HOME RANGE SIZE AND HABITAT USE OF PREMONTANE RAINFORESTS BY LONG-TAILED MANAKINS (*CHIROXIPHIA LINEARIS*)

by

RYAN ANDREW MALLOY

(Under the Direction of Robert J. Cooper)

ABSTRACT

Although fragmentation is widely studied in birds, it is unclear exactly how Neotropical forest songbirds react to different levels of deforestation and habitat fragmentation. In the Upper San Luis valley in Costa Rica, there is a rich history of relatively small-scale human-dominated land use which has resulted in a landscape matrix of forest and various agricultural practices. This study assessed habitat use in a mixed-use landscape by a frugivorous forest songbird, the Long-tailed Manakin (*Chiroxiphia linearis*), at several spatial scales. Results showed that relative rank of habitat use differed by scale. In addition, results indicated that low-intensity cattle ranching, which makes use of forested hedgerows and windbreaks, may provide necessary habitat structure for some forest songbirds, such as the Long-tailed Manakin. However, there is likely to be a threshold for the amount of open habitat in a landscape that Long-tailed Manakins and other forest birds will tolerate.

INDEX WORDS: Long-tailed Manakin, Chiroxiphia linearis, habitat use, home range size, compositional analysis, low-intensity agriculture, Neotropics, Costa Rica

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DEDICATION

This thesis is dedicated to my family, for providing a good dose of laughter and humility, and whose continued support has allowed me to follow my dreams and fulfill my goals. And to my wife, Mia, who has always shared my love and interest in birds and life.

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INTRODUCTION, LITERATURE REVIEW, AND STUDY OVERVIEW

INTRODUCTION

Habitat loss is one of the primary reasons for population declines of species worldwide (Martinez-Morales 2005, Cayuela et al. 2006, Hale 2006). The dominant form of habitat loss, deforestation, is occurring in the Neotropics at an estimated rate of over 5 million hectares per year (Rainforest Alliance 2008). In Costa Rica, deforestation occurred at an annual loss of 4.2% during 1986-1991, with the majority of loss occurring in cloud forest ecosystems of the cordilleras (Sader and Joyce 1988, Sanchez-Azofeifa et al. 2001, Martinez-Morales 2005). The majority of cleared land has been subsequently converted into cattle pasture. While the Costa Rican government limits deforestation, there is an increasing trend toward converting both forest and small shade coffee plantations into pasture land. Shade coffee plantations are thought to act as suitable habitat for forest dwelling bird species (both residents and migrants), but how they do so is poorly understood (Greenberg et al. 1997, Tejeda-Cruz and Sutherland 2004, Sekercioglu et al. 2007). Within the Monteverde region of Costa Rica, the Long-tailed Manakin (*Chiroxiphia linearis*) resides almost exclusively within forested landscapes, although some Long-tailed Manakins will use shade coffee plantations, mostly making use of forested windbreaks (R.A. Malloy personal observation).

The Monteverde region of Costa Rica has extraordinary biodiversity (Haber 2000). With the majority of the planet’s species found in such a relatively small area, it is imperative that conservation measures be implemented for extant species before they are lost. The Monteverde cloud forest ecosystem contains over 3000 plant species, which provide a myriad of niches for many taxa, including birds (Haber 2000). Many of the 450 bird species that occupy these ecosystems can often be found utilizing shade coffee plantations. In San Luis, located approximately 200 meters down slope from the Monteverde region, a majority of the landscape is dominated by forest and mixed agricultural land cover classes. These land cover types provide refuge for hundreds of resident and migratory birds. Historically, San Luis has been known as a quiet agricultural community with families occupying small parcels of land used for subsistence farming. With a changing economy, many individuals are abandoning traditional farm-related work and seeking employment in ecotourism (in Monteverde). Within the nearby community of San Luis, most of the subsistence farms are still relatively small (1-2 hectares per farm); however, the pressure of converting agricultural plots to cattle pastures is being felt by a changing economy, as traditional agricultural practices are not being passed down to future generations. Located immediately down slope from Upper San Luis is Lower San Luis. Farms in Lower San Luis are larger and structurally more similar to many other cattle ranching operations throughout Costa Rica and other parts of Central America (Kricher 1999). If the higher intensity form of cattle ranching continues upslope from Lower San Luis to Upper San Luis, there could be a negative impact to forest birds, such as the Long-tailed Manakin. Daily et al. (2001) found that while forest birds may use human-dominated landscapes, they likely will not persist in those areas, especially with continued intensification of land use. This study aims to better understand how forest birds such as the Long-tailed Manakin are using low-intensity human-dominated landscapes, such as those found in Upper San Luis.

LITERATURE REVIEW

Historical and current land use of Costa Rica and Monteverde

Prior to European settlement (before 1500 AD), Costa Rica was inhabited by an indigenous population of approximately 80,000 (estimates range from 27,000 to 300,000) (Evans 1999). There were approximately nine loosely associate tribes that inhabited the country when Christopher Columbus arrived in 1502 AD. The tribes were described as hunter-gatherer and simple agrarian communities (Evans 1999). Three hundred years later, coffee was introduced to Costa Rica, as it was discovered that the climate and fertile soils were perfect for cultivating coffee. The introduction of banana and pineapple shortly followed, and led to a drastic change in Costa Rica's landscape (Evans 1999). Government incentives were given to land prospectors to convert forested areas into agriculturally productive landscapes (Evans 1999, Kricher 1999, Grau and Aide 2008). In the twentieth century, deforestation in Costa Rica resulted in a loss of over 60% of primary forests, with the highest rate of deforestation occurring during 1960 – 1980 (Sader and Joyce 1988). The intensification in deforestation coincided with a shift in land use from Pacific mountain slopes, after Pacific lowland forests were cleared, to Atlantic coast lowland forests. The delay between Pacific lowland forest conversion to agriculture and Atlantic lowland forest conversion to agriculture is thought be attributed to a higher degree of difficulty to access the Atlantic slope due to greater annual precipitation (Sader and Joyce 1988). Starting in the mid 1960s and early 1970s, Costa Rica started protecting natural areas from further deforestation (Rosero-Bixby and Palloni 1998, Evans 1999, Kricher 1999). Today > 25% of Costa Rica's land is protected in the form of national parks, biological preserves, wildlife refuges, protected zones, indigenous reserves, and other areas (Evans 1999).

Land use changes in Monteverde

Pottery shards and crops such as sugarcane, and cuadrado (a close relative of banana) are some of the only remnants of the indigenous inhabitants of the Monteverde area (Griffith et al. 2000). In the 1950s, a small Quaker community from the United States settled in Monteverde. Familiar with dairy farming, the Quakers were quick to help the dairy production increase in the Monteverde area. As dairy farming in the Monteverde area increased so did deforestation. Following deforestation, exotic pasture grasses were introduced, and East African grasses such as Kikuyu (*Pennisetum clandestinum*) and Eastern Star Grass (*Cynodon sp.*), became more and more common (Griffith et al. 2000). The dairy industry took an economic down-turn in the 1970s and did not recover on an national economic level until the 1990s (Griffith et al. 2000). The financial troubles associated with cattle ranching and dairy farming led some individuals to consider alternate uses for the landscape. Many turned to coffee. At first, coffee plants were grown in marginal habitat for cattle, usually restricted to the steeper slopes. Coffee soon spread throughout the Monteverde area as a supplemental crop for some, but increasingly a primary crop for others. By the mid-1980s there were approximately 60 coffee farms with about 60 – 90 ha of coffee (Griffith et al. 2000). Coffee was still slow to develop in this area because managing a successful coffee farm, even a small farm, requires more laborers than a small dairy farm. In 1989 a small coffee farming cooperative formed, and many of the labors associated with coffee farming were coordinated, streamlined, and completed through a group effort (Griffith et al. 2000). The shade coffee agroecosystem was put into practice in areas such as San Luis, where farmers typically had < 2ha of land from which to farm productively and sustainably (Griffith et al. 2000).

Habitat loss and fragmentation in the Neotropics

A study conducted by the United Nations Food and Agriculture Organization (2006) estimated that between 1990 – 2005, approximately 17.3% of rainforests in Central America were deforested. Habitat loss, such as deforestation, continues to occur in Central America at an average annual rate of 1.23% (FAO 2006) and is considered the number one contributing factor to global declines in biodiversity (Dirzo and Raven 2003). New species are still being identified in some parts of the Neotropics (Patterson 2000). With continued habitat loss, it is inevitable that species go extinct before they are even identified by scientists. Furthermore, for some species that have been identified in the Neotropics, there is still a relatively poor understanding of very basic species-habitat relationships (Young and Zuchowski 2003). Therefore, it is very difficult to understand exactly how certain species will respond to changes in habitat across the landscape at different scales.

Fragmentation of forest habitats is also associated with decreases in biodiversity within the Neotropics (Laurance et al. 2002). A long-term, large-scale habitat fragmentation study has been underway in the Amazonian rainforest over the past few decades (Lovejoy et al. 1986, Laurance et al. 2002). Results from these studies have documented and quantified the effects of forest fragmentation and isolation on many species across multiple taxa. It has been shown that forest fragmentation typically has an overall negative influence on forest species through an alteration of abiotic factors that influence habitat use (Lovejoy et al. 1986, Laurance et al. 2002).

