FACTORS AFFECTING ALTITUDINAL MIGRATION OF LONG-TAILED MANAKINS (*CHIROXIPHIA LINEARIS*) IN A TROPICAL AGRICULTURAL LANDSCAPE

by

AN CHEE HSIUNG

(Under the Direction of Richard Chandler)

ABSTRACT

Altitudinal migration exists in many taxa around the world, yet our understanding of the factors influencing the behavior is limited. The objectives of this study were to gain a deeper understanding of altitudinal migration by synthesizing existing knowledge and by studying migratory propensity of a tropical bird species. First, I conducted a literature review highlighting common patterns and drivers of altitudinal migration, current knowledge gaps, and conservation implications of the behavior. I then investigated altitudinal migration of long-tailed manakins (*Chiroxiphia linearis*) in an agricultural landscape in Costa Rica. Capture-recapture and radio telemetry data were collected at low and high elevations between January and April of 2016. Five of the 12 tracked manakins migrated upslope during the study. Manakin abundance decreased in small forest fragments at low elevation and increased at high elevation, while abundance increased at both low and high elevations in large fragments. However, my results did not demonstrate that individual traits such as age, sex, and body size affect migratory propensity.

INDEX WORDS: Altitudinal migration, elevational movement, partial migration, long-tailed manakin, *Chiroxiphia linearis*, Costa Rica

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CHAPTER 1

INTRODUCTION

Background

Altitudinal migration is characterized by seasonal movements of animals between breeding and non-breeding sites located at different elevations (Rappole 2013). Altitudinal migration behavior exists in a variety of taxa, including mammals (Takatsuki et al. 2000, Parrini et al. 2003, Sawyer et al. 2005, Rice 2008, Skidmore et al. 2008, Bohrer et al. 2014, Wen et al. 2014), insects (Shapiro 1973, Hunt et al. 1999, Gutiérrez and Wilson 2014, Slager and Malcolm 2015), and birds (Rabenold and Rabenold 1985, Burgess and Mlingwa 2000, Gillis et al. 2008, Garwood et al. 2009, Boyle et al. 2010, Hardesty and Fraser 2010, Powell and Bjork 2010, Papeş et al. 2012). Despite being a widespread behavior exhibited by many species around the world, altitudinal migration and the factors that influence the behavior are poorly understood. In temperate regions, altitudinal migration typically involves individuals moving between lower elevation winter ranges and higher elevation summer ranges, and the timing of migration often occurs during spring and autumn when the climate is shifting within the animal's range (Hahn et al. 2004, Hebblewhite et al. 2008, Rice 2008, Díaz et al. 2013, Green et al. 2015). In tropical regions, the timing of migration often coincides with the shift between wet and dry seasons (Boyle et al. 2010, Powell and Bjork 2010, Bohrer et al. 2014).

Migration often involves trade-off between costs and benefits of movement between habitats (Baker 1978, Dingle and Drake 2007). Seasonal fluctuation of food resources is one of

the major drivers behind migration in general, and can also be applied to altitudinal migration. It is common that the amount of food resources within a habitat vary seasonally due to change in climate throughout the year. Many studies, especially of ungulates, have demonstrated how individuals migrate altitudinally to track food resources (Festa-Bianchet 1988, Takatsuki et al. 2000, Hebblewhite et al. 2008). Similar patterns can also be found in the Neotropical avian species, especially in frugivorous and nectivorous birds whose food resources often vary between wet and dry seasons (Stiles 1985, 1988, Levey 1988, Blake and Loiselle 1991, Solorzano et al. 2000, Chaves-Campos 2003, 2004).

The climatic changes at different altitudes throughout the year can also be a major driving force behind altitudinal migration (Parrini et al. 2003, Igota et al. 2004, Boyle et al. 2010, Green 2010). An example of a weather element that affects altitudinal migratory behaviors is snow. Snow cover drives altitudinal migration in many ungulate species around the world, such as roe deer (*Capreolus capreolus*, Mysterud 1999, Ramanzin et al. 2007), sika deer (*Cervus nippon*, Igota et al. 2004), and ibex (*Capra ibex*, Parrini et al. 2003), and mule deer (*Odocoileus hemionus*, Sawyer et al. 2005). In the case of the American Dippers (*Cinclus mexicanus*) in Canada, the movement of birds from higher elevation breeding site to lower elevation wintering site might be caused by cold stress (Morrissey et al. 2004).

Most altitudinal migratory species are also partially migratory, in that only a subset of the population migrate annually (Rappole 2013). Partial migration is common across taxa and is exhibited in both temperate and tropical environments, and has been especially well-documented in birds (Ketterson and Nolan Jr 1979, Festa-Bianchet 1988, Takatsuki et al. 2000, Jahn et al. 2010, Belthoff and Gauthreaux 2013, Mcguire and Boyle 2013, Perez et al. 2014). Variation among characteristics of individuals, such as sex, age, and body weight cause individual animals

to react differently to changes in the environment due to their different needs. For example, larger-sized individuals within a population may not migrate far from the breeding grounds during the nonbreeding season because they can withstand the severe weather during the winter compared to smaller individuals (Ketterson and Nolan 1976). Additionally, dominant individuals of a population occupy habitats of higher quality while subdominant individuals are forced to migrate to suboptimal habitat due to competitive exclusion (Ketterson and Nolan 1979). These hypotheses have been tested on many long-distance migrants, however, little is known about their applicability to altitudinal migratory species (Lundberg 1985, Boyle 2008, Jahn et al. 2010, Norbu et al. 2013).

Many species in the tropics also exhibit altitudinal migratory behavior (Boyle 2008, Chaves-Campos et al. 2003). Our knowledge of tropical altitudinal migrants is limited. The lack of understanding of seasonal movements of altitudinal migratory species in the tropics is detrimental to conservation efforts of tropical biodiversity because there is insufficient knowledge of their year-round habitat requirements (Chaves-Campos et al. 2003, Powell and Bjork 2010). Moreover, without information about how the factors influences migratory propensity, it is impossible to predict how ongoing rapid environmental change will affect altitudinal migrants.

To gain a deeper understanding of animal altitudinal migration, I conducted a thorough literature review of documented patterns and drivers, and I identified current knowledge gaps and conservation implications of the behavior (Chapter 2). I then tested hypotheses related to partial altitudinal migration using the long-tailed manakins (*Chiroxiphia linearis*) as a study species (Chapter 3). Chapter 4 includes the major findings and conclusions of the research, and offers potential management implications for altitudinal migratory bird species in the tropics.

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CHAPTER 2

ALTITUDINAL MIGRATION: ECOLOGICAL DRIVERS, KNOWLEDGE GAPS, AND CONSERVATION IMPLICATIONS[1]

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Abstract

Animal migration has been the subject of intensive research for more than a century. Most research has focused on long-distance migration, and relatively little is known about the ecology of short-distance migration, such as altitudinal migration. In particular, information is lacking about the biotic and abiotic factors that influence migratory behavior and individual propensity to migrate. Without this information, it is difficult to predict how rapid environmental changes will affect the viability of short-distance migrant populations, which are widespread and highly diverse both geographically and taxonomically. To assess current state of knowledge of altitudinal migration, we reviewed and synthesized the peer-reviewed literature on altitudinal migration of all studied taxa. The extrinsic drivers that have received the most support are variation in food resources and climatic factors. Additionally, hypotheses regarding intrinsic factors such as sex, age, and body size of individuals within a population have also received support from various studies. We then discussed knowledge gaps in our understanding of the system and presented conservation implications of the behavior. Some of the gaps that still exist in our understanding of altitudinal migration include the effects of changes in landscape composition and configuration caused by habitat loss and fragmentation, and impacts on altitudinal migratory species by changes in global climate change. Lastly, we presented conservation implications of altitudinal migration in the face of changing environments, and provided ideas for future research on altitudinal migratory species.

Keywords: altitudinal migration, elevational movement, partial migration

Introduction: Migration Overview

In his book "The History of Animals", Aristotle (350 B.C.) provided one of the first descriptions of migratory behaviors in several animals, including fish who "migrate from the outer seas in towards shore, and from the shore towards the outer seas, to avoid the extremes of cold and heat" and birds that "in winter and frosty weather come down to the plains for warmth, and in summer migrate to the hills for coolness". The next two thousand years saw little progress in human understanding of animal migration, as evidenced by Linnaeus' (1757) treatise on avian migration, "Migrationes Avium", in which he explained that swallows disappeared during the winter because they dove under the water in the lakes and hibernated until the next spring.

Substantial progress in the study of animal migration began in the 19th century with discoveries in the physiology and underlying mechanisms of the behavior. Several books on avian migration were published with detailed documentation of timing and direction of bird migration and description of migration flight (Harvie-Brown and Cordeaux 1879, Whitlock 1897). The 20th century saw an explosion of research on migration, with great advances made by experimental studies of migration orientation strategies. For example, the indigo bunting (*Passerina cyanea*) was observed to use the celestial system to navigate (Emlen 1967). More recently, it was discovered that some species of sea turtles use magnetic fields to navigate during migration (Lohmann and Lohmann 1996). Important discoveries were also made about the wide array of migratory strategies used by different animal taxa, ranging from certain insect species that only migrate once in a lifetime for short distances (Baker 1978, Dingle and Drake 2007) to extensive long-distance latitudinal migration systems displayed by many avian, mammalian, reptile, and lepidopteran species (Luschi et al. 2003, Rappole 2013, Hansson and Akesson 2014, Vidal and Rendón-Salinas 2014).

Despite centuries of observations and research on animal migration, researchers have yet to agree on a definition for this common behavior. From the spatial point of view, some researchers have made the distinction between inter-habitat movement which they term "migration", and intra-habitat movement which is "non-migration" or "trivial movement" (Baker 1978). However, this definition suffers from the difficulty associated with objectively classifying habitat types. Other researchers have tried to use non-spatial classification schemes to define migration. For example, entomologists have defined migration as a large number of individuals "flying steadily in one definite direction" (Williams 1957). However, certain animal migrations do not fall under this definition, such as green sea turtles (*Chelonia mydas*) who migrate by being carried by ocean currents, and certain locust species migrate by being carried by the wind (Baker 1978). Ornithologists have defined migration as seasonal back-and-forth movements on a geographical scale (Baker 1978). Newton (2008) described migration as a behavior "in which individuals make regular return movements, at about the same times each year, often to specific destinations". To add even greater confusion, plant ecologists often equate migration with range shifts of plant species (Zhu et al. 2014). For the purpose of this paper, we will use the definition proposed by Rappole (2013), who stated that migration is "an annually repeated, seasonal movement between the breeding range and those regions where breeding does not occur… to exploit two or more environments whose relative suitability in terms of survival or reproduction changes over time."

There are many reasons for animals to migrate and each migratory behavior has its associated costs and benefits. Some benefits of migration include the ability to take advantage of seasonal availability of resources, to avoid predation, and to meet the resource needs at different life stages (Milner-Gulland et al. 2011). Some costs of migration include increased metabolic

expenditure during migration, increased risk of predation en route, delayed reproduction, and cost of settlement (Milner-Gulland et al. 2011). As a result, migratory behaviors are determined by the trade-off between the costs and benefits of moving from one location to another (Baker 1978, Milner-Gulland et al. 2011). These trade-offs also shape the evolution of migration, and in migratory decisions of individuals within a population. For example, the elk (*Cervus canadensis*) population in Banff National Park contains both migrant and resident individuals, and although migratory females are able to exploit higher quality food and have higher quality calves by migrating to summer ranges, they risk exposure to predators during migration and thus have lower survival rate (Hebblewhite and Merrill 2011). Similar behavior was observed in the cyprinid fish in southern Sweden, where the fish migrated from lakes to streams to minimize predation risk during the winter, and migrated back to lakes during the spring when foraging opportunities outweighed predation risk (Brönmark et al. 2008).

Animal migration can be categorized based on characteristics such as frequency and distance (Baker 1978, Rappole 2013). For the purpose of this paper, we will use distance to distinguish different types of migration. However, we recognize that the definition of long- vs. short-distance migration is a relative distinction simplifying the reality that the extent of migration is a continuum, rather than a dichotomy. Nonetheless, many taxa do exhibit bimodal distributions of migratory distance, and by categorizing each species into long- or short-distance migrants help researchers compare and contrast these systems and elucidate evolutionary history of migration. Rappole (2013) defined long-distance migration as movement of all individuals of a population over 2,000km away, often to a different continent. Examples of this include the leatherback sea turtle (*Dermochelys coriacea*) that can make inter-nesting movements for approximately 7000km (Hughes et al. 1998), Alaskan bar-tailed godwit (*Limosa lapponica*) that

can migrate for >11,000km from Alaska to New Zealand, and Humpback whales (*Megaptera novaeangliae*) who can migrate for > 7000 km a year (Hansson and Akesson 2014). Some animals perform rather short migrations. For example, green darners (*Anax junius*) in North America migrate for <12km daily on average (Wikelski et al. 2006). White bass (*Marone chrysops*) migrate for only a few kilometers between the open water and their spawning sites (Baker 1978). Amphibians and certain reptiles also do not migrate far from their wetland breeding sites due to risk of desiccation (Semlitsch and Bodie 2003).

Altitudinal migration is a type of short-distance migration in which animals migrate seasonally between breeding and nonbreeding grounds that differ in elevation (Rappole 2013). Altitudinal migration is found across many taxa, including mammals (Mysterud 1999, Takatsuki et al. 2000, Loucks et al. 2003, Mcguire and Boyle 2013, Bohrer et al. 2014), birds (Burgess and Mlingwa 2000, Chaves-Campos et al. 2003, Hahn et al. 2004, Powell and Bjork 2004, 2010, Boyle et al. 2011b, Norbu et al. 2013), insects (Alcock and Dodson 2008, Gutiérrez and Wilson 2014), and reptiles (Blake et al. 2013). Although widespread, both geographically and taxonomically, studies of altitudinal migration and the mechanisms underlying the behavior are limited. For example, numerous studies have been conducted examining movement patterns and migration routes of long-distance migrants (Hughes et al. 1998, Thirgood et al. 2004, Stutchbury et al. 2009, Horton et al. 2001, Rappole 2013, Trier weiler et al. 2014), but similar studies on altitudinal migrants are limited in contrast (Powell and Bjork 2004, 2010, Blake et al. 2013, Norbu et al. 2013).

Numerous hypotheses have been proposed to explain why animals migrate altitudinally, and in this paper, we (1) compile and synthesize published literature on altitudinal migration in all studied animal taxa, (2) evaluate existing hypotheses explaining altitudinal migration with

examples demonstrating the mechanisms, (3) identify knowledge gaps in the area of research, (4) evaluate conservation implications of altitudinal migration, and (5) propose potential future research directions.

