (Rappole and Warner 1980). Territoriality is also suggested by the lack of overlapping home ranges.

Large home range size and territorial behavior may explain why golden-winged warblers are not reported to be common anywhere throughout their non-breeding range (Johnson 1980, Morton 1980, Orejuela et al. 1980, Powell et al. 1992, Wallace et al. 1996, Komar 1998, Blake and Loiselle 2000). Territoriality may also affect how golden-winged warblers respond to habitat loss because limited habitat can lead to competitive interactions resulting in losers that do not gain territories. For ovenbirds in Jamaica, where predation pressure is low, there appears to be costs and benefits associated with the territorial and non-territorial social systems (Brown and Sherry 2008). These authors suggested that territorial individuals were able to access stable resources and minimize space use and energy expenditure whereas non-territorial birds exploited temporary resources more effectively. Wood thrush in contrast conform to an ideal despotic population model in which territory owners in primary forest relegate subordinate individuals to low quality habitat (Fretwell and Lucas 1969, Winker et al. 1990). These "floaters" wander over large areas and incur higher mortality (Rappole et al. 1989). I did not encounter any non-territorial golden-winged warblers (Chapter 5), so this possibility will require future study.

Golden-winged warblers exhibited strong site fidelity both within and among non-breeding seasons. High site fidelity indicates that it is adaptive for an individual to learn information regarding food availability and predator risk associated with a particular location. Deforestation may negatively affect species exhibiting high site fidelity because they are forced to find new habitats in which they have no prior experience (Rappole and Morton 1985), or adopt nomadic movement patterns that can lead to lower survival (Rappole et al. 1989).

I found some evidence that tolerance was higher between the sexes than within the sexes. Home range overlap was higher for male-female neighbors than for male-male neighbors. Generally male-female neighbors did not occur within close proximity of each other, although one male consistently foraged within 5 m of an unbanded female without displaying any aggression. I also found no evidence of differences in foraging behavior among the sexes; however, with data on only three females, a larger sample is necessary before conclusive statements can be made regarding sex-specific foraging behavior. Furthermore, as with most foraging behavior studies in tropical forests, there is bias in my sample due to the fact that it was difficult to effectively observe golden-winged warblers when they were either very high in the canopy or in low thickets. This may be an important source of bias because two of the three females studied used very dense understory vegetation and I was only able to record foraging behavior when they came up from the thickets. The possibility therefore exists that female forage at lower heights than males as has been observed for other Nearctic migrants.

My findings that male-female tolerance was higher than male-male tolerance, and that foraging behavior did not differ between the sexes contrast with many studies demonstrating sexual habitat segregation and dominance (Morton et al. 1987, Marra 2000); however, male-female tolerance during the non-breeding season has been observed for other Neotropical-Nearctic migrants including prothonotary warblers (*Protonotaria citrea*), Canada warblers, and golden-cheeked warblers (Morton 1980, Rappole et al. 1999). Pairs (presumably male-female) of Philadelphia vireos, blue-headed vireos, and gray vireos (*Vireo vicinior*) have been reported suggesting that some species may exhibit pair-territoriality as do stonechats (*Saxicola torquata*) and white wagtails (*Motacilla alba*) (Zahavi 1971, Tramer and Kemp 1982, Gwinner et al. 1994, E. Morton pers. comm.). In other species, the sexes may occur randomly distributed within a habitat type (Brown and Sherry 2008), or may have horizontally overlapping territories, but stratify vertically (Rappole 1988, Wunderle 1992). The reason for higher intersexual tolerance in golden-winged warblers is unclear, and deserves further study. The primary conservation implication of the absence of sexual habitat segregation is that differential rates of habitat loss would not lead to biased sex ratios. However, in spite of high tolerance and overlapping home ranges, there was an apparent sex ratio bias within the study area (Chapter 3) indicating that the sexes may segregate geographically, which would be an alternate route to a skewed sex ratio.

Golden-winged warblers occurred with mixed species flocks 85% the time. Some researchers have contrasted territoriality with flock participation; however, many species that regularly join mixed-species flocks are highly territorial. These species may either defend the flock itself against conspecifics (Munn and Terborgh 1979) or have distinct territory boundaries and drop out of the flock when these boundaries are crossed (Powell 1979, Munn 1985). Territorial flock participants often occur as lone individuals or pairs and will attack conspecifics that attempt to enter the flock (Buskirk 1976, Hutto 1987). Other species such as cerulean warblers (*Dendroica cerulea*) will occur in large groups within mixed species flocks and show little conspecific aggression (Bakermans 2008). This variation in flock participation has obvious impacts on area requirements and space use. In addition, reliance on mixed-species flocks increases a species' vulnerability deforestation and fragmentation because these processes can prevent flock cohesion (Rappole and Morton 1985, Stouffer et al. 2006). Furthermore this dependence upon mixed-species flocks indicates that conserving nuclear species, around which flocks are formed, will be necessary to ensure population viability.

Mixed-species flock participation has other important conservation implications because it can reduce predation risk, increase foraging efficiency, or both (Pulliam 1973, Buskirk 1976, Munn and Terborgh 1979, Powell 1985). In addition to the potential benefits, flocking may impose important costs. If flocks are joined primarily to reduce predation risk, then flocking may not be an optimal foraging strategy (Hutto 1988, Hake and Ekman 1988). This suggests energetic costs. Golden-winged warblers moved continually and rapidly throughout the day at speeds ranging between 75-200 m/hr. Day length was approximately 12 hours and thus some birds probably traveled at least 2 km within their home ranges each day and approximately 400 km over the course of the non-breeding season. Passerines can travel similar distances in the course of a few days during migration (Stutchbury et al. 2009b), suggesting that these movements may not impose high energetic costs. However, birds require extensive fat reserves to complete long-distance migrations, and during non-breeding season when food may be limiting, movement rate may be an important component of an individual's energy budget (Moore and Kerlinger 1987, Sherry et al. 2005, Bowlin et al. 2005). If so, the fact that movement rate was positively related to basal area and negatively related to canopy height suggests that tall forests with high tree densities may not be high quality habitat; however, the relationship between movement rate and survival would need to be established to determine this possibility. Nonetheless, this is consistent with my finding in Chapter 3 indicating that golden-winged warblers preferred forests characterized by intermediate disturbance. My results also indicated that species richness of mixed-species flock was larger in primary forest. Predation risk reduction hypotheses predict that flock size should be negatively related to predation risk (Moynihan 1961, Pulliam 1973, Powell 1985); therefore, primary forest with natural disturbance features may offer high quality habitat for golden-winged warblers.

My results support the hypothesis that social systems develop as an outcome of resource availability and foraging behavior. Golden-winged warblers exhibit a specialized foraging strategy in which they primarily probe hanging dead leaves and epiphytes. This foraging strategy is shared by many species of several Neotropical families (Capitonidae, Formicaridae, Furnariidae, Troglodytidae), as well some Neotropical-Nearctic migrants (Morton 1980, Remsen and Parker 1984, Greenberg 1987, Rosenberg 1993). Dead leaves provide habitat for numerous large-bodied arthropods, especially roaches (Blattaria), spiders (Araneae), and Orthopterans (Gradwohl and Greenberg 1982, Rosenberg 1993, pers. obs.). Arthropod density and biomass can be much higher in dead leaves than in live leaves, due to the larger body sizes and different taxonomic composition (fewer Hymenopterans and Dipterans, Rosenberg 1997). Accessing these resources, however, requires skills that non-specialized species do not possess (Rosenberg 1993). Golden-winged warblers clearly exhibit these specializations and their lack of rictal bristles may indicate that this specialization process has a long evolutionary history. They were also capable of consuming large-bodied insects as demonstrated by my observation (18 February 2008) of a male that spent 75 seconds manipulating and consuming a 3-cm long katydid removed from a dead leaf.

The benefits of accessing abundant food resources in dead leaves are associated with two important costs. First, dead leaves are much less abundant than live leaves and are patchily distributed (Remsen and Parker 1984). Dead leaf foragers must therefore travel further than live leaf foragers, which may partially explain the large home range size of golden-winged warblers; flock participation may be another explanation. Second, dead leaf foraging may increase predation risk because it is a noisy process and precludes vigilance since the entire head is often inside a curled leaf (Morton 1980, pers. obs.). This behavior probably explains why virtually all regular dead leaf foragers participate in mixed-species flocks (Remsen and Parker 1984, Rosenberg 1997). The flocks joined by golden-winged warblers were highly variable in terms of species composition as demonstrated by the low co-occurrence probabilities for all species. This finding supports the hypothesis that flocks were joined to reduce predation risk, not to gain foraging benefits derived from other species. This hypothesis is also supported by my finding that foraging behavior did not differ between flocking states.

The reliance upon a high-quality, patchily-distributed food resource may also explain territoriality in golden-winged warblers. Arthropod populations in dead leaves can be quickly diminished by avian predators, but colonization rate is also high (Gradwohl and Greenberg 1982, Rosenberg 1993). Therefore, successfully defending an area with many dead-leaf clusters could ensure adequate food supply throughout the non-breeding season. In accordance with this hypothesis, most dead-leaf foraging resident species occur as single individuals or pairs in mixed-species foraging flocks and actively defend territories against conspecifics (Powell 1979, Munn and Terborgh 1979).

My results suggest that the energetic costs and high predation risk associated with the golden-winged warbler social system will only increase as flock size decreases and home range size increases. Because this social system is inextricably linked to its foraging behavior, this species may not be able to adapt to the novel conditions imposed by habitat loss and degradation. However, forest fragments and advanced secondary forests often contain many vine tangles and hanging dead leaves. Therefore this species may force into secondary forests within these landscapes even if the large flocks are not present. This situation raises the possibility that fragmented landscapes could serve as ecological traps if survival is low. Future studies should compare non-breeding ground behavior and survivorship between fragmented and contiguous forests. Direct energetic measurements and their influences on body condition would also be helpful in identifying high quality habitat. Even without this information, conservation plans for the golden-winged warbler must recognize the role of behavior in influencing potential carrying capacity. Specifically their social system potentially limits carrying capacity, and their apparent dependence upon mixed-species flocks suggests that successful conservation will depend upon conserving resident nuclear species that are key to flock formation.

Table 4.1 Home-range size summary statistics for 20 golden-winged warblers. Data are from radio-telemetry collected during three non-breeding seasons 2006-2009 in the Cordillera de Tilarán, Costa Rica.

Estimator	Level	Mean	SD	Min	Max
Kernel	50%	1.99	0.95	0.44	4.00
	75%	4.13	1.98	1.00	8.75
	95%	8.77	4.69	2.31	19.50
Minimum convex polygon	50%	0.83	0.56	0.13	1.96
	75%	1.56	0.99	0.32	4.00
	95%	3.16	2.13	0.81	9.87

Table 4.2. Multiple linear regression models of movement and flocking variables. The best models of home range size and percent time flocking did not include any covariate effects and are therefore not presented. PC refers to percent cover. Data are from 26 golden-winged warblers radio-tracked in the Cordillera de Tilarán, 2006-2009.

Response	Parameter	Estimate	SE	*t*	*P*(>|*t*|)	R^2
Movement rate	Intercept	143.15	18.12	7.90	0.000	0.90
	Home range size	3.48	1.50	2.25	0.075	
	Basal area	11.43	2.54	4.50	0.006	
	Canopy height	-4.24	1.43	-2.95	0.032	
	Habitat types	-30.28	12.0	-2.52	0.053	
Flock size	Intercept	-15.27	7.17	-2.13	0.056	0.66
	Canopy height	0.83	0.33	2.51	0.029	
	Tracking days	1.95	0.59	3.29	0.007	
	PC primary forest	0.16	0.07	2.10	0.059	

Table 4.3 Co-occurrence probabilities for species observed flocking with 26 golden-winged warblers on > 5% of observation days. Probabilities are averages weighted by observation effort. Migratory species are in bold. Data collected while radio-tracking birds during three non-breeding seasons 2006-2009 in the Cordillera de Tilarán, Costa Rica.

Species	Co-occurrence probability
Myioborus miniatus	0.37
Chlorospingus ophthalmicus	0.36
Wilsonia pusilla	0.36
Dendroica virens	0.36
Dendroica pensylvanica	0.35
Mniotilta varia	0.34
Vermivora peregrina	0.29
Tangara icterocephala	0.18
Vireo philadelphicus	0.16
Myiarchus tuberculifer	0.16
Mionectes olivacea	0.14
Vireo flavifrons	0.12
Basileuterus culcivorous	0.10
Saltator maximus	0.09
Hylophilus decurtatus	0.08
Turdus grayi	0.08
Basileuterus tristriatus	0.08
Elaenia frantzii	0.07
Basileuterus rufifrons	0.07
Ramphocelus passerinii	0.07
Thraupis episcopus	0.06
Xiphorhynchus erythropygius	0.06
Euphonia hirundinacea	0.06
Phlogothraupis sanguinolenta	0.05
Piranga rubra	0.05
Premnoplex brunnescens	0.05

Table 4.4. Mixed-effects models of golden-winged warbler foraging behavior. Data are 122 observations recorded for 11 color-banded individuals. Fixed effects included flocking status (flocking, associating, solo) and sex. The reference level (*ß0*) refers to females that were not flocking. Random effects are reported as standard deviations. For the normally distributed response variables, ε represents the standard deviation of residuals. Data collected in the Cordillera de Tilarán, 2006-2009.

Response	Parameter	Type	Estimate	SE	t^a	$P(>\|t\|)$
Bird height	*ß0*	Fixed	5.71	1.32	4.31	0.000
	FlockAssoc	Fixed	-1.15	2.03	-0.57	0.286
	FlockCohesive	Fixed	0.50	0.97	0.52	0.302
	SexMale	Fixed	0.08	1.12	0.07	0.472
	Individual	Random	0.83			
	ε	Random	4.05			
Tree height	*ß0*	Fixed	8.57	1.84	4.66	0.000
	FlockstateAssoc	Fixed	-2.53	2.75	-0.92	0.180
	FlockstateYes	Fixed	-0.24	1.32	-0.18	0.429
	SexMale	Fixed	0.42	1.59	0.26	0.397
	Individual	Random	1.29			
	ε	Random	5.50			
Distance from stem	*ß0*	Fixed	1.44	0.64	2.24	0.014
	FlockstateAssoc	Fixed	0.30	1.15	0.26	0.398
	FlockstateYes	Fixed	-0.06	0.52	-0.11	0.456
	SexMale	Fixed	0.40	0.47	0.85	0.199
	Individual	Random	0.00			
	ε	Random	2.06			
Maneuver	*ß0*	Fixed	1.15	0.82	1.41	0.159
	FlockstateAssoc	Fixed	15.51	1857.16	0.01	0.993
	FlockstateYes	Fixed	-0.07	0.57	-0.12	0.902
	SexMale	Fixed	0.30	0.73	0.41	0.680
	Individual	Random	0.62			

[a] For the maneuver model with a binomial response, a *z* test was used instead of a *t* test.