Edge effects introduced by forest fragmentation in the Neotropics are far reaching and vary by species spatially and temporally (Turner 1996, Laurance et al. 2002). Effects of edges on individual survival and species persistence can be altered through a myriad of ways including loss of important food resources and nesting habitats, changes in biotic conditions such as introduction of invasive species and exposure to predators, and abiotic conditions such as increased temperature and wind (Laurance et al. 2002). In the Neotropics, habitat loss and fragmentation have resulted in limited use of disturbed areas (i.e., edges) by insectivorous birds (Stouffer and Bierregaard Jr 2008). However, Restrepo and Gomez (1998) showed that some Neotropical frugivorous birds may preferentially use edges during the rainy season and avoid edges during the dry season. The extent to which frugivorous birds use edges associated with forest and pastures is still poorly understood (Sekercioglu et al. 2007). Patch size could be an important factor in determining habitat use of forest/pasture edges, as small forest fragments in the Amazon have been shown to support a lower density of plants that bear fleshy fruits (e.g., Rubiaceae, Lauraceae, Myrtaceae, and Sapotaceae) (Tabarelli et al. 1999). The effects of patch size are further complicated by temporal lag effects associated with habitat fragmentation (Pimm and Askins 1995, Brooks et al. 1999). Daily et al. (2008) cautioned that the mere fact that forest species were found using human-dominated landscapes in southern Costa Rica does not necessarily indicate that these were viable populations.

In Costa Rica, deforestation in lowland areas has been shown to lift low-base cloud cover from montane areas such as Monteverde (Lawton et al. 2001, Nair et al. 2003). If the extent of deforestation in lowland Caribbean rainforests persists, cloud forest ecosystem processes could be altered by lower exposure to wind driven cloud water (Clark et al. 2000), which is a major hydrologic input for the Monteverde area. In turn, the alteration of hydrologic processes could affect the species that inhabit these ecosystems by potentially altering the phenology of plant’s flowering/fruiting cycles, which could have cascading affects on the organisms that depend on these plants as a food resource.

Species-habitat relationships

Understanding species-habitat relationships has been an important issue for biologists and ecologists for over a century (Block and Brennan 1993, Morrison et al. 2006). Improving understanding of how animals use the landscape has important implications for the preservation of many threatened and endangered species, as well as species for which there exists little information about habitat requirements. Data deficiency seems to be the rule rather than the exception for many species that inhabit the Neotropics (Patterson 2000, Young and Zuchowski 2003).

Powell et al. (2000) used radio telemetry to monitor the seasonal elevational movements of the Resplendent Quetzal (*Pharomacrus mocinno*) and were able to uncover important habitat linkages based on the elevational migration undertaken by this species every year. Similar research has been conducted in Costa Rica for the declining Three-wattled Bellbird (*Procnias tricarunculata*). Powell and Bjork (2004) also used radio telemetry to discover one of the most complicated circumnavigated migrations of a large-bodied Neotropical frugivore. Both of these studies led to efforts to preserve and connect important habitats that are vital for these elevational migrants for completing their complex annual journey across multiple life zones (Holdridge 1966, Powell et al. 2000, Powell and Bjork 2004). While there is an increasing literature regarding species descriptions and general habitat requirements in the Neotropics, there is still a pressing need to better understand how animals are responding to changes in the landscape. Sekercioglu et al. (2007) examined habitat use of forest thrushes (Turdidae) in human-dominated landscapes, while Daily et al. (2008) looked at the effects of forest fragmentation on forest birds in southern Costa Rica. In addition, Ruiz-Gutierrez et al. (2008) investigated effects of forest fragmentation on the survival of the White-ruffed Manakin (*Corapipo altera*). The previous 3 studies were conducted in southern Costa Rica in a fragmented landscape that is very similar to San Luis. To date, there have been no extensive studies conducted in San Luis which focus on species-habitat requirements for frugivorous forest birds, such as the Long-tailed Manakin.

Species account

The Long-tailed Manakin (*Chiroxiphia linearis,* Family: Pipridae) is a suboscine songbird ranging from southern Mexico to central Costa Rica. In Costa Rica, Long-tailed Manakins are considered common in a variety of forest habitats from tropical dry forests (sea level) to premontane wet forests (ca. 1500 meters) (Holdridge 1966, Stiles and Skutch 1989). Habitat for Long-tailed Manakins is described as both large canopy forests with a minimal understory layer (Foster 1976) and dry or humid forests with abundant undergrowth (Stiles and Skutch 1989).

Adult males are described as mostly black, with a red crown, sky blue back, and long central rectrices. For a few years, females and immature males closely resemble one another, with an overall olive-green appearance, red crown (present in some older females), and various pre-definitive stages consisting of black, blue, and red patches in immature males (<5 years old). In a male’s fifth year, it obtains the definitive plumage adorned by conspecific mature males, as well as full testicular development (Foster 1987, Stiles and Skutch 1989, Doucet et al. 2007). Adults from both sexes are long-lived with some color-banded individuals returning to known lek sites for over 13 years (Trainer and McDonald 1993).

Nesting for Long-tailed Manakins generally starts in March and can last until September (Foster 1976, Stiles and Skutch 1989). Females are responsible for building the nest, incubating the eggs, and rearing the young, while males contribute nothing more than DNA. Clutch size is usually two eggs, light brown in color with a strong band of chocolate brown spots toward the larger end of the egg. Females incubate mostly during the afternoon, but little is known regarding their behavior during the remaining daylight hours (Foster 1976).

Long-tailed Manakins are a subcanopy species that employs a lek-based mating system. After young fledge and no longer require parental care, immature males will join groups of approximately 3-11 individuals in varying stages of predefinitive molts and begin practicing vocalizations and display behavior. However, it is only two definitive males from the group, one alpha and one beta, who perform for the females within a display arena, or lek, in order to gain the opportunity to mate. If a particular duet is chosen by a receptive female, only the dominant alpha male will mate.

Relative to other manakins, Long-tailed Manakins are a well-studied species in Costa Rica. Detailed studies of male-male cooperative displays relating to delayed plumage and maturation (Foster 1987, Arevalo and Heeb 2005, Doucet et al. 2007), as well as song learning and variation and vocal repertoire (Trainer and McDonald 1993, Trainer and Parsons 2001), have previously been conducted in Costa Rica. Only one study performed by Foster (1976) attempted to evaluate the nesting biology of Long-tailed Manakins. Foster (1976) focused her survey on a discrete population of Long-tailed Manakins in the northwest region of Costa Rica within the lowland tropical dry forest habitat of the Guanacaste Province. She reported that females spent much of the day away from the nest and out of sight. This is not surprising, as females tend to be highly secretive, and very difficult to detect (R.A. Malloy personal observation). Additional habitat use and nesting biology studies are needed for Long-tailed Manakins throughout more of its extensive range. No such studies have been performed focusing on montane populations in Costa Rica.

STUDY OVERVIEW

This study examined home range size and habitat use of a frugivorous forest species, the Long-tailed Manakin, during the breeding season. This species was chosen for this study because: 1) they are considered to be common throughout their range (Stiles and Skutch 1989); 2) they are considered to be a forest species (Foster 1976;1977a;b;1987, Stiles and Skutch 1989) that will inhabit areas near human-dominated landscapes; 3) there is still relatively little known about its habitat-use requirements; and 4) there is very little information available about female Long-tailed Manakins (Foster 1976).

The primary objectives of this study were to: 1) establish home range estimates for female Long-tailed Manakins; 2) quantify habitat use of a human-dominated landscape by Long-tailed Manakins at multiple spatial scales and; 3) quantify microhabitat selection for nest sites by female Long-tailed Manakins by comparing vegetation measurements from nest sites to paired non-nest sites. A better understanding of how forest birds use human-dominated agricultural landscapes could help to better manage and preserve forest species by managing for landscape features that benefit these species (e.g., forested hedgerows, old growth remnant trees in pastures, and maintaining high densities of fruit-bearing plants.).

This thesis is divided into three chapters. It has been written in a format that combines the three objectives of this study stated above. Chapter one provides an overall literature review of the historical land use trends of Costa Rica and the Monteverde area, trends of habitat loss and some of their potential effects on birds, and an overview of the motivation of biologists for examining habitat use and some of the ways in which this has been achieved in the past. Chapter two focuses on quantifying home range size and habitat use of the Upper San Luis landscape by female Long-tailed Manakins at multiple spatial scales during the breeding season. Chapter three summarizes the major conclusions and findings of this study and suggests potential directions of future studies.

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CHAPTER 2

HOME RANGE SIZE AND HABITAT USE OF PREMONTANE RAINFORESTS BY LONG-TAILED MANAKINS (*CHIROXIPHIA LINEARIS*)

Malloy, R. A., and Cooper, R. J. To be submitted to The Auk.

ABSTRACT

Although fragmentation is widely studied in birds, it is unclear exactly how Neotropical forest songbirds react to different levels of deforestation and habitat fragmentation. In the Upper San Luis valley in Costa Rica, there is a rich history of relatively small-scale human-dominated land use which has resulted in a landscape matrix of forest and various agricultural practices. This study assessed habitat use in a mixed-use landscape by a frugivorous forest songbird, the Long-tailed Manakin (*Chiroxiphia linearis*), at several spatial scales. Results showed that relative rank of habitat use differed by scale. In addition, results indicated that low-intensity cattle ranching, which makes use of forested hedgerows and windbreaks, may provide necessary habitat structure for some forest songbirds, such as the Long-tailed Manakin. However, there is likely to be a threshold for the amount of open habitat in a landscape that Long-tailed Manakins and other forest birds will tolerate.

INTRODUCTION

Habitat loss is one of the primary reasons for population declines of species worldwide (Martinez-Morales 2005, Cayuela et al. 2006, Hale 2006). The dominant form of habitat loss, deforestation, is occurring in the Neotropics at an estimated rate of over 5 million hectares per year (Rainforest Alliance 2008). In Costa Rica, deforestation occurred at an annual loss of 4.2% during 1986-1991, with the majority of loss occurring in cloud forest ecosystems of the cordilleras (Sader and Joyce 1988, Sanchez-Azofeifa et al. 2001, Martinez-Morales 2005). The majority of cleared land has been subsequently converted into cattle pasture. While the Costa Rican government limits deforestation, there is an increasing trend toward converting both forest and small shade coffee plantations into pasture land. Shade coffee plantations are thought to act as suitable habitat for forest dwelling bird species (both residents and migrants), but how they do so is poorly understood (Greenberg et al. 1997, Tejeda-Cruz and Sutherland 2004, Sekercioglu et al. 2007). Within the Monteverde region of Costa Rica, the Long-tailed Manakin (*Chiroxiphia linearis*) resides almost exclusively within forested landscapes, although some Long-tailed Manakins will use shade coffee plantations, mostly making use of forested windbreaks (R.A. Malloy personal. observation).