Published Literature on Altitudinal Migration

Literature search

We searched the published literature using the online database *Web of Science* and search engine *Google Scholar*. We searched for the terms "animal altitudinal migration", "elevational movement", and "altitudinal movement". We also combined each search term with different taxa including birds, bats, reptiles, ungulates, and insects. We augmented the list of papers with literature discovered during our search. Current research on altitudinal migration that has not yet been published are not included in this synthesis. Furthermore, we included literature published in languages other than English. However, we recognize that there exists other literature written in foreign languages that are inaccessible to us and that we cannot include them because of limitations in our ability to understand them. Table 1 is a compilation of the literature covered by this review, including study species, location of studies, authors, and year of publication.

Factors Driving Altitudinal Migration

Food limitation hypothesis

Seasonal fluctuation of food resources is one of the major drivers of migration in general, and it is often used to explain altitudinal migration. It is common that the amount of food resources within a habitat vary seasonally in response to climate fluctuations throughout the year. Bohrer et al. (2014) discovered that the timing of altitudinal migration of elephants in Kenya coincided

with change in seasonal availability of vegetation at various elevations which was closely associated with change in precipitation. The elephants moved to areas with more vegetation during the dry season and moved upslope when the vegetation at lower elevations senesced (Bohrer et al. 2014). Fluctuation in food resources has also been identified as a major driver behind altitudinal migration in ungulates. In the Rocky Mountains, bighorn sheep (*Ovis canadensis*) ewes and yearlings migrate between lower elevation winter range and higher elevation summer range to take advantage of higher forage quality at those areas (Festa-Bianchet 1988). The sika deer (*Cervus nippon*) in Japan also migrate altitudinally while tracking forage (i.e. bamboo grass) downslope during the winter (Takatsuki et al. 2000, Igota et al. 2004). The huemul deer (*Hippocamelus bisulcus*) in the Argentinian Andes perform seasonal altitudinal migration which appeared to be driven by seasonal variation in food availability because they have been found to select for vegetaion common at lower elevations during the winter and vegetation common at higher elevations during the summer (Díaz et al. 2013).

Tracking seasonal vegetation availability by ungulates has been termed as "surfing the green wave" (Fryxell and Avgar 2012), and individuals within a population may employ different strategies for such behavior. For example, some individuals in a population of red deer (*Cervus elaphus*) in Norway choose to "surf" the green wave by tracking the "crest" of the green wave where vegetation availability and quality are the highest, while the other individuals moved ahead of the wave and arrive at a habitat in anticipation of increase in vegetation availability (Fryxell and Avgar 2012).

Although food availability is often invoked to explain altitudinal migration, forage quality may be equally important. Hebblewhite et al. (2008) tested a closely-related food limitation hypothesis which they named the "forage maturation hypothesis" (FMH). The FMH

predicts that altitudinal migration of certain ungulates is driven by selection of younger vegetation with intermediate biomass that is higher quality forage than more mature vegetation. The reason that animals select for younger plants is that higher biomass in mature plants requires longer handling time and more effort to digest. As a result, the net energy intake for an animal decreases after plants reach an intermediate biomass (Hebblewhite et al. 2008). One prediction of this hypothesis is that migratory individuals within a population will be better able to track habitats with higher quality forage, or plants with intermediate biomass, than resident individuals. In agreement with the prediction, migrant elk in the Canadian Rocky Mountains selected higher quality forage than residents at both landscape and homerange scales, while residents selected for vegetation with high biomass but low quality (Hebblewhite et al. 2008). Similar behavior was observed in a population of female red deer (*Cervus elephus*) in Norway (Albon and Langvatn 1992).

The food limitation hypothesis has also found support in studies of tropical avian species, especially in frugivores and nectivores (Stiles 1985, 1988, Levey 1988, Blake and Loiselle 1991, Solorzano et al. 2000, Kimura et al. 2001), whose food resources are known to vary seasonally. Many of these studies examined the change in pattern of species diversity over elevation gradients over time, and correlated it with seasonal change in fruit abundance (Levey 1988, Stiles 1988, Blake and Loiselle 1991). Several studies of avian communities in Costa Rica found evidence that abundance of frugivorous birds tended to increase at higher elevations and decrease at lower elevations during the dry season (January-April), and exhibit the opposite pattern during the wet season (May-December) (Levey 1988, Blake and Loiselle 1991, Loiselle and Blake 1991). This pattern coincided with peak fruiting season of plants that are important part of the diet of these species (Levey 1988, Blake and Loiselle 1991, Loiselle and Blake 1991).

Other support for the food limitation hypothesis include frugivorous and nectivorous bats that have been found to track resources while migrating altitudinally (Mcguire and Boyle 2013). The flowering of some columnar cactus species has been suggested to be an attractant for nectivorous bats who migrate altitudinally (Valiente-Banuet et al. 1997). Furthermore, some insectivorous bats migrate over an elevational gradient to follow seasonal fluctuation of prey abundance at different elevations (Mcguire and Boyle 2013). For example, the Hawaiian hoary bats (*Lasiurus cinereus semotus*) migrate upslope to track the irruption of moth abundance during the winter (Menard 2001). In insects, resource availability explains altitudinal migration of certain butterfly species, such as the common brimstone (*Gonepteryx rhamni*) in Spain where some individuals migrate downhill during the winter because the density of host plants is the highest at lower elevation at the time (Gutiérrez and Wilson 2014).

Migration driven by weather-induced food shortage is exhibited in the social wasps of the genus *Polistes* and *Mischocyttarus* in Guanacaste, Costa Rica who have been observed to migrate to high elevations during the dry season where the temperature is colder compared to lower elevations (Hunt et al. 1999). The reason for this migration was thought to be that the dry climate at lowlands resulted in low food availability, while the colder temperature at high elevations provided ideal climate for the wasps to be dormant (Hunt et al. 1999). As soon as the wet season started, the wasps once again descended to low elevations to reproduce. Similar movement patterns were observed in some butterfly species in Costa Rica as well, where the adults moved upslope to the montane forests and spent approximately eight to eleven months in the state of reproductive diapause. The downslope migration of these butterflies generally happened in April and May and was often cued by the first rain shower of the wet season (Haber and Stevenson 2004).

However, not all studies of the food limitation hypothesis have found evidence supporting the hypothesis. Boyle (2010) tested the food limitation hypothesis in white-ruffed manakins (*Corapipo altera*) in Costa Rica by measuring fruit abundance at different elevations within her study area over one year and examined the relationship between abundance of fruit and manakins (Boyle 2010). Contrary to expectations, little evidence was found to support the food limitation hypothesis in the study (Boyle 2010). While the uphill migration of white-ruffed manakins coincided with peak fruiting season, fluctuation in fruit availability did not explain the downhill migration in this species, suggesting altitudinal migration in White-ruffed Manakins is driven by more than one variable (Boyle 2010).

Predation hypothesis

Several studies have revealed difference in predation risk of animals between low and high latitudes, and also low and high elevations (Skutch 1985, Martin 2015). The effects of predation risks can be classified as either consumptive or non-consumptive depending on whether predation affects survival rates, reproductive performance, or foraging behavior (Sih et al. 2010). Both consumptive and non-consumptive effects of predation risk could be important drivers of altitudinal migration.

In birds, the relationship between nest predation rates and elevation is equivocal. In the tropics, nest predation rates have been observed to be higher at lower elevations compared to higher elevations (Skutch 1985). The underlying mechanism is thought to be that there is lower species richness, and lower abundance of predators in general. Therefore, it is more advantageous for birds to breed at higher elevations in order to increase their nest success and, ultimately, their fitness. However, other studies have found the difference to be not significant

(Badyaev and Ghalambor 2001). Furthermore, artificial nest predation experiments have revealed conflicting evidence to support this prediction. A study conducted on the Caribbean slope of Costa Rica revealed a weak inverse relationship between artificial nest predation rate and elevation (Boyle 2008b). Another study conducted in Cameroon found a decrease in nest survival with increasing altitude (Djomo Nana et al. 2015). Thus, it is possible that nest predation risk is not a strong driver of altitudinal migration for birds that breed at higher elevations.

Predation of offspring can be a migratory driver, especially in mammals. A study of bighorn sheep migration in the Canadian Rockies revealed that predation risk of lambs, in combination with forage quality, could be drivers behind altitudinal migration of ewes (Festa-Bianchet 1988). It was observed that pregnant ewes migrated upslope to give birth to their lambs during the spring while the forage quality at lower elevations were better than that of the lambing area (Festa-Bianchet 1988). Additionally, pregnant ewes migrated upslope earlier than non-pregnant ewes during the spring where the terrain provided more protection against predators. Therefore, the reason for upslope movement during the spring for the pregnant ewes is to reduce predation risk of the lambs (1988).

While lower predation rates at a certain elevation may be an incentive for animals to migrate altitudinally, migrants often expose themselves to predators during migration as well. By moving to higher elevation summer ranges, the migrant elk in Banff National Park reduced their predation risk by 70% compared to that of the resident individuals that remain at lower elevation (Hebblewhite and Merrill 2007). However, by migrating between winter and summer ranges, migrant elks also exposed themselves to higher wolf predation risk while moving, thus migrants face a trade-off between decreased predation risk at higher elevation summer ranges and increased predation risk during migration (Hebblewhite and Merrill 2007).

Weather-driven hypothesis

Availability of food resource at different elevations may be associated with changes in climatic conditions which dictates the growing season of vegetation. Weather conditions and food availability are often highly correlated, thus it is unclear if it is the cold temperature, snow cover, or lack of above ground forage due to snow cover that is the reason for altitudinal migration in some animals. As such, it is difficult to tease apart weather-driven hypotheses from food limitation hypotheses. Typically, the availability of above ground vegetation depends on the initiation and duration of the growing season. Therefore, the lack of access to vegetation for forage due to high snow depth could be the reason why montane ungulates migrate downslope during the winter (Takatsuki et al. 2000, Parrini et al. 2003).

Some studies have suggested that weather variables alone, such as temperature and precipitation, may be a driver behind altitudinal migration of animals. In temperate regions, altitudinal migrants occupy lower elevation ranges during the winter to avoid the harsh weather at higher elevations. An example of a weather element that affect altitudinal migratory behaviors is snow. Snow cover drive altitudinal migration in many ungulate species around the world, including roe deer (*Capreolus capreolus*, Mysterud 1999, Ramanzin et al. 2007), sika deer (Igota et al. 2004), ibex (*Capra ibex*, Parrini et al. 2003), and mule deer (*Odocoileus hemionus*. Sawyer et al. 2005). Some individuals of the sika deer population in Japan migrate downslope during the winter, while others migrate upslope (Igota et al. 2004). Upslope migration during the winter is unique because it has not been documented in other cervids (Igota et al. 2004). One explanation for this behavior is that there is more coniferous cover at higher elevations during the winter creating shelter from harsh weather elements and predators (Igota et al. 2004). Regardless of upslope or downslope migration, the deer selected winter home ranges within habitats that had

less snow cover than their summer home ranges, suggesting the main driver for migration is precipitation (Takatsuki et al. 2000, Igota et al. 2004). Another example of weather as a migratory driver is evidenced in an American dipper (*Cinclus mexicanus*) population in Canada which moved from higher elevation breeding site to lower elevation wintering site to avoid cold stress (Morrissey et al. 2004b).

Limited foraging opportunities hypothesis

While severe weather could be the reason why animals migrate to lower elevations during the nonbreeding season, it has been proposed that it is not the weather per se that drives the animals to migrate, but the reduced foraging time caused by suboptimal weather (Boyle et al. 2010). A strong correlation was found between downhill migration of white-ruffed manakins and the timing of tropical storms in Costa Rica (Boyle et al. 2010). There was a dramatic increase in manakin captured at lower elevation sites following a storm during the study (Boyle et al. 2010). Additionally, birds that stayed at higher elevations during the storm have higher levels of stress hormones compared to birds that migrated downhill (Boyle et al. 2010). Thus, birds that stay at higher elevations tend to withstand long periods without foraging opportunities, unlike the migratory individuals (Boyle et al. 2010). Christmas Bird Count data from the Caribbean slope of Costa Rica also revealed that rainfall prior to counts are positively correlated with increase in known altitudinal bird species abundance at lowlands, which is consistent with the limited foraging opportunities hypothesis (Boyle 2011).

In California, high elevations in coastal mountain ranges receive more rainfall than lower elevations which is believed to reduce foraging opportunities for female bats during reproduction and lead to their downhill migration (Mcguire and Boyle 2013). Additionally, the upslope

migration of the Hawaiian hoary bats can also be explained by the increase in frequency of storms in the lowlands during the non-breeding season which reduces opportunities for the bats to feed on aerial preys (Mcguire and Boyle 2013).

Reproduction-related hypothesis

The Reproductive Constraints Hypothesis was proposed by researchers who have observed that in certain bat species, females migrate downslope during the winter because the low temperature and decreased food availability at higher elevations limit their ability to produce young (Mcguire and Boyle 2013). Migratory elk in Banff National Park had higher pregnancy rates and higher quality offspring than resident elks due to higher forage quality during calf season, which could be the driver of altitudinal migration in female elk (Hebblewhite and Merrill 2011). However, female and calf survival are also lower for migrant elk in the same area possibly due to predation (Hebblewhite and Merrill 2011). While migrating to a more suitable habitat with better climate could facilitate breeding success for some species, studies have found that uphill migration before the breeding season could be a result of intraspecific competition for suitable breeding habitats. For example, in the American dipper population in Canada, individuals that migrate upslope before the breeding season produce less offspring and provide food of lower quality to their young (Morrissey 2004, Gillis et al. 2008).

Synergistic factors

As previously alluded to in several examples, it is likely that a number of factors act synergistically to influence altitudinal migration. A classic example of synergistic factors is in the seasonal migration of many species of Lepidoptera to and from the dry forests of Guanacaste

Province, Costa Rica. In these forests, the hot, dry conditions combined with a lack of food during the dry season make them inhospitable, and the >3100 species of Lepidoptera of the area have evolved a variety of behaviors to adapt to these unfavorable conditions (Janzen 1987, 1988, 1993). Many species spend the bulk of the year in cooler, moister, higher elevation rainforests. Adults migrate to lower elevation dry forests with the onset of the wet season, with the primary cue being temperature. The dry forest changes from largely brown and leafless (many tree species are deciduous) to green and fully leafed within a few weeks, thus providing ample food for newly emerging caterpillars. However, although the rainy season can last up to six months, and new vegetation continues to leaf out over that span, most Lepidoptera are finished with reproduction after about only 1-3 months, a time when green vegetation is nearing its peak and the weather is still relatively cool and humid. Janzen (1988, 1993) explained that myriad predators and parasitoids are also at their annual low in numbers at the onset of the rainy season. Their pronounced functional response but delayed numerical response to increased numbers of caterpillar prey is such that only the first half of the rainy season is a profitable time for reproduction by butterflies and moths. Newly emerged adults migrate back to rainforest at this time. Thus, hypotheses related to weather, food availability (and perhaps quality), reproduction and predation are all relevant and likely act in concert to determine patterns of altitudinal migration in these species.