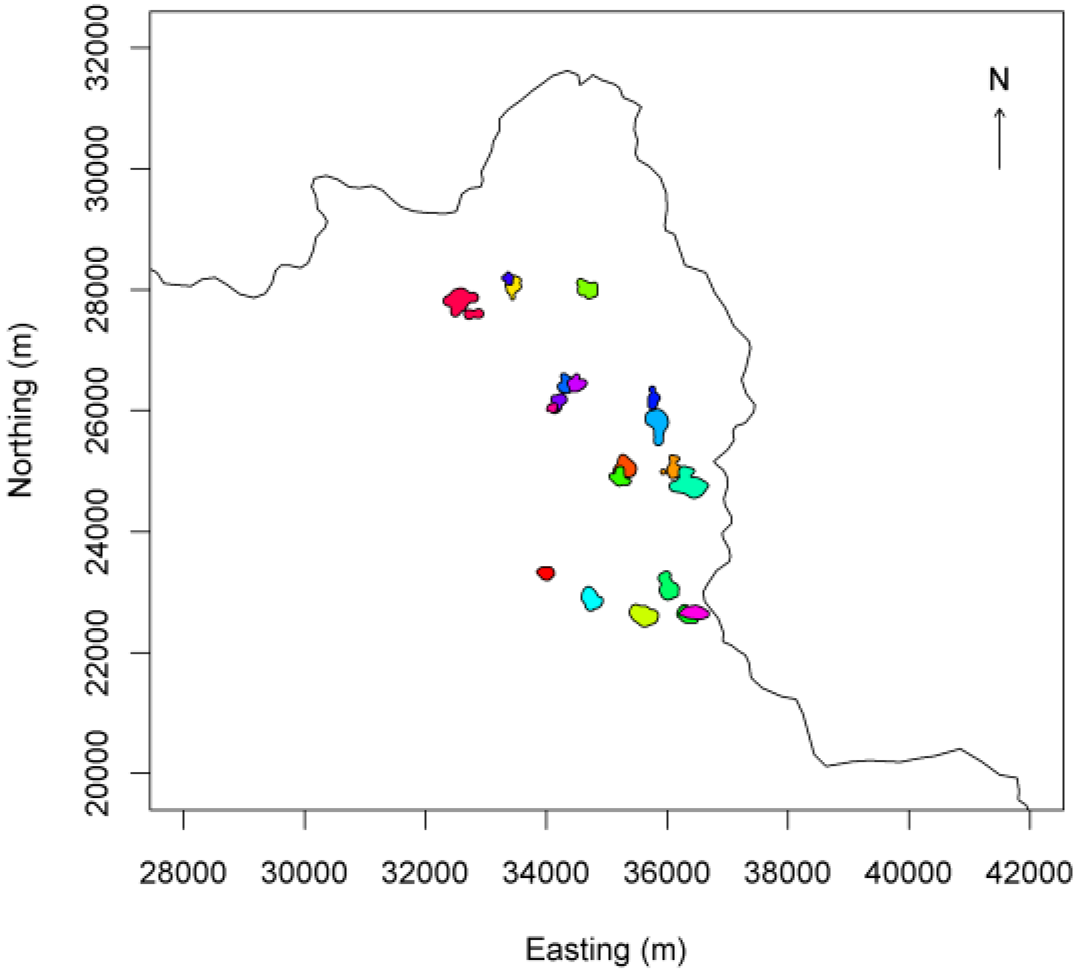

Figure 4.1. Distribution of golden-winged warbler home ranges across study area. Solid line is the continental divide. Radio-telemetry data are from three non-breeding seasons 2006-2009 in the Cordillera de Tilarán, Costa Rica.

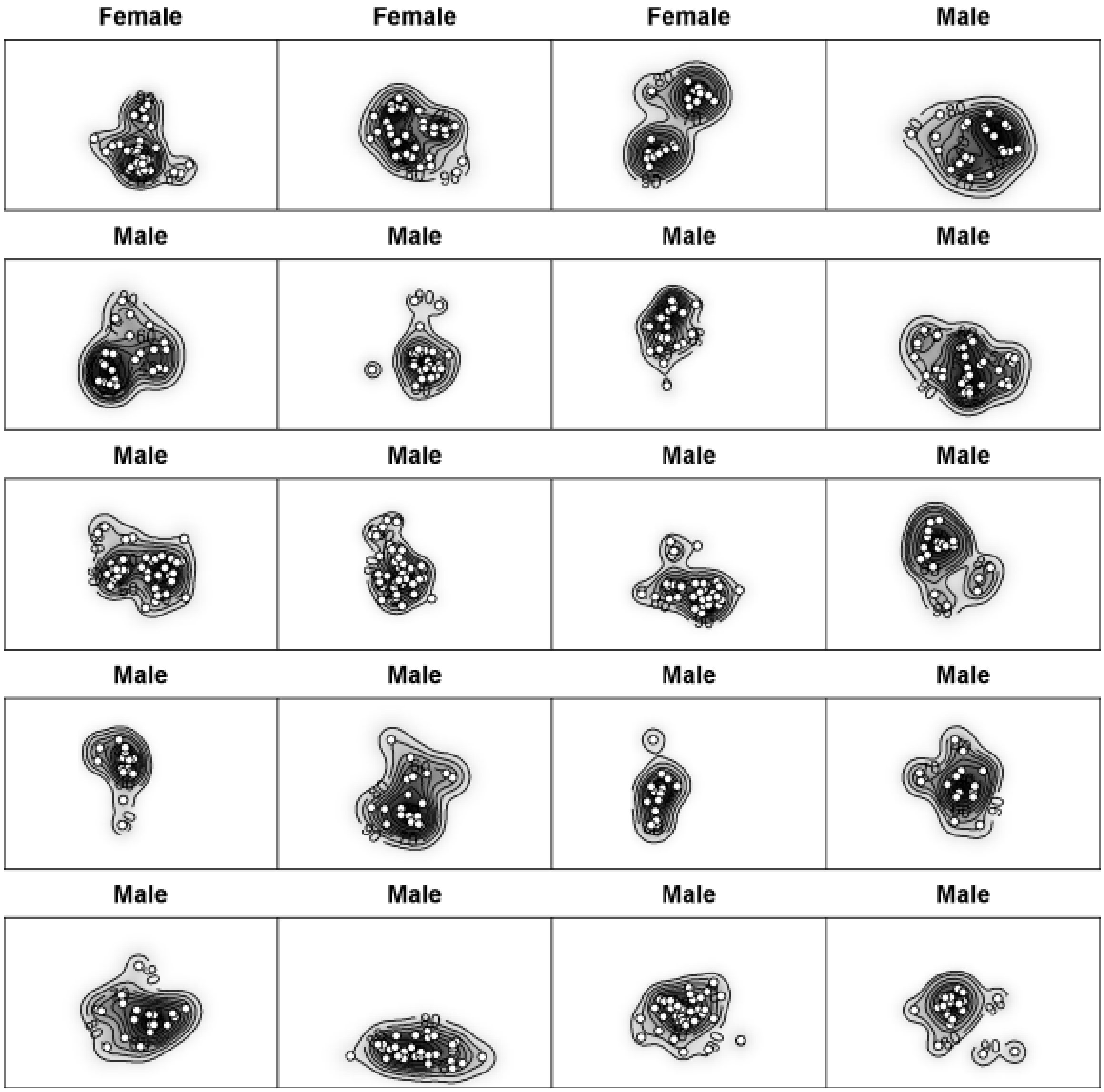

Figure 4.2 Kenel utilization distributions and location points for 17 male and 3 female golden-winged warblers with at least 15 location points. Contour lines represent home range levels. Data are from the Cordillera de Tilarán, Costa Rica, 2006-2009.

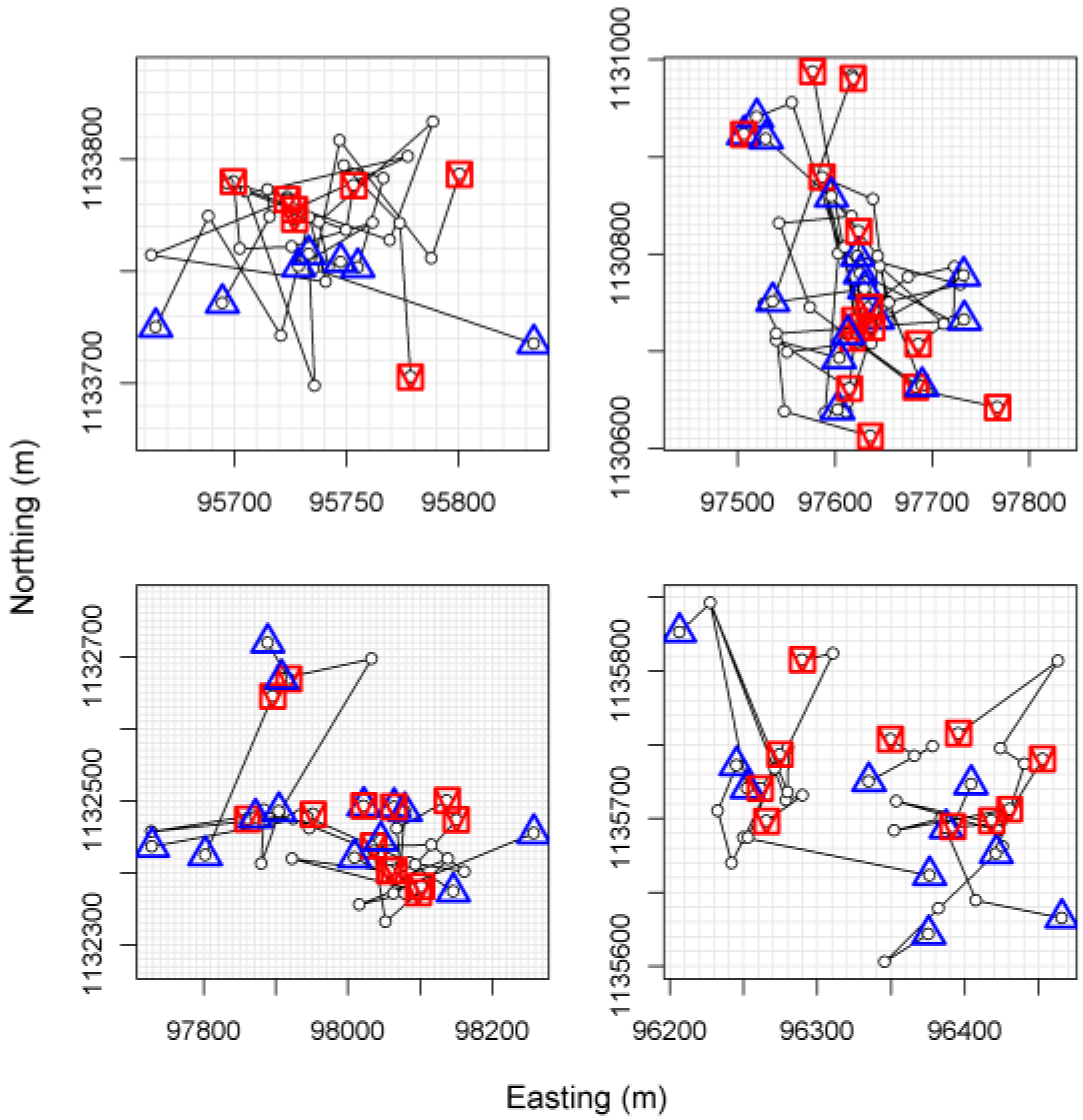

Figure 4.3. Examples of daily movement patterns for four golden-winged warblers. Each day of tracking is represented by segments starting from a blue triangle and ending at a red enclosed-triangle. Segments represent 30 minute time intervals. Movements are superimposed over 10-m grids. Data are from the Cordillera de Tilarán, Costa Rica, 2006-2009.

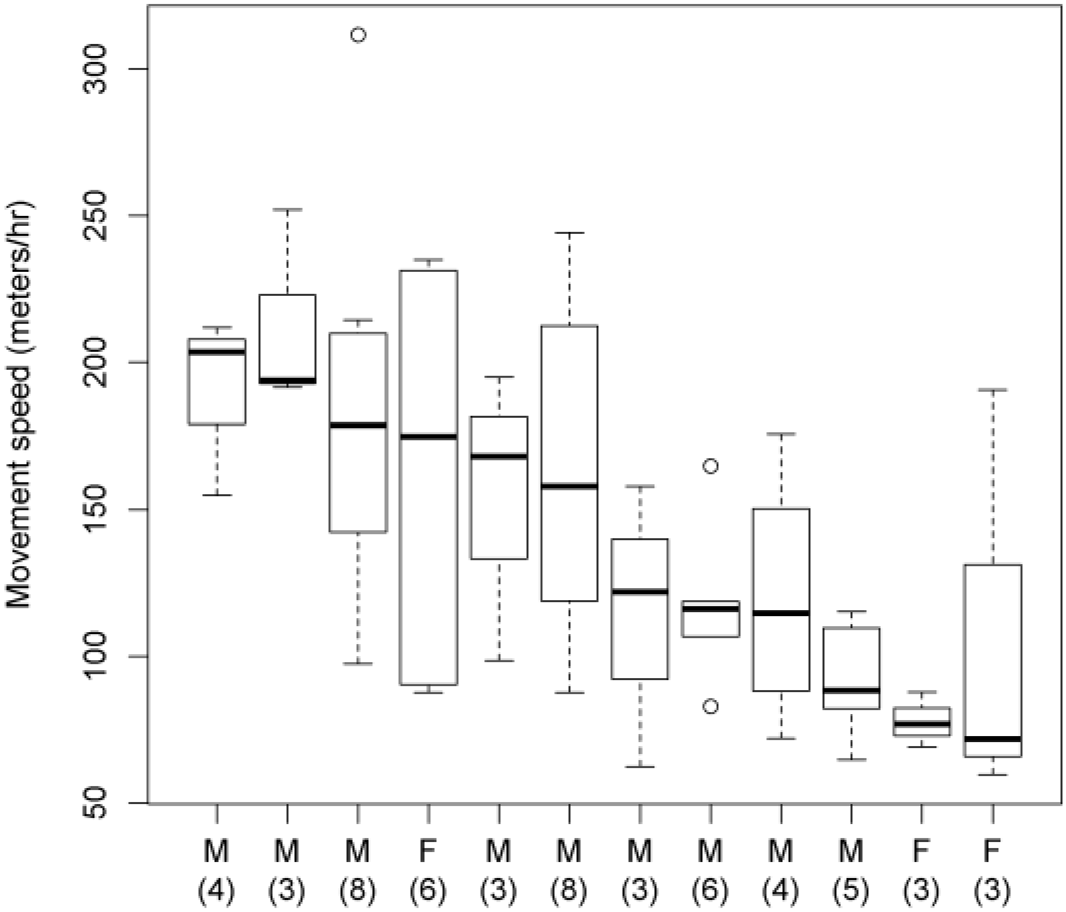

Figure 4.4. Boxplots of movement speeds of 12 golden-winged warblers labeled by sex (M=male, F=female) and ranked by median movement speed. Samples sizes in parenthesis are the number of observation days with at least four locations spaced by 30 minutes. Horizontal lines within boxes are medians. Box edges are first and third quartiles. Whiskers extend to extreme values unless outliers are present. Data are from the Cordillera de Tilarán, Costa Rica, 2006-2009.