The Monteverde region of Costa Rica has extraordinary biodiversity (Haber 2000). With the majority of the planet's species found in such a relatively small area, it is imperative that conservation measures be implemented for extant species before they are lost. The Monteverde cloud forest ecosystem contains over 3000 plant species, which provide a myriad of niches for many taxa, including birds (Haber 2000). Many of the 450 bird species that occupy these ecosystems can often be found utilizing shade coffee plantations. In San Luis, located approximately 200 meters down slope from the Monteverde region, a majority of the landscape is dominated by forest and mixed agricultural land cover classes. These land cover types provide refuge for hundreds of resident and migratory birds. Historically, San Luis has been known as a quiet agricultural community with families occupying small parcels of land used for subsistence farming. With a changing economy, many individuals are abandoning traditional farm-related work and seeking employment in ecotourism (in Monteverde). Within the nearby community of San Luis, most of the subsistence farms are still relatively small (1-2 hectares per farm); however, the pressure of converting agricultural plots to cattle pastures is being felt by a changing economy, as traditional agricultural practices are not being passed down to future generations. Located immediately down slope from Upper San Luis is Lower San Luis. Farms in Lower San Luis are larger and structurally more similar to many other cattle ranching operations throughout Costa Rica and other parts of Central America (Kricher 1999). If the higher intensity form of cattle ranching continues upslope from Lower San Luis to Upper San Luis, there could be a negative impact to forest birds, such as the Long-tailed Manakin. Daily et al. (2001) found that while forest birds may use human-dominated landscapes, they likely will not persist in those areas, especially with continued intensification of land use. This study aims to better understand how forest birds such as the Long-tailed Manakin are using low-intensity human-dominated landscapes, such as those found in Upper San Luis. Unlike previous research on this species, I used radiotelemetry and focused entirely on habitat use by females. I hypothesized that, as forest birds, Long-tailed Manakins would use forest preferentially over other habitats, and that home ranges containing more forest would be smaller than home ranges containing other open habitat types.

METHODS

Study site

This study was conducted at the University of Georgia (UGA) San Luis Research Station (10^{o} 17’N, 84^{o} 48’W), which is located on the Pacific slope of the Cordillera de Tilaran mountain range within the municipality of Puntarenas and has an elevation of approximately 1100 m asl (Figure 2.1). Receiving approximately 2.5 m of precipitation annually, this region is considered premontane wet forest (Holdridge 1966). The temperature varies from 18 - 24 ^{o}C throughout the year. The UGA station property is approximately 62 ha and is surrounded by a mosaic of both secondary and primary forest, as well as shade-grown coffee plantations, mixed agriculture farms, and pastures (Figure 2.2).

Bird sampling/ Telemetry

Birds were captured via mist nets set up at lek sites within the forest. Four mist nets (combination of 10 m x 3 m, and 8 m x 3 m 36 mm mesh) were operated around the periphery of each lek site, as well as between lek sites. Nets were opened before dawn, checked every 15-20 minutes, and closed at approximately 4:00 pm. Net locations and operation times were adjusted as needed to coincide with Long-tailed Manakin activity. Radio transmitters (Lotek Wireless, Ontario, Canada) which weighed 1g were attached to 21 females following the attachment method described by Kershner et al. (2004) and Rappole and Tipton (1991), which involves fitting the radio transmitter on the female using a backpack-style harness. Each female was weighed, measured, checked for breeding condition (presence/absence of vascularized brood patch), photographed, fitted with a radio (if considered in breeding condition), banded, and weighed again with transmitter before being released at the site of capture. Birds were monitored immediately following attachment of a radio for approximately one to three hours after release to detect behavioral irregularities (Sekercioglu et al. 2007). Previous radio telemetry studies with passerines show that the presence of transmitters weighing < 5% of the total mass show negligible effects on bird behavior and survival (Caccamise and Hedin 1985). Female Long-tailed Manakins used in this study were 21.1g ± 0.41 (mean ± SE). In addition, a 24 - 48-hour acclimation period was allowed prior to tracking. Radio-marked birds were tracked daily from sunrise until dusk using a homing technique. A three-element Yagi antennae and a SRX 400 receiver (Lotek Wireless, Ontario) were used to detect and track individual female Long-tailed Manakins. When a radio-marked bird was located, visual confirmation of the individual was made if possible prior to recording a waypoint using a Trimble GEO XM GPS (Trimble, Los Altos, California) and ArcPad 7.0 (ESRI, Redlands, California) which allowed for the locations to be loaded directly into a shapefile. When satellite coverage was insufficient to record locations on the GPS, the location was placed on a georeferrenced field map and later manually entered into a point location shapefile in ArcGIS 9.3 (ESRI, Redlands, California). In many cases, a visual observation of the bird was not possible; therefore, the closest location possible was recorded, and an estimate of the bird's distance and/or height above the observer was made (Rivera et al. 2003). Battery life for transmitters was approximately 100 days.

Generating home ranges

Long-tailed Manakin home ranges were generated using ArcGIS 9.3 from point locations which were gathered from May – August in both 2008 and 2009 from 21 female Long-tailed Manakins fitted with radio transmitters (see above). Average number of points per individual used to generate home ranges was 26 ± 2.13 (mean ± SE).

Home ranges were generated using 3 different methods: minimum convex polygon (MCP), kernel density estimation (KDE), and local convex hull (LoCoH). Home ranges refer to areas travelled by an animal to carry out feeding, mate finding/selection, and/or caring for offspring (Burt 1943). To avoid including spurious movements, 90% home ranges were constructed. Barg et al. (2006) found that Cerulean Warblers (*Dendroica cerulea*) showed nonrandom space use in core areas within territories relative to other available areas within home ranges. Therefore, 50% core areas were also generated using each home range tool.

MCPs were generated in order to allow comparison with other home range and habitat use studies (Harris et al. 2008). MCPs are computationally simple, and they are very user-friendly in that it does not require much in the way of equipment or statistical/computer knowledge to perform. Simply put, for any given point location file that is deemed appropriate to use for home range analysis, the outermost points are connected, and the result is a polygon that encompasses all the other point locations from that individual. Though relatively simple to create and comprehend, there are a few shortcomings associated with MCPs. They do not reveal any information regarding internal configuration or how a particular area was used (Worton 1987, Barg et al. 2005). Also, they can sometimes include peripheral habitats that were sure to have not been used by an animal (Barg et al. 2005). MCPs were generated using the Home Range Estimator extension tool (Rogers and Carr 1998) within ArcGIS 9.3.

KDE represents a utilization distribution (UD) in that the area generated from the point locations is a probability density function which represents space-use by an animal (Worton 1987, White and Garrott 1990, Barg et al. 2005). Fixed radius kernels were generated from location data (Worton 1989), and a least-squares cross-validation (LSCV) smoothing parameter was used (Gitzen and Millspaugh 2003). KDEs were generated using the Home Range Estimator extension tool (Rogers and Carr 1998) within ArcGIS 9.3.

LoCoH is a UD that is generated by connecting each point location with its k – 1 nearest neighbors in order to construct convex hulls. Convex hulls are straight-edged polygons that connect a specified number of points. This process is repeated for each of the points within an individual animal’s point location set. Next, the convex hulls are joined in an iterative process until the desired isopleth level is reached, in this case 90% isopleths (Getz and Wilmers 2004, Getz et al. 2007). The value of k was determined by plotting area vs. k charts for each individual. A value of k = 8 was chosen, as this was the point where higher values of k showed no increase in area (Figure 2.3; Getz et al. 2007). LoCoH home ranges were generated using the LoCoH web application interface tool (http://locoh.cnr.berkeley.edu/).

A Randomized Complete Block Design ANOVA was used to examine if there was a difference in home range size between the three different methods. Each territory was considered as an individual block, and home range estimators were considered as the treatments. Additionally, a paired t-test was used for each home range estimator to examine whether or not there was a significant difference in home range size between years. All statistical analyses were performed in SAS 9.1 (SAS Institute Inc., Cary, NC).

GIS: Generating habitat data

A satellite image (1:24,000) was used to digitize land cover types for the upper San Luis valley (Figure 2.2). Land cover types were classified as forest, agriculture, pasture, or gap. Forest land cover types consisted of either secondary or primary forest. As most of the landscape was cleared approximately 40-50 years ago, much of the current landscape consists of secondary forest. However, some steep hilltops maintain small patches of primary forest. Agriculture habitat consisted of mostly multistrata polyculture plots (Somarriba et al. 2004). These were primarily shade coffee (*Coffea arabica)* plots with various citrus (Rutaceae), banana (Musaceae), and fig (Moraceae) tree cover and various mid – low strata vegetation. Pastures were almost exclusively Kikuyu (*Pennisetum clandestinum*) and African Star Grass (*Cynodon sp.*) and were occupied by cattle and horses (Griffith et al. 2000). Gaps were considered to be any clearing not falling into any of the above categories and ranged from houses and buildings to small roads, trails, landslides, and even stream and river clearings.

The study area was defined by generating a large polygon, approximately 660 ha that spanned the entire upper San Luis valley, beyond the farthest home range generated from kernel density estimation (Figure 2.2). Within this area, Long-tailed Manakins were known to occur based on both direct observation and/or anecdotal information. In addition, each of the four habitat types was available throughout the sampling area. Within the polygon, 20 random points were generated using Hawth’s tools (Beyer 2004) in ArcGIS 9.3. Each point was separated by

500 m in order to ensure that there was adequate coverage of the study area. Buffers around each point were created that had a 200 m radius, and no buffers were allowed to overlap. All land cover within each buffer was digitized and classified into the land cover categories defined above. The sampling buffer size used was equivalent to the largest home range size averaged across all three home range tools, approximately 12.5 ha. Proportions of each habitat type were used as estimates of habitat availability within the study area.