Partial Migration in Altitudinal Migrants

While the above hypotheses help explain how extrinsic mechanisms facilitate altitudinal migration, there are certain individual traits such as age, sex, and body conditions that may result in differentiation of individual migratory strategies within a population. The hypotheses

pertaining to environmental changes such as variation in food and weather explain the altitudinal migration over relatively short time scales. In contrast, the hypotheses regarding individual characteristics that determine migratory propensity help explain how the combination in environmental factors and individual traits result in partially migratory populations and the evolution of altitudinal migration.

Partial migration is a phenomenon in which a subset of the population of animals migrate annually, while the others stay sedentary, and it is common across taxa in both temperate and tropical environments (Ketterson and Nolan Jr 1979, Festa-Bianchet 1988, Takatsuki et al. 2000, Jahn et al. 2010, Belthoff and Gauthreaux 2013, Mcguire and Boyle 2013, Perez et al. 2014). Variation among characteristics of individuals, such as sex, age, and body weight cause individual animals to react differently to changes in the environment due to their different needs. The question of "why do some individuals of a population migrate while others do not" has lead researchers to test several hypotheses that may explain these patterns (Boyle and Conway 2007, Jahn et al. 2010, Boyle et al. 2011a). Altitudinal migratory species that also exhibit partial migration behavior are ideal systems for studying what drives migration patterns because the seasonal variations between the locations, resources, and climates are not as drastic, thus more controlled, as those of long-distance migrants (Boyle and Conway 2007, Boyle 2008a).

Hypotheses on partial migration

Several hypotheses have been proposed to explain partial migration, especially with regards to birds, and some of them have been investigated within the context of partial altitudinal migration (Boyle 2008a). Ketterson and Nolan (1976, 1979) proposed three hypotheses explaining partial avian migratory behaviors: the body size hypothesis, the dominance hypothesis, and the arrival

time hypothesis, which they tested using Dark-eyed juncos (*Junco hyemalis*) in North America as a model species. With respect to the body size hypothesis, they predicted that larger-sized individuals within a population would not migrate far from the breeding grounds during the nonbreeding season because they could withstand the severe weather during the winter compared to smaller individuals (1976). The dominance hypothesis predicted that dominant individuals of a population occupy habitats of higher quality while subdominant individuals were forced to migrate to suboptimal habitat due to competitive exclusion (Ketterson and Nolan 1979). The arrival time hypothesis predicted that the males of the population did not migrate far from the breeding grounds before the nonbreeding season because it was advantageous for them to stay close to the breeding grounds in order to occupy better territories during the upcoming breeding season (Ketterson and Nolan 1979). These hypotheses have been tested on many long-distance migrants, however, little is known about their applications in altitudinal migratory species (Lundberg 1985, Boyle 2008a, Jahn et al. 2010, Norbu et al. 2013).

Partial altitudinal migration

American dippers in southeast British Columbia exhibit partial migratory behavior where migrants and residents gather at low elevation wintering sites during the nonbreeding season, and migrants move to higher elevation sites during the breeding season (Morrissey 2004, Gillis et al. 2008). Researchers found that the migrants of this partial migratory population have lower reproductive success than the residents, and they concluded that the migrants are likely forced out of ideal breeding habitats due to competitive exclusion, consistent with the dominance hypothesis (Gillis et al. 2008, Mackas et al. 2010, Green et al. 2015).

The white-ruffed manakins in Costa Rica also exhibit partially migratory behaviors in which both migrants and residents breed at higher elevation sites, and after the breeding season migrants move downslope to the nonbreeding grounds (Boyle 2008a). Neither dominance nor arrival time hypotheses explain partial migration in this species, because the younger individuals are not more likely to migrate than older (more dominant) individuals, and females are not more likely to migrate than males (Boyle 2008a). The body size hypothesis may explain partial migration in this species, because smaller individuals are more likely to migrate compared to larger individuals (Boyle 2008a).

Most montane ungulate populations are partially migratory where the migrants and residents share low elevation wintering range and migrants move upslope to their summer range after the winter (Mysterud 1999, Takatsuki et al. 2000, Parrini et al. 2003, Ramanzin et al. 2007, Hebblewhite et al. 2008, Hebblewhite and Merrill 2011). Such pattern can be explained by the dominance hypothesis. For example, the summer grounds of roe deer in the Italian Alps are of poorer quality than the lower elevation habitats (Ramanzin et al. 2007). Therefore, it was hypothesized that subdominant individuals were forced to migrate to higher elevations during the summer (Ramanzin et al. 2007).

Sex-biased partial migration is common among bats in the temperate world where females usually occur at lower elevations than males during the summer (Mcguire and Boyle 2013). The arrival time hypothesis may explain this pattern, as mating for several bat species occur at higher elevations during hibernation. Thus, male bats that remain at higher elevation hibernation sites during the summer instead of migrating downslope have a better chance of gaining access to females (Mcguire and Boyle 2013). Conversely, female bats benefit from

migrating downslope before hibernation because of reduces the cost of going into torpor which has negative impact on fetal development (Mcguire and Boyle 2013).

The Galapagos tortoises (*Chelonoides nigra*) on the Santa Cruz Island in the Galapagos archipelago are partially migratory and have been observed to migrate altitudinally to track changes in seasonal vegetation dynamics (Blake et al. 2013). Contrary to the predictions of the body size and dominance hypothesis, the larger and presumably more dominant individuals of the population have higher tendency to migrate altitudinally (Blake et al. 2013).

Current Knowledge Gaps

In general, the hypotheses regarding extrinsic factors that have found the most support in empirical studies are the ones concerning fluctuation in resources (food) and climatic variables. Furthermore, these variables affect individuals within a population differently because of variations among individual traits, such as age, sex, and body size. As a result, intrinsic factors within a population shape altitudinal migratory patterns of partially migratory species. Within the major partial migration hypotheses, each has received some support from various studies across taxa. However, there exists a need for linkage between the results of these studies to current human-modified environments, and how changes in the ecosystems may affect altitudinal migratory species. Below we discuss examples of such knowledge gaps and offer suggestions for future research directions to address these issues.

Potential impacts of rapid environmental change on altitudinal migration

Many of the studies of altitudinal migrations have alluded to the potential negative impact of habitat fragmentation to altitudinal migrants, especially forest fragmentation in the tropics

(Chaves-Campos et al. 2003, Powell and Bjork 2004, 2010). Researchers have found that forest fragmentation can potentially alter movement behavior of animals and ultimately decrease their survival rate (Rappole et al. 1989, Cohen and Lindell 2004, Hadley and Betts 2009). For example, wood thrushes (*Hylocicha mustelina*) that winter in Mexico have been observed to become "wanderers" who are not territorial during the non-breeding season, and evidence suggested that the mortalities observed during the study were mostly suffered by wanderers (Rappole et al. 1989). Thus, rapid change in human-modified landscape may force altitudinal migrants to traverse areas where they are more susceptible to predation and consequently experience lower survival rates, as in the migrant elk population in Banff National Forest in Canada (Hebblewhite and Merrill 2007).

Moreover, forest or habitat conversion to agriculture leads to decrease in available resources, increase in predation risk, and increase in human-wildlife conflict (Takatsuki et al. 2000, Bohrer et al. 2014). Because of continuous encroachment of agricultural and residential developments near protected areas, the separation between humans and wildlife has also decreased drastically. Deer and elephants have been reported to damage crops through consumption and movements on crop land (Takatsuki et al. 2000, Bohrer et al. 2014). Further investigation is needed to assess the degree at which altitudinal migrants are affected by modified landscape and to implement appropriate actions to mitigate the impact.

Global climate change has affected weather conditions in various habitats, forcing animals to cope by adjusting their behavior (Cotton 2003). A growing body of literature has shown that climate change has resulted in temperature warming at the wintering grounds of many species, leading to earlier departure dates for long-distance migrants (Cotton 2003, Cox 2010, Seebacher and Post 2015). The effects of climate change on altitudinal migrants, on the

other hand, has rarely been investigated (Inouye et al. 2000). It is possible that altitudinal migrants are more sensitive to climate change than long-distance migrants, because their range of distribution is often smaller thus more sensitive to changes in climatic variables such as temperature and precipitation. Thus, changes in climate and condition of the winter or summer grounds of these species significantly reduces optimal habitat for them. If these species are unable to alter their behavior or physiological needs, they could face drastic range contraction, as has been observed in several sedentary species (Moritz et al. 2008, Gibson et al. 2010).

Furthermore, climate change can lead to mismatches between animal phenology (timing of seasonal life-cycle events) and plant production for altitudinal migrants (Inouye et al. 2000). In the Colorado Rocky Mountains, climate change has resulted in temperature warming of lower altitudes during the winter (Inouye et al. 2000). As a result, American robins (*Turdus migratorius*) within the mountain range have been migrating earlier from lower elevation nonbreeding grounds to higher elevation breeding grounds (Inouye et al. 2000). Because of certain plasticity within the migratory behavior of some animals, some facultative migrants that summer at higher latitudes have lost their migratory propensity because warmer temperatures at higher latitudes leads to less severe winter conditions (Wilcove and Wikelski 2008). The same might occur within altitudinal migratory populations as well if winters at their breeding grounds become tolerable, causing loss of migratory propensity of the previously migratory individuals of the population.

Aside from changes in temperature, frequency and severity of precipitation associated with global climate change may also alter migratory behaviors of altitutdinal migrants. Since tropical storms have been proposed to be the cause for downhill migration of White-ruffed Manakins during the nonbreeding season, the projected increase in frequency and severity of

tropical storms in the future may force more individuals to migrate and share the habitats in the lowlands which have been decreasing due to human modification (Boyle 2008a).

Potential future research directions

While numerous studies on altitudinal migratory behavior have been conducted, the question of how change in landscape matrix affect altitudinal movements of animals remain mostly unanswered. Variables such as patch size, distance to neighbor, patch density, total edge, and edge density can have profound impact on animal movements (Hadley and Betts 2009). However, their effects on movements of altitudinal migrants have rarely been examined. New methods have been developed to estimate landscape resistant coefficients and connectivity using animal movement data (Royle et al. 2013, Graves et al. 2014). Similar methods could be applied to understand how landscape structure influences the movement patterns of altitudinal migrants. Factors such as change in temperature, forest cover, land use, and sea level can be incorporated into climate and spatial models to predict change in migratory behaviors of animals and, ultimately, species persistence in the face of changing environment.

Additionally, little is known about how, following habitat fragmentation, the size of fragments affects migratory propensity of altitudinal migrants. It has been suggested that resources availability is a major driver behind altitudinal migration patterns. However, no empirical study has attempted to make the connection between resource abundance and habitat fragment size, and how that may affect migratory behaviors of animals that depend on these fragments. Therefore, modeling migratory propensity against landscape variables such as fragment size, fragment distance, and landscape barriers will shed light on how habitat fragmentation might affect movements of altitudinal migrants.

The importance of conserving habitat patches to satisfy seasonal habitats needs of altitudinal migrants has been emphasized in several studies (Chaves-Campos et al. 2003, Powell and Bjork 2004, 2010, Bohrer et al. 2014). Because altitudinal migrants do not make drastic moves in one migration burst over hundreds of kilometers, they need connectivity between habitat patches for movement, foraging, and shelter. The intensification of deforestation in areas where altitudinal migratory species reside result in increase in distance between suitable habitats and barriers impeding animal movements. Therefore, preservation of corridors between habitat patches for this type of migrants is paramount (Chaves-Campos et al. 2003, Powell and Bjork 2004, 2010). The results of further studies on altitudinal migration can help develop reserve designs that incorporate such corridors as they will benefit not only the altitudinal migrants, but also other short distance migrants that require linkages and stop-over sites between their seasonal habitats.

Partial migration within altitudinal migratory species can also have important conservation implications. The variation in migratory propensity among individuals can have profound effects on population dynamics and persistence. For example, if the dominance hypothesis holds true such that subdominant individuals are forced to migrate to habitats of poorer quality, resulting in decrease in survivorship and reproduction, then the population as a whole could suffer from decreased annual recruitment rates. Additionally, if the arrival hypothesis holds true, females of a population would migrate further than males. The increase in migration distance could decrease their survivorship due to increase in predation and weather-related mortalities. Further investigations involving modelling individual fitness and migratory propensity can help shed light on effects of habitat changes on individuals and altitudinal migratory population dynamics as a whole.

Conclusions

Altitudinal migration is a phenomenon that exists in many species representing a wide array of taxa. In this paper, we reviewed the different altitudinal migration behavior exhibited by various species from mammals, birds, reptiles, and insects. Many studies have been conducted on examining drivers behind altitudinal migration, although our knowledge in causes making animals migrate altitudinally is still lacking. Currently, most supported hypotheses concerning altitudinal migration are related to resource availability and weather conditions. We also pointed out some knowledge gaps that still exist within the research of altitudinal migration and offered possibilities for future research.

First, even though numerous studies have documented altitudinal migration, there exists a lack of consensus as to what drive these migratory behaviors. It is likely because that there is not an over-arching theory that can explain altitudinal migration across all taxa given drastic differences between animal life histories. However, there is still a debate regarding why species migrate even within the same taxa (Stiles 1988, Boyle et al. 2010, Mcguire and Boyle 2013). In most cases, a combination of multiple drivers dictates altitudinal migratory behavior of a population, and also cause within-population variations as demonstrated in many birds (Gillis et al. 2008, Boyle 2010), mammals (Hebblewhite and Merrill 2007, Hebblewhite et al. 2008), and insects (Gutiérrez and Wilson 2014), which can make studying of the behavior complicated.

Second, little is known about how recent environmental changes, such as habitat fragmentation and climate change affect altitudinal migration behavior of animals. Altitudinal migration is common both taxonomically and geographically, and it exists in ecosystems that are under threat due to anthropogenic developments. To gain understanding of such impact is

essential due to the demonstrated negative impact of these changes on wildlife populations and global biodiversity (Dirzo and Raven 2003, Sodhi et al. 2008, Korfanta et al. 2012).

Lastly, important conservation implications have emerged from altitudinal migration research, including how population dynamics of partially migratory species may be affected by habitat fragmentation, and how reserve and corridor designs could incorporate elements that would aid in movements of altitudinal migrants. Our knowledge of the mechanism of altitudinal migration leaves much to be desired. Gaining further understanding in this migratory system will not only help decipher the evolution history of migration, but also obtain information of habitat needs of altitudinal migrants while managing for these species and their populations.

