SEASONALITY AND ELEVATIONAL MIGRATION IN AN ANDEAN BIRD COMMUNITY

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by
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The undersigned, appointed by the dean of the Graduate School, have examined the dissertation entitled

ELEVATIONAL MIGRATION OF BIRDS
ON THE EASTERN SLOPE OF THE ANDES
IN SOUTHEASTERN PERU

presented by Christopher L. Merkord,

a candidate for the degree of doctor of philosophy,

and hereby certify that, in their opinion, it is worthy of acceptance.

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Professor James Carrel

Professor Raymond Semlitsch

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Professor Miles Silman

For mom and dad…

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TABLE OF CONTENTS

LIST OF TABLES

Chapter 1

Chapter 2

Chapter 3

Chapter 4

LIST OF FIGURES

Chapter 1

Chapter 2

Chapter 3

Chapter 4

ABSTRACT

The distribution of species and individuals along environmental gradients is a central question in biogeography, from both ecological and conservation perspectives. Our understanding of factors affecting species distributions at a global scale is hindered by a lack of information on many tropical species. Simply describing the distribution of many species along environmental gradients is complicated when individuals perform regular two-way migrations along the gradient, as is the case with elevationally migratory insects, birds, and mammals. While elevational migration is known to be widespread in birds, in the Neotropics the phenomenon has only been studied along elevational gradients in Central America. Here I provide the first community-level assessment of avian elevational migration in South America. I used point counts and mist netting and focal observations of a mid-elevation mixed species flock to document patterns of avian elevational migration along a 2.7 km elevational gradient in Manu National Park, southeastern Peru.

To effectively study elevational migration, some knowledge of the annual cycles of birds is required. Despite the tropics often being perceived as aseasonal, climate varies significantly throughout the year at our study sites. Measurements of daily temperature and rainfall along the gradient reveal a cool dry season from May to August, and a warmer rainy season from August to April, with rainfall peaking in February. Patterns of monthly fruit production along the gradient are complicated, but on average fruit volume peaks in February and fruit number peaks in July. Breeding of birds begins to increase at the start of the wet season and peaks in October and November. Molt, the annual replacement of feathers, was rare during the dry season and early wet season, and increased thereafter to peak during the height of the wet season, 2-3 months after the peak in breeding, resulting in a strong correlation between molt and rainfall. Molt timing varied little along the elevational gradient, except that perhaps middle elevation birds complete their molt earlier than high or low elevation birds. Elevational migrants appear to molt more quickly than nonmigrants, suggesting a possible mechanism for the apparent differences among elevations. Feeding guild also appears to affect molt timing, with insectivores and nectarivores molting earlier than frugivores and omnivores.

Mixed-species bird flocks are a common phenomenon throughout the world, reaching their highest diversity and size in the tropics, where flocks often defend permanent territories from neighboring flocks. Through a combination of mist netting, color banding, resighting, and behavioral observations I documented the composition of one particularly large and diverse mixed-species flock from a middle elevation site at 1400 m a.s.l. Individuals of many species observed in the flock appeared to be elevational migrants, including the two most abundant species in the flock, the Deep-blue Flowerpiercer *Diglossa glauca* and the Streak-necked Flycatcher *Mionectes striaticollis*. A polyspecific subgroup originally captured in the mixed species flock was recaptured at a nearby ridge, suggesting the possibility that individuals in this subgroup maintained the interspecific bonds created on their nonbreeding grounds during part of their upslope migration, a first for a polyspecific group of terrestrial migrants.