Statistical Analysis: Influence of landscape variables on home range size

Linear regression analysis (Neter et al. 1990) was used to evaluate the relationship of landscape variables with home range size. Variables included were: percentage of land cover types- Gap, Agriculture, Forest, and Pasture; distance from female territories to male lek sites (point of capture); and edge density (m/ha) within home ranges. All data used in this analysis were generated from 90% fixed kernel home ranges, and edge density was calculated using FRAGSTATS 3.0 (McGarigal et al. 2002). This approach was used to better understand landscape-scale mechanisms that influence home range size in the San Luis area. In order to avoid effects of the unit-sum constraint (Johnson 1980, Aitchison 1983), multiple sets of models were constructed removing each habitat-type once. Removing a habitat type typically helped reduce multicollinearity among the predictor variables. In addition to removing habitat types in order to avoid effects of multicollinearity in the statistical models, variables with Pearson's $|r| > 0.6$ were excluded.

An information theoretic approach (Burnham and Anderson 2002) was used to create and assess the relative fit of the linear regression models. Four global models were constructed containing all predictor variables minus one habitat type as well as 9 subsets of models from each global model; these corresponded to different hypotheses to explain variability in home range size (Table 2.1). Akaike's Information Criteria (AIC; Akaike 1973) were calculated with the small-sample bias adjustment (AICc; Hurvich and Tsai 1989) to assess the fit of each candidate model. The relative fit of each model was assessed by calculating and comparing Akaike weights (Burnham and Anderson 2002) which range from 0 to 1. Therefore, the most parsimonious model would be the model with the greatest Akaike weight.

Model selection uncertainty was incorporated by calculating model-averaged estimates of regression coefficients and their respective standard errors (b-hat averaging as described by Burnham and Anderson 2002). Weighted Akaike weights for the estimated coefficients and their standard errors from each candidate model were summed across different models, and a composite model was created. All model inferences were based on composite models. Ratios of Akaike weights from candidate models were used to determine relative support for each model, and a 12% rule was used to create a confidence set of models (Royall 1997, Thompson and Lee 2000, Rieman et al. 2006). Model averaged parameter estimates were only calculated for those parameters within the confidence set. Precision of the model-averaged estimates was based 95% confidence intervals. If a confidence interval included zero, the nature of the relationship given the data was not able to be determined. Goodness-of-fit was evaluated by examining the residual and normal probability plots, as well as R^2. Non-transformed data were used which may have violated some of the assumptions of linear regression; therefore, model selection and parameter estimate values could be imprecise.

Orders of selection

Second order: Home range use vs. landscape availability

Second order selection compares habitats use at the animal's home range level to habitats available at the landscape scale (Johnson 1980). Available habitats were quantified using a landscape sampling technique (see *GIS: Generating habitat data*). Habitat use was quantified as the proportion of each habitat type found within the 21 home ranges. Compositional analysis was used to quantify whether or not any of the four habitats were used disproportionally to their availability (Aebischer et al. 1993). BYCOMP.SAS with randomization (Ott and Hovey 1997) was used to analyze habitat use vs. availability.

Third order: Core area use vs. home range availability

Third order selection compares habitat use within the core area with habitats available within the 90% home ranges. Proportions of habitats within the 50% core areas were quantified similarly to second order selection. Again, compositional analysis was used to quantify whether or not any of the four habitats were used disproportionally to their availability (Aebischer et al. 1993). BYCOMP.SAS with randomization (Ott and Hovey 1997) was used to analyze habitat use vs. availability.

Fourth order selection: Nest site selection

Fourth order selection describes habitat selection at the finest scale (Johnson 1980). This approach is often used to determine how an animal uses a particular resource within a home range in order to satisfy a life need (e.g., food resource selection or nest site selection). In order to estimate microhabitat nest site selection by female Long-tailed Manakins, vegetation measurements were taken within both 5 and 11-meter radii at both nest sites and paired non-nest sites, which were located within 25 meters of the nest. A slightly modified BBIRD protocol (Martin et al. 1997) was followed for data collection. Variables used in logistic regression models were: number of large stems (dbh > 2.5 cm), percent green cover, small trees (dbh 8-23 cm), large trees (dbh > 23 cm), small snags (dbh < 12 cm), and large snags (dbh > 12 cm). At nest sites only, I measured dbh of the nest tree (cm), orientation (degrees) of nest, tree height of nest tree, diameter of supporting branch (cm), nest height from ground (cm), distance from trunk of supporting tree (cm), distance from nest to forest edge (m), percent vegetation cover above nest, and average percent vegetation cover from each cardinal direction around the nest (Table 2.2).

Logistic regression analysis (Hosmer and Lemeshow 1989, Johnson et al. 2006) was used to see if there was a relationship between nest presence and variables measured. Again an information theoretic approach described by Burnham and Anderson (2002) was used in order to assess the relative influence that each measured variable had on nest presence. This approach uses information in the data to approximate a best fitting model and provides strength of evidence for alternative models. In order to avoid effects of multicollinearity in the statistical models, variables with Pearson's $|r| > 0.6$ were excluded.

A global model was constructed which contained all variables measured at both nest and paired non-nest sites (see above). Then, 12 subsets of the global model were created which represented competing hypotheses for predicting nest presence (Table 2.3). Akaike's Information Criteria (AIC; Akaike 1973) were calculated with the small-sample bias adjustment (AICc; Hurvich and Tsai 1989) to assess the relative fit of each candidate model. Relative fit was determined by evaluating Akaike weights (Burnham and Anderson 2002) that range from 0 to 1, thus the most parsimonious model will be reflected by the greatest Akaike weight. Ratios of Akaike weights from candidate models to determine relative support for each model, and a 12% rule was used to create a confidence set of models (Royall 1997). To evaluate goodness-of-fit, the Hosmer and Lemeshow (1989) goodness-of-fit test was used.

Model averaging was used to account for model uncertainty in model selection by calculating model-averaged estimates of regression coefficients and their respective standard errors (b-hat averaging as described by Burnham and Anderson 2002). In addition, odds ratios were calculated to determine relative effects of each predictor variable on probability of presence of Long-tailed Manakin nests. The precision of the predictor variable estimates was assessed by whether or not the standard errors and 95% confidence limits overlapped with one. Measurements taken only at the nests were averaged and summarized.

RESULTS

Home range size

Mean home range size for MCP, KDE, and LoCoH was 1.93ha ± 0.5, 3.32ha ± 1.23, and 1.02 ± 0.41ha (mean ± SE), respectively. Results from the ANOVA showed that there was a significant difference in home range size between the three home range tools ($F_{2, 40} = 5.92$, $p = 0.006$). Tukeys HSD showed that there was no significant difference between MCP and KDE; however, there was a significant difference between both MCP and KDE with LoCoH (Figure 2.4). In addition, there was a significant block effect ($F_{20, 40} = 6.46$, $p < 0.0001$) indicating that there were differences between territory sizes among home range estimators. There was no difference in home range size between years for KDE home ranges ($t = -1.3695$, 19 df, $p = 0.19$) or LoCoH home ranges ($t = -2.0831$, 19 df, $p = 0.051$). However, there was a significant difference in home range size between years for MCP ($t = -2.6451$, 19 df, $p = 0.016$).

Mean home range size for KDE was 3.32 ha ± 1.23 (mean ± SE). Mean edge density was approximately 365 m/ha within KDE home ranges. Mean distance from female territories to male lek sites was approximately 336 meters, with a range from 67 – 666 m. Mean proportions of Gap, Agriculture, Forest, and Pasture were 0.04 ± 0.01; 0.02 ± 0.01; 0.86 ± 0.02; and 0.08 ± 0.02 (mean ± SE), respectively.

Influence of landscape variables on home range size: AIC model selection

When Pasture was withheld, the model that contained Agriculture alone was the best approximating model and was 1.70 times more likely that the second best approximating model, which was Forest alone. When Forest was withheld, the Agriculture alone model was the best approximating model and was 1.76 times more likely than the second best model, which was distance from female home range to male lek site alone. When Agriculture was withheld, the Forest alone model was the best approximating model and was 1.04 times more likely than the second best model, which contained distance from female home range to male lek site alone. When Gap was withheld, the Agriculture alone model was the best approximating model and was 1.70 times more likely than the second best model, which contained Forest alone (Table 2.4).

Averaged composite model

Agriculture had the largest effect on female Long-tailed Manakin home range size. With every 1% increase in Agriculture, home range size increased by 0.15 ha. With every 1% increase in Forest and Pasture, there was a decrease in home range size by 0.047- and 0.043 ha, respectively. As Gap increased by 1% there was an average increase of 0.094ha in home range size. As Edge density increased by 1m/ha, there was a decrease in home range size of 0.023ha. With every 1m increase in distance from female territories to male lek sites, there was an increase of 0.011 ha in home range size (Table 2.5). Model fit for the global models was relatively poor (R^2 = 0.19; adjusted R^2 = -0.09). It should be noted that the 95% confidence intervals for all variables overlapped 0; therefore, interpretation of these parameters could be imprecise.

Orders of selection

Second order selection: Landscape vs. home range

For MCP, habitat use differed from availability ($F_{3,18} = 13.27$, $p < 0.0001$). For KDE, habitat use differed from availability at the second order ($F_{3,18} = 8.69$, $p = 0.001$). For LoCoH, habitat use also differed from availability ($F_{3,18} = 47.69$, $p < 0.001$). At the second order, habitat rankings were the same for all three home range estimators: Forest was ranked highest, followed by gap, pasture, and agriculture, respectively (Table 2.6).