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Table 2.1 Summary of literature pertaining to animal altitudinal migration arranged by taxa

Taxon	Species	Location	Reference
Ungulate	Mountain Goat	British Columbia, Canada	Poole & Heard (2003)
	Mountain Goat	Washington, USA	Clifford G. Rice (2008)
	Sika Deer	Japan	Takatsuki *et al.* (2000)
	Sika Deer	Japan	Igota *et al.* (2004)
	roe deer	Italy	Ramanzin *et al.* (2007)
	roe deer	Portugal	Carvalho *et al.* (2008)
	roe deer	Norway	Mysterud (1999)
	bighorn sheep	Alberta, Canada	Festa-Bianchet (1988)
	Golden Takin	China	Skidmore *et al.* (2008)
	huemul deer	Patagonia	Diaz *et al.* (2013)
	Alpine ibex	Italy	Parrini *et al.* (2003)
	Alpine ibex	Italy	Aublet *et al.* (2009)
	Elk and deer	British Columbia, Canada	Poole & Mowat (2005)
	Mule deer	Wyoming, USA	Sawyer & Hoffman (2011)
	Mule deer and pronghorn	Wyoming, USA	Sawyer *et al.* (2005)
	Pronghorn	Nevada, USA	Collins (2016)
	Elk/wapiti	Canada	Morgantini & Hudson (1989)
	Elk	Banff NP, Canada	Hebblewhite & Merrill (2007)
	Elk	Banff NP, Canada	Hebblewhite *et al.* (2008)
	Elk	Banff NP, Canada	Hebblewhite & Merrill (2011)
	Red deer	Norway	Albon & Langvatn (1992)
	Woodland caribou	Yukon, Canada	Oosenbrug and Theberge (1980)
Bats	Natal long-fingered bat	Mount Kilimanjaro, Tanzania	Voigt *et al.* (2014)
	Hawaiian hoary bat	Hawaii	Bonaccorso *et al*. (2009)
	Lesser long-nosed bat	Mexico	Herrera-Montalvo (1997)
	Ipanema bat	Brazil	Esbérard *et al.* (2011)
	Bats (review)	Worldwide	McGuire & Boyle (2013)
	Multiple species of bats	Honduras	Erzberger *et al.* (2011)
	Big Brown bats	Colorado, USA	Neubaum *et al.* (2006)
	Daubentons bat	Germany	Encarnação *et al.* (2005)
	Neotropical bats	Neotropics	Fraser *et al.* (2010b)
Other mammals	Asiatic black bear	Japan	Izumiyama & Shiraishi (2004)
	Black-and-white monkey	China	Li *et al.* (2008)

Taxon	Species	Location	Reference
Other mammals	Giant Pandas	China	Loucks *et al.* (2003)
	Elephant	Kenya	Bohrer *et al.* (2014)
	small mammals	China	Wen *et al.* (2014)
	Orangutans	Malaysia	Buij *et al.* (2002)
Birds	White-ruffed Manakins	Costa Rica	Rosselli (1994)
	White-ruffed Manakins	Costa Rica	Boyle (2008a)
	White-ruffed Manakins	Costa Rica	Boyle (2008b)
	White-ruffed Manakins	Costa Rica	Boyle *et al.* (2010)
	White-ruffed Manakins	Costa Rica	Boyle (2010)
	Neotropical frugivores	Costa Rica	Boyle (2011)
	Neotropical frugivores	Costa Rica	Boyle *et al.* (2011b)
	Neotropical frugivores	Costa Rica	Boyle *et al.* (2011a)
	American Dipper	British Columbia, Canada	Morrissey (2004)
	American Dipper	British Columbia, Canada	Morrissey *et al.* (2004a)
	American Dipper	British Columbia, Canada	Middleton et al. (2006)
	American Dipper	British Columbia, Canada	Gillis *et al.* (2008)
	American Dipper	British Columbia, Canada	Mackas *et al.* (2010)
	American Dipper	British Columbia, Canada	Green *et al.* (2015)
	American Dipper	California, USA	Garwood *et al.* (2009)
	Dark-eyed Juncos	Southern Appalachiains, USA	Rabenold & Rabenold (1985)
	Blue Grouse	Colorado, USA	Cade & Hoffman (1993)
	Columbian Sharp-tailed Grouse	Colorado, USA	Boisvert *et al.* (2005)
	Mountain Quail	California, USA	Brennan *et al.* (1987)
	Mountain Chickadee	Utah, USA	Dixon & Gilbert (1964)
	White-crowned Sparrow	California, USA	Hahn *et al.* (2004)
	White-crowned Sparrow	California, USA	Breuner and Hahn (2003)
	Spotted Owl	California, USA	Laymon (1989)
	Little Greenbul	Tanzania	Werema (2014)
	Wetmore's Bush-Tanager	Veraruz, Mexico	Winker *et al.* (1997)
	Three-wattled Bellbirds	Costa Rica	Powell & Bjork (2004)
	Three-wattled Bellbirds	Costa Rica	Papes *et al.* (2012)

Taxon	Species	Location	Reference
Birds	Resplendent Quetzals	Costa Rica	Solorzano *et al.* (2000)
	Resplendent Quetzals	Costa Rica	Powell & Bjork (2010)
	Bare-necked Umbrellabird	Costa Rica	Chaves-Campos *e al.* (2003)
	Blue-tailed Hummingbird	Nicaragua	Fraser *et al.* (2010a)
	Citril Finch	Spain	Borras *et al.* (2010b)
	Citril Finch	Spain	Borras *et al.* (2010a)
	Woodlark	Italy	Brambilla and Bubolini (2009)
	Krüper's Nuthatch	Mediterranean Turkey	Albayrak *et al.* (2010)
	Crested Guans & Black Guans	Costa Rica	Chaves-Campos (2003)
	Sharpbill	Brazil	da Silva (1993)
	Yellow-legged Thrush and White-necked Thrush	South-eastern Brazil	De Castro (2012)
	Hawaiian Goose	Hawaii, USA	Leopold & Hess (2014)
	Wallcreeper	Slovakia	Saniga (1995)
	Black Rosy Finch	Western USA	French (1959)
	Rosy Finches	Utah, USA	King and Wales, Jr. (1964)
	Frugivores	Borneo, Malaysia	Kimura *et al.* (2001)
	Multiple species	Brazil	Bencke & Kindel (1999)
	Neotropical birds	Argentina	Capllonch *et al.* (2007)
	Multiple species	Costa Rica	Chaves-Campos (2004)
	Satyr tragopan	Himalaya	Norbu *et al.* (2013)
	Brown Accentor	Tibet	Lu (2006)
	Multiple species	Mexico	Nocedal (1994)
	Neotropical raptors	Latin America	Bildstein (2004)
	Multiple species	Brazil	Bencke and Kindel (1999)
	Frugivores	Costa Rica	Levey (1988)
	Hummingbirds	Ecuador	Hobson *et al.* (2003)
	Neotropical birds	Nicaragua	Fraser *et al.* (2008)
	African birds	Africa	Burgess & Mlingwa (2000)
	Neotropical birds	Costa Rica	Blake & Loiselle (1991)
	Frugivores	Costa Rica	Loiselle & Blake (1991)
	Nectivores	Hawaii, USA	Hart *et al*. (2011)
	Neotropical birds	Costa Rica	Stiles (1988)
	Hummingbirds	Ecuador	Hardesty & Fraser (2010)
	Multiple species	Spain	De la Hera (2014)
	Multiple species	Southern Africa	Brooke (1994)
	Multiple species	South Africa	Johnson & Maclean (1994)
	Multiple species	South Africa	Brown (2006)

Taxon	Species	Location	Reference
	Multiple species	Peru	O'Neill and Parker III (1978)
Birds	Multiple species	Taiwan	Chang *et al.* (2011)
	Honeyeaters	Australia	Keast (1968)
	Multiple species	Australo-Papaun region	Dingle (2004)
Insects	Brimstone	Spain	Gutiérrez & Wilson (2014)
	Multiple butterfly species	California, USA	Shapiro (1973)
	Southern Monarch butterfly	Bolivia and Argentina	Slager & Malcolm (2015)
	Pacific Dotted-Blue	Washington, USA	Peterson (1997)
	Wasps	Costa Rica	Hunt *et al.* (1999)
	Agelaia wasps	Costa Rica	Hunt *et al.* (2001)
	Multiple moth species	Costa Rica	Janzen (1988, 1993)
	Multiple butterfly species	Costa Rica	Henderson (2010)
	Wasps and butterflies	Worldwide	Alcock and Dodson (2008)
Reptile	Galapagos tortoise	Galapagos	Blake *et al*. (2013)

CHAPTER 3

FACTORS INFLUENCING ALTITUDINAL MIGRATION OF LONG-TAILED MANAKINS (*CHIROXIPHIA LINEARIS*) IN AN AGRICULTURAL LANDSCAPE IN COSTA RICA[2]

[2]Hsiung, A. and R. B. Chandler. To be submitted to *The Auk*.

Abstract

Altitudinal migration is exhibited by many species across a wide range of taxa, and is especially prominent among Neotropical resident bird species. However, the mechanisms governing altitudinal migration and individual migratory propensity are largely understudied. Additionally, some Neotropical resident bird populations are partially migratory. The need for understanding seasonal altitudinal migratory patterns of Neotropical resident birds is necessitated by the rapid disappearance of their habitats. The objectives of this study were to provide evidence of altitudinal migration of a Neotropical bird species, the long-tailed manakins (*Chiroxiphia linearis*), and examine individual and landscape factors that influence migratory propensity and spatio-temporal variation in abundance. Capture-recapture data were collected using constant-effort mist-netting at both low (n=4) and high (n=4) elevation sites between January and April of 2016. Additionally, radio transmitters were placed on 12 individuals within the study area and their movements were monitored. Results from capture-recapture analyses demonstrated that manakin abundance decreased in small forest fragments and increased in large fragments at low elevations. At high elevations, abundance increased at both small and large forest fragments, indicating upslope movement of individuals. Five of the 12 individuals with radio transmitter migrated upslope at the beginning of the breeding season. However, neither mist-net nor telemetry data supported the hypothesis that individual traits such as sex, age and body weight affect migratory propensity. Our study presents the first empirical evidence of altitudinal migration in long-tailed manakins, and highlights the need to understand how behavioral responses to forest fragmentation affect the viability of Neotropical resident bird populations.

Keywords: altitudinal migration, partial migration, *Chiroxiphia linearis*, long-tailed manakin

Introduction

Seasonal migration of animals has been studied extensively over many decades, with long-distance, latitudinal migrations receiving most of the attention (Dingle and Drake 2007). Conversely, the ecology of short-distance migrations is understudied. Short-distance migration has been defined in a number of ways, one of which defines short-distance migration as a migration pattern in which animals migrate for less than 2,000km to reach their destination (Rappole 2013). A common form of short-distance migration is altitudinal migration, characterized by seasonal movements of animals along an elevational gradient (Oosenbrug and Theberge 1980, Mysterud 1999, Boyle 2010, Rappole 2013). In temperate regions, altitudinal migration involves individuals moving between lower elevation winter ranges and higher elevation summer ranges (Hahn et al. 2004, Morrissey et al. 2004, Hebblewhite et al. 2008, Rice 2008). In tropical regions, the timing of altitudinal migration often coincides with the shift between wet and dry seasons (Boyle et al. 2010, Powell and Bjork 2010, Bohrer et al. 2014).

Altitudinal migration behavior exists in a variety of taxa, including mammals (Takatsuki et al. 2000, Parrini et al. 2003, Sawyer et al. 2005, Rice 2008, Skidmore et al. 2008, Bohrer et al. 2014, Wen et al. 2014), insects (Shapiro 1973, Hunt et al. 1999, Gutiérrez and Wilson 2014, Slager and Malcolm 2015), and birds (Rabenold and Rabenold 1985, Burgess and Mlingwa 2000, Gillis et al. 2008, Garwood et al. 2009, Boyle et al. 2010, Hardesty and Fraser 2010, Powell and Bjork 2010, Papeş et al. 2012). Gaining a deeper understanding of animal altitudinal migration will help shed light on mechanisms driving migratory behavior in animals, but also help reveal the evolutionary process of migration in general (Levey and Stiles 1992, Boyle and Conway 2007).

Tropical resident bird species were previously thought of as "sedentary" (Winker et al. 1997), but recent studies have found that many of these species are altitudinal migrants (Stiles 1988, Rosselli 1994, Powell and Bjork 2004, 2010, Fraser et al. 2010). Stiles (1988) provided empirical evidence demonstrating that approximately 25% of the avian community on the Caribbean slope of Cost Rica perform seasonal altitudinal migrations. One example is the white-ruffed manakin (*Corapipo altera*) which occurs on the Caribbean slopes of Costa Rica (Rosselli 1994, Boyle et al. 2010, 2011, Boyle 2010). *C. altera* aggregate at higher elevations during the breeding season (April-June), and some individuals migrate downhill between October and January during the nonbreeding season, then subsequently migrate uphill again between February and March to breed (Rosselli 1994, Boyle 2010). Other species of tropical resident birds that perform annual altitudinal migration include the three-wattled bellbird (*Procnias tricarunculata*), the umbrellabird (*Cephalopterus glabricollis*), the resplendent quetzal (*Pharomacrus mocinno*), and many species of hummingbirds (Solorzano et al. 2000, Chaves-Campos et al. 2003, Hobson et al. 2003, Powell and Bjork 2004, 2010, Hardesty and Fraser 2010, Papeş et al. 2012).

One of the most supported hypotheses of altitudinal migration driver is the "food limitation hypothesis", which states that the temporal variation of resources at different elevations cause animals to make elevational movements in order to take advantage of peak resource availability (Levey 1988, Loiselle and Blake 1991, Chaves-Campos 2004, Bohrer et al. 2014). Seasonal variation in climate is thought to be another major driver of altitudinal migration. Many ungulate species in the temperate region are believed to migrate elevationally from high to low elevations during the fall and winter in order to avoid harsh weather conditions (Parrini et al. 2003, Igota et al. 2004). Several avian species, including the white-crowned

sparrow (*Zonotrichia leucophrys*) in California (Hahn et al. 2004) and dark-eyed junco (*Junco hyemalis*) in North Carolina (Rabenold and Rabenold 1985) migrate altitudinally to avoid harsh weather during the winter at high elevations.

In addition to the extrinsic factors listed above, migratory propensity varies among individuals. Most altitudinal migratory species are considered partial migrants, meaning that only a subset of the populations migrates every year. Several hypotheses have been developed to explain partial migration. Ketterson and Nolan (1976, 1979) proposed three of the most well-known hypotheses. The body size hypothesis predicts that larger individuals within a population will not migrate far from the breeding grounds during the nonbreeding season because they can withstand the severe weather during the winter compared to smaller individuals (Ketterson and Nolan 1976). The dominance hypothesis predicts that dominant individuals of a population occupy habitats of higher quality while subdominant individuals are forced to migrate to suboptimal habitat due to competitive exclusion (Ketterson and Nolan 1979). The arrival time hypothesis predicts that males would not migrate far from the breeding grounds because it is advantageous for them to stay close in order to occupy better breeding sites (Ketterson and Nolan 1979). These hypotheses have been tested on many long-distance migrants, however, little is known about their relevance to altitudinal migratory species (Lundberg 1985, Boyle 2008, Jahn et al. 2010, Blake et al. 2013, Norbu et al. 2013).