To identify other elevationally migratory species I first needed to outline a method of analyzing abundance estimates from point count data. First I divided the year into three seasons (dry, early wet, late wet) and divided the elevational range of each species into 2 to 5 elevational zones, depending on the number of point counts I conducted within the species' range. I estimated the relative abundance of each species in each season at two spatial levels: the elevational zone and the survey point. Relative abundance estimates were derived separately using two methods: 1) by calculating the average number of birds per point for species with a sufficient number of detections, and 2) using the multiple covariate distance sampling engine in program Distance to estimate relative density for those species with a sufficient number of detections for which the distance to the individual could be measured. For each season I calculated the mean elevation of occurrence as the mean elevation of zone midpoints weighted by relative abundance. In paired seasonal comparisons I measured the shift in mean elevation of occurrence and tested for the key characteristics of a down- or upslope movement (an increase at one elevation and a corresponding decrease at another elevation) by measuring the significance of a season*elevation interaction effect in a two-way ANOVA. A combination of a significant interaction effect and a significant shift down- or upslope was taken as indication of a seasonal movement. This is the first time abundance has been used in this way to statistically test for movement along an environmental gradient. I scored each species as a migrant or resident based on the results of the point count data analysis. In addition, I scored each species using relative abundance estimates from mist netting, flock observations, and using a combination of all datasets, and averaged all available scores for each species. The cumulative score represents the combined weight of evidence in favor of designating each species as an elevational migrant or a resident. I discuss alternative hypotheses to explain the seasonal variation in density distributions, and offer comments on study design and the interpretation of my results.

Sufficient data was obtained to assign 234 species a residency status. Of these, 55 (24%) were classified as elevational migrants and 169 (76%) as residents. Included as elevational migrants are 4 species whose movements may in fact turn out to latitudinal or trans-Andean. We conducted a meta-analysis of studies describing the migratory status of birds at other Neotropical sites and compared those results to our Peruvian study site. The percentage of latitudinal migrant species in Neotropical bird communities decreases from north to south while the percentage of elevational migrant species, the percentage of resident nonmigratory species, and the ratio of elevational migrants to residents all increase from north to south. Additional studies in the Atlantic Forest of Brazil, the Guiana Shield, and on both slopes of the Andes, including temperate latitudes, and are urgently needed in order to determine how patterns of elevational migration vary within South America. Only by first understanding broad patterns of migration and distribution along elevational gradients can we begin to ask detailed questions about the proximate and ultimate causes of distributional patterns. Our results fill in a critical information gap on migration in the Andes and provide a method of quantifying distributions along environmental gradients that can be applied to other taxa and gradients. Understanding the factors that affect the elevational distribution of organisms is particularly urgent as global climate change increasingly threatens montane biota.

CHAPTER 1.

TIMING OF MOLT IN A PERUVIAN MONTANE RAIN FOREST

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ABSTRACT

The timing of molt in tropical regions is less well understood than in temperate regions. The same generality can be made for humid forests versus dry forests and savannas, and for highlands versus lowlands. We describe the timing of molt in a tropical humid montane forest on the eastern slope of the Andes in Peru. We captured and scored birds for molt along a continuous elevational gradient from 800–3500 m a.s.l. Despite the tropics often being perceived as aseasonal, climate varied significantly throughout the year at our study sites. We measured daily temperature and rainfall and monthly fruit production along the gradient. Molt was rare during the dry season and early wet season, and increased thereafter to peak during the height of the wet season, resulting in a strong correlation between molt and rainfall. Breeding began to increase at the start of the west and peaks 2–3 months before the peak in molt. We found little difference in the timing of molt along the elevational gradient, except that perhaps middle elevation birds completed their molt earlier than high or low elevation birds. Elevational migrants appeared to molt more quickly than nonmigrants, suggesting a possible mechanism for the apparent differences among elevations. Feeding guild also appeared to affect molt timing, with insectivores and nectarivores molting earlier than

frugivores and omnivores. We discuss the implications of our findings on the study of life history traits, including life stage phenology.