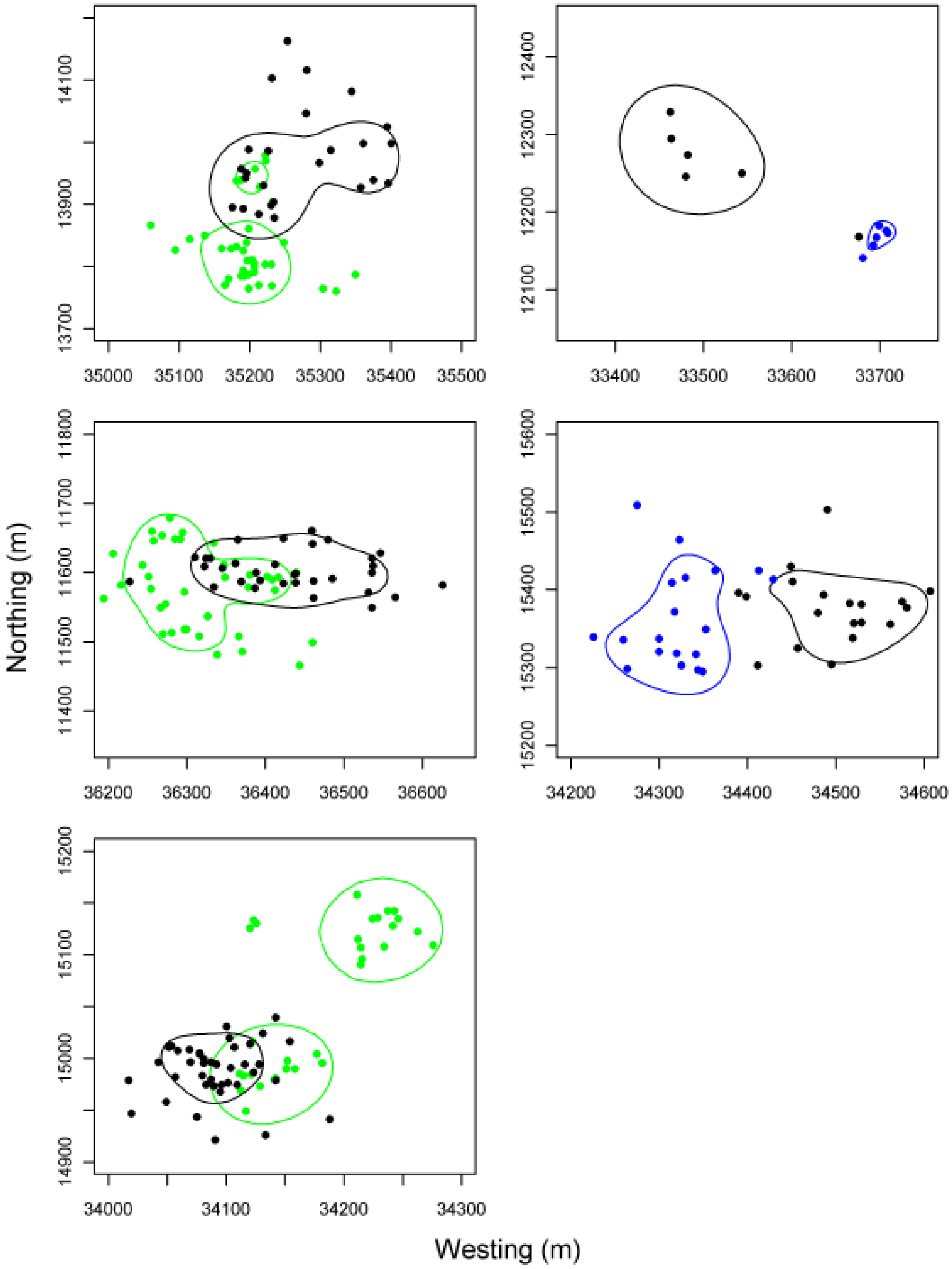

Figure 4.5. Home range overlap for five neighboring pairs of golden-winged warblers. Females are in green, males are in blue and black. Lines represent 50% kernel density home range estimates. Only neighbors that were radio-tracked simultaneously and had at least 5 location points are shown. Data are from the Cordillera de Tilarán, Costa Rica, 2006-2009.

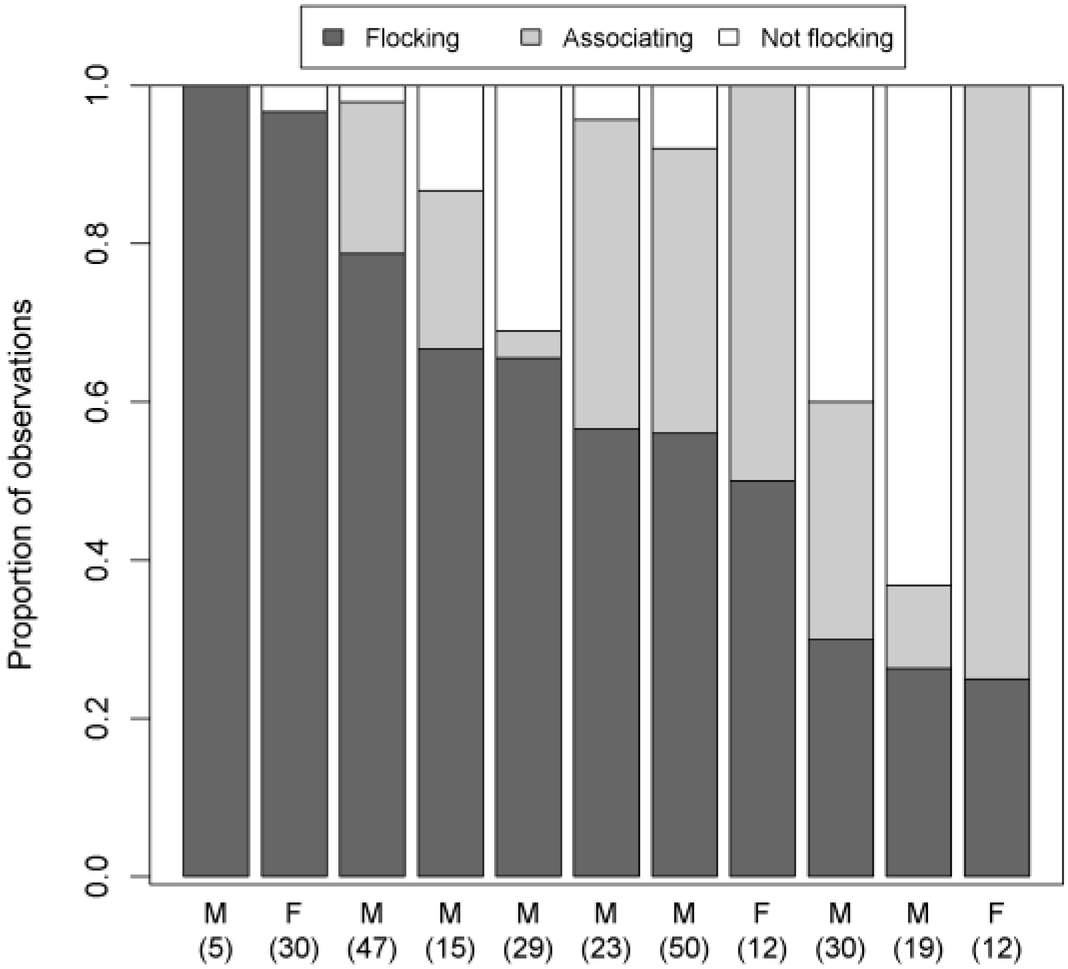

Figure 4.6. Proportion of observations in which 11 golden-winged warblers were flocking. Associating refers to cases where the bird occurred with other species, but were not moving together in concert. Individuals referenced by sex (M=male, F=female) and sample size, in parentheses. Data are from the Cordillera de Tilarán, Costa Rica, 2006-2009.

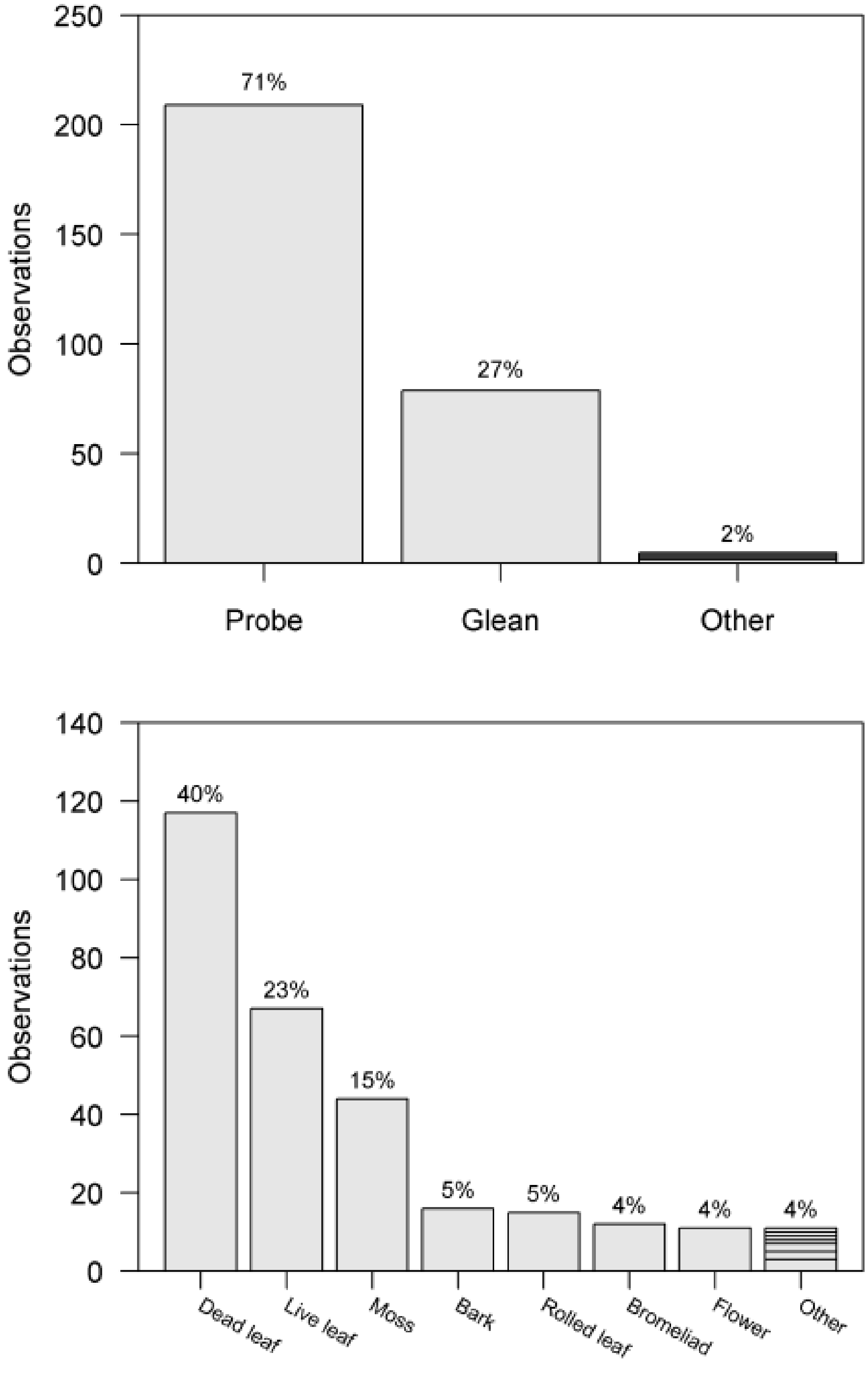

Figure 4.7. Barplots of foraging maneuvers (top) and substrates (bottom). Data are from the Cordillera de Tilarán, Costa Rica, 2006-2009.

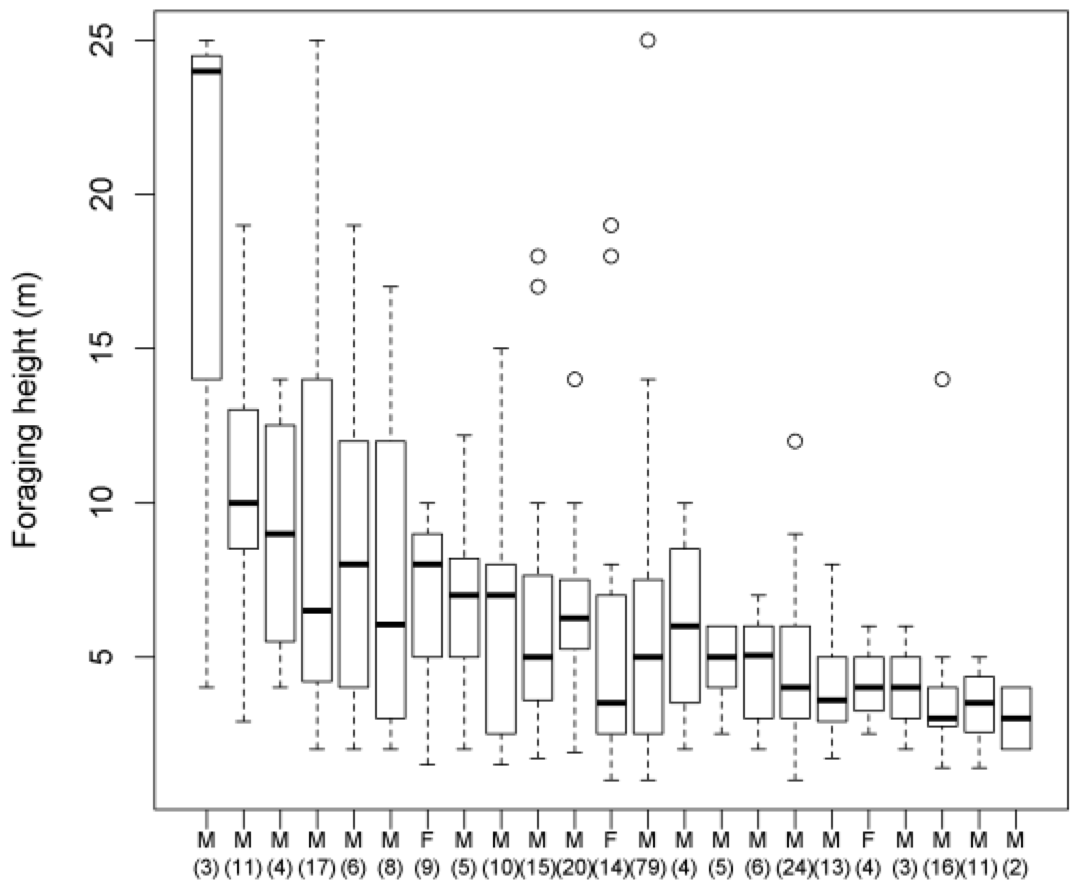

Figure 4.8. Boxplots of foraging heights in meters for 20 male and 3 female golden-winged warblers. Sample size for each individual is shown in parentheses. Horizontal lines within boxes are medians. Box edges are first and third quartiles. Whiskers extend to extreme values unless outliers are present. Data are from the Cordillera de Tilarán, Costa Rica, 2006-2009.