An example of a partial altitudinal migratory species in the temperate region is the American dipper (*Cinclus mexicanus*) in southeast British Columbia where migrants and residents gather at low elevation wintering sites during the nonbreeding season, and migrants move to higher elevation sites during the breeding season (Morrissey 2004, Gillis et al. 2008). The migrants of this partial migratory population have lower reproductive success than the

residents, which indicates that the migrants are likely forced out of ideal breeding habitats due to competitive exclusion, consistent with the dominance hypothesis (Gillis et al. 2008, Mackas et al. 2010, Green et al. 2015). Additionally, *C. altera* in Costa Rica also exhibit partial migratory patterns where both migrants and residents breed at higher elevation breeding sites, and migrants move downslope to the nonbreeding grounds after the breeding season (Boyle 2008). Boyle (2008) found that neither the dominance hypothesis nor the arrival time hypothesis explained partial migration in this population. However, she did find evidence to support a variation of the body size hypothesis. Her results indicated that smaller bodied individuals migrate downslope during the nonbreeding (wet) season because the harsh weather reduced opportunities for foraging at higher elevations. Thus, smaller individuals migrate to lower elevations because they cannot withstand long periods of starvation (Boyle et al. 2010).

Aside from individual characteristics, landscape composition and configuration may also affect migratory propensity of birds. The effect of habitat patch size and quality on avian demography have been studied extensively (Hoover et al. 1995, Hokit and Branch 2003, Skagen et al. 2005). With respect to birds in fragmented Neotropical landscapes, researchers found that wood thrushes (*Hylocichla mustelina*) in Mexico were more likely to be wanderers between different habitat patches compared to wood thrushes that reside in continuous landscape who hold consistent winter territories (Rappole et al. 1989). Therefore, it is possible that within a partially altitudinal migratory population, individuals that reside in smaller habitat fragments during the nonbreeding season have a higher tendency to migrate in search for better habitat during the breeding season. So far, few studies examined individual movements of altitudinal migrants, and even fewer considered potential impacts of landscape factors on these behaviors within human-modified landscapes (Powell and Bjork 2004, 2010, Norbu et al. 2013).

Understanding which species perform seasonal altitudinal migration and their migratory patterns is important because these species will require different conservation strategies than sedentary species (Chaves-Campos et al. 2003, Powell and Bjork 2004, 2010). Tropical rainforests have been cleared at a rapid rate within the past several decades, and the resulting habitat loss and fragmentation can greatly restrict wildlife movements between fragments due to lack of connectivity between patches (Brooks et al. 1997, Thiollay 1999, Hadley and Betts 2009, Kinnaird et al. 2010, Sodhi et al. 2010, Volpe et al. 2014). Thus, further studies of movement patterns and migratory behavior of tropical bird species will aid in conservation of these populations.

The objectives of this study were to (1) present empirical evidence of altitudinal migratory behavior of a Neotropical resident bird species within tropical agricultural landscapes and (2) examine individual and landscape factors affecting individual migratory propensity. We tested the dominance hypothesis, the arrival time hypothesis, and the body size hypothesis, along with a landscape level hypothesis which we termed the patch size hypothesis. We used long-tailed manakins (*Chiroxiphia linearis*), a Neotropical resident frugivore, as our target species for this study. The reason for choosing *C. linearis* was three-fold: (1) dominance is known to be a function of age, which can be easily determined in the field (Lukianchuk and Doucet 2014), (2) pilot data from 2015 indicate that some individuals of the population migrated from lower elevation nonbreeding ground to higher elevation breeding ground, and (3) they are partially dependent on forest fragments within agricultural landscapes (Chandler et al. 2013).

For the dominance hypothesis, we predicted that there would be more young individuals at higher elevations and greater abundance of older (dominant) individuals at lower elevation during the wet (nonbreeding) season due to competitive exclusion from higher quality

nonbreeding habitats at lower elevations. For the arrival time hypothesis, we predicted that there would be similar abundance of males at higher and lower elevation during the nonbreeding season because of the advantage of being closer to potential breeding sites when breeding season arrives. Conversely, we expected that there would be more female *C. linearis* at lower elevations during the nonbreeding season compared to higher elevations because the weather is more tolerate at lower elevations and they do not need to secure quality breeding sites. For the patch size hypothesis, we predicted that a larger proportion of individuals would migrate from the smaller habitat patches than from larger patches because the resources within small patches would not be sufficient to sustain the individuals during the breeding season.

Study System and Species

Study Area

The study was conducted within the Montes de Oro region in Puntarenas Province, Costa Rica (N10°13' W84°39') between elevations 600m and 1200m above sea level (Figure 1). The area is located within the Río Aranjuez watershed and adjacent to the Monteverde Cloud Forest Reserve. The major land use within the area is agriculture, including pasture and plantations with coffee, bananas, sugar cane, tomatoes, and bell peppers. The area encompasses the premontane moist forest life zone (Janzen 1983). Some common trees in the study area belong to the families *Anacardiaceae*, *Bombacaceae*, *Moraceae*, *Malvaceae*, *Cecropiaceae*, *Mimosaceae*, and *Estercuriaceae*. The climate within the area exhibits two distinct seasons: the dry season (January-April) with little rain and higher temperature and the wet season (May-December) with frequent tropical storms and lower temperatures. Most of the remaining forests in the landscape consists of patches of secondary forests that were selectively logged for timber and firewood.

Study species

The long-tailed manakins (*Chiroxiphia linearis*) is a Neotropical resident bird species in the family Pipridae. The range of *C. linearis* extends from southern Mexico to northern Costa Rica (Stiles and Skutch 1989). The breeding season of *C. linearis* starts as early as mid-February and lasts until as late as September (Stiles and Skutch 1989). C. *linearis* have unique mating behaviors characterized by lekking of males during the breeding season where males gather at a lek to perform courtship display to attract females (Foster 1977a, McDonald 1989a, McDonald and Potts 1994). Male *C. linearis* do not reach their mature plumage until their fifth year, and the age of sub-adult males can be determined before then by intermediate stages of plumage (Doucet et al. 2007, Wolfe et al. 2009). During courtship display, a group of alpha and beta male manakins perform their songs and dance at a lek (McDonald 1989b). Typically, only the alpha males of a lek can copulate with the females, and beta males simply aid in the courtship (McDonald and Potts 1994, Lukianchuk and Doucet 2014). As a frugivore, the main diet of *C. linearis* consists of berries and fruits form Neotropical plants, especially plants of the *Ardisia* genus (Foster 1977b, Stiles and Skutch 1989). *C. linearis* is common within our study area in Costa Rica, and can occur in primary forests, secondary forests, and agricultural areas such as coffee plantations (Chandler et al. 2013).

Pilot season observations in 2015 suggested that some of the *C. linearis* in our study area are altitudinal migrants. More individuals were observed aggregating at lower elevations during the non-breeding season compared to higher elevations. Furthermore, at the beginning of the dry season which also coincides with the start of the breeding season, more individuals are present at higher elevations (Hsiung personal observation).

Methods

Bird capture

The study was conducted between January and April of 2016. Eight field sites were selected, each consisting of a forest fragment surrounded by small agricultural plantations and cattle pastures. The four high elevation field sites were located between 1000m and 1200m, and the four low elevation sites were located between 600m and 900m (Table 3.1). To examine whether forest patch size affect migratory propensity of *C. linearis*, two of the forest patches within each elevation range were small (< 4ha), and two were large (> 10ha).

The field season was divided into three mist-netting cycles (primary sampling occasion), and each site was sampled for two days (secondary sampling occasion) during each of the three primary periods, consistent with a robust design (Pollock 1982). Within each site, five 2.5m x 12m mist-nets with mesh size of 38mm (Avinet) were set up in two lines (three in one line and two in the other), and the spacing between the nets was 25m when the terrain permitted. The nets were opened at sunrise for six consecutive hours and were checked every 30 minutes. Vocalizations of male *C. linearis* were played near the nets to maximize captures. Birds were extracted promptly when encountered in the nets during net checks. During processing, all birds were given a metal leg band with a unique identification number. The Neotropical resident birds were given custom-made metal bands (National Band and Tags Co.) while the Neotropical migrant birds were given USGS metal bands. Additionally, each *C. linearis* captured was given a unique combination of metal and color bands for re-sighting in the field. The sex and age of the bird were determined whenever possible, and measurements of the birds were taken, including wing length, tail length, muscle condition, fat reserve, exposed culmen length, bill width, and evidence of molt.

Radio Telemetry

During the first primary sampling period, three manakins within each of the four lower elevation sites were fitted with a radio transmitter with a unique frequency (Advanced Telemetry Systems, Inc.). We deployed the transmitters during the first sampling period because it was prior to the start of the breeding season, and before the manakins started to migrate. The battery life of the transmitters was 90 days which was long enough to allow us to keep track of the movement of radio-tagged birds prior and during migration. The transmitters were attached to the back of the birds using the harness design proposed by Rappole and Tipton (1991). The total weight of the transmitter with harness did not exceed 5% of the weight of the birds to ensure that their mobility of was not restricted. Radio tracking began one day after the birds were released.

Radio tracking was conducted between January and April, and each bird was tracked with 3-element Yagi antenna and a receiver (Communications Specialists, Inc.) every 1-3 days between 0600 and 1300 hours both on foot and by car. When a bird was located, the observer attempted to obtain a visual observation of the bird, although most of the time it was not possible. In order to obtain an accurate location of the birds, the observer would get as close to a bird as possible (10-15m) without flushing it before recording the location. The location and elevation of the bird was marked with a GPS unit (Garmin Ltd.) and the surrounding habitat was also recorded. When a location of a bird was inaccessible to the observer, a waypoint was projected from the location of the observer based on the best estimation of its location. In the case where a mortality was encountered, the transmitter was collected.

Statistical Analysis

We modeled variation in the abundance of *C. linearis* using multinomial N-mixture models accounting for variation in capture probability (Chandler and King 2011). These models allow for variation in abundance among sites and between primary sampling occasions. The total number of individuals that use a site is denoted by M_i, a Poisson random variable with mean λ_i. The proportion of the population actually using site *i* and during primary period *j* is denoted by N_{ij}, a Binomial random variable with an expected value of $M_i\phi_{ij}$ where ϕ_{ij} is the probability of an individual being in site *i* during primary period *j*. The capture-recapture data (y_{ijk}) represent the number of individuals with encounter history *k* at site *i* during the j^{th} primary occasion. The probabilities of observing a particular capture history are denoted by π (p_{ij}).

To model overall abundance of *C. linearis*, we used a log-linear function with elevation and forest fragment size as predictor variables. The proportion of the population occurring on the plot during primary period was modeled using a logit-linear function with elevation, forest fragment size, and standardized Julian date treated as fixed effects. We modeled capture probability using a behavioral response model because we expected capture probability to decrease after first capture. The hierarchical model can be summarized as follows:

$M_i \sim Poisson(\lambda_i)$	Overall population at site *i*
$N_{ij} \sim Binomial(M_i, \phi_i)$	Proportion of population available for sampling at site *i* during primary sampling occasion *j*
$y_{ijk} \sim Multinomial(N_{ij}, \pi(p_{ij}))$	Number of individuals observed at site *i* during primary sampling occasion *j* with encounter history *k*

Abundance of males and females were analyzed separately using the same modeling framework. Additionally, we categorized each individuals as second-year or after-second-year, and modeled the abundance of each age group with the same models used for analyzing overall abundance. A set of candidate models was generated with the predictor variables for all of the analyses. For each model set, a null model was also considered. We then used Akaike information criterion (AIC) for model selection (Burnham and Anderson 2002). Models within a model set with $\Delta AIC < 2$ were considered the top models explaining variation in manakin abundance. In cases where more than one model received substantial support, we used model averaging for parameter estimates (Burnham and Anderson 2002).

For the birds that were tracked with radio telemetry, an individual that had two distinct nonbreeding and breeding home ranges with difference in elevation of more than 100m were classified as migrants. We modeled migratory propensity with logistic regression models in which individual traits (sex, age, body weight) and forest fragment size (where the individual was originally captured) were treated as fixed effects. All statistical analyses were conducted using program R 3.2.1. Capture-recapture models were fitted using the "gmultmix" function in the "unmarked" package (Fiske and Chandler 2011, R Core Team 2014).

Results

A total of 84 *C. linearis*, including 51 males and 33 females, were captured during 1423 net hours (Table 3.2). Aside from *C. linearis*, 80 other species were captured during the study (Appendix A). The top models for the overall population trend of *C. linearis* included the interaction between elevation, forest fragment size, and time, indicating that abundance changed over time at low and high elevations, and the change in abundance within small forest fragments

differ from that within large fragments (Table 3.3). The top models for overall abundance also included the variable for behavioral effect, indicating that capture probability decreased after birds were captured for the first time (Table 3.3). Model-averaged estimates showed that manakin abundance decreased at low elevation sites and increased at high elevation sites within small forest fragments (Fig. 3.2). In contrast, abundance increased at both low and high elevations within large forest fragments, with rate of increase higher at high elevation compared to low elevation (Fig. 3.2).

The top models explaining variation in male abundance included the interaction between forest fragment size and time, but not with elevation, suggesting elevation does not have an effect on male abundance over time (Table 3.4). For females, the top model was not substantially better than the null model (ΔAIC = 2.39), indicating that the predictor variables had little effect on the female abundance parameters (Table 3.5). The top models for predicting second-year manakin abundance include the interaction between elevation, time, and fragment size (Table 3.6). However, model-averaging produced unrealistic estimates and standard errors for second-year abundance, suggesting sample size may be too small for making inferences about the population. The top model for estimating after-second-year abundance included an interaction between time and fragment size for variation in proportion of population available over time, indicating elevation had no effect on change in after-second-year abundance (Table 3.7).

The 12 *C. linearis* that were tracked with radio telemetry included three females and nine males; three individuals were second-year and nine were after-second year adults (Table 3.8). A total of 427 locations were recorded with an average of 35.6±5.65 locations per bird (Fig. 3.3, Table 3.8). Five individuals had distinct nonbreeding and breeding home ranges that differed in elevation, thus were categorized as migrants (Table 3.8). Two of the 12 individuals with

transmitters died during the study, but the mortalities did not appear to be research related, as the birds did not show difficulty flying away after release, and the mortality events occurred several weeks after the birds were equipped with the transmitters. The tracking data clearly indicated that individuals could be classified as migratory or non-migratory (Fig. 3.4). The migrants not only gained elevation during migration, but also had distinct non-breeding and breeding home ranges (Fig. 3.4, Fig. 3.5). Timing of migration occurred between March 4th and March 14th (Table 3.8). The average difference in elevation between the center of the individual's home ranges before and after migration was 254.5±136.3m. The average distance between the center of the individual's pre- and post-migration home ranges was 2.25±1.83km (Table 3.9). Results from the logistic regression models indicated that migratory propensity could not be explained by the individual traits (i.e., age, sex, and body weight) or by patch size (Table 3.10). Although non-significant (P=0.099), the effect of patch size requires additional investigation given that two-thirds of the birds with radio transmitters in small fragments migrated, compared to only one-third that migrated from the large fragments (Fig. 3.6)

Discussion

To our knowledge, this is the first study that offers empirical evidence of altitudinal migratory behavior of *C. linearis*, a Neotropical resident bird species. Results from this study indicate that *C. linearis* are partial migrants, with the migratory individuals departing the low elevation non-breeding grounds to select breeding sites at higher elevations. Our capture-recapture data indicate that the abundance of *C. linearis* decreased over time at low elevation (600m-900m) and increased at high elevations (1000m-1200m) from January to April within small forest fragments (Fig. 3.2). In large forest fragments, manakin abundance increased at both low and high

elevations, and the rate of increase was higher at high elevation (Fig. 3.2) This demonstrates an upslope movement of individuals along the elevational gradient within our study area. These results are similar to the altitudinal migratory pattern of a closely related species, the white-ruffed manakin. Individuals of white-ruffed manakins on the Caribbean slope in Costa Rica aggregate at higher elevations during the breeding season, and some individuals migrate after breeding (Boyle 2010).