INTRODUCTION

Molt is the periodic loss and replacement of feathers, and is necessary as feathers become worn or damaged over time. For most species, molt occurs on an annual cycle, with feather replacement progressing in a specific timing and sequence (Palmer 1972). Molt entails increased metabolic rates and energy expenditure (Payne 1972, Lindström et al. 1993). If enough feathers are molted at once, insulatory capacity may be reduced and flight capabilities inhibited, the latter possibly resulting in increased predation risk (Schieltz and Murphy 1997, Hedenström 2003). These costs set up a variety of physiological and ecological trade-offs between molt and breeding and between molt and migration as individuals adjust the amount of time and resources allocated to each activity (Lindström et al. 1994, Hemborg and Lundberg 1998, Hemborg 1999). Depending on an individual's response to those tradeoffs, molt may overlap to varying degrees with breeding (Foster 1975, Hahn et al. 1992), and individuals may postpone molt of some or all feathers until they reach more favorable environmental conditions either during or after migration (Rohwer et al. 2005). Thus the timing of molt and degree of molt-breeding overlap are interrelated with other natural history parameters such as clutch size, length of breeding season, number of nesting attempts, and mortality rates (Foster 1974, Flinks et al. 2008).

Life history strategies are known to vary between populations and species due to extrinsic factors such as food availability and predation rates (Martin 1995, 1996), resulting in a "slow-fast" continuum of life history strategies (Ricklefs and Wikelski 2002, Wiersma et al. 2007). To some extent, this slow-fast continuum is correlated with latitude. Temperate birds tend to have higher metabolic rates (Wikelski et al. 2003, Wiersma et al. 2007), grow faster (Ricklefs 1976), mature sooner, have larger clutches (Martin et al. 2000), invest less heavily in juvenile care (Russell et al. 2004), and have shorter lifespans (Peach et al. 2001) than tropical birds. Given that so many life history traits covary along the temperate-tropic gradient, it should be expected that the phenology of life stages such as breeding, molt, and migration should vary as well. The rate of molt in Stonechats (*Saxicola torquata*), for example, is faster in temperate than tropical populations, presumably due to the shorter window of opportunity for molting at higher latitudes (Helm and Gwinner 1999, 2001). Unfortunately, temperate-tropical comparisons of life stage phenology are hampered by a general lack of knowledge of 1) the relative timing of breeding and molt in the tropics (Echeverry-Galvis and Córdoba-Córdoba 2008), and 2) the direction, timing, and extent of intratropical migrations (Faaborg et al. 2010). A major challenge facing tropical ecologists is to fill in the many gaps in basic natural history information of tropical species.

Tropical montane ecosystems are particularly poorly known considering the high levels of biodiversity they harbor. Valuable contributions to ecology have resulted from detailed studies of bird distributions along elevational gradients (e.g., Terborgh 1971, 1977). Furthermore, elevational gradients support variation in environmental conditions across relatively short distances, providing an excellent laboratory for the study of variation in life history traits, including those related to breeding, molt, and migration. In some respects, birds at higher elevations appear to fall on the fast end of the fast-slow continuum compared to birds at lower elevation. High elevation birds appear to have short, well-defined molting periods (Echeverry-Galvis and Córdoba-Córdoba 2008), short breeding periods (Bears et al. 2009), smaller body size (Janes 1994) and thus probably higher metabolic rates (Bennett and Harvey 1987). On the other hand, inter- and intra-specific studies have shown lower annual fecundity, increased parental care, and increased survival at higher elevations (Badyaev 1997, Badyaev and Ghalambor 2001, Bears et al. 2009), all placing high elevation birds on the slow end of the life history continuum. Competing theories about avian life history variation on elevational gradients have largely been tested in temperate regions. In the tropics, where lowland species already exhibit a slow pace of life, do their high-elevation counterparts exhibit an even slower one? Clearly there remain many questions regarding the effects of elevational gradients on avian life history and the relative importance of extrinsic and intrinsic factors in determining life history variation.

One life history strategy – to migrate or not to migrate, and if so when and where – has received particularly little attention in the montane Neotropics (Faaborg et al. 2010). Elevational migration is a widespread if understudied phenomenon in montane regions (Merkord 2010 Chapter 4), and should be considered when interpreting the timing of other life history events such as breeding and molt along an elevational gradient. Migratory individuals in a population of Silvereyes (*Zosterops lateralis*), a partial latitudinal migrant, tend to molt earlier and more synchronously than sedentary individuals (Munro et al.