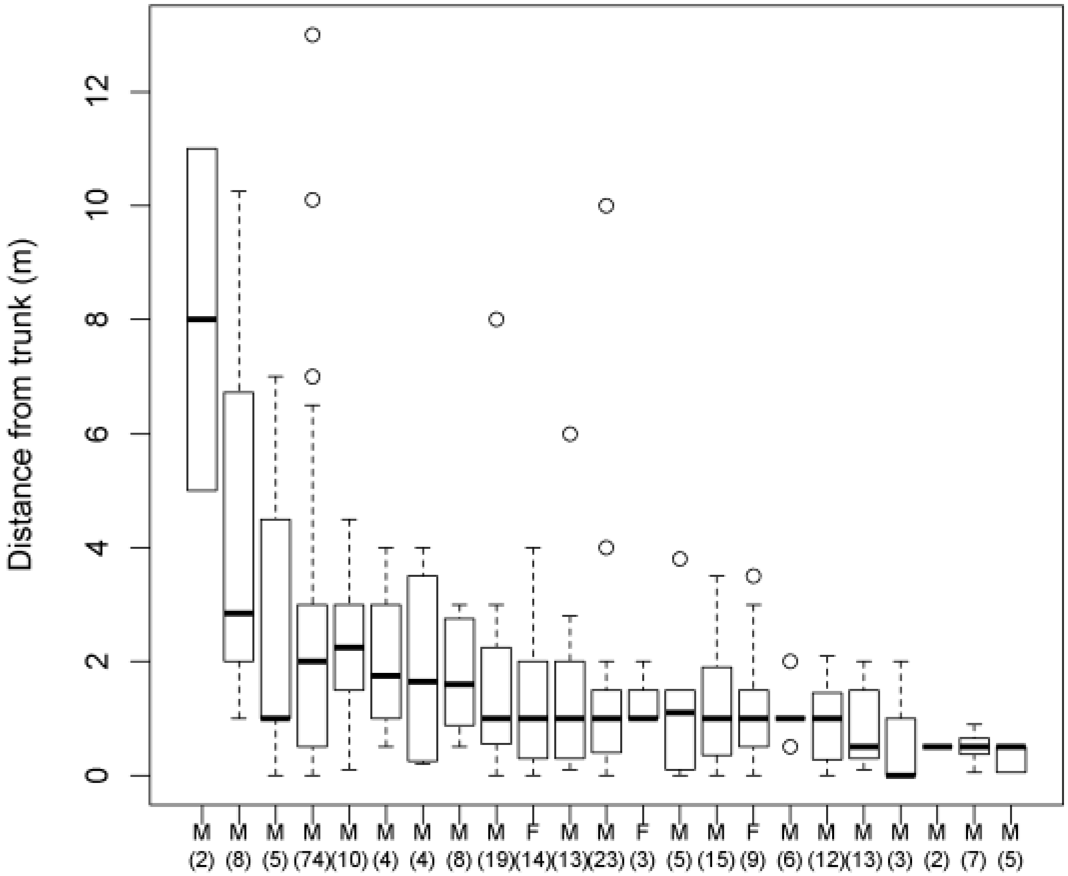

Figure 4.9. Boxplots of foraging distances from trunk for 20 male and 3 female golden-winged warblers. Horizontal lines within boxes are medians. Box edges are first and third quartiles. Whiskers extend to extreme values unless outliers are present. Data are from the Cordillera de Tilarán, Costa Rica, 2006-2009.

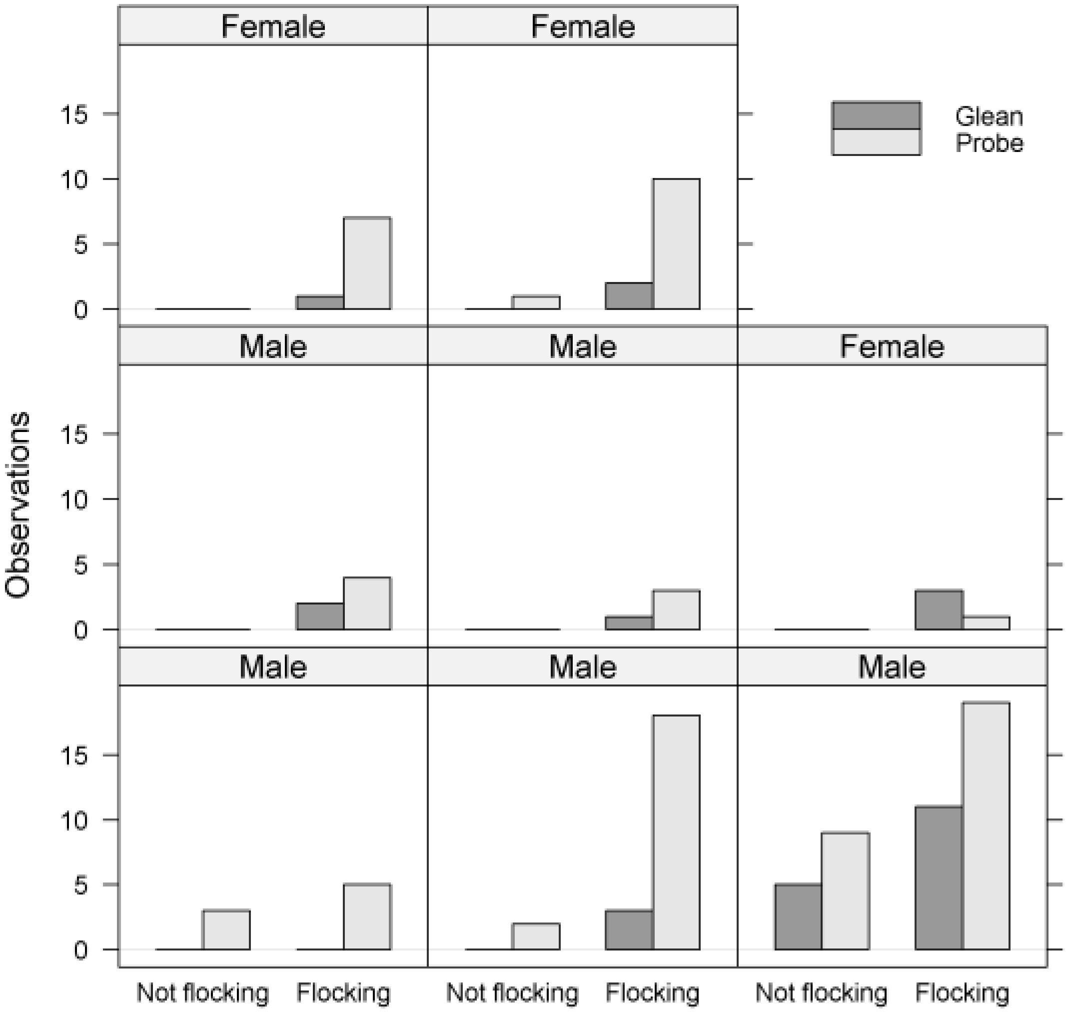

Figure 4.10. Barplots of foraging maneuvers for golden-winged warblers in and out of mixed-species foraging flocks. The five male and three females shown are those with at least four observations that could be unambigiously classified as flocking or not. Data are from the Cordillera de Tilarán, Costa Rica, 2006-2009.

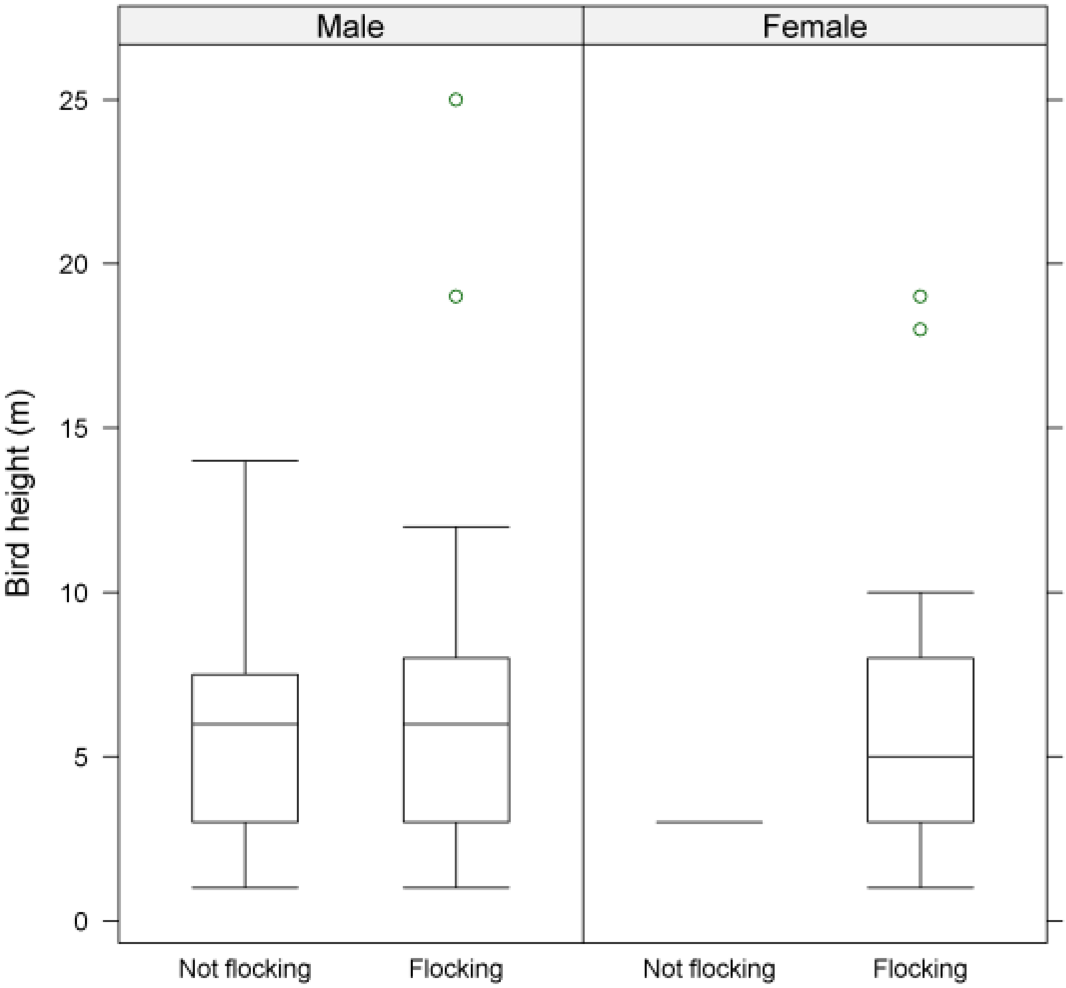

Figure 4.11. Boxplots of foraging heights stratified by sex and flocking status. Horizontal lines within boxes are medians. Box edges are first and third quartiles. Whiskers extend to extreme values unless outliers are present. Data are from the Cordillera de Tilarán, Costa Rica, 2006-2009.

CHAPTER 5

SEASONAL AND ANNUAL ESTIMATES OF GOLDEN-WINGED WARBLER SURVIVORSHIP

5.1 Introduction

Seasonal survival rates are often the most influential demographic parameters affecting population growth of migratory birds (Schmutz et al. 1997, Podolsky et al. 2007, Buehler et al. 2008). For many species of Neotropical-Nearctic migrants, survival is highest during the breeding season (Powell et al. 2000b, Sillett and Holmes 2002, Jones et al. 2004), indicating that non-breeding season survival rates may regulate populations. However, it has not been possible to quantitatively determine which factors regulate these populations because few non-breeding season demographic data exist (Holmes 2007). This problem is concerning because many Neotropical-Nearctic migrants are declining, and low survival rates have been reported for some species during the stationary non-breeding season (Rappole et al. 1989, Sauer et al. 2008).

The golden-winged warbler has declined at a rate of 2.8% per year since 1966 according to the Breeding Bird Survey (Sauer et al. 2008). Although habitat loss on the breeding or non-breeding grounds could explain this population decline, reduced vital rates due to habitat loss, habitat degradation, or hybridization with blue-winged warblers (*Vermivora pinus*) may also be responsible (Buehler et al. 2007). All the demographic data available to assess the relative importance of these factors has come from the breeding grounds. Nest success and fecundity data have been reported from the southern Appalachian Mountains where this species is listed among the species of highest conservation concern (Rich et al. 2004). Interestingly, nest success in this region appears to be greater than 50% and 3-6 young are fledged per nest (Klaus and Buehler 2001, Bulluck and Buehler 2008). Because golden-winged warblers readily renest after nest failure, productivity is extremely high in this region. Furthermore hybridization with blue-winged warblers is rare because golden-winged warblers occur at higher elevations than blue-winged warblers, and nest parasitism by brown-headed cowbirds (*Molothrus ater*) is uncommon (Buehler et al. 2007, Vallender et al. 2007a, Bulluck and Buehler 2008). Comparable productivity rates have been found in other parts of the breeding range (Will 1986, Amber Roth personal communication).

These data suggest that neither reproductive rates nor competition and hybridization with blue-winged warblers are a satisfactory explanation for the local declines of golden-winged warblers in at least some portions of the breeding range. This raises the possibility that survivorship during the non-breeding season could be a contributing factor; however, no published studies focusing on the non-breeding demography of golden-winged warblers during the non-breeding season exist. The objectives of this component of my research were to 1) provide the first seasonal and annual estimates golden-winged warbler survival, and 2) determine if recruitment was high enough to offset mortalities on the non-breeding grounds.

5.2 Methods

5.2.1 Field methods

I collected data on golden-winged warbler survival using a combination of radio-telemetry and mark-resight techniques. Radio-telemetry makes it possible to determine the causes of mortality, and greatly reduces the uncertainty regarding an individual's fate because resight probability is generally close to one. However, studying small animals using radio-telemetry can only be done on short time scales because of inherent battery lifespan limitations. The use of radio-telemetry also raises concerns about the effect of transmitters on survival probability (Burger et al. 1991, but see Powell et al. 1998). Monitoring color-banded individuals provides a complementary approach because individuals can be studied over much longer time periods, and survival probability is unlikely to be affected (Zann 1994). Combining data from these two field methods can increase precision of parameter estimates (Powell et al. 2000a).

I captured birds using 6-12 m mist-nets with 32-36 mm mesh sizes. I used both constant effort passive methods and target methods. The constant effort approach involved setting arrays of 10 nets spaced by 25m, and running them for eight hours a day over three consecutive days (see Chapter 2 for details of the study design). The target netting method involved attracting birds to nets using broadcast vocalizations and a painted clay decoy positioned between two parallel nets. All individuals caught were banded with two color bands and one USGS metal band. Most individuals were also outfitted with 0.43 g radio-transmitters (Holohil BD-2N), which had battery life spans lasting up to 28 days.

Birds with functioning transmitters were relocated using 4-element yagi antenna and VHS receivers (Telonics, Inc. model TR-4). To resight birds without functional transmitters, I searched areas within 500 m of the capture location for 30 minutes, broadcasting recorded vocalizations. An effort was made to resight birds with transmitters every 1-2 days; whereas birds without transmitters were searched for approximately once per month.

Recruitment here is defined as the rate at which new individuals enter the population. I could not measure this directly without color-banding the entire population; however, as a proxy I used the proportion of vacated territories that were recolonized. Thus, during territory searches, unbanded individuals were noted when encountered.

5.2.2 Statistical methods

I modeled apparent survival (ϕ) and resight probability (p) using a hierarchical implementation of the Cormack-Jolly-Seber (CJS) model (Royle 2008, Royle and Dorazio 2008). Apparent survival is the probability that an individual survives and does not move off the study area. This model can be 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 state variable describing if individual i was alive at time t, and $y(i, t)$ is the observed data. Apparent survival after the initial capture is determined by the status of the individual in the previous time period (0 if dead, 1 if alive) multiplied by the survival probability. In other words, if an individual is alive at time t-1, it survives (or permanently emigrates) with probability ϕ. This survival process cannot be directly observed because resight probability is typically less than one. Thus, an individual not detected may be either dead or alive and unseen. To account for this observation process, the model assumes that the observed data $y(i, t)$ arise from a Bernoulli distribution with probability equal to $z(i, t)$ multiplied by p. This ensures that dead individuals have a zero encounter probability, and living individuals are detected with probability p. Unlike conventional implementations of the CJS model (Lebreton et al. 1992), this formulation allows for incorporation of individual- and time-specific covariates affecting ϕ and p.

A more important advantage of modeling the underlying state variable $z(i, t)$ is that it overcomes an often ignored limitation of virtually all multi-season mark-resight studies of Neotropical-Nearctic migrants. Specifically, researchers normally confound early and late portions of the non-breeding season with other phases of the annual cycle because mark-resight efforts start and stop at intermediate dates within the non-breeding season. Thus, birds dying during the stationary non-breeding season, but outside of the observation period, will be treated by the CJS model as dying outside of the stationary non-breeding season. By setting up the golden-winged warbler encounter histories by day, rather than month, and using a clear definition of the stationary non-breeding season (1 October – 15 April, based upon arrival and departure dates), this model could better differentiate between apparent mortalities within and among non-breeding seasons. This approach also explicitly accounts for non-constant time intervals between resight attempts.