Third order selection: Core area use vs. home range availability

Habitat use differed from availability for MCP ($F_{3,18} = 3.85$, $p = 0.027$), KDE ($F_{3,18} = 8.32$, $p = 0.001$), and LoCoH ($F_{3,18} = 3.98$, $p = 0.025$). Habitat selection differed between the different home range estimators. For MCP, forest ranked highest followed by gap, agriculture, and pasture, respectively. For KDE, forest ranked highest followed by pasture, gap, and agriculture, respectively. For LoCoH, forest ranked highest followed by agriculture, gap, and pasture, respectively (Table 2.6).

Fourth Order selection: Nest site selection

Mean large stem count was approximately 38. Mean canopy cover was approximately 95% with a range of 91 - 97% (Table 2.7). Mean number of large trees was approximately 17. Mean number of small snags was 18, and mean number of large snags was approximately 9 (Table 2.7).

The Hosmer and Lemeshow goodness of fit results indicated that model fit was sufficient for analysis ($p = 0.1135$). The best approximating model for predicting the presence of a nest contained the large snag variable alone and was 3.36 times more likely than the next best approximating model, which was small snag alone. Other models included within the confidence set were: large stem alone, percent cover alone, small tree alone, and large tree alone (Table 2.8).

The composite logistic regression model of the probability of nest presence indicated that nests were 1.04 times more likely to occur for every 1-unit increase in large stems. For every 1% increase in canopy cover, nests were 1.25 times more likely to occur. For every one unit increase in small trees nests were 1.02 times less likely to occur. For every one unit increase in large trees, nests were 1.03 times less likely to occur. For every one unit increase in small snags, nests were 1.10 times less likely to occur, and for every one unit increase in large snags, nests were 1.37 times more likely to occur (Table 2.9). It should be noted that the 95% confidence intervals for all variables overlapped 1; therefore, interpretation of these parameters could be imprecise.

Nest measurements

Nests were typically found in small trees or shrubs which were an average height of 191 cm, with an average diameter of 1.5 cm. On average, nests were 126 cm off of the ground on small supporting branches that were an average diameter of 0.7cm. Nests were located an average distance of 32 cm from the trunk of the tree oriented at approximately 186º. Nests were relatively well concealed with an average side cover of 72.3% and an average top cover of 79.2%. Nests were found an average distance of 38.7 m from the forest edge (Table 2.10).

DISCUSSION

Home range size

Home range size varied significantly by estimator. This result was expected given the differences in how each method generated home ranges, and that sample size was relatively small (Seaman et al. 1999). KDEs were approximately 1.71 times larger than MCPs. This is likely due to relatively small sample size used in this study (n < 50), which has been shown to lead to large KDE home ranges relative to MCP (Wauters et al. 2007). Mean home range sizes generated by MCPs and KDEs were 1.91 and 3.27-times larger than mean home ranges generated by LoCoH, respectively. Korte (2008) found similar trends in differences in mean home range size between MCP and LoCoH estimates of forest buffalo in Africa (MCP home ranges approximately 1.18 times larger than LoCoH estimates). This result lends support to the idea that careful *a priori* planning regarding which home range estimator will be used should be carried out prior to conducting field work. Some home range estimators better capture true barriers restricting movement (Getz and Wilmers 2004, Getz et al. 2007); however, to be able to adequately do so, a certain sample size may need to be reached as shown by Getz and Wilmers (2004).

Habitat use

Although models relating home range size to landscape-level variables were judged to have adequate fit based on a visual assessment of a plot of the residuals from the global model, 95% confidence intervals around parameter estimates included zero for all coefficients. The reader is cautioned that parameter estimates and their interpretations could be imprecise. Still, coefficient signs (and direction of ecological relationships) were largely as predicted, and while the estimates of the landscape variables were relatively imprecise when used to predict home range size, there was a significant effect found for habitat selection. Therefore, the effects of the landscape parameters are discussed in detail below.

Second order selection and effects of habitat variables on home range size

Habitat selection at the second order showed that forest had the highest relative rank of all habitat-types considered in this study, which makes sense, because the Long-tailed Manakin is a forest species (Stiles and Skutch 1989), and one would expect that forest cover is higher quality habitat than the other habitat types. Though the 95% confidence interval overlapped zero, the model averaged forest parameter estimate showed a decreasing effect on average home range size. The food-value theory (Stenger 1958) suggests that territoriality is a mechanism to space individuals over an area to ensure the food needed to raise offspring successfully, and has been repeatedly supported in the literature via an inverse relationship between territory size and food density. For example, Dunk and Cooper (1994) showed that increasing habitat quality within territories of Black-shouldered Kites (*Elanus caeruleus*) via increased prey abundance decreased mean territory size. Smith and Shugart (1987) showed a similar decreasing trend in territory size of Ovenbirds (*Seiurus aurocapillus)* with increasing prey abundance. Marshall and Cooper (2004) showed the same relationship with a canopy-dwelling songbird whose territory was measured in three dimensions. While forest habitat was selected highest overall, the magnitude of the effect of forest habitat on home range size was not very large relative to the increasing effect of agriculture. This is likely due to the fact that fruiting plants that are actually bearing fruit at any given time are rare, even in forest, so manakins still have to travel long distances within forest patches to find fruit. Many plants produce fruit within the rainy season; however, it is common for fruiting plants to show high levels of asynchrony within season (Murray 2000). Furthermore, small fruiting plants are not overly abundant throughout the understory stratum of the forest, where Long-tailed Manakins spend most of their time. Therefore, finding fruiting plants within the forest understory can be difficult. It has been documented that Long-tailed Manakins have an enlarged hippocampus relative to other songbirds (McDonald 2000). This could be important in understanding how manakins use the landscape, as the hippocampus is associated with spatial memory in birds (Krebs et al. 1989). It is possible that female Long-tailed Manakins map local important habitat features (i.e., location of fruiting plants and lek sites) within season and potentially between seasons (Foster 1977a, McDonald and Potts 1994). In addition, Long-tailed Manakins' ability to travel relatively long distances to find fruit could be evolutionarily beneficial to fruiting plants, as traveling manakins are not very likely to deposit seeds near the site of fruit consumption. Thus, seeds carried away from a small understory fruiting plant have a better probability of colonizing a new area or even escaping local density dependent pressures such as competition with parent plants (Murray et al. 2000). It is likely that manakins still need to travel frequently and sometimes quite far in order to locate sporadically fruiting plants within the forest understory. Females showed a tendency to place nests farther away from edges (see below) than where fruiting plants and/or lek sites may have been located. This could have also been a contributing factor for why the magnitude of the effect of forest was not equal to that of gap and/or agriculture.

Gap was ranked second and was selected over pasture and agriculture. This result shows that at the landscape level, forest edge habitats are important to female manakins, probably due to the high abundance of fruiting plants associated with forest edges (Murray et al. 2000). In fact, edge density had a decreasing effect on home range size, suggesting that at the home range scale, female manakins may need a certain amount or certain types of forest edge habitat to find fruit. Also, many of the gaps were relatively small and were likely to be easily crossed by manakins in search for fruiting plants, leks, or nest sites, a result also observed with fragmented habitat use by Blue Manakins (*Chiroxiphia caudata*) in South America (Hansbauer et al. 2008). Gap habitats also had the second highest increasing effect on home range size, after agriculture. It could be that, for female Long-tailed Manakins, gap habitats are lower in quality than forest. The proportion of lower quality habitat within female manakin's home range could be playing an important role in determining overall home range size, though more data are needed to properly determine the effect of gap habitat on home range size. It is important to note that for the purposes of this study, naturally formed gaps and gaps caused from anthropogenic factors (e.g., clearings for roads and buildings) were lumped together into one habitat classification. It is possible that many of the gaps present on this landscape did not provide as much in the way of fruiting plants or trees as did forest cover. Lastly, it could also be that some of these gaps in Upper San Luis were associated with areas of relatively high human-use and were therefore avoided by female Long-tailed Manakins. Many gaps associated with human-dominated areas have been exposed to increased construction over the last 5 years, as this area continues to develop.

Pastures were selected third and were selected over agriculture. Many pastures have forested windbreaks or hedgerows which connect adjacent forest patches together, facilitating movement by forest birds such as manakins (Hinsley and Bellamy 2000). Pasture also had a decreasing effect on home range size of female Long-tailed Manakins. Many of the pastures in the Upper San Luis area are small relative to large-scale cattle ranches found in other parts of Costa Rica (Kricher 1999, Nadkarni and Wheelwright 2000), and these pastures would be considered low-intensity according to Bignal and McCracken (1996). Bignal and McCraken (1996) found that low-intensity cattle ranching habitats can still support forest dwelling song birds. If this is in fact the case in the Upper San Luis area, then perhaps these low-intensity cattle pastures are viewed similarly as the low-intensity agricultural plots, which have been shown to be beneficial to birds (Perfecto et al. 1996, Moguel and Toledo 1999, Perfecto et al. 2003). However, fewer studies have considered low-intensity cattle ranching as having a similar effect on wildlife, including birds. In addition, there are quite a few solitary old growth remnant trees that persist within most pastures, which have been shown to play an important role in post-agriculture forest succession (Murray et al. 2008). Some of these species are fruit bearing trees from the family Melastomataceae, which is a food source for many forest frugivorous birds including Long-tailed Manakins (Wheelwright et al. 1984). Sekercioglu et al. (2007) found that old-growth remnant trees were important factors in open habitat use by forest birds. Proximity from connected forest patches via forested windbreaks likely plays a part in whether or not forest birds such as Long-tailed Manakins will use these corridors for movement (Hinsley and Bellamy 2000, Ferraz et al. 2007). Additionally, it may not be that low-intensity cattle ranching is beneficial to birds, rather at this scale it may simply be that this habitat is not a deterrent to forest birds with respect to movement and feeding (Mordecai et al. 2009). Nests were never located within forested hedgerows, indicating that there is a limit to the benefit of these corridors for Long-tailed Manakins. Similar relationships were found by Roberts et al. (2000) who showed that some forest birds demonstrated limited use of shade coffee landscapes (i.e., feeding but not nesting). At larger scales, forest fragmentation and isolation, which results from high intensity agriculture, has been shown to decrease biodiversity, including the presence of forest birds (Solórzano et al. 2003, Ferraz et al. 2007). The habitat adjacency matrix generated from FRAGSTATS 3.0 showed that the dominant habitat adjacencies in the Upper San Luis area were forest and pasture. Therefore, for forest birds such as Long-tailed Manakins, occupying forest patches in Upper San Luis could mean that encountering pastures is very commonplace. In fact, because there is typically a high amount of fruiting plants along the forest-pasture interface, these types of habitats could actually serve as important areas for frugivorous forest birds.