2006). Theory would predict the same pattern among individuals in elevationally migratory populations: migratory individuals should molt more quickly than nonmigratory.

We describe the timing of avian molt along an elevational gradient on the eastern slope of the Andes. First we compare the timing of molt among individuals along the elevational gradient. Then we attempt to measure the relationship between molt and environmental factors that may influence molt. Finally we compare the timing of molt between migratory and nonmigratory species, and between species of different foraging guilds. We discuss the implications of our finding on the use of stable isotopes to track seasonal elevational movements of birds. These data will provide basic natural history information on Andean birds and offer insights into the variation of a major life history trait along an elevational gradient.

METHODS

Study sites were distributed throughout the Kosñipata and Tono valleys in the buffer and core zones of Manu National Park, Cusco region, Peru, along an elevational gradient from approx. 800–3400 m a.s.l. The climate is fairly seasonal, with a short but pronounced dry season from Apr to Jul. For most species, breeding activities increases with the onset of the rainy season in Aug and peak between Sep and Dec (G. Londoño, *pers. comm.*). Over 1,000 species of birds have been recorded in Manu National Park, including over 700 species within the elevational range covered by this study (Walker et al. 2006).

We established 48 net sites, with 4 to 16 nets per site. Nets ranged in elevation from 795–3387 m a.s.l. We sampled during four distinct time periods: Jun 19–Aug 15, 2005; Jun 27–Nov 14, 2006; Feb 21–Mar 30, 2007; and Jul 10–Oct 31, 2007. Most net sites were sampled once, but several were sampled multiple times for a total of 58 sampling periods. During each sampling period, we netted for three days, opening the nets 30 minutes before dawn and closing the nets at dusk, except on the third day when nets were sometimes closed in late morning. We closed the nets if rain was too heavy, so there was much variation in effort between days and netting periods. Netting periods ranged in effort from 33 to 551 net hours, for a total of 12,491 net hours. Summing across years, monthly sampling effort ranged from 456 to 4,027 net hours (Table 1). Time permitting, we scored each captured individual for molt in the flight feather, wing and tail coverts, and body feathers. Individuals were considered to be molting flight feathers if they showed approximately symmetrical molt in the remiges or rectrices, while individuals were considered to be molting covert or body feathers if a total of at least 3 feathers were molting in all covert or body feather tracts combined, to account for occasional adventitious molt.

Weather data were collected at 5 locations along the elevational gradient (1500, 1800, 2750, 2850, 3450 m a.s.l.) using HOBO Microstation Data Loggers (H21-002, Onset Computer Corporation) fitted with Temperature/Relative Humidity Smart Sensors (S-THB-M002, Onset Computer), 0.2 mm Rainfall Smart Sensors (S-RGB-M002, Onset Computer), Photosynthetic Light (PAR) Smart Sensors (S-LIA-M003, Onset Computer), and Wind Speed and Direction Smart Sensors (S-WCA-M003, Onset Computer). The sensors were mounted on poles approximately 1 meter above the canopy, and the temperature/relative humidity sensors were fitted with sun shields. Microstations logged data every 10 minutes during 2007–2009. Fruit data was collected at 14 1-ha plots situated every 250 m in elevation from 800–3450 m a.s.l. (M. R. Silman, *unpubl. data*). In each plot, 100 fruit fall traps were distributed every 10 m in a grid layout. We checked traps every 2 weeks throughout 2007 and measured and identified all seeds (all to family, many to species).