My model building process began with a global model that contained an interaction of season (within vs. among) and transmitter on ϕ and transmitter on p. This global model allowed me to estimate survival within and among seasons for birds wearing and not wearing transmitters (whether the batteries were functional or not). It also accounted for the fact that birds were easier to resight when outfitted with functioning radio transmitters. I then used a backwards selection process to arrive at the most parsimonious model. This process involved removing non-significant covariates and comparing the reduced model to the global model using the Deviance Information Criterion (Spiegelhalter et al. 2002). DIC is computed as the mean deviance plus the effective number of parameters (pD). Various methods exist to calculate pD, and here I used one half the variance of deviance (Gelman 2004). Because the global model had four survival parameters and two resight parameters plus the latent *z(i,t)* variables, and my sample size was small (see Results), I was not able to include other covariates such as age, sex, or habitat type.

I estimated model parameters using Markov-chain Monte Carlo (MCMC) methods implemented in the program OpenBUGS (Lunn et al. 2009) and run from R using the BRugs package (Thomas et al. 2006). MCMC is a Bayesian method of approximating the posterior distributions of model parameters, and can easily accommodate latent variables, non-constant sampling periods, and missing data. Posterior distributions are the probability distributions of model parameters. Thus they allow for direct inference regarding the probability that a value corresponds to the true population parameter. For instance, the median of the posterior is the most likely value given the data. Bayesian data analysis requires specifying prior distributions for all model parameters. I chose non-informative priors because no previous estimates of golden-winged warbler survival or resight probability exist. Specifically, I used a Uniform(0, 1) prior for all parameters, except for within-season monthly survival for which I used a Uniform(0.5, 1) prior because monthly survival less than 0.5 is equivalent to total mortality over the non-breeding season. I summarized posterior distributions using 200,000 draws from two independent chains thinned by 20 after discarding the 100,000 burn-ins. I assessed convergence using visual inspections and Gelman-Rubin diagnostics (Gelman and Rubin 1992) .

5.3 Results

I captured and monitored 28 male and 4 female golden-winged warblers over five non-breeding seasons (Fig 5.1). I discarded data from one male captured on 26 March 2008 and never seen again because this bird was probably a transient. All other individuals were captured before 15 March. This procedure resulted in 447 resight attempts for 31 individuals. Twenty seven of these birds were tracked using radio-telemetry over a total of 269 days.

5.3.1 Survivorship during stationary non-breeding season

I found strong evidence that golden-winged warbler survival differed among phases of the annual cycle and was affected by transmitters among seasons. I found no evidence of a within-season transmitter effect on ϕ (mean difference = 0.14, $P = 0.11$). I therefore removed this term and modeled within-season survival as constant among individuals. Clearly, variation in survival probability exists among individuals, but given the small data set, this was the most parsimonious parameterization as was demonstrated by the lower DIC value for the reduced model (145.5) than the global model (153.5). Gelman-Rubin statistics were less than 1.1 for all model parameters indicating convergence. Furthermore, posterior distributions showed no sign of multi-modality (Fig. 5.2).

Apparent monthly survival was 0.93, equivalent to a 0.63 probability of surviving the entire 6.5 month stationary non-breeding season (Table 5.1). Resight probability was close to unity for birds with functioning radio transmitters as expected. For birds without functioning transmitters, resight probability was 0.42, indicating that 2, 3, 4, and 5 searches would result in cumulative probabilities of 0.66, 0.80, 0.88, and 0.93 respectively, conditional on an individual being alive.

One mortality event was directly observed while radio-tracking. A first-year male was depredated by a striped palm pit-viper (*Bothriechis lateralis*) on 17 October 2007, less than one month after making its first arrival on the non-breeding grounds (Fig 5.3). This species of snake is a sit-and-wait predator (Savage 2005), ambushing prey that passes within close range. This suggests that the transmitter did not increase this golden-winged warbler's susceptibility to predation, which is consistent with the lack of a statistically significant effect of transmitter on within season apparent survival. This bird was tracked for nine days before being depredated, and occurred exclusively in 18 year old secondary forest regenerating after pasture abandonment (Fig 5.4). *B. lateralis* was encountered six times, always in this habitat type, during the course of the study.

5.3.2 Among season and annual apparent survival

Five individuals were encountered in multiple seasons; one individual survived at least four seasons, one for three seasons, and three for two season (Fig 5.1). Birds that apparently migrated with transmitters survived the migratory and breeding intervals at a much lower rate (0.26) than those that departed without transmitters (0.85)(Table 5.1). This apparent survival probability includes both annual migrations and the breeding season, spanning a total of 5.5 months. Only two birds that apparently departed with transmitters were resighted in ensuing seasons, and in both cases the transmitters had fallen off in the interval.

Annual apparent survival probability for birds departing without transmitters was 0.53, which was estimated as a derived parameter by multiplying the within season apparent survival and the among season survival for birds without transmitters.

5.3.3 Recruitment

Of 25 vacated territories (territories where the previous occupants had died or emigrate), only 16 (64%) were colonized by unbanded birds in at least one subsequent season. Several territories were left vacated for multiple seasons. Two territories were unoccupied for all three seasons following vacancy, and four territories remained unoccupied for two seasons. In total, 28 of 55 (51%) of possible colonization opportunities were made. These statistics should be considered minimum values because the possibility exists that some colonizing individuals died prior to being discovered or were present but not detected.

5.4 Discussion

The annual survival rate of 0.53 reported here for golden-winged warblers lies within the range of estimates for many species of Neotropical-Nearctic migrants (DeSante et al. 2001, Sillett and Holmes 2002, Jones et al. 2004, Stutchbury et al. 2009a, Saracco et al. 2010); however, in contrast to a growing body of literature indicating that survival probability is lowest during migration, most mortality within my study area apparently occurred during the stationary non-breeding season, as indicated by lower apparent survival rates during the non-breeding season. For example, Sillett and Holmes (2002) found extremely high apparent monthly survival rates (0.987-0.990) of black-throated blue warblers (*Dendroica caerulescens*) wintering in Jamaica, which is equivalent to a 0.92 probability of surviving a 6.5 month non-breeding season. Thus they determined that mortality rates were 15 times higher during migration than during stationary periods. Similar high apparent survival rates for migrants during the stationary non-breeding season have been reported by others (Wunderle and Latta 2000, Johnson et al. 2006). For golden-winged warblers, however, apparent monthly survival during the stationary non-breeding season was only 0.93, lower than the abovementioned studies, and among-season apparent survival was 0.85, higher relative to these studies.

The difference between these survival rates cannot be attributed to the use of ratio-transmitters because my estimate is for individuals not wearing transmitters. The difference may be explained by the fact that most studies reporting high survival during the stationary non-breeding season occurred in the West Indies. These islands host a much smaller community of potential predators than do the mainland Neotropics. In Costa Rica, for example, there are 10 species of (semi-) diurnal birds of prey occur that specialize on small passerines, three species of *Glaucidium*, four species of *Accipiter* and three species of *Micrastur* (Garrigues 2007). Seven of these species were observed in my small study area. In Cuba on the other hand, which is twice as large as Costa Rica, only three species within this guild exist (Garrido and Kirkconnell 2000). Similarly, over 100 species of snakes occur in Costa Rica compared to 14 in Cuba (Savage 2005). Although higher species richness of predators does not necessarily equate to higher predation pressure, lower predation pressure on the islands is also suggested by the lower occurrence of mixed-species flocks (Beauchamp 2004) and by studies indicating that most predator densities are low and that birds comprise a small proportion of the diets of some potential predators (Henderson and Crother 1989, Delannoy 1997).

In contrast to results from the Greater Antilles, apparent survival estimates from the mainland are often as low as or lower than the rates in my study (Rappole et al. 1989, Winker et al. 1990). A study of cerulean warblers (*Dendroica cerulea*) wintering in shade coffee farms in Venezuela reported high monthly survival rates (0.97) for cerulean warblers classified as territorial, but most individuals captured were deemed non-territorial and had much lower rates (0.81) (Bakermans et al. 2009). Bakermans et al. (2009) did not report an overall within season survivorship estimate but a mixture of these two sampling distributions yields an approximate monthly rate of 0.88, which ranks among the lowest reported for any Neotropical-Nearctic migrant.

The proximate causes of mortality for Neotropical-Nearctic migrants have rarely been determined, making it difficult to establish if low survival rates are due to novel threats imposed by human induced habitat modifications. Radio-telemetry is typically required to locate dead birds and many species are too small to be monitored for sufficient durations to adequately quantify causes of mortality. The few studies that have reported mortality events suggest that predation is the primary cause of mortality. Of six wood thrush mortalities observed by Rappole et al. (1989), mammalian and avian predators each were responsible for equal numbers. These researchers demonstrated that low survival was attributable to anthropogenic influences in that, habitat loss prevented many individuals from acquiring territories and these individuals suffered higher mortality.

I only observed one mortality event and could not model habitat-specific survival, thus it was not possible to determine the causes of the low survival rate in my study. However, it is important to realize that this study was conducted in a highly fragmented agricultural landscape. Future research should compare survival rates between fragmented and unfragmented landscapes. Furthermore, it is interesting that the one depredated individual was a juvenile inhabiting secondary forest soon after arriving on the non-breeding grounds. Although no research has addressed this for Neotropical-Nearctic migrants, the onset of the stationary non-breeding season is probably a stressful period, especially for juveniles, as birds must compete for territories and experience novel predation pressures after finishing a long migration (Snell-Rood and Cristol 2005). Furthermore, October-December can be inhospitable months of the year in much of the golden-winged warbler winter range because they inhabit some of the wettest places on earth, and rainfall and wind speeds can peak in these months (Clark et al. 2000).

Low survival rates during the stationary non-breeding season warrant concern because both high fecundity and high survival rates during migration and the breeding season would be required to maintain stable populations. I found that apparent survival was indeed high during the intervening interval (0.85) relative to previous studies (Sillett and Holmes 2002). This finding coupled with reports of high productivity on the breeding grounds suggests that mortalities during the stationary non-breeding season should be offset by high recruitment. However, recruitment was low in this population, as evidenced by low colonization rates of vacated territories. This finding is consistent with results from Chapter 3 in which I found no evidence of site-level recruitment within or among seasons. However, this finding along with the rarity of floater in my study area stands in stark contrast to numerous studies in which surplus birds quickly claimed vacated territories (Rappole and Warner 1980, Stutchbury 1994, Marra 2000, Studds and Marra 2005, Brown and Long 2007).

Three hypotheses may explain how recruitment could be low when productivity and among season survival are high. First, juvenile survival may be low during either the post-fledging pre-migration period or during fall migration. Second, juveniles may not be able to find available habitat. Third, my recruitment estimates may be biased low if colonizing individuals died early in the non-breeding season or were present but not detected. The first hypothesis needs further investigation because low post-fledging survival rates have been reported for many species (King et al. 2006, Rush and Stutchbury 2008, Moore et al. 2010). This prediction could be tested by estimating annual survival of juveniles on the breeding grounds. Furthermore, the possibility exists that abnormally low survival rates of juveniles during migration could result from hybridization with blue-winged warblers; however, the influence of hybridization on migration patterns and return rates has not been studied. The second hypothesis may be true if the population size is small relative to the amount of available habitat. Estimates of habitat extent and carrying capacity are needed to evaluate this possibility (Rappole et al. 2003a). The latter hypothesis is not supported by my data because territories were typically surveyed three times per season including one season when territory surveys began in early October.

Although these estimates provide the first insight into golden-winged warbler demographics during the non-breeding season, I did not have enough data to estimate habitat-, sex-, or age-specific survival rates, and precision was low. Habitat-specific survival rates are needed to identify and conserve high quality habitat. Testing for differences between the sexes is important because studies from the breeding grounds have found evidence that females return less frequently than males (Will 1986, David Buehler personal communication). Such a disparity would bias sex ratios thereby lowering effective population size and potentially increasing hybridization rates with blue-winged warblers (Rappole and McDonald 1994, Vallender et al. 2007b). Future research should therefore aim to increase the precision of these estimates and attribute variation in within-season survival rate among habitat types and sex and age cohorts. This could be accomplished by increasing mark-resight effort at the beginning and end of the non-breeding season. An assessment of temporal change in survival, and survival rates from other regions of the non-breeding range are also needed. Radio telemetry should not be used if annual survival is of interest due to the difficulty of removing transmitters from golden-winged warblers and the low among season apparent survival rates of birds departing with transmitters. In addition, constant effort mist-netting methods are not likely to be effective due to low capture rates (Chapter 2).

Migratory bird populations may be limited by habitat availability at any stage of the annual cycle, or by recruitment rates too low to offset mortalities (Goss-Custard et al. 1995, Sutherland 1996, Peach et al. 1999, Runge and Marra 2005). For golden-winged warblers, hybridization poses an additional extinction risk (Dabrowski et al. 2005, Vallender et al. 2007b). Here I found that vital rates of golden-winged warblers wintering in Costa Rica were not high enough to maintain a stable population. Although approximately 53% of birds appeared to survive annually, mortality was high during the stationary non-breeding season, and recruitment appeared to be below thresholds necessary for vacated territories to be colonized. Low recruitment does not appear to be due to low productivity, but may be attributed to low juvenile survival prior to arriving on the non-breeding grounds, in which case it would not be clear how management actions could improve this situation. However, survival rates during the stationary non-breeding season could potentially be increased by conserving high quality habitat. Future research should focus on identifying theses habitat types.

Table 5.1 Summaries of posterior distributions from the most parsimonious Cormack-Jolly-Seber model of golden-winged warbler survival. Bayesian credible intervals (CI) are highest posterior density regions. See Fig 5.2 for graphical displays of posterior distributions. Data were collected on 31 individuals monitored for up to five years in the Cordillera de Tilarán, Costa Rica, 2006-2010.