Individual traits and migratory propensity

Several altitudinal migratory species include partially migratory populations in which only a subset of the population migrate annually (Boyle 2008, Mackas et al. 2010, Blake et al. 2013, Norbu et al. 2013). It has been observed that individual traits, in combination with environmental factors, may explain differences in individual migratory propensity within a population (Ketterson and Nolan 1976, Ketterson and Nolan 1979). In our study, we tested the partial migration hypotheses: the arrival time, body size, and dominance hypotheses. The results from our study did not support theses hypotheses. With the arrival time hypothesis, we predicted that females would be more likely to migrate between the breeding and non-breeding season compared to males because males are more inclined to stay within their breeding area during the nonbreeding season in order to secure breeding sites for next year. Our results did not support the arrival time hypothesis, as the model with the effect of interaction between elevation and time on female abundance was not better than the null model. Furthermore, the top models for estimating male abundance did not include interaction between elevation and time, indicating variation in male abundance was not explained by elevation over time. For the dominance hypothesis, we predicted that there would be more young individuals at higher elevations and more old

individuals at lower elevation during the wet (nonbreeding) season. The results from our capture-recapture data did not support this hypothesis, as our top models did not include the interaction between elevation and time indicating change in abundance over time at both elevations. Our telemetry data further demonstrated partial migration within the *C. linearis* population in our study area because five of the 12 individuals with radio transmitters made substantial elevational movements between the nonbreeding and breeding seasons compared to the residents. However, the results from the logistic regression models did not provide support for the partial migration hypotheses.

Effect of patch size on migratory propensity

Variability in habitat patch size can result in variability in resources and habitat quality which may lead to lower survival of individuals within a population (Korfanta et la. 2012). Therefore, smaller habitat patches could have lower resources, and it may be more advantageous for the animals to migrate from a small patch compared to a large habitat patch. Thus, we predicted that the abundance of *C. linearis* within small forest patches at low elevations would decrease more drastically compared to larger patches, because the individuals from the smaller patches are more motivated to emigrate in search for resources once the breeding season starts. Conversely, the larger patches at higher elevation will experience a higher influx of *C. linearis* compared to smaller patches during the breeding season because they are preferable destinations for the migrants.

At low elevation, our data suggest that *C. linearis* abundance did decrease drastically within small patches between January and April while abundance increased within larger patches (Fig. 3.2). The population trend at high elevation supported our prediction, with higher

population increase of *C. linearis* within larger forest patches compared to small forest patches (Fig. 3.2). Although the results from the logistic regression model of tracked *C. linearis* migratory propensity and forest patch size was not significant, four of the five individuals that migrated between the nonbreeding and breeding season were originally captured in a small forest patch, suggesting that smaller habitat patch size could affect migratory propensity (Fig. 3.6). The reason for such pattern could be that, while small forest fragments may suffice for some manakins during the nonbreeding season when weather at lower elevations are more tolerable than that at higher elevation, it is more advantageous for individuals to migrate from those patches to higher elevations as soon as the weather improves. The weather at the lower elevation sites within our study area becomes extremely warm and windy during the dry season (Hsiung personal observation). Thus, higher elevation habitats may become more tolerable compared to those at lower elevations during the dry season. Additionally, as the growing season starts at high elevation during the dry season, food resources would increase. At high elevations, the larger patches contain more resources during the breeding season, thus are preferable breeding sites compared to smaller patches and attracting more individuals.

Study limitations

Because our study was conducted during the pre-breeding season migration, we only obtained data documenting uphill migration of *C. linearis*. As many studies have suggested, the causes for uphill and downhill migration of altitudinal migrants may differ (Rice 2008, Boyle et al. 2010, Boyle 2010, Mcguire and Boyle 2013). Therefore, the downhill migration of the manakins may exhibit a different pattern compared to the uphill migration. Additionally, the geographical range of our study area was also limited. *C. linearis* occurs in habitats from lowland dry forests to

montane wet forests in Costa Rica (Foster 1976, Stiles and Skutch 1989). Our study area only covers habitats between 600m and 1200m in elevation. Furthermore, time was consistently an important predictor variable in our models, indicating that the *C. linearis* abundance did vary within the study timeframe. Thus, a clearer altitudinal migratory pattern of *C. linearis* may be observed if a larger elevational range was sampled. For example, the increase in manakin abundance in our low elevation study sites may have been a result of upslope migration of manakins from elevations below 600m into the study area. If additional field sites were sampled at elevations below 600m, we may see a decrease in manakin abundance even within large forest fragments, indicating upslope migration of individuals from this elevation. Additionally, our sample size for manakins with radio transmitters was possibly too small to detect effect of individual traits on migratory propensity. Further studies of altitudinal migration of *C. linearis* at a larger scale, both temporal and spatial, will allow us to obtain better understanding of seasonal movement patterns of this species.

Conservation implications

Many Neotropical resident bird species have low forest dependency, thus do not have high occupancy within forests. However, recent studies have presented evidence that even species with low forest dependency have higher occupancy in forest compared to non-forest habitats (Ruiz-Gutiérrez et al. 2010). In our study area, although manakins have been observed within agricultural areas such as coffee plantations, they are rarely observed in open areas such as pastures, and are most often observed in forest fragments (Chandler et al. 2013). Furthermore, certain tropical bird species spend most of their time in forest fragments within agricultural landscapes even though the availability of those habitats are low (Sekercioglu et al. 2007).

Therefore, connectivity between habitat patches for altitudinal migrants in the tropics may be crucial for aiding in their conservation, as it is likely that they need forest for moving between habitat patches to exploit available resources.

Future research should attempt to monitor the migratory paths of Neotropical altitudinal migrants to understand the composition and configuration of forest patches needed for these species to persist in the rapidly changing human-dominated landscapes. Current technology is somewhat limited in studying movement patterns of Neotropical songbirds, however, as the available automated tracking devices are often too large to use on smaller birds, and the tracking method involving VHF transmitters often collects insufficient data and involves large amount of effort. The continuing discoveries of migratory behavior of Neotropical resident species highlights the need for information about their movement patterns and implications of rapid land use change on population viability and connectivity.

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Table 3.1 Elevation, forest patch size, and location of study sites in Montes de Oro, Costa Rica.

Site	Elevation	Patch size	Latitude	Longitude
William	720	Small	10.2093667	-84.7201
Moya	865	Large	10.2143833	-84.7184833
Domingo	610	Small	10.2075500	-84.725900
Quino	620	Large	10.2029	-84.7163833
Caco	1075	Large	10.2272167	-84.70445
Melvin	1050	Small	10.23	-84.6775
Tonio	1158	Large	10.2234167	-84.6704167
Ricardo	1070	Small	10.2172667	-84.66895

Table 3.2 Age strucutre of *C. linearis* captured with mist-net between January and April 2016 in Montes de Oro, Costa Rica.

Sex	Age	Number captured
Male	Second-year	13
	Third-year	8
	After-third-year	2
	Fourth-year	7
	After-fourth-year	21
	Total	51
Female	Second-year	4
	After-second-year	29
	Total	33

Table 3.3 Model selection results for long-tailed manakin abundance in Montese de Oro, Costa Rica. λ is overall population within the study area, ϕ is the portion of the population available for detection, and *p* is the detection probability. A dot (.) signifies that the parameter is constant (no covariate effect).

λ	Proportion on plot at time *j* (ϕ)	*p*	K	AIC	ΔAIC	weight
Fragment size	Fragment size × Time × Elevation	Behavior	12	45.63	0.00	0.45
Fragment size +Elevation	Fragment size × Time × Elevation	.	13	46.85	1.21	0.25
.	Fragment size × Time × Elevation	Behavior	11	47.38	1.75	0.19
Elevation	Fragment size × Time	Behavior	12	49.37	3.74	0.069
.	Fragment size × Time	Behavior	7	52.46	6.83	0.015
Fragment size	Fragment size × Time	Behavior	8	52.83	7.20	0.012
Elevation	Fragment size × Time	Behavior	8	54.15	8.52	0.001
Fragment size +Elevation	Elevation × Time + Fragment size	Behavior	10	54.75	9.12	0.000
Fragment size +Elevation	Fragment size × Time	Behavior	9	54.81	9.18	0.000
.	Elevation × Time + Fragment size	Behavior	8	55.80	10.17	0.000
Fragment size	Elevation × Time × Fragment size	.	11	58.61	12.98	0.000
.	Fragment size × Time	.	6	59.98	14.35	0.000
Fragment size	Elevation × Time + Fragment size	.	8	60.89	15.26	0.000
Fragment size	Time	.	5	61.30	15.67	0.000
.	Elevation × Time	Behavior	7	61.64	16.01	0.000
Fragment size +Elevation	Elevation × Time + Fragment size	.	9	62.04	16.41	0.000
Elevation	Elevation × Time	Behavior	8	63.63	18.00	0.000
Elevation	Elevation + Time	Behavior	7	63.66	18.03	0.000
.	Time	Behavior	5	64.03	18.40	0.000
.	Elevation + Time	Behavior	6	64.90	19.27	0.000
Elevation	Time	Behavior	6	65.91	20.28	0.000
.	.	.	3	71.92	26.29	0.000

AIC, Akaike Information Criterion

Table 3.4 Model selection results for **male** long-tailed manakin abundance in Montes de Oro, Costa Rica. λ is overall population within the study area, ϕ is the portion of the population available for detection, and *p* is the detection probability. A dot (.) signifies that the parameter is constant (no covariate effect).

λ	Proportion on plot at time *j* (ϕ)	*p*	K	AIC	ΔAIC	weight
.	Fragment size × Time	Behavior	7	82.41	0.00	0.26
Fragment size	Fragment size × Time	Behavior	8	83.55	1.14	0.15
Elevation	Fragment size × Time	Behavior	8	84.18	1.77	0.11
Fragment size	Time	.	5	84.79	2.38	0.079
.	Elevation × Time + Fragment size	Behavior	8	84.90	2.49	0.075
.	Fragment size × Time	.	6	85.37	2.96	0.059
Fragment size + Elevation	Fragment size × Time	Behavior	9	85.44	3.03	0.057
.	Elevation × Fragment size × Time	Behavior	11	85.44	3.03	0.057
Fragment size + Elevation	Elevation × Time + Fragment size	Behavior	10	85.96	3.55	0.044
Fragment size	Elevation × Fragment size × Time	Behavior	12	86.33	3.92	0.037
Elevation	Elevation × Fragment size × Time	Behavior	12	86.83	4.42	0.028
Fragment size + Elevation	Elevation × Fragment size × Time	Behavior	13	87.55	5.14	0.020
Fragment size	Elevation × Time + Fragment size	.	8	88.13	5.71	0.015
Fragment size + Elevation	Elevation × Time + Fragment size	.	9	89.59	7.17	0.010
Fragment size	Elevation × Fragment size × Time	.	11	90.86	8.45	0.004
.	Time	Behavior	5	91.98	9.56	0.002
.	Elevation × Time	Behavior	7	93.27	10.86	0.001
Elevation	Time	Behavior	6	93.83	11.42	0.000
.	Elevation + Time	Behavior	6	93.96	11.55	0.000
Elevation	Elevation × Time	Behavior	8	95.23	12.82	0.000
Elevation	Elevation + Time	Behavior	7	95.41	13.00	0.000
.	.	.	3	101.08	18.67	0.000

Table 3.5 Model selection results for **female** long-tailed manakin abundance in Montes de Oro, Costa Rica. λ is overall population within the study area, ϕ is the portion of the population available for detection, and *p* is the detection probability. A dot (.) signifies that the parameter is constant (no covariate effect).

λ	Proportion on plot at time *j* (ϕ)	*p*	K	AIC	ΔAIC	weight
.	Elevation × Time + Fragment size	Behavior	8	96.68	0.00	0.298
.	Time	Behavior	5	98.14	1.47	0.143
.	.	.	3	99.07	2.39	0.090
.	Elevation + Time	Behavior	6	99.33	2.65	0.079
Elevation	Time	Behavior	6	99.65	2.98	0.067
Fragment size +Elevation	Elevation × Time + Fragment size	Behavior	10	100.65	3.97	0.041
Elevation	Elevation + Time	Behavior	7	100.89	4.21	0.036
.	Elevation × Time	Behavior	7	101.00	4.32	0.034
Fragment size	Elevation × Time + Fragment size	.	8	101.26	4.58	0.030
.	Fragment size × Time × Elevation	Behavior	11	101.34	4.67	0.030
.	Fragment size × Time	Behavior	7	101.80	5.12	0.023
Elevation	Elevation × Time	Behavior	8	101.93	5.26	0.022
Elevation	Fragment size × Time Fragment size × Elevation	Behavior	12	102.18	5.50	0.020
Fragment size	Time	Behavior	5	102.25	5.58	0.020
Fragment size + Elevation	Elevation × Time + Fragment size	.	9	102.97	6.30	0.013
Fragment size	Elevation × Time × Fragment size	Behavior	12	103.03	6.35	0.013
Elevation	Fragment size × Time	Behavior	8	103.19	6.52	0.012
Fragment size + Elevation	Elevation × Time × Fragment size	Behavior	13	103.32	6.65	0.011
Fragment size	Fragment size × Time	Behavior	8	103.45	6.77	0.010
.	Fragment size × Time	.	6	103.46	7.79	0.010
Fragment size + Elevation	Fragment size × Time	Behavior	9	105.07	8.40	0.004
Fragment size	Elevation × Time × Fragment size	.	11	106.60	9.92	0.002

Table 3.6 Model selection results for **second-year** long-tailed manakin abundance in Montes de Oro, Costa Rica. λ is overall population within the study area, ϕ is the portion of the population available for detection, and *p* is the detection probability. A dot (.) signifies that the parameter is constant (no covariate effect).