During data analysis, we divided all flight feather molt observations into three elevational zones: low (795–1300 m a.s.l.), medium (1300–2000 m a.s.l.), and high (2000–3387 m a.s.l.). The cutoffs between elevational zones were set at 1300 and 2000 m a.s.l. so that netting effort was relatively similar between zones. We then assigned bird species to simplified foraging guilds—frugivores, nectarivores, insectivores, omnivores, carnivores, and aquatic feeders—based on a variety of published sources (Parker and O'Neill 1980, Isler and Isler 1987, Terborgh et al. 1990, Poulin et al. 1994, Restrepo and Gómez 1998, Herzog et al. 2003). We measured the correlation between molt frequency and environmental factors using a cross-correlational analysis using a maximum time lag of 6 months (Wikelski et al. 2000). Analyses including migratory status use the results of Merkord (2010 Chapter 4) to classify species as elevational migrants or nonmigrant residents.

RESULTS

We captured 3,492 individuals and scored 2,983 of them for flight and contour feather molt. Summing across years, the number of individuals scored per month ranged from 99 to 861 (Table 1). Birds scored for molt comprised 8 orders, 36 families, 186 genera, and 270 species. For 55 species, only one individual was scored, but for 20 species at least 40 individuals were scored; 183 individuals were scored of the most commonly captured species, Streak-necked Flycatcher (*Mionectes striaticollis*). Flight feather molt was observed in 107 species and covert-body molt in 195 species.

The percentage of individuals molting flight feathers varied from 3.8% during the dry season to 31% at the peak of the wet season (Fig. 2). Covert-body molt ranged from 23% at the end of the dry season and beginning of the rainy season to 76% at the end of the wet season (Fig. 2). As expected, flight feather molt was always less common than covert-body molt, and the percentage of individuals molting flight feathers was significantly correlated with the percentage molting covert or body feathers ($r = 0.98$). The frequency of flight feather molt was most strongly correlated with rainfall ($r = 0.92$; Table 2). There was also a correlation with temperature during the previous month ($r = 0.66$), fruit volume during the previous month ($r = 0.66$), and fruit number 4 months later ($r = 071$), but not with solar radiation (Table 2).

The timing of flight feather molt is fairly consistent along the elevational gradient (Fig. 3a). In all elevational zones, the percentage of birds molting is low (2.0–6.1%) during the dry season and the beginning of the wet season (Jun–Aug). Molt activity increases gradually through the middle of the wet season (Nov) and peaks in the late wet season (Feb or Mar). The only noticeable difference in the percentage of birds molting occurs during Mar, when proportion of molting birds increases from 0.29 ($n = 146$) to 0.43 ($n = 14$) at lower elevation and decreases from 0.29 ($n = 7$) to 0.16 ($n = 49$) at middle elevations. Molt at high elevations that month (0.36; $n = 96$) is similar to that at low elevations. The net effect is that in Mar a smaller percentage of birds are molting at middle elevations compared to high and low elevations. The apparent variation in molt rates in Mar between birds in different elevational zones is intriguing, but whether the variation is a biological phenomenon or an artifact of small sample sizes in either Feb or Mar is unclear. Variation in fruit volume or fruit number do not appear to be correlated with the mid-elevation decrease in the percentage of birds molting (Figs. 3b, 3c), nor is there any climatic variation that might readily explain the observed pattern (Merkord 2010 Chapter 3 Fig. 2).

Four foraging guilds—frugivores, nectarivores, insectivores, and omnivores—were captured in sufficient numbers to estimate the percentage of birds molting during all sampled months. The monthly trends in flight feather molt are broadly similar to those of all species combined, but some variation among foraging guilds is apparent (Fig. 4). Among all four guilds, molt is rare during the dry season (Jun–Jul). As the breeding/wet season progresses, however the percentage of insectivores, and to some degree nectarivores, increases markedly. This contrasts sharply with the percentage of molt in frugivores and omnivores, which remains low through Nov. During the months of peak precipitation (Feb–Mar), the percentage of birds molting was high in all guilds. Frugivores, which show the lowest percentage of molt during Nov, show the highest percentage during Feb. Overall, it appears that frugivores and omnivores initiate molt later than insectivores and nectarivores. Unfortunately due to our lack of data in Dec–Jan and Apr–May, we are unable to ascertain whether molt occurs more rapidly in frugivores and omnivores, or if it is just shifted to later in the season.