Agriculture was selected last and also showed the largest effect on home range size. In the Upper San Luis area, most of the agricultural plots are very similar, structurally, to forests.

Agricultural plots contain mostly shade coffee and forested wind breaks that could act as potential corridors for movement and even foraging habitat for female Long-tailed Manakins. In addition, many farmers plant flowering and fruiting shrubs and trees to attract various types of pollinators and seed dispersers (Peters et al. 2010). However, most of the agricultural plots are concentrated in the northwest region of Upper San Luis; therefore, radiotagged female manakins in this particular study may have had relatively less access to these habitats. Due to the fact that home ranges were fairly small, and there were enough lek sites closer to the San Luis Research Station (i.e., near the point of capture for all birds), female manakins were not likely to travel to agricultural plots located in the northwest area of San Luis. Thus, more time and effort may be spent foraging along forest-pasture edges for fruiting plants than traveling long distances to visit shade coffee parcels. Even though there were some agricultural plots dispersed across the landscape, low selection of agriculture by female manakins could have been a function of the distance to most of the shade coffee plots on the landscape. Previous studies in the San Luis area focusing on avian communities in coffee and forest systems found that Long-tailed Manakins do use the extensive poly-agricultural plots in Upper San Luis (Hernandez-Divers 2008). However, the individuals used in this study were captured an average distance of 650 m from the farm plots used by Hernandez-Divers (2008), which is approximately two-times the average distance travelled by females in this study. In addition, because female Long-tailed Manakins seemed to be able to find a necessary amount of fruiting plants and lek sites within the forests around the San Luis Research Station (point of original capture), they apparently did not make the journey to the agricultural plots for these resources.

Third order selection: Core area use vs. home range availability

Relative rank of habitat selection at the third order was different than selection at the second order and showed different trends for each of the three home range estimators (Table 6). Forest was selected first in each case, which shows that at the core area scale, forest is still most important for female Long-tailed Manakins. Agriculture and gap were selected second by female Long-tailed Manakins (MCP – agriculture; and both KDE and LoCoH – gap, respectively). This result shows that forest-edge habitat is also important at finer scales for female manakins, which is likely due to the proximity of fruiting plants and perhaps the proximity to lek sites for some individuals. Distance to lek sites from female home ranges increased average home range sizes. It could be that some females are being pushed out to the periphery of the interior, higher quality forest habitats by more dominant females (if some measure of territoriality exists). However, territoriality is not known among this species and was never directly observed. Furthermore, a small number of female manakins in this study tended to show overlapping home ranges during the same temporal period indicating that these females were using the same parts of the landscape during the same time. Another potential explanation for habitat selection of open areas and increases in home range size with increasing distance to lek sites is that males are placing lek sites in higher quality areas. Studies that focused on lek placement found that for some species of manakins, leks were located where there was a higher density of fruiting plants, supporting the hotspot hypothesis (Emlen and Oring 1977, Westcott 1994, Ryder et al. 2006). In the Upper San Luis area, it could be that male manakins are placing lek sites near areas of high fruiting densities, and females are nesting around these areas accordingly. Females that are farther away from lek sites could be farther away from quality habitats, and therefore this metric could be an indirect measure of female home range quality.

Longer distance to travel to quality habitats could mean longer time spent away from nests leaving unprotected young exposed to potential diurnal nest predators, and would therefore be less than ideal for nesting females in areas prone to high nest-depredation such as the Neotropics (Skutch 1985). Pasture was always selected last at the third order, which can be explained by the fact that pasture habitats offer very little in the way of nesting cover or protection (Foster 1976, Stiles and Skutch 1989). It appears that while low intensity agriculture can provide suitable habitat for foraging and/or movement for female Long-tailed Manakins, it does not provide the necessary cover for nesting purposes. This behavior has been shown by other species of Neotropical birds that will use human-dominated landscapes such as shade coffee plots in order to meet some life needs but only in a limited capacity (Roberts et al. 2000). Furthermore, the degree of human-use may dictate the extent of use by forest species (Hinsley and Bellamy 2000, Ferraz et al. 2007).

Fourth order selection: Nest site selection

Large snag was the most important variable for predicting the probability of nest presence. Large snags are associated with older-aged forest stands and are not commonly found in young scrub-shrub habitat. In addition, large stems also contributed to increased probability of nest presence. High frequencies of large stems could be an indicator for higher amount of local canopy cover within a lower vegetation stratum beneath the canopy of tall forest trees (Murray et al. 2000). Canopy cover also proved to be an important factor in predicting nest presence, as increased canopy cover can increase nest concealment thereby reducing nest exposure to potential predators, either diurnal or nocturnal (Martin 1996).

Based on these results, female manakins are selecting microhabitat sites for nest placement that are away from immediate forest edges and that are not overly dense with smaller shrubs. Instead, manakins seem to prefer slightly more open understory habitats than those commonly associate with early successional forests. Long-tailed Manakins, either male or female, were never observed feeding, displaying, or even traversing areas of the forest understory that were densely vegetated by shrubs, small trees, and new-growth forms of lianas and vines typical of tree fall gaps. Instead, they were often found in slightly more open habitats with a mixed vegetation age and size class. This behavior may actually serve to protect nests from predators by placing nests in low-lying trees that are not immediately adjacent to other small shrubs. Nests were typically highly concealed from all sides and even protected by an added layer of camouflage along the outer layer of nest material (Foster 1976). If nest predators are using the small shrubs as means of travelling from plant to plant, an isolated plant located in more open areas would be visited less by these types of predators. Higher frequencies of large stems as well as large snags may be indicative of higher amounts of canopy cover as well, which was an important variable at finer scales.

Female Long-tailed Manakins placed nests within relatively small understory trees that were found within a forest structure of mixed size/age classes. Habitat heterogeneity within the forest understory is likely to be a very important factor in microhabitat selection by female Long-tailed Manakins. On average, small size/age class stems seemed to decrease the probability of nest presence; however, nests were typically placed in relatively small trees (dbh < 2cm). This behavior would suggest that female manakins were selecting nest sites that are heterogeneous with respect to forest stand type. While forest edges seemed to be important to female Long-tailed Manakins at larger scales, probably for feeding, nest placement was typically not near edges. This result is likely due to increased nest depredation associated with forest edges in the Neotropics (Skutch 1985, Gibbs 1991, Burkey 1993, Roper and Goldstein 1997), as well as changes in microhabitat characteristics (e.g., wind and temperature) that are also associated with forest edges (Ferraz et al. 2007).

In conclusion, female Long-tailed Manakins preferentially selected forest habitats over pasture, gap, and agriculture habitats at both the landscape and home range scales. In addition, Long-tailed Manakins do not seem to be responding to the landscape matrix of Upper San Luis as would be expected by a forest species in a human-dominated agroecosystem. Apparently, this landscape still offers similar benefits to that of the forest, while harboring different human land uses such as small scale farming and cattle ranching. Small agricultural plots with a high level of structural diversity between crop-types likely maintains a rich diversity of forest species in these areas (Hernandez-Divers 2008, Peters et al. 2010). However, low-intensity cattle ranching also seems to contribute to forest species using other parts of the landscape within the Upper San Luis valley where a lower density of polyculture farm plots are found. Together, small polyculture farm plots and relatively low-intensity cattle ranching contribute to the persistence of frugivorous forest birds, such as the Long-tailed Manakin, in this area. In addition, relative remoteness of the San Luis township, and low human population density likely contribute to the success of forest species in this area.

If land use intensity increases, perhaps with a potential increase in cattle ranching, it is likely that forest species, such as the Long-tailed Manakin, will cease to use the landscape in the manner observed during this study. If local or regional goals are to maintain or increase the number of forest dwelling bird species in this area, management of the landscape with respect to human use should be top priority. This requires a transparent dissemination of information regarding the potential effects of human land use on forest birds from biologists to local land owners.

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Table 2.1. Hypotheses and candidate models of the effects of various landscape characteristics on home range size.

Hypothesis	Candidate model
Home range size is a function of overall habitat quality which is made up of edge density, distance to lek site, Gap, Agriculture, Forest, and Pasture together.	Edge density + Distance to lek site + Gap + Agriculture + Forest + Pasture
Home range size is a function of edge density alone	Edge density
Home range size is determined by the distance from a female's territory to the nearest male lek site	Distance to lek site
Home range size is determined by relative proportions of habitat types alone: Gap, Forest, Pasture, and Agriculture	Gap + Agriculture + Forest + Pasture*
Home range size is determined by the amount of gap alone	Gap
Home range size is a function of the amount of agriculture habitat available	Agriculture
Home range size is a function of the amount of Forest habitat alone	Forest
Home range size is a function of the amount of agriculture habitat alone	Agriculture

* One habitat type withheld each time during model selection process

Table 2.2. Vegetation measurements within 5 - and 11m radii at both nest and paired non-nest points.

Variable	Description
5m radius	
large stems	number of stems > 2.5 cm dbh
canopy cover	percent canopy cover
11m radius	
small trees	number of trees dbh 8-23cm
large trees	number of trees dbh > 23cm
small snags	number small snags < 12cm circumference
large snags	number small snags > 12cm circumference
Nest only	
nest tree size	dbh (cm) of the nest tree
nest orientation	orientation (degrees) of the nest
tree height	height of the nest tree (cm)
branch diameter	diameter (cm) of the branch supporting the nest
nest height	height of the nest from the ground (cm)
distance from trunk	distance from the trunk of the nest tree to nest (cm)
distance to edge	distance from nest to the forest edge
top vegetation cover	percent vegetation covering the nest
side vegetation cover	percent vegetation cover averaged from each side of the nest (N, S, E, and W)

Table 2.3. Hypotheses and candidate models of the effects of various landscape characteristics on the presence of Long-tailed Manakin nests.