				95% CI	
Parameter	Mean	SD	Median	Lower	Upper
Within season apparent survival (monthly)	0.93	0.033	0.93	0.87	0.99
Within season apparent survival (1 Oct - 15 April)	0.63	0.14	0.64	0.37	0.90
Among season apparent survival (no transmitter)	0.85	0.12	0.87	0.60	1.00
Among season apparent survival (with transmitter)	0.26	0.13	0.24	0.032	0.52
Annual apparent survival (no transmitter)	0.53	0.13	0.53	0.29	0.77
Resight probability (no transmitter)	0.42	0.058	0.42	0.31	0.54
Resight probability (with transmitter)	0.99	0.0059	0.99	0.98	1.00

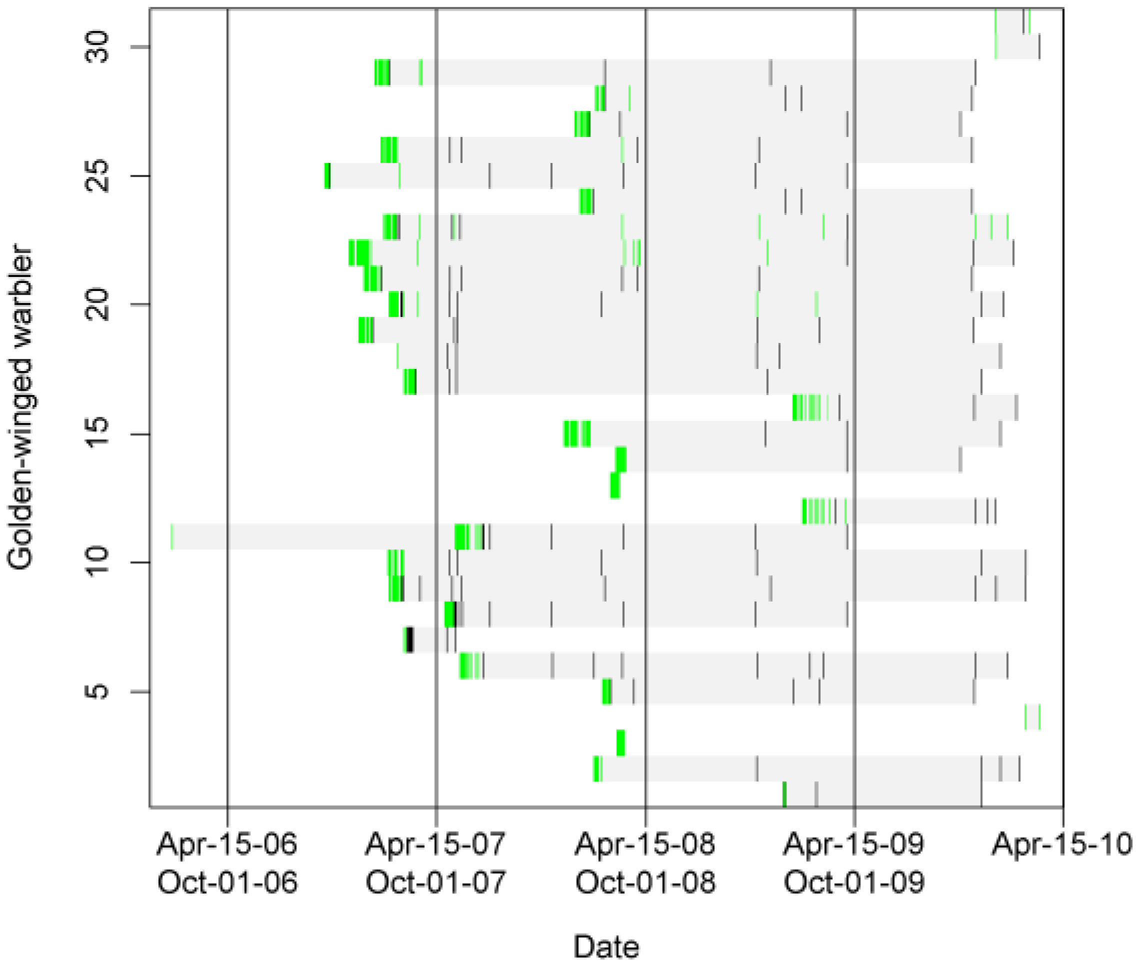

Figure 5.1. Graphical displays of the 31golden-winged warbler encounter histories used in the Cormack-Jolly-Seber model. Filled areas represent days between first capture and last search. Encounters are shown in green and non-detections in black. Vertical lines separate the five non-breeding seasons. Note that most effort was concentrated in the latter half of the non-breeding season with the exception of the 2007-2008 season. Data are from the Cordillera de Tilarán, Costa Rica.

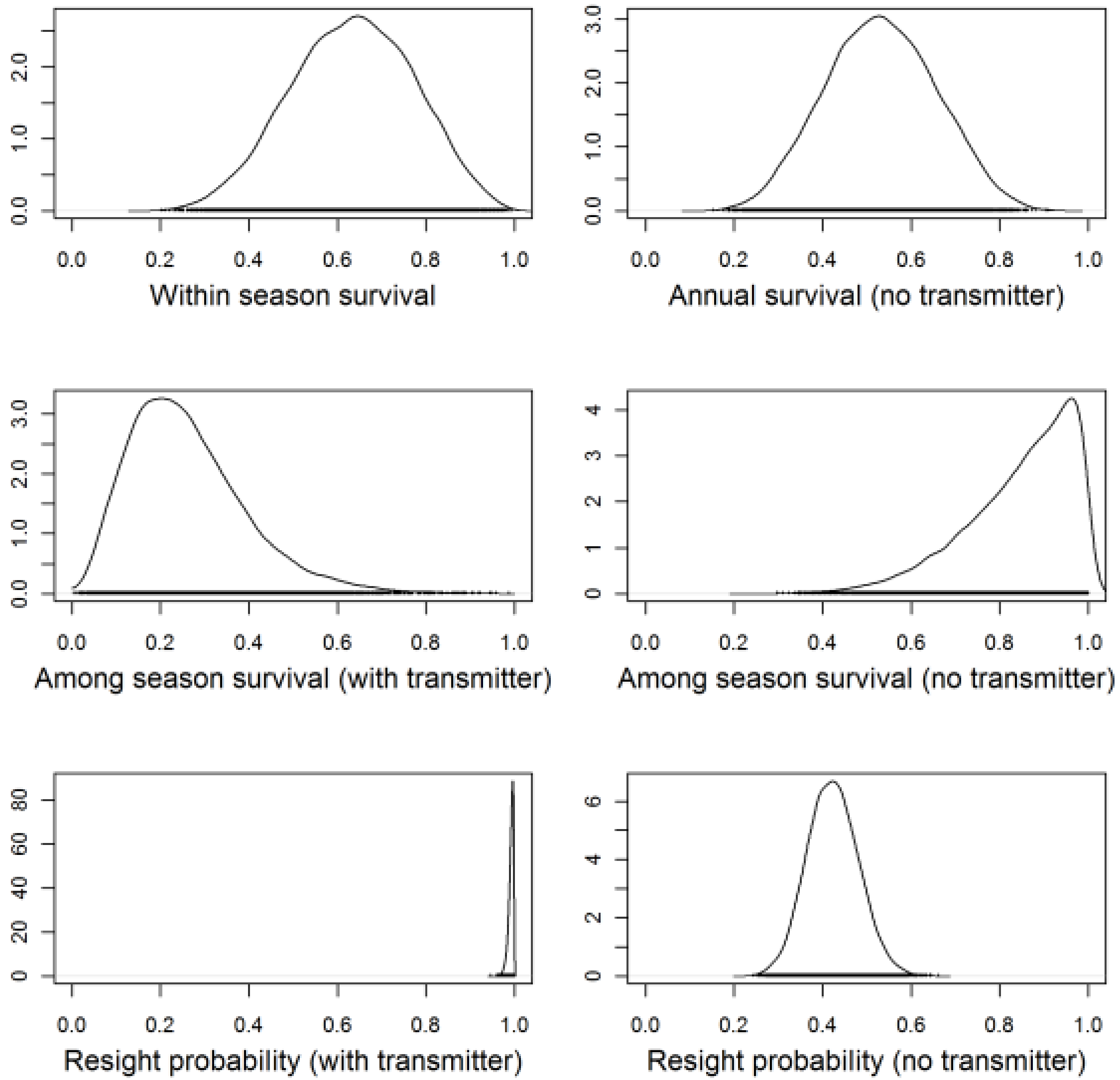

Figure 5.2. Posterior distributions for golden-winged warbler survival and detection probability parameters. All survival estimates are apparent survival. Within season apparent survival refers to the stationary non-breeding season. Among season apparent survival is for the interval 15 April – 10 October, which includes spring and fall migration as well as the breeding season. Data are from the Cordillera de Tilarán, Costa Rica, 2006-2010.

Figure 5.3. Striped palm-pitviper (*Bothriechis lateralis*) digesting a jeuvenile male golden-winged warbler (large bulge) with functioning radio transmitter. *B. lateralis* were regularly encountered in secondary forest such as this (see Figure 5.2). The tree species is "tubú" (*Montanoa guatemalensis*). Photograph by author, from the Cordillera de Tilarán, Costa Rica.

Figure 5.4. Location of golden-winged warbler mortality (yellow box). The habitat was 18-year old secondary forest resulting from pasture abandonment. Photograph by author, from the Cordillera de Tilarán, Costa Rica.

APPENDIX A

SPECIES LIST FOR STUDY AREA

			Relative abundance[a]		
			Life zone[b]		
Common name	Scientific name	Family	PM	MW	PW
Highland Tinamou	*Nothocercus bonapartei*	Tinamidae		R	R
Gray-headed Chachalaca	*Ortalis cinereiceps*	Cracidae	U	U	
Black Guan	*Chamaepetes unicolor*	Cracidae		C	
Crested Guan	*Penelope purpurascens*	Cracidae		R	R
Magnificent Frigatebird	*Fregata magnificens*	Fregatidae	O		
Cattle Egret	*Bubulcus ibis*	Ardeidae	O		
Great Blue Heron	*Ardea herodias*	Ardeidae	O		
Great Egret	*Ardea albus*	Ardeidae	O		
Black Vulture	*Coragyps atratus*	Cathartidae	C	C	C
Turkey Vulture	*Cathartes aura*	Cathartidae	C	C	C
King Vulture	*Sarcoramphus papa*	Cathartidae		O	
Great Black-Hawk	*Buteogallus urubitinga*	Accipitridae		R	
Swallow-tailed Kite	*Elanoides forficatus*	Accipitridae	C	U	
Black Hawk-Eagle	*Spizaethus tyrannus*	Accipitridae		R	
Ornate Hawk-Eagle	*Spizaethus ornatus*	Accipitridae		R	R
Red-tailed Hawk	*Buteo jamaicensis*	Accipitridae	U	U	
White-tailed Kite	*Elanus leucurus*	Accipitridae	R		
Sharp-shinned Hawk	*Accipiter striatus*	Accipitridae	R		
Cooper's Hawk	*Accipiter cooperii*	Accipitridae	R		
Gray Hawk	*Buteo nitidus*	Accipitridae	U		
White Hawk	*Leucopternis albicollis*	Accipitridae	U	U	U
Zone-tailed Hawk	*Buteo albonotatus*	Accipitridae	R		
Bicolored Hawk	*Accipiter bicolor*	Accipitridae		R	
Double-toothed Kite	*Harpagus bidentatus*	Accipitridae		R	
Barred Hawk	*Leucopternis princeps*	Accipitridae		O	R
Solitary Eagle	*Harpyhaliaetus solitarius*	Accipitridae		O	
Hook-billed Kite	*Chondrohierax uncinatus*	Accipitridae	O		
Tiny Hawk	*Accipiter supercilosus*	Accipitridae		O	

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Bat Falcon	*Falco rufigularis*	Falconidae		R	
Lauging Falcon	*Herpetotheres cachinnans*	Falconidae	U		
Barred Forest-Falcon	*Micrastur ruficolis*	Falconidae	U	R	R
Collared Forest-Falcon	*Micrastur semitorquatus*	Falconidae		U	
American Kestrel	*Falco sparverius*	Falconidae	O		
Peregrine Falcon	*Falco peregrinus*	Falconidae		O	
Crested Caracara	*Caracara cheriway*	Falconidae	O		
Gray-necked Wood-Rail	*Aramides cajanea*	Rallidae	U	C	
White-throated Crake	*Laterallus albigularis*	Rallidae	U	U	
Sunbittern	*Eurypyga helias*	Eurypygidae	R		
Spotted Sandpiper	*Actitis macularius*	Scolopacidae		U	
White-fronted Parrot	*Amazona albifrons*	Psittacidae	C	U	
Orange-chinned Parakeet	*Brotogeris jugularis*	Psittacidae	C	U	
Brown-hooded Parrot	*Pionopsitta haematotis*	Psittacidae		O	
Crimson-fronted Parakeet	*Aratinga finschi*	Psittacidae			O
Red-lored Parrot	*Amazona autumnalis*	Psittacidae	O	R	
White-crowned Parrot	*Pionus senilis*	Psittacidae		O	
Red-fronted Parrotlet	*Touit costaricensis*	Psittacidae		R	
Squirrel Cuckoo	*Piaya cayana*	Cuculidae	U	U	
Groove-billed Ani	*Crotophaga sulcirostris*	Cuculidae	C	U	
Lesser Ground-Cuckoo	*Morococcyx erythropygus*	Cuculidae	O		
Spectacled Owl	*Pulsatrix perpicillata*	Strigidae		R	R
Mottled Owl	*Ciccaba virgata*	Strigidae	U	U	
Ferruginous Pygmy-Owl	*Glaucidium brasilianum*	Strigidae		O	
Vermiculated Screech-Owl	*Otus guatemalae*	Strigidae		O	
Common Pauraque	*Nyctidromus albicollis*	Caprimulgidae	C	C	
Short-tailed Nighthawk	*Nyctidphrynus ocellarus*	Caprimulgidae		R	
White-collared Swift	*Streptoprocne zonaris*	Apodidae	C	C	
Vaux's Swift	*Chaetura vauxi*	Apodidae	U		
Purple-throated Mountain-gem	*Lampornis calolaema*	Trochilidae		C	
Stripe-throated Hermit	*Phaethornis striigularis*	Trochilidae	U	U	U
Green Hermit	*Phaethornis guy*	Trochilidae		C	C

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Canivet's Emerald	*Chlorostilbon canivetii*	Trochilidae	U		
Coppery-headed Emerald	*Elvira cupreiceps*	Trochilidae		C	
Striped-tailed Hummingbird	*Eupherusa eximia*	Trochilidae		C	
Violet Saberwing	*Campylopterus hemileucurus*	Trochilidae	U	U	
White-tipped Sicklebill	*Eutoxeres aquila*	Trochilidae		R	
Green-crowned Brilliant	*Heliodoxa jacula*	Trochilidae		U	R
Ruby-throated Hummingbird	*Archilochus colubris*	Trochilidae	R	R	
Steely-vented Hummingbird	*Amazilia saucerrottei*	Trochilidae	C	R	
Rufous-tailed Hummingbird	*Amazilia tzacatl*	Trochilidae	C	U	
White-bellied Mountain-gem	*Lampornis hemileucus*	Trochilidae		R	
Plain-capped Starthroat	*Heliomaster constantii*	Trochilidae	U	R	
Purple-crowned Fairy	*Heliothryx barroti*	Trochilidae		R	
Green Violet-ear	*Colibri thalassinus*	Trochilidae		O	
Magenta-throated Woodstar	*Calliphlox bryantae*	Trochilidae		R	
Violet-crowned Woodnymph	*Thalurania colombica*	Trochilidae			O
Green-fronted Lancebill	*Doryfera ludovicae*	Trochilidae			O
Orange-bellied Trogon	*Trogon aurantiiventris*	Trogonidae		C	U
Resplendent Quetzal	*Pharomachrus mocinno*	Trogonidae		U	
Slaty-tailed Trogon	*Trogon massena*	Trogonidae			O
Violaceous Trogon	*Trogon violaceus*	Trogonidae			O
Blue-crowned Motmot	*Momotus motmota*	Momotidae	C	U	
Turquoise-browed Motmot	*Eumomota superciliosa*	Momotidae	R		
Broad-billed Motmot	*Electron platyrhynchum*	Momotidae		O	
Rufous Motmot	*Baryphthengus martii*	Momotidae			R
Rufous-tailed Jacamar	*Galbula ruficauda*	Galbulidae		U	R
Black-thighed Grosbeak	*Caryothraustes poliogaster*	Cardnalidae			U
Rose-breasted Grosbeak	*Pheucticus ludovicianus*	Cardnalidae	C	R	
Indigo Bunting	*Passerina cyanea*	Cardnalidae	O		