λ	Proportion on plot at time *j* (ϕ)	*p*	K	AIC	ΔAIC	weight
.	Fragment size × Time × Elevation	Behavior	11	68.13	0.00	0.193
Elevation	Fragment size × Time × Elevation	Behavior	12	69.02	0.89	0.124
Fragment size	Fragment size × Time × Elevation	.	11	69.23	1.10	0.111
Fragment size	Fragment size × Time × Elevation	Behavior	12	69.64	1.51	0.090
Fragment size + Elevation	Elevation × Time + Fragment size	Behavior	10	69.66	1.53	0.090
.	Time	Behavior	5	70.46	2.33	0.060
Fragment size	Time	.	5	70.62	2.48	0.056
Fragment size + Elevation	Elevation × Time + Fragment size	Behavior	13	70.64	2.51	0.055
Fragment size + Elevation	Elevation × Time + Fragment size	.	9	71.45	3.31	0.037
Fragment size	Fragment size × Time	Behavior	8	71.81	3.68	0.031
Elevation	Time	Behavior	6	72.19	4.06	0.025
.	Elevation + Time	Behavior	6	72.28	4.14	0.024
Elevation	Fragment size × Time	.	6	72.66	4.53	0.020
.	Fragment size × Time	Behavior	7	72.95	4.81	0.017
.	Elevation × Time	Behavior	7	73.36	5.22	0.014
Fragment size + Elevation	Fragment size × Time	Behavior	9	73.81	5.67	0.011
Elevation	Elevation + Time	Behavior	7	73.99	5.86	0.010
.	Elevation × Time + Fragment size	Behavior	8	74.06	5.93	0.010
Elevation	Fragment size × Time	Behavior	8	74.66	6.53	0.007
Elevation	Elevation × Time	Behavior	8	75.33	7.20	0.005
.	.	.	3	75.39	7.25	0.005
Fragment size	Elevation + Time	Behavior	8	75.65	7.52	0.005

Table 3.7 Model selection results for **after-second-year** long-tailed manakin abundance in Montes de Oro, Costa Rica. λ is overall population within the study area, ϕ is the portion of the population available for detection, and *p* is the detection probability. A dot (.) signifies that the parameter is constant (no covariate effect).

λ	Proportion on plot at time *j* (ϕ)	*p*	K	AIC	ΔAIC	weight
.	Fragment size × Time	Behavior	8	73.26	0.00	0.587
Fragment size + Elevation	Elevation × Time + Fragment size	Behavior	10	76.96	3.70	0.092
Elevation	Elevation × Time × Fragment size	Behavior	12	77.65	4.38	0.066
Fragment size	Elevation × Time + Fragment size	.	8	77.86	4.59	0.059
Fragment size	Elevation × Time × Fragment size	Behavior	12	78.28	5.02	0.048
.	Elevation × Time × Fragment size	Behavior	11	78.46	5.19	0.044
Fragment size + Elevation	Elevation × Time × Fragment size	Behavior	13	78.64	5.37	0.040
Fragment size + Elevation	Fragment size × Time + Fragment size	.	9	79.83	6.57	0.022
Fragment size	Elevation × Time × Fragment size	.	11	80.52	7.26	0.016
.	Fragment size × Time	.	6	82.52	9.26	0.006
.	Fragment size × Time	Behavior	7	82.64	9.38	0.005
Elevation	Fragment size × Time	Behavior	8	82.87	9.61	0.005
Fragment size	Time	.	5	84.35	11.08	0.002
Fragment size	Fragment size × Time	Behavior	8	84.62	11.36	0.002
Fragment size + Elevation	Fragment size × Time	Behavior	9	84.66	11.40	0.002
.	Time	Behavior	5	85.98	12.72	0.001
Elevation	Elevation + Time	Behavior	7	86.25	12.99	0.001
Elevation	Time	Behavior	6	86.28	13.01	0.001
.	Elevation + Time	Behavior	6	87.62	14.35	0.000
Elevation	Elevation × Time	Behavior	8	88.25	14.99	0.000
.	Elevation × Time	Behavior	7	88.72	15.46	0.000
.	.	.	3	89.92	16.71	0.000

Table 3.8 *C. linearis* captured and tagged with radio transmitter in Montes de Oro, Costa Rica.

Date captured	Patch size	ID	Age	Sex	Weight (g)	Migratory	Migration date	Locations	Fate
1/20/2016	Small	AYOG	ASY	M	18.5	Yes	03/10/2016	36	Alive
1/29/2016	Small	ARWW	ASY	M	17.6	Yes	03/10/2016	36	Alive
1/29/2016	Small	ABBY	ASY	F	19.8	Yes	03/14/2016	33	Dead
1/15/2016	Large	AUYG	SY	M	17.4	No		44	Alive
1/28/2016	Large	AORW	ASY	M	17.7	No		34	Alive
1/28/2016	Large	AGOB	ASY	F	19	No		22	Dead
1/22/2016	Large	AGRY	ASY	M	18.6	No		40	Alive
1/22/2016	Large	AYUO	SY	M	17.6	No		37	Alive
1/23/2016	Large	ABGW	ASY	M	16.8	Yes	03/07/2016	39	Alive
1/13/2016	Small	ABRY	ASY	M	20.3	Yes	03/04/2016	41	Alive
1/25/2016	Small	AYUG	SY	M	17.5	No		34	Alive
1/28/2016	Small	AGWR	ASY	F	18.4	No		31	Alive

Table 3.9 Elevation gain and distance between pre- and post-migration home ranges for migrant *C. linearis* in Montes de Oro, Costa Rica between January and April 2016.

ID	Elevation gain (m)	Distance between home ranges (km)
ABBY	484.43	4.25
ABRY	271.21	4.23
ABGW	150.48	0.65
AYOG	174.65	0.73
ARWW	191.67	1.44

Table 3.10 General linear model results of migratory propensity of *C. linearis* with radio transmitters.

Model	Estimate	Std. error	z value	|Pr|>z
Migratory propensity ~ weight	0.598	0.632	0.947	0.344
Migratory propensity ~ patch size	2.303	1.396	1.649	0.0992
Migratory propensity ~ sex	0.47	1.40	0.337	0.736
*Migratory propensity ~ age	-18.79	3765	-0.005	0.996

* Model failed to converge

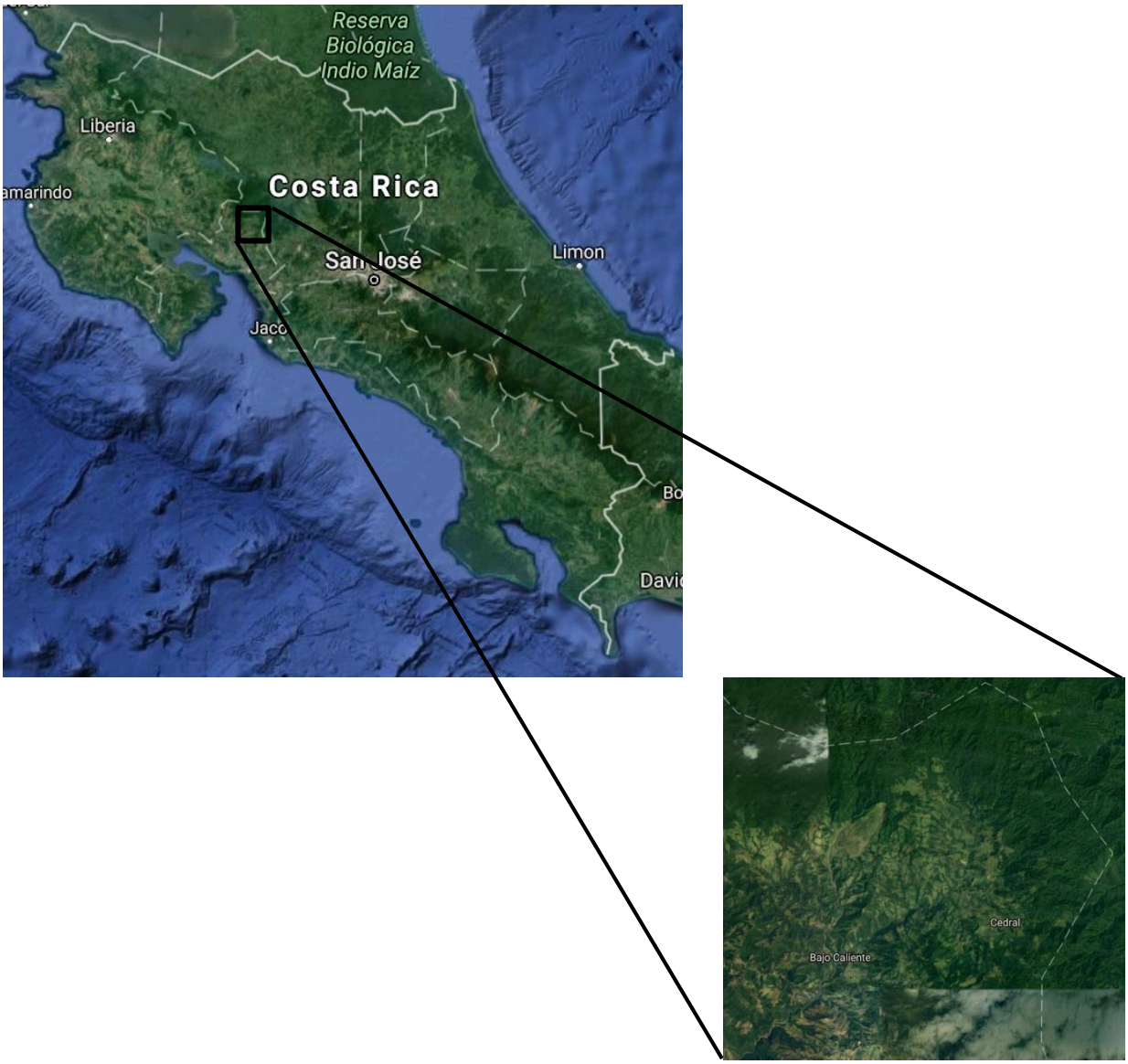

Figure 3.1 Location of study area in Montes de Oro, Puntarenas Province, Costa Rica.

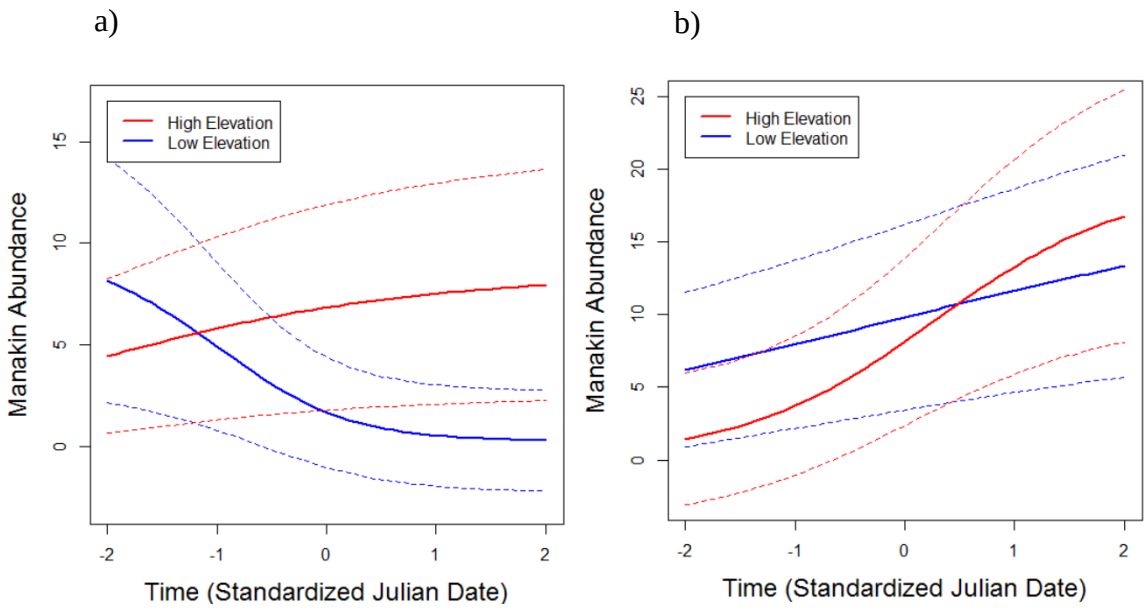

Figure 3.2 Model-averaged abundance estimate of *C. linearis* between January and April 2016 at low and high elevations in Montes de Oro. a) indicate abundance estimate in small forest fragments. b) indicate abundance estimate in large forest fragments. Dotted lines represent ± 1SE.

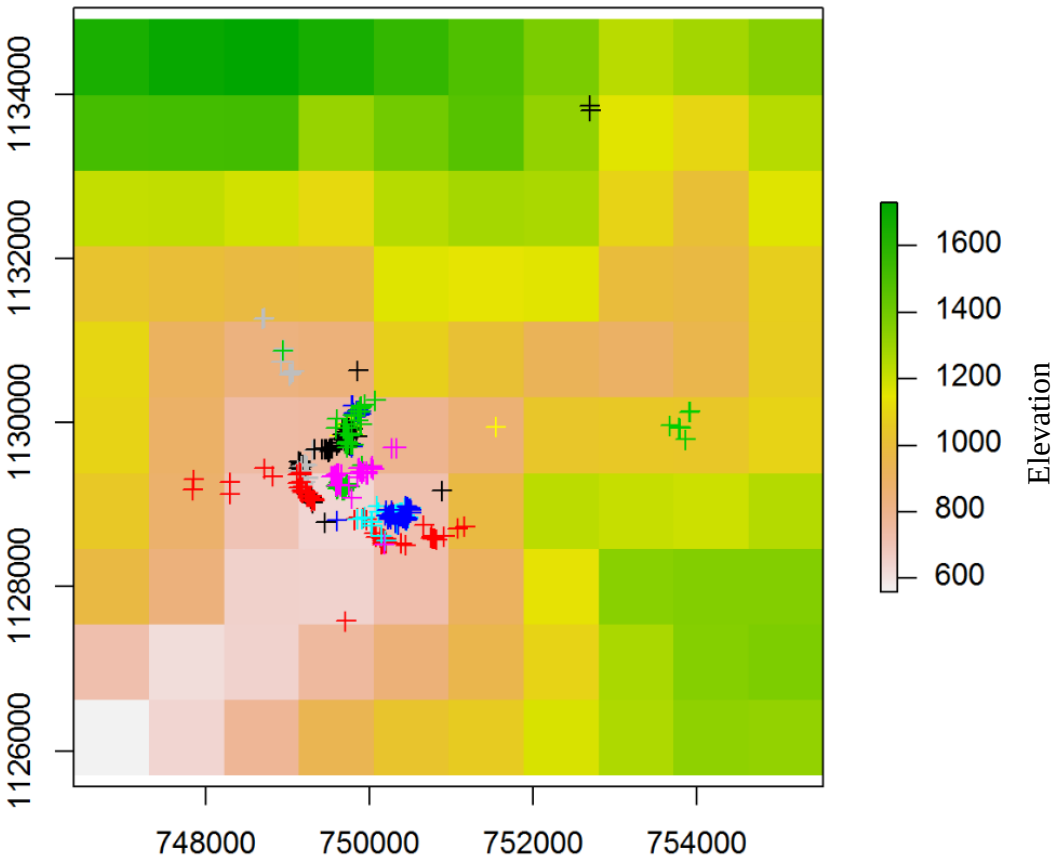

Figure 3.3 Locations of *C. linearis* within the study area with radio transmitters and tracked between January and April 2016 on an elevation map. Points with different colors represent different individuals.