Hypothesis	**Candidate model**
Nest presence is a function of the number of large stems, percent canopy cover, number of small trees, number of large trees, number of small snags, and number of large snags	Large stems + Canopy cover + Small tree + Large tree + Small snag + Large snag
The amount of large stems alone determines nest presence for Long-tailed Manakins	Large stem
The amount of canopy cover alone determines nest presence for Long-tailed Manakins	Canopy cover
The number of small trees alone determines whether or not Long-tailed Manakins will nest in a particular area	Small tree
The number of large trees alone determines whether or not Long-tailed Manakins will nest in a particular area	Large tree
The number of small snags alone determines whether or not Long-tailed Manakins will nest in a particular area	Small snag
The number of large snags alone determines whether or not Long-tailed Manakins will nest in a particular area	Large snag

Table 2.4. Predictor variables, number of parameters (K), log likelihood (LogL), AICc, ΔAICc, and Akaike weights (w) for the set of candidate models (i) for predicting home range size of female Long-tailed Manakins. Models are listed in order of decreasing plausibility based on Akaike weights.

Model	K	LogL	AICc	ΔAICc	w_i	percent w_i
Gap, Agriculture, and Forest						
Agriculture	3	-34.944	77.601	0.000	0.262	100.000
Forest	3	-35.473	78.659	1.057	0.154	58.934
Distance to lek	3	-35.508	78.730	1.129	0.149	56.877
Edge density	3	-35.510	78.732	1.131	0.149	56.801
Gap	3	-35.514	78.741	1.140	0.148	56.564
Gap Agriculture	4	-34.865	80.852	3.251	0.052	19.686
Agriculture Forest	4	-34.883	80.887	3.286	0.051	19.338
Gap Forest	4	-35.472	82.067	4.465	0.028	10.724
Gap Agriculture Forest	5	-34.856	84.818	7.217	0.007	2.710
Global Model	7	-34.729	94.850	17.249	0.000	0.019
Gap, Agriculture, and Pasture						
Agriculture	3	-34.944	77.601	0.000	0.266	100.000
Distance to lek	3	-35.508	78.730	1.129	0.151	56.880
Edge density	3	-35.510	78.732	1.131	0.151	56.801
Gap	3	-35.514	78.741	1.140	0.150	56.564
Pasture	3	-35.536	78.785	1.184	0.147	55.329
Gap Agriculture	4	-34.865	80.852	3.251	0.052	19.688
Agriculture Pasture	4	-34.941	81.004	3.403	0.048	18.238
Gap Pasture	4	-35.507	82.135	4.534	0.028	10.364
Gap Agriculture Pasture	5	-34.856	84.818	7.217	0.007	2.711
Global Model	7	-34.729	94.850	17.249	0.000	0.019
Gap, Forest, and Pasture						
Forest	3	-35.473	78.659	0.000	0.184	100.000
Distance to lek	3	-35.508	78.730	0.071	0.177	96.505
Edge density	3	-35.510	78.732	0.074	0.177	96.375
Gap	3	-35.514	78.741	0.082	0.176	95.972
Pasture	3	-35.536	78.785	0.126	0.172	93.876
Forest Pasture	4	-35.319	81.761	3.102	0.039	21.202
Gap Forest	4	-35.472	82.067	3.408	0.033	18.197
Gap Pasture	4	-35.507	82.135	3.477	0.032	17.582
Gap Forest Pasture	5	-34.856	84.818	6.159	0.008	4.600

Global Model	7	-34.729	94.850	16.191	0.000	0.033
Agriculture, Forest, and Pasture						
Agriculture	3	-34.944	36.647	0.000	0.477	100.000
Agriculture Pasture	4	-34.941	39.823	3.176	0.098	20.437
Agriculture Forest	4	-34.883	39.831	3.184	0.097	20.353
Distance to lek	3	-35.508	40.117	3.470	0.084	17.640
Edge density	3	-35.510	40.418	3.770	0.072	15.181
Forest	3	-35.473	40.648	4.001	0.065	13.526
Pasture	3	-35.536	40.885	4.237	0.057	12.019
Global Model	7	-34.729	42.959	6.312	0.020	4.259
Agriculture Forest Pasture	5	-34.856	43.519	6.871	0.015	3.220
Forest Pasture	4	-35.319	43.753	7.105	0.014	2.866

Table 2.5. Model-averaged results for composite model of landscape variables that affect Long-tailed Manakin home range size.

Parameter	Parm_est	std_err	upper 95% CI	lower 95% CI
Intercept	2.7676	2.3948	7.4615	-1.9262
Edge density	-0.0024	0.0848	0.1639	-0.1687
Distance to lek	0.0109	0.0818	0.1712	-0.1493
Gap	0.0940	0.4516	0.9791	-0.7912
Agriculture	0.1494	0.7091	1.5393	-1.2405
Forest	-0.0471	0.4054	0.7476	-0.8417
Pasture	-0.0432	0.4413	0.8217	-0.9081

Table 2.6. Simplified ranks of habitat selections by female Long-tailed Manakins. Higher numbers indicate selection.

	MCP		KDE		LoCoH	
Habitat type	2nd Order	3rd Order	2nd Order	3rd Order	2nd Order	3rd Order
Gap	3	3	3	2	3	2
Agriculture	1	2	1	1	1	3
Forest	4	4	4	4	4	4
Pasture	2	1	2	3	2	1

Table 2.7. Summary statistics of vegetation measurements taken within 5 - and 11m radii at both nest and paired non-nest points.

Variable	N	Mean	SE	Minimum	Maximum
5m					
Small stem	12	297.417	15.390	183.000	390
Large stem	12	37.750	3.804	22.000	60
Green cover (%)	12	53.646	2.997	43.750	80
Leaf litter (%)	12	55.417	8.335	13.750	96.250
Canopy cover (%)	12	94.973	0.556	91.160	96.880
11m					
Small tree	12	38.75	4.02	21.00	71
Large tree	12	16.58	2.14	7.00	35
Small snag	12	18.00	2.18	7.00	29
Large snag	12	8.92	1.50	3.00	22

Table 2.8. Predictor variables, number of parameters (K), log likelihood (LogL), AICc, ΔAICc, and Akaike weights (w) for the set of candidate models (i) for 5 -and 11m variables predicting nest presence. Models are listed in order of decreasing plausability based on Akaike weights.

Model	**K**	**LogL**	**AICc**	**ΔAICc**	**w_i**
Large snag	2	-6.555	22.110	0.000	0.456
Small snag	2	-7.767	24.533	2.423	0.136
Large stem	2	-7.953	24.906	2.796	0.113
Canopy cover	2	-7.979	24.958	2.848	0.110
Small tree	2	-8.144	25.287	3.177	0.093
Large tree	2	-8.251	25.501	3.391	0.084
Canopy cover Small snag Large snag	4	-5.319	30.637	8.527	0.006
Canopy cover Small tree Large snag	4	-6.298	32.595	10.485	0.002
Large stem Canopy cover Small tree	5	-6.003	40.805	18.695	0.000
Large stem Small tree Large tree Large snag	5	-6.100	40.999	18.889	0.000
Large stem Canopy cover Small tree Large tree	5	-6.781	42.362	20.252	0.000
Global Model	7	-5.100	74.200	52.090	0.000

Table 2.9. Model averaged results for logistic regression model of nest presence.

Parameter	**Parameter est**	**SE**	**Odds ratio**	**Upper 95% CI**	**Lower 95% CI**
Intercept	-3.590	7.544	0.028	72904.088	0.000
Large stem	0.040	0.048	1.041	1.145	0.947
Canopy cover	0.227	0.362	1.255	2.553	0.617
Small tree	-0.024	0.047	0.976	1.071	0.890
Large tree	-0.030	0.083	0.970	1.142	0.824
Small snag	-0.092	0.091	0.912	1.089	0.764
Large snag	0.318	0.226	1.374	2.139	0.882

Table 2.10. Summary statistics of variables measured at nests only.

	N	Mean	SE	Minimum	Maximum
nest tree size (cm)	6	1.500	0.165	1	2
nest orientation (degrees)	6	185.833	19.850	95	230
tree height (cm)	6	191.167	18.798	150	250
branch diameter (cm)	6	0.700	0.052	0.5	0.9
nest height (cm)	6	126.000	13.429	80	170
distance from trunk (cm)	6	32.667	8.273	12	70
distance to edge (m)	6	38.667	8.413	12	60
top vegetation cover (%)	6	79.167	5.974	60	95
side vegetation cover (%)	6	72.333	4.211	61.25	86.25