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Buff-throated Saltator	*Saltator maximus*	Cardnalidae	C	C	
Grayish Saltator	*Saltator coerulescens*	Cardnalidae	R		
Painted Bunting	*Passerina ciris*	Cardnalidae	O		
American Dipper	*Cinclus mexicanus*	Cinclidae		U	U
Band-tailed Pigeon	*Columba fasciata*	Columbidae		U	U
Ruddy Pigeon	*Patagioenas subvinacea*	Columbidae		U	U
Short-billed Pigeon	*Patagioenas nigrirostris*	Columbidae		U	U
White-tipped Dove	*Leptotila verreaux*	Columbidae	C	C	
Red-billed Pigeon	*Columba flavirostris*	Columbidae	C	U	
Inca Dove	*Columbina inca*	Columbidae	U		
Common Ground-Dove	*Columbina passerina*	Columbidae	U		
Buff-fronted Quail-Dove	*Geotrygon costaricensis*	Columbidae		O	
Chiriqui Quail-Dove	*Geotrygon chiriquensis*	Columbidae		O	
Violaceous Quail-Dove	*Geotrygon violacea*	Columbidae		O	
Ruddy Quail-Dove	*Geotrygon montana*	Columbidae		O	
White-winged Dove	*Zenaida asiatica*	Columbidae	O		
Brown Jay	*Cyanocorax morio*	Corvidae	C	C	
Azure-hooded Jay	*Cyanolyca cucullata*	Corvidae		U	
White-throated Magpie-Jay	*Calocitta formosa*	Corvidae	U		
Three-wattled Bellbird	*Procnias tricarunculata*	Cotingidae		U	
Bare-necked Umbrellabird	*Cephalopterus glabricollis*	Cotingidae			O
Rufous Piha	*Lipaugus unirufus*	Cotingidae		O	
Yellow-faced Grassquit	*Tiaris olivacea*	Emberizidae	C	C	
Rufous-collared Sparrow	*Zonotrichia capensis*	Emberizidae	C	U	
White-naped Brush-Finch	*Atlapetes albinucha*	Emberizidae	C	U	
Blue-black Grassquit	*Volatinia jacarina*	Emberizidae	U	U	
White-collared Seedeater	*Sporophila torqueola*	Emberizidae	U	U	
Variable Seedeater	*Sporophila aurita*	Emberizidae	U	U	
Chestnut-capped Brush-Finch	*Buarremon brunneinucha*	Emberizidae		U	
White-eared Ground-Sparrow	*Melozone leucotis*	Emberizidae	C		
Thick-billed Seed-Finch	*Oryzoborus funereus*	Emberizidae		O	

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Blue Seedeather	*Amaurospiza concolor*	Emberizidae		O	
Orange-billed Sparrow	*Arremon aurantiirostris*	Emberizidae			R
Sooty-faced Finch	*Lysurus crassirostris*	Emberizidae		C	
Peg-billed Finch	*Acanthidops bairdii*	Emberizidae		R	
Slaty Flowerpiercer	*Diglossa plumbea*	Emberizidae		O	
Olive Sparrow	*Arremonops rufivigatus*	Emberizidae	O		
Prevost's Ground Sparrow	*Melozone biarcuata*	Emberizidae	O		
Scaled Antpitta	*Grallaria guatimalensis*	Formicariidae		O	
Black-headed Antthrush	*Formicarius nigricapillus*	Formicariidae			R
Ochre-breasted Antpitta	*Grallaricula flavirostris*	Formicariidae		O	
Golden-browed Chlorophonia	*Chlorophonia callophrys*	Fringillidae		U	
Yellow-throated Euphonia	*Euphonia hirundinacea*	Fringillidae	C	U	
Tawny-capped Euphonia	*Euphonia annaeae*	Fringillidae		U	
Elegant Euphonia	*Euphonia elegantissima*	Fringillidae		O	
Lesser Goldfinch	*Carduelis psaltria*	Fringillidae	U		
Spotted Woodcreeper	*Xiphorhynchus flavigaster*	Furnariidae		C	
Olivaceous Woodcreeper	*Sittasomus griseicapillus*	Furnariidae	R		
Wedge-billed Woodcreeper	*Glyphorhynchus spirurus*	Furnariidae		U	
Ruddy Woodcreeper	*Dendrocincla homochroa*	Furnariidae	U	U	
Barred Woodcreeper	*Dendrocolaptes certhia*	Furnariidae	O		
Streaked-headed Woodcreeper	*Lepidocolaptes souleyetii*	Furnariidae	U	R	
Brown-billed Scythebill	*Campylorhmphus pusillus*	Furnariidae		R	R
Cocoa Woodcreeper	*Xiphorhynchus susurrans*	Furnariidae	O		
Plain-brown Woodcreeper	*Dendrocincla fulginosa*	Furnariidae			R
Ruddy Treerunner	*Margarornis rubiginosus*	Furnariidae		R	

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Spotted Barbtail	*Premnoplex brunnesscens*	Furnariidae		C	
Striped Woodhaunter	*Hyloctistes subulatus*	Furnariidae			O
Tawny-throated Leaftosser	*Sclerurus mexicanus*	Furnariidae		U	
Gray-throated Leaftosser	*Sclerurus albigularis*	Furnariidae		R	R
Plain Xenops	*Xenops minutus*	Furnariidae			O
Red-faced Spinetail	*Cranioleuca erythrops*	Furnariidae		R	
Buff-fronted Foliage-gleaner	*Automolus ochrolaemus*	Furnariidae		R	R
Buffy Tuftedcheek	*Pseudocolaptes lawrencii*	Furnariidae		O	
Linneated Foliage-gleaner	*Syndactyla subalaris*	Furnariidae		R	
Blue-and-white Swallow	*Tachycineta thalassina*	Hirundinidae	C		
Northern Rough-winged Swallow	*Stelgidopteryx serripennis*	Hirundinidae	U		
Montexuma Orpendola	*Psarocolius montezuma*	Icteridae	C	C	
Chestnut-headed Oropendola	*Psarocolius wagleri*	Icteridae	R	R	
Yellow-billed Cacique	*Amblycercus holosericeus*	Icteridae	R		
Eastern Meadowlark	*Sturnella magna*	Icteridae	U		
Baltimore Oriole	*Icterus galbula*	Icteridae	C	U	
Bronzed Cowbird	*Molothrus aeneus*	Icteridae	R		
Melodious Blackbird	*Dives dives*	Icteridae	C	U	
Black-cowled Oriole	*Icterus dominicensis*	Icteridae		R	
Great-tailed Grackle	*Quiscalus mexicanus*	Icteridae	C		
Orchard Oriole	*Icterus spurius*	Icteridae	O		
Sharpbill	*Oxyruncus cristatus*	Oxyruncidae		O	R
Black-and-white Warbler	*Mniotilta varia*	Parulidae	U	U	U
Yellow Warbler	*Dendroica petechia*	Parulidae	U		
Slate-throated Redstart	*Myioborus miniatus*	Parulidae	U	C	U
Northern Waterthrush	*Seiurus noveboracensis*	Parulidae		U	
Three-striped Warbler	*Basileuterus tristriatus*	Parulidae		C	
Wilson's Warbler	*Wilsonia pusilla*	Parulidae	C	C	U
Chestnut-sided Warbler	*Dendroica pensylvanica*	Parulidae	C	C	
Black-throated Green Warbler	*Dendroica virens*	Parulidae	R	C	

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Rufous-capped Warbler	*Basileuterus rufifrons*	Parulidae	C	R	
Golden-winged Warbler	*Vermivora chrysoptera*	Parulidae	O	U	R
Mourning Warbler	*Oporornis philadelphia*	Parulidae	O		
Golden-crowned Warbler	*Basileuterus culicivorus*	Parulidae	R	C	U
Louisiana Waterthrush	*Seiurus motacilla*	Parulidae		O	
Gray-crowned Yellowthroat	*Geothlypis poliocephala*	Parulidae	U		
Ovenbird	*Seiurus aurocapillus*	Parulidae	U	R	
Tennessee Warbler	*Vermivora peregrina*	Parulidae	C	U	U
Buff-rumped Warbler	*Phaeothlypis fulvicauda*	Parulidae			U
Collared Redstart	*Myioborus torquatus*	Parulidae		U	
Townsend's Warbler	*Dendroica townsendi*	Parulidae		R	
Tropical Parula	*Parula pitiayumi*	Parulidae		R	U
Blackburnian Warbler	*Dendroica fusca*	Parulidae		O	
Yellow-rumped Warbler	*Dendroica coronata*	Parulidae			O
Kentucky Warbler	*Oporornis formosus*	Parulidae		O	
MacGillivray's Warbler	*Oporornis tolmiei*	Parulidae	O		
American Redstart	*Stetophaga ruticillia*	Parulidae	O	O	
Canada Warbler	*Wilsonia canadensis*	Parulidae		O	
Wrenthrush	*Zeledonia coronata*	Parulidae		R	
Blue-winged Warbler	*Vermivora pinus*	Parulidae		O	
Worm-eating Warbler	*Helmitheros vermivorum*	Parulidae		O	
Black-breasted Wood-Quail	*Odontophorus leucolaemus*	Phasianidae		U	R
Pale-billed Woodpecker	*Campephilus guatemalensis*	Picidae	R	R	
Golden-olive Woodpecker	*Piculus rubiginosus*	Picidae		U	
Hoffman's Woodpecker	*Melanerpes hoffmannii*	Picidae	C	U	
Lineated Woodpecker	*Dryocopus lineatus*	Picidae	R	R	
Black-cheeked Woodpecker	*Melanerpes pucherani*	Picidae			R
Smoky-brown Woodpecker	*Veniliornis fumigatus*	Picidae		U	
Rufous-winged Woodpecker	*Piculus simplex*	Picidae			O
Yellow-bellied Sapsucker	*Sphyrapicus varius*	Picidae		O	

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White-ruffled Manakin	*Corapipo leucorrhoa*	Pipridae		U	U
Long-tailed Manakin	*Chiroxiphia linearis*	Pipridae	C	U	
White-collared Manakin	*Manacus candei*	Pipridae		O	
Least Grebe	*Tachybaptus dominicus*	Podicipedidae	R		R
Black-and-yellow Silky-Flycatcher	*Phainoptila melanoxantha*	Ptilogonatidae		R	
Prong-billed Barbet	*Semnornis frantzii*	Ramphastidae		U	
Red-headed Barbet	*Eubucco bourcierii*	Ramphastidae		R	R
Emerald Toucanet	*Aulacorhynchus prasinus*	Ramphastidae	U	U	U
Collared Araçari	*Pteroglossus torquatus*	Ramphastidae			R
Keel-billed Toucan	*Ramphastos sulfuratus*	Ramphastidae	U	U	U
Silvery-fronted Tapaculo	*Scytalopus argentifrons*	Rhinocryptidae		C	U
Tawny-faced Gnatwren	*Microbates cinereiventris*	Sylviidae			R
Long-billed Gnatwren	*Ramphocaenus melanurus*	Sylviidae		R	
Immaculate Antbird	*Myrmeciza immaculata*	Thamnophilidae		C	
Bicolored Antbird	*Gymnopithys leucaspis*	Thamnophilidae		O	
Ocellated Antbird	*Phaenostictus mcleannani*	Thamnophilidae			R
Slaty Antwren	*Myrmotherula schisticolor*	Thamnophilidae		U	U
Plain Antvireo	*Dysithamnus mentalis*	Thamnophilidae		U	U
Barred Antshrike	*Thamnophilus doliatus*	Thamnophilidae	R		
Russet Antshrike	*Thamnistes anabatinus*	Thamnophilidae			R
Dull-mantled Antbird	*Myrmeciza laemosticta*	Thamnophilidae			U
Scarlet-rumped Tanager	*Ramphocelus passerinii*	Thraupidae	C	U	
Summer Tanager	*Piranga rubra*	Thraupidae	U	U	
Silver-throated Tanager	*Tangara icterocephala*	Thraupidae		U	U
Spangled-cheeked Tanager	*Tangara dowii*	Thraupidae		U	R
Red-legged Honeycreeper	*Cyanerpes cyaneus*	Thraupidae	R		
Green Honeycreeper	*Chlorophanes spiza*	Thraupidae			O
Scarlet-thighed Dacnis	*Dacnis venusta*	Thraupidae		U	
Crimson-collared Tanager	*Phlogothraupis sanguinolenta*	Thraupidae	O	U	U
Blue-gray Tanager	*Thraupis episcopus*	Thraupidae	C	C	

Continues on the next page

Common Bush-Tanager	*Chlorospingus ophthalmicus*	Thraupidae		C	C
Palm Tanager	*Thraupis palmarum*	Thraupidae	R		
Bay-headed Tanager	*Tangara gyrola*	Thraupidae		R	
Black-and-yellow Tanager	*Chrysothlypis chrysomelas*	Thraupidae			R
Blue-and-gold Tanager	*Buthraupis arcaei*	Thraupidae			R
White-lined Tanager	*Tachyphonus rufus*	Thraupidae		O	
Hepatic Tanager	*Piranga flava*	Thraupidae			R
Scarlet Tanager	*Piranga olivacea*	Thraupidae		O	
Blue Dacnis	*Dacnis cayana*	Thraupidae			R
Sooty-capped Bush-Tanager	*Chlorospingus pileatus*	Thraupidae		R	
Olive Tanager	*Chlorothraupis carmioli*	Thraupidae			O
Emerald Tanager	*Tangara florida*	Thraupidae			O
White-throated Shrike-Tanager	*Lanio leucothorax*	Thraupidae			O
Red-crowned Ant-tanager	*Habia rubica*	Thraupidae	R		
Masked Tityra	*Tityra semifasciata*	Tityridae	U	U	
Rose-throated Becard	*Pachyramphus aglaiae*	Tityridae	O		
House Wren	*Troglodytes aedon*	Troglodytidae	C	C	
Rufous-breasted Wren	*Thryothorus rutilus*	Troglodytidae	R		
Rufous-and-white Wren	*Thryothorus rufalbus*	Troglodytidae	C	R	
Gray-breasted Wood-Wren	*Henicorhina leucophrys*	Troglodytidae		C	
White-breasted Wood-Wren	*Henicorhina leucosticta*	Troglodytidae			C
Plain Wren	*Thryothorus modestus*	Troglodytidae	C	U	
Ochraceous Wren	*Troglodytes ochraceus*	Troglodytidae		U	
Nightingale Wren	*Microcerculus philomela*	Troglodytidae			R
Rufous-naped Wren	*Campylorhynchus*	Troglodytidae	O		
Pale-vented Robin	*Turdus obsoletus*	Turdidae		U	U
White-throated Robin	*Turdus assimilus*	Turdidae		R	
Slaty-backed Nightingale-Thrush	*Catharus fuscater*	Turdidae		C	
Orange-billed Nightingale-Thrush	*Catharus aurantiirostris*	Turdidae	C	U	
Swainson's Thrush	*Catharus ustulatus*	Turdidae		U	

Continues on the next page

Black-headed Nightingale-Thrush	*Catharus mexicanus*	Turdidae			R
Ruddy-capped Nightingale-Thrush	*Catharus frantzii*	Turdidae		O	
Mountain Robin	*Turdus plebejus*	Turdidae		R	
Wood Thrush	*Hylocichla mustelina*	Turdidae		R	U
Black-headed Solitare	*Myadestes melanops*	Turdidae		C	U
Clay-colored Robin	*Turdus grayi*	Turdidae	C	U	
Bright-rumped Attila	*Attila spadiceus*	Tyrannidae		U	
Golden-bellied Flycatcher	*Myiodynastes hemichrysus*	Tyrannidae		R	
Streaked Flycatcher	*Myiodynastes maculatus*	Tyrannidae		O	
Sulphur-bellied Flycatcher	*Myiodynastes luteiventris*	Tyrannidae		O	
Yellowish Flycatcher	*Empidonax flavescens*	Tyrannidae		U	
Dusky-capped Flycatcher	*Myiarchus tuberculifer*	Tyrannidae	C	C	
Great-creasted Flycatcher	*Myiarchus crinitus*	Tyrannidae		O	
Tropical Pewee	*Contopus cinereus*	Tyrannidae		R	
Common Tody-Flycatcher	*Todirostrum cinereum*	Tyrannidae	U	U	
Mountain Elaenia	*Elaenia frantzii*	Tyrannidae		U	
Eye-ringed Flatbill	*Rhynchocyclus brevirostris*	Tyrannidae		U	
Black Pheobe	*Sayornis nigricans*	Tyrannidae	U	U	U
Scale-crested Pygmy-Tyrant	*Lophotriccus pileatus*	Tyrannidae		U	U
Mistletoe Tyrannulet	*Zimmerius vilissimus*	Tyrannidae		U	
Olive-striped Flycatcher	*Mionectes olivaceus*	Tyrannidae		C	U
Yellow-bellied Flycatcher	*Empidonax flaviventris*	Tyrannidae	R	R	
White-throated Spadebill	*Platyrinchus mystaceus*	Tyrannidae		U	R
Tropical Kingbird	*Tyrannus melancholicus*	Tyrannidae	C	C	
Social Flycatcher	*Myiozetetes similis*	Tyrannidae	C	R	
Great Kiskadee	*Pitangus sulphuratus*	Tyrannidae	C	U	
Boat-billed Flycatcher	*Megarhynchus pitangua*	Tyrannidae		U	
Yellow-bellied Elaenia	*Elaenia flavogaster*	Tyrannidae	U	R	