Migratory status also appears to affect the frequency of molt. Molt frequency is highly correlated between elevational migrants and nonmigrants ($r = 0.95$; Fig. 5). Elevational migrants, however, showed a consistently lower frequency of molt than nonmigrants, except in July when slightly more migrants were molting. This pattern is consistent with the theory that elevational migrants spend, on average, less time molting than nonmigrants. In other words, that elevational migrants molt more quickly than nonmigrants, making observation of the molt less likely. Our results agree with other studies that have shown migratory populations to molt more quickly than nonmigratory populations (Helm and Gwinner 1999, 2001). That Jul was the only month when the frequency of molt in migrants equaled that of nonmigrants is interesting because that is the time of year when most migrants are on their nonbreeding grounds. This pattern may suggest that some migrants molt during the dry season to take advantage of resources not available to them during other seasons. Due to our lack of sampling in some key months, it is impossible to ascertain whether molt also occurs earlier in elevational migrants, as might be expected if they need to finish molting in time to migrate. As expected, we observed no flight feather molt in either boreal or austral migrants, which complete their prebasic molts on their breeding grounds.

DISCUSSION

Molt was rare during the dry season and the early wet season, and increased dramatically to peak during the middle and late wet season. This pattern is consistent with the expectation that birds undergo their prebasic molt shortly after breeding (Palmer 1972). Our personal observations, combined with extensive data on nesting behavior by Gustavo Londoño (*unpubl. data*), suggest that most species in our study area initiate nesting during the period from Sep to Nov, the late part of the dry season and the early part of the wet season. Thus peak molting appears to follow 2–3 months after peak breeding. The general timing of seasonal precipitation, breeding activity, and molt in our study area closely matches that found in the cerrado of south-central Brazil (Oniki and Willis 1999, Piratelli et al. 2000, Marini and Durães 2001).

Fruit number is almost certainly not a driving force in the timing of breeding or molt, because peak numbers of fruits occur during the middle of the dry season at least 2 months before most birds begin breeding. The dry season peak in fruit number may be due to wind-dispersed species, which are dispersed mostly during the dry season. This pattern is largely driven by the higher elevation sites where wind-dispersed species are more common. The volume of fruit, however, *is* fairly well correlated with molt frequency, albeit with a one month lag between the two peaks. Assuming a rough 3 month delay between peak nesting and peak molting activities (Marini and Durães 2001), for many species the peak in fruit abundance would likely occur during the postfledging stage. Studies have shown that while many species feed their nestlings on protein-rich arthropods, including otherwise frugivorous species (Riehl and Adelson 2008), fruit can be an important resource for recently fledged juveniles (White et al. 2005). We have measurements of all sampled fruit seeds, and have identified most of them, so it would be possible to classify the available fruit into size classes. Conducting further analyses where the timing of breeding or molt is correlated only with fruits of the appropriate size for any given individual may yield even better correlations between fruit volume and molt.

Nevertheless, rainfall was a much stronger correlate of molt frequency than the other environmental parameters. Other studies have documented that tree diameter growth rates in the study area peak during the early wet season (J. Rapp, *unpublished data*). This peak in growth rates is probably correlated with a peak leaf flushing.. Peak herbivory is correlated with leaf flushing (Gombauld and Rankin-de Merona 1998, Williams-Linera 1999), so a peak in the biomass of arthropod herbivores is likely at this time. Many studies suggest that birds time their breeding so that food availability is highest when adults are feeding nestlings and juveniles (Perrins 1970, van Noordwijk et al. 1995). A general pattern begins to emerge in our data, where tree growth and presumably foliar growth are timed with increases in temperature and rainfall at the end of the dry season. Breeding activity