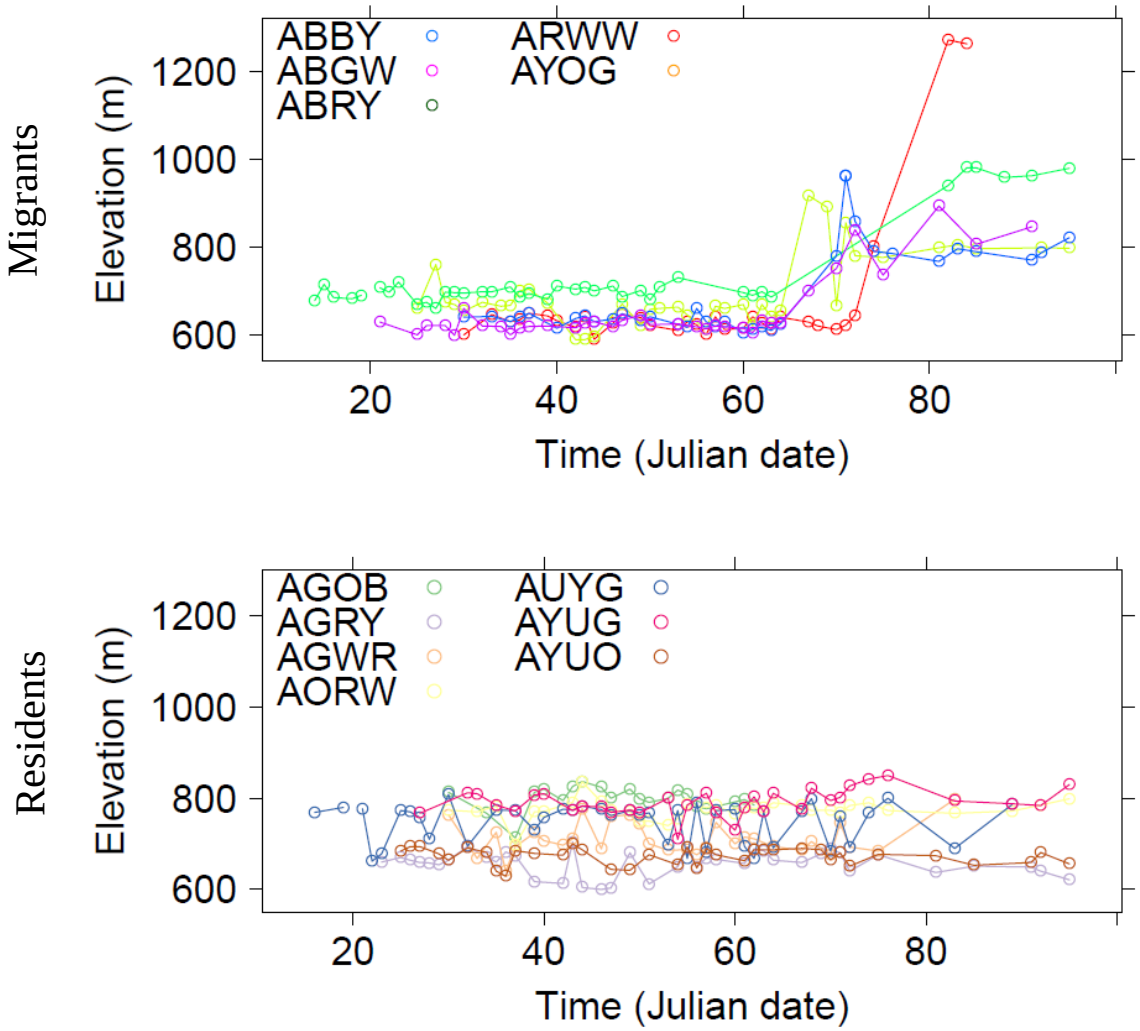

Figure 3.4 Comparison of elevation changes between migrant and resident *C. linearis* between January and April 2016 within Montes de Oro, Costa Rica.

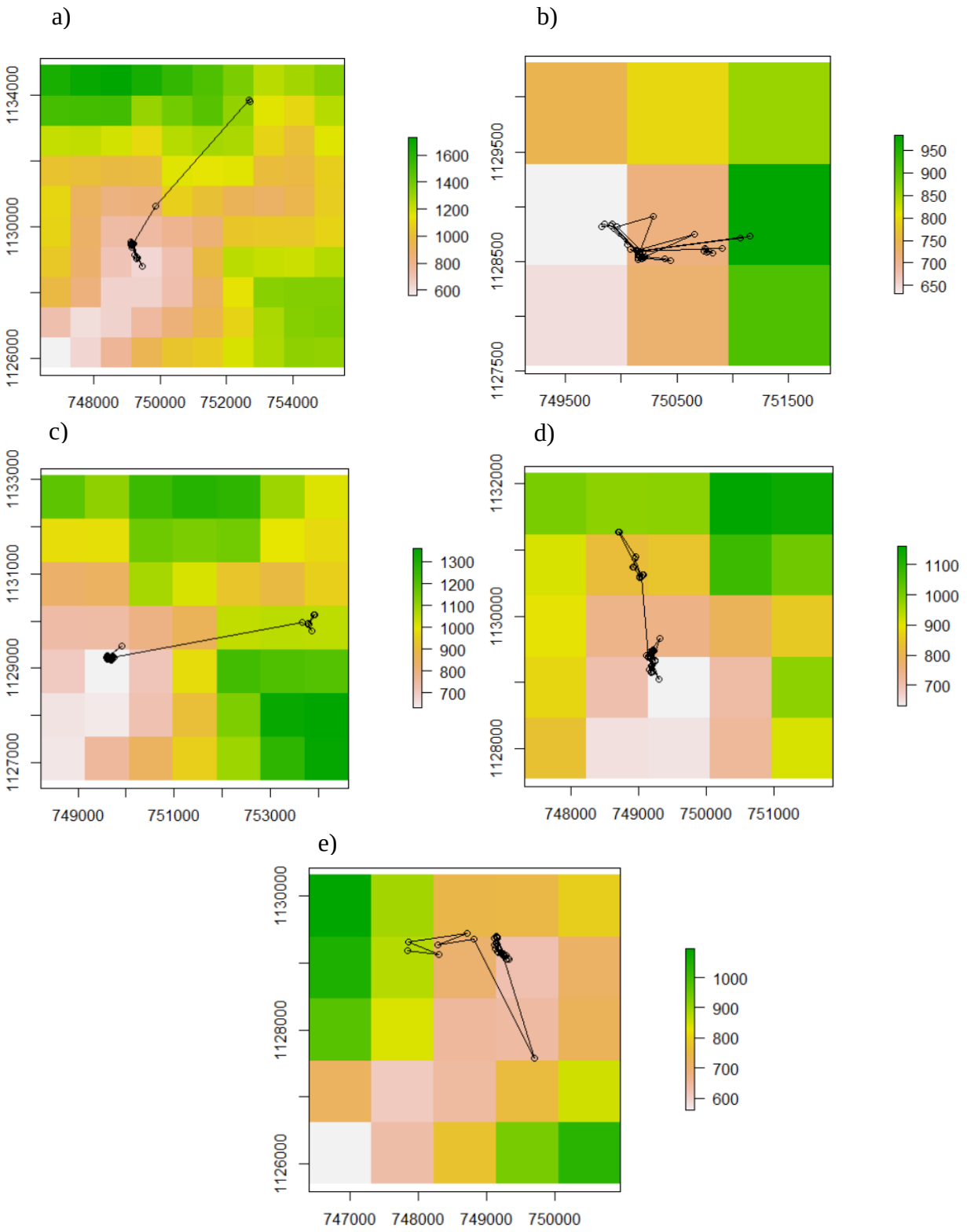

Figure 3.5 Examples of movement trajectories of migrant *C. linearis* between January and April 2016 within Montes de Oro, Costa Rica. Individual IDs are as follows: a) ABBY, b) ABGW, c) ABRY, d) ARWW, e) AYOG. Legend indicates elevation in meters.

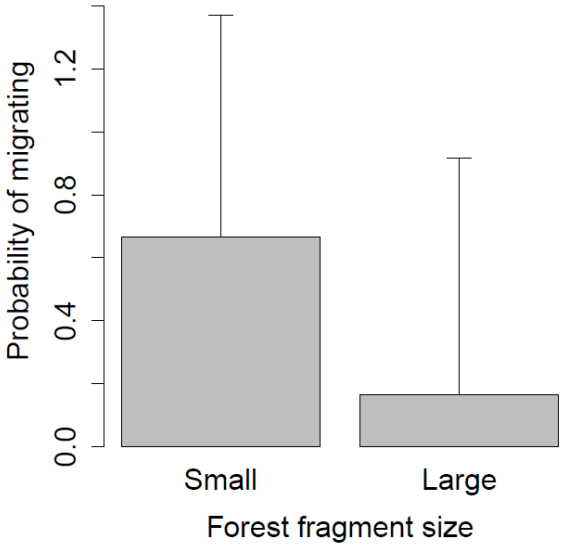

Figure 3.6 Proportion of *C. linearis* with radio transmitters that migrated from small and large forest fragments in Montes de Oro, Costa Rica.

CHAPTER 4

CONCLUSIONS

Major Findings

Altitudinal migration is defined by seasonal elevational movements of animals between breeding and non-breeding seasons, and is a behavior exhibited by animals across several taxa around the world (Burgess and Mlingwa 2000, Loucks et al. 2003, Hahn et al. 2004, Boyle et al. 2010, Blake et al. 2013, Mcguire and Boyle 2013, Bohrer et al. 2014). Many studies have been conducted to examine movement patterns and drivers of altitudinal migratory species. Through a thorough literature review in Chapter 2, I examined various hypotheses regarding drivers of altitudinal migration, identified gaps in the current knowledge of altitudinal migration, and conservation implications. Hypotheses pertaining to variation in food resources and climatic conditions are the most supported by empirical studies of altitudinal migration, especially in ungulates and Neotropical frugivorous birds (Parrini et al. 2003, Igota et al. 2004, Powell and Bjork 2004, 2010, Rice 2008, Boyle 2010). Additionally, the interaction between changes in the environmental conditions and individual traits (e.g. sex, age, and body size) result in partial altitudinal migratory populations, in which only part of the population migrate annually (Ketterson and Nolan 1979, Boyle et al. 2011, Blake et al. 2013, Norbu et al. 2013). I also presented potential conservation implications of altitudinal migration, including challenges faced by altitudinal migrants in the face of rapid global changes of land use and climate. For example,

forest fragmentation could impede movements of altitudinal migrants which could have negative impact on the vital rates of their populations.

In Chapter 3, I examined altitudinal migration of long-tailed manakins (*Chiroxiphia linearis*) in agricultural landscapes of Costa Rica. I used capture-recapture data collected from constant-effort mist-netting between January and April of 2016 to estimate spatio-temporal variation in manakin abundance between their breeding and non-breeding seasons. I also investigated the effect of individual traits on migratory propensity of the manakins. Twelve radio transmitters were deployed on manakins to track individual movements within the same time period. Results showed that the abundance in small forest fragments decreased at low elevation and increased at high elevation over time. At high elevation, manakin abundance increased at both low and high elevations. Five of the 12 manakins with radio transmitters migrated upslope in early March. However, individual traits (i.e. sex, age, and body size) did not explain migratory propensity. This study provided the first evidence of altitudinal migration of long-tailed manakins. A growing body of literature has documented altitudinal migratory behavior in species historically categorized as "sedentary". Gaining a deeper understanding of this type of migration is important in meeting seasonal habitat needs of altitudinal migrants, which will in turn aid in conservation of these species.

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APPENDIX A

LIST OF BIRD SPECIES AND NUMBER OF CAPTURES BETWEEN JANUARY AND APRIL 2016 IN MONTES DE ORO, COSTA RICA

Species	Captures
Amazilia saucerrottei	13
Amazilia tzacatl	24
Amblycercus holosericeus	1
Archilocus colubris	3
Arremon brunneinucha	9
Arremonops rufivirgatus	13
Aulacorhynchus prasinus	1
Basileuterus culicivorus	3
Basileuterus rufifrons	37
Campephilus guatemalensis	2
Campylopterus hemileucurus	27
Cantorchilus modestus	2
Cardellina pusilla	2
Catharus aurantiirostris	23
Catharus ustulatus	35
Chiroxiphia linearis	98
Chlorospingus ophthalmicus	5
Chlorostilbon canivetii	2
Corapipo altera	6
Dendrocincla homochroa	13
Dendrocolaptes sanctithomae	2
Dysithamnus mentalis	5
Empidonax flaviventris	5
Empidonax minimus	1
Eupherusa eximia	9
Euphonia anneae	2
Euphonia hirundinacea	5
Geothlypis formosa	2
Glyphorynchus spirurus	13
Heliodoxa jacula	1
Heliomaster constantii	3
Helmitheros vermivora	1
Henicorhina leucosticta	3
Hylocharis eliciae	1
Hylocichla mustelina	6
Lampornis calolaema	2
Lampornis hemileucurus	1
Lepidocolaptes souleyetti	2
Lophotriccus pileatus	3
Micrastur ruficollis	1
Mionectes olivaceus	18
Momotus coeruliceps	9
Myadestes melanops	2
Myiarchus tuberculifer	2
Nyctidromus albicollis	1
Oreothlypis peregrina	5
Pachysylvia decurtatus	1
Parkesia novaboracensis	1
Passerina ciris	1
Phaethornis guy	11
Phaethornis striigularis	3
Pheugopedius rutilus	4
Picoides fumigatus	1
Platyrinchus mystaceus	3
Premnoplex brunnescens	3
Pteroglossus torquatus	1
Ramphocelus passerini	1
Saltator maximus	15
Sclerurus mexicanus	1
Seiurus aurocapillus	11
Setophaga pensylvanica	1
Sittasomus griseicapillus	11
Sporophila corvina	2
Tangara dowii	1
Thamnophilus doliatus	4
Thryophilus rufalbus	16
Tiaris olivaceus	6
Tolmomyias sulphurescens	7
Trogon aurantiiventris	1
Turdus assimilis	4

Species	Captures
Turdus grayi	19
Turdus obsoletus	1
Vireo flavifrons	1
Vireo flavoviridis	1
Vireo philadelphicus	1
Xiphorhynchus susurrans	2
Xyphorynchus erythropygius	1