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Ochre-belled Flycatcher	*Mionectes oleagineus*	Tyrannidae		R	
Slaty-capped Flycatcher	*Leptopogon oleagineus*	Tyrannidae		R	
Tufted Flycatcher	*Mitrephanes phaeocercus*	Tyrannidae		U	
Western Wood-pewee	*Contopus sordidulus*	Tyrannidae		O	
White-throated Flycatcher	*Empidonax albigularis*	Tyrannidae		O	
Olive-sided Flycatcher	*Contopus cooperi*	Tyrannidae		O	
Sepia-capped Flycatcher	*Leptopogon amaurocephalus*	Tyrannidae			O
Rough-legged Tyrannulet	*Phyllomyias burmeisteri*	Tyrannidae		O	
Nutting's Flycatcher	*Myiarchus nuttingi*	Tyrannidae	O		
Least Flycatcher	*Empidonax minimus*	Tyrannidae	O		
Sulphur-rumped Flycatcher	*Myiobius sulphureipygius*	Tyrannidae			O
Torrent Tyrannulet	*Serpophaga cinerea*	Tyrannidae			R
Rufous-browed Tyrannulet	*Phylloscartes superciliaris*	Tyrannidae			O
Brown-crested Flycatcher	*Myiarchus tyrannulus*	Tyrannidae	O		
Bananaquit	*Coereba flaveola*	Uncertain		U	C
Cinnamon Becard	*Pachyramphus cinnamomeus*	Uncertain			R
Gray-headed Piprites	*Piprites griseiceps*	Uncertain			R
Philadelphia Vireo	*Vireo philadelphicus*	Vireonidae		U	
Lesser Greenlet	*Hylophilus decurtatus*	Vireonidae		R	
Yellow-throated Vireo	*Vireo flavifrons*	Vireonidae		R	
Brown-capped Vireo	*Vireo leucophrys*	Vireonidae		R	R
Rufous-browed Peppershrike	*Cyclarhis gujanensis*	Vireonidae	R		
Blue-headed Vireo	*Vireo solitarius*	Vireonidae		O	

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[a] These are subjective categories based upon species lists maintained at Costa Rican field stations run by the Organization for Tropical Studies. O = occasional, not likely to be found in appropriate habitat, R = rare, found sporadically in appropriate habitat, U = uncommon, occurring at low abundances in appropriate habitat, C = common, often encountered in appropriate habitat.

[b] PM = premontane moist, 700-900m on the Pacific slope, MW = montane wet, above 1100 m on both slopes, PW = premontane wet, below 900 m on Caribbean slope. Intermediate elevations are transition zones.

APPENDIX B

LIST OF GOLDEN-WINGED WARBLERS, BLUE-WINGED WARBLERS, AND THEIR HYBIRDS ENCOUNTERED BETWEEN 2006-2010 IN THE CORDILLERA DE TILARÁN, COSTA RICA

Species	Date	Sex	Habitat[a]	Longitude[b]	Latitude[b]	Elev. (m)
Vermivora chrysoptera	20-Nov-06	M	SF	84.67577	10.20401	1073
Vermivora chrysoptera	16-Dec-06	F	SF	84.67768	10.23513	1216
Vermivora chrysoptera	16-Dec-06	M	SF	84.67374	10.23640	1043
Vermivora chrysoptera	31-Dec-06	M	SF	84.67643	10.20508	1215
Vermivora chrysoptera	23-Jan-07	M	PF	84.67409	10.23650	1076
Vermivora chrysoptera	1-Feb-07	M	SF	84.67302	10.23316	1120
Vermivora chrysoptera	6-Feb-07	M	RI	84.68588	10.23935	1076
Vermivora chrysoptera	9-Feb-07	F	SF	84.68850	10.24873	1200
Vermivora chrysoptera	16-Feb-07	M	PF	84.70473	10.25148	1450
Vermivora chrysoptera	23-Feb-07	M	RI	84.68505	10.23884	1018
Vermivora chrysoptera	24-Feb-07	M	SF	84.69559	10.25501	1395
Vermivora chrysoptera	1-Mar-07	M	PF	84.69254	10.21014	1287
Vermivora chrysoptera	2-Mar-07	M	PF	84.70462	10.25728	1464
Vermivora chrysoptera	2-Mar-07	M	SF	84.69396	10.21075	1232
Vermivora chrysoptera	16-Mar-07	M	SF	84.68350	10.20601	1142
Vermivora chrysoptera	16-Mar-07	M	SF	84.67254	10.20076	1269
Vermivora chrysoptera	8-Oct-07	M	SF	84.67457	10.20689	1171
Vermivora chrysoptera	15-Oct-07	M	SF	84.69555	10.25412	1381
Vermivora chrysoptera	19-Oct-07	M	SF	84.67459	10.20386	1235
Vermivora chrysoptera	19-Oct-07	F	SF	84.69254	10.21014	1287
Vermivora chrysoptera	23-Oct-07	F	SF	84.67332	10.20399	1229
Vermivora chrysoptera	23-Oct-07	M	SF	84.69504	10.25412	1363
Vermivora chrysoptera	6-Nov-07	M	PF	84.64643	10.21529	1174
Vermivora chrysoptera	8-Nov-07	M	ND	84.67938	10.20944	1075
Vermivora chrysoptera	11-Nov-07	M	PF	84.67061	10.20195	1286
Vermivora chrysoptera	21-Nov-07	M	SF	84.69965	10.24986	1453
Vermivora chrysoptera	23-Nov-07	M	RI	84.69157	10.25889	1309
Vermivora chrysoptera	24-Nov-07	M	SF	84.67938	10.19224	1408
Vermivora chrysoptera	30-Nov-07	M	PF	84.64975	10.27568	1257
Vermivora chrysoptera	1-Dec-07	F	RI	84.64621	10.26470	1031
Vermivora chrysoptera	6-Dec-07	M	SF	84.69659	10.26105	1412
Vermivora chrysoptera	7-Dec-07	F	PF	84.68098	10.24969	1112
Vermivora chrysoptera	10-Dec-07	M	PF	84.65565	10.23947	1268

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Vermivora chrysoptera	14-Dec-07	M	PF	84.64634	10.24534	1074
Vermivora chrysoptera	18-Jan-08	M	SF	84.68986	10.26320	1313
Vermivora chrysoptera	18-Jan-08	M	SF	84.69447	10.25525	1364
Vermivora chrysoptera	19-Jan-08	M	SF	84.66349	10.22059	1174
Vermivora chrysoptera	25-Jan-08	M	PF	84.64247	10.21315	1076
Vermivora chrysoptera	26-Jan-08	M	ND	84.68799	10.20084	1263
Vermivora chrysoptera	26-Jan-08	M	SF	84.68870	10.20949	1201
Vermivora chrysoptera	28-Jan-08	M	SF	84.67199	10.21047	1059
Vermivora chrysoptera	30-Jan-08	M	RI	84.67163	10.20796	1129
Vermivora chrysoptera	31-Jan-08	F	SF	84.67123	10.20975	1101
Vermivora chrysoptera	8-Feb-08	M	SF	84.66796	10.20477	1258
Vermivora chrysoptera	13-Feb-08	F	RI	84.68869	10.23547	1115
Vermivora chrysoptera	13-Feb-08	F	SF	84.66795	10.20452	1297
Vermivora chrysoptera	26-Feb-08	M	SF	84.69060	10.21094	1218
Vermivora chrysoptera	27-Feb-08	M	RI	84.68904	10.23538	1127
Vermivora chrysoptera	5-Mar-08	M	PF	84.67103	10.22611	1090
Vermivora chrysoptera	13-Mar-08	F	SF	84.67943	10.22521	922
Vermivora chrysoptera	18-Mar-08	M	SF	84.66912	10.20441	1269
Vermivora chrysoptera	19-Mar-08	M	SF	84.67836	10.22804	955
Vermivora chrysoptera	12-Jan-09	M	PF	84.67049	10.20173	1289
Vermivora chrysoptera	13-Jan-09	M	ND	84.68890	10.20954	1179
Vermivora chrysoptera	13-Jan-09	M	SF	84.69447	10.21026	1236
Vermivora chrysoptera	13-Jan-09	M	AF	84.68098	10.21318	1019
Vermivora chrysoptera	13-Jan-09	M	SF	84.68144	10.20637	1113
Vermivora chrysoptera	15-Jan-09	F	SF	84.68717	10.23860	1050
Vermivora chrysoptera	17-Jan-09	M	RI	84.66859	10.21555	1003
Vermivora chrysoptera	17-Jan-09	M	SF	84.66904	10.21752	999
Vermivora chrysoptera	17-Jan-09	M	SF	84.66859	10.21555	1003
Vermivora chrysoptera	19-Jan-09	M	SF	84.64973	10.23165	1127
Vermivora chrysoptera	21-Jan-09	M	SF	84.67210	10.21167	1123
Vermivora chrysoptera	23-Jan-09	M	SF	84.68483	10.20442	1140
Vermivora chrysoptera	24-Jan-09	M	SF	84.66996	10.22930	1142
Vermivora chrysoptera	24-Jan-09	M	SF	84.66946	10.22405	1140
Vermivora chrysoptera	30-Jan-09	M	PF	84.69675	10.26171	1483
Vermivora chrysoptera	30-Jan-09	M	ND	84.68373	10.25327	1174
Vermivora chrysoptera	30-Jan-09	M	PF	84.69453	10.25891	1384
Vermivora chrysoptera	7-Feb-09	M	SF	84.68459	10.20461	1146
Vermivora chrysoptera	12-Feb-09	M	PF	84.68110	10.25271	1196
Vermivora chrysoptera	16-Feb-09	M	ND	84.67101	10.22814	1016
Vermivora chrysoptera	17-Feb-09	M	SF	84.66898	10.22583	1144

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Vermivora chrysoptera	19-Feb-09	M	SF	84.69305	10.25844	1347
Vermivora chrysoptera	20-Feb-09	M	ND	84.62715	10.23032	743
Vermivora chrysoptera	24-Feb-09	F	ND	84.68880	10.23549	1131
Vermivora chrysoptera	24-Feb-09	M	SF	84.66102	10.21635	1222
Vermivora chrysoptera	4-Mar-09	M	PF	84.68539	10.25583	1193
Vermivora chrysoptera	6-Mar-09	M	AF	84.69262	10.23931	1191
Vermivora chrysoptera	6-Mar-09	M	SF	84.70614	10.24621	1517
Vermivora chrysoptera	7-Mar-09	M	AF	84.68890	10.22970	1007
Vermivora chrysoptera	7-Mar-09	M	PF	84.66593	10.22356	1229
Vermivora chrysoptera	9-Mar-09	M	ND	84.68655	10.25710	1195
Vermivora chrysoptera	10-Mar-09	M	ND	84.68819	10.20085	1249
Vermivora chrysoptera	11-Mar-09	M	AF	84.68013	10.23933	987
Vermivora chrysoptera	12-Mar-09	M	ND	84.62859	10.22012	792
Vermivora chrysoptera	14-Mar-09	M	ND	84.66401	10.21113	1252
Vermivora chrysoptera	17-Mar-09	M	SF	84.69548	10.25531	1390
Vermivora chrysoptera	19-Mar-09	M	PF	84.66640	10.22879	1199
Vermivora chrysoptera	21-Mar-09	M	SF	84.65650	10.21567	1159
Vermivora chrysoptera	8-Jan-10	M	SF	84.67445	10.20399	1228
Vermivora chrysoptera	8-Jan-10	M	PF	84.66197	10.20002	1425
Vermivora chrysoptera	12-Jan-10	M	SF	84.66405	10.22169	1202
Vermivora chrysoptera	14-Jan-10	M	PF	84.63169	10.22410	823
Vermivora chrysoptera	19-Jan-10	M	SF	84.68464	10.24883	1180
Vermivora chrysoptera	29-Jan-10	M	SF	84.68234	10.24401	1095
Vermivora chrysoptera	1-Feb-10	M	SF	84.63732	10.23780	926
Vermivora chrysoptera	3-Feb-10	M	PF	84.68641	10.25663	1215
Vermivora chrysoptera	5-Feb-10	F	SF	84.68144	10.20637	1113
Vermivora chrysoptera	8-Feb-10	M	PF	84.62943	10.22594	786
Vermivora chrysoptera	10-Feb-10	F	SF	84.68242	10.24993	1079
Vermivora chrysoptera	10-Feb-10	M	SF	84.68444	10.25470	1149
Vermivora chrysoptera	10-Feb-10	F	SF	84.69068	10.25709	1273
Vermivora chrysoptera	11-Feb-10	M	PF	84.70566	10.25699	1477
Vermivora chrysoptera	15-Feb-10	M	SF	84.68928	10.20971	1220
Vermivora chrysoptera	15-Feb-10	M	SF	84.68253	10.21420	991
Vermivora chrysoptera	20-Feb-10	F	SF	84.67298	10.23367	1104
Vermivora chrysoptera	20-Feb-10	M	PF	84.63804	10.24053	842
Vermivora chrysoptera	22-Feb-10	M	AF	84.68574	10.24437	1134
Vermivora chrysoptera	24-Feb-10	M	PF	84.64857	10.25233	1096
Vermivora chrysoptera	27-Feb-10	F	AF	84.68578	10.22597	901
Vermivora chrysoptera	2-Mar-10	M	SF	84.66921	10.22483	1215
Vermivora chrysoptera	2-Mar-10	M	SF	84.68589	10.20331	1181

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Vermivora chrysoptera	10-Mar-10	F	SF	84.69967	10.20499	1416
Vermivora chrysoptera		F	SF	84.66831	10.21343	1080
Vermivora chrysoptera		F	SF	84.69475	10.25448	1350
Vermivora chrysoptera		F	RI	84.67768	10.23513	1006
Vermivora chrysoptera		F	SF	84.68850	10.24873	1200
Vermivora chrysoptera		F	SF	84.68350	10.20601	1142
Vermivora chrysoptera		M	SF	84.67577	10.20401	1230
Vermivora chrysoptera		M	RI	84.68588	10.23935	1076
Vermivora chrysoptera		M	RI	84.68044	10.21351	1014
Vermivora sp. [c]		M	SF	84.68350	10.20601	
Vermivora sp. [d]	15-Feb-10	M	SF	84.67161	10.20981	1149
Vermivora pinus	18-Mar-08	M	AF	84.67872	10.22592	930
Vermivora pinus	14-Feb-09	M	SF	84.66978	10.22174	1096

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[a] PF = primary forest, SF = secondary forest, RI = riverside forest, ND = naturally disturbed forest such as large canopy gaps, AF = agroforest such as shade coffee farm.

[b] Coordinates recorded in decimal degrees using a WGS84 datum.

[c] Lawrence’s type hybrid

[d] Brewster’s type hybrid

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