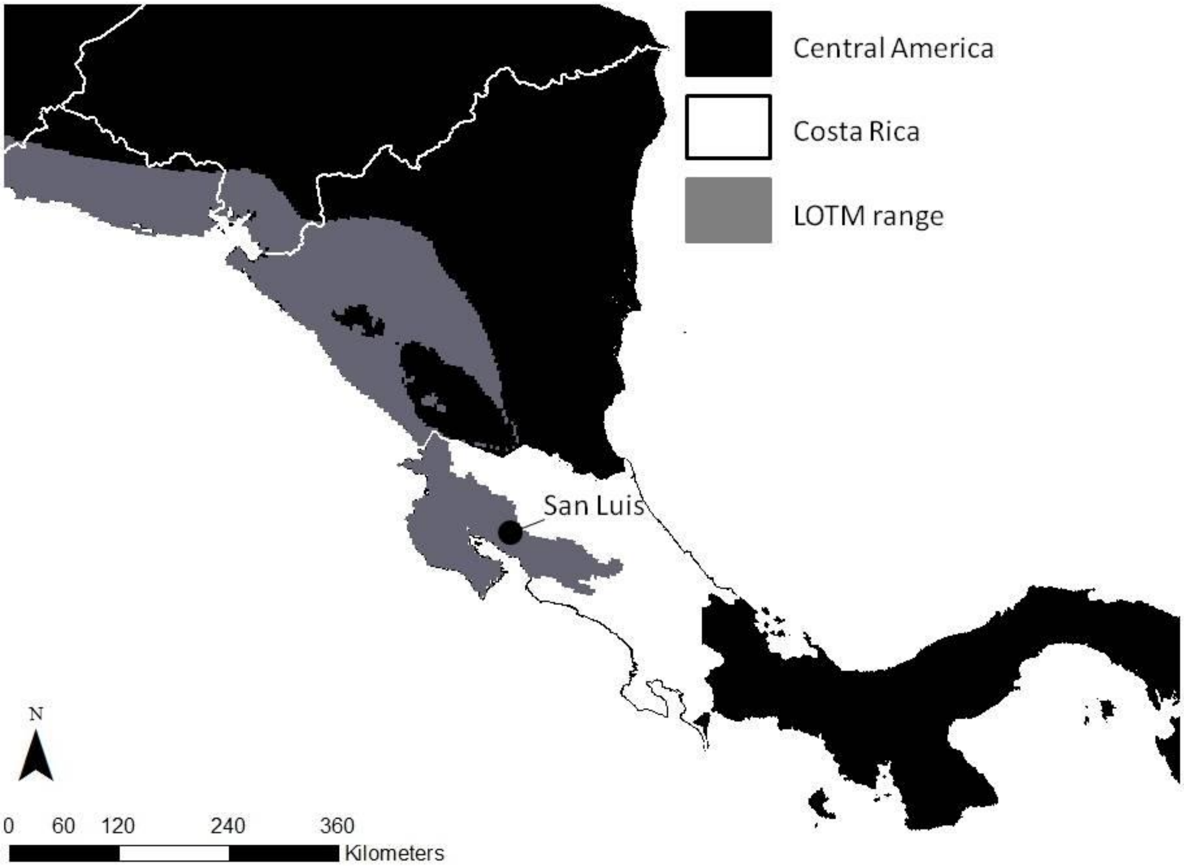

Figure 2.1. Long-tailed Manakin range within Central America. Study area was San Luis, Costa Rica.

Figure 2.2. Upper San Luis valley. Study area considered to be all area within polygon.

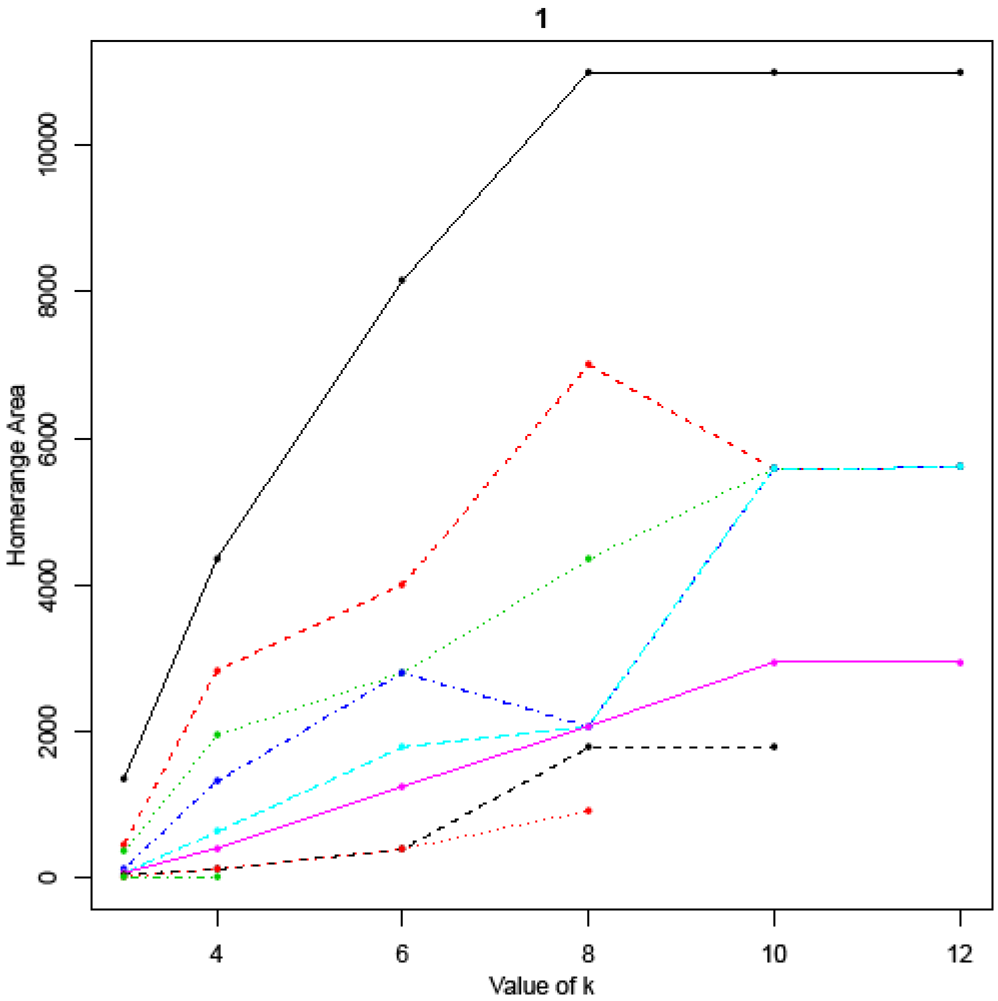

Figure 2.3. Area vs. k plot for individual #34. Home range size levels off at a value of k = 8 (solid line).

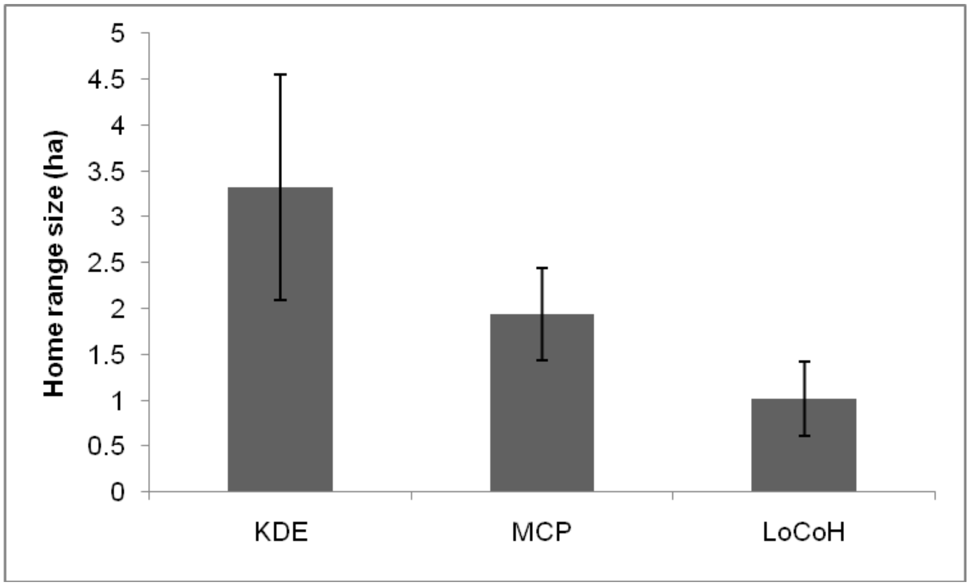

Figure 2.4. Mean Home range size for female Long-tailed Manakins generated by 3 different home range estimators. Error bars represent standard error.

CHAPTER 3
MAJOR CONCLUSIONS AND FINDINGS

Forested landscapes in the Neotropics are continually threatened by deforestation for many reasons, a main driving factor being cattle ranching. Often times this land use practice results in the displacement or loss of forest dwelling species in these areas. While it has been shown that some Neotropical forest species may persist for some time after habitat loss and fragmentation, it is thought that many forest species will not persist in highly fragmented landscapes for very long (Pimm and Askins 1995, Daily et al. 2008). Results from this study showed that female Long-tailed Manakins use human-dominated landscapes that include both small polyculture agricultural plots and low-intensity cattle ranches with forested windbreaks or hedgerows during the breeding season. Edge habitats showed to be important areas and were heavily used by female Long-tailed Manakins throughout the breeding season, which is likely due to the high abundance of fruiting plants located along forest edges during the rainy season (Restrepo and Gómez 1998). While edge habitats provided an adequate source for food finding, nest locations were found to be closer to the forest interior, where a moderate level of structural habitat heterogeneity is maintained.

While there have been other studies that have addressed habitat use of human-dominated landscapes by forest species in the Neotropics, none has considered the effects of low-intensity cattle ranching systems on habitat use. Furthermore, no other study has focused solely on female Long-tailed Manakins, thus very little has been known about habitat use within any part of their extensive range (Stiles and Skutch 1989).

A better understanding of habitat requirements for forest birds, such as Long-tailed Manakins, could potentially help land managers decide the future direction of conservation decisions in the Upper San Luis valley, which is connected to the Monteverde Cloud Forest Preserve and Children's Eternal Rainforest. The process of protecting forest habitat in Costa Rica, as well as throughout the Neotropics, will likely have to be a system that works with agrarian communities such as the Upper San Luis valley. Small farming parcels with a high level of crop/cover diversity have been shown to provide relatively good habitat for certain levels of utilization by forest species. In addition, low-intensity cattle ranching has shown that it too may be an effective way to harbor forest species. This information, in the hands of the landowners of San Luis, can help to foster conservation efforts that benefit forest species, such as the Long-tailed Manakin, as well as to continue to provide goods and services from the land for the local communities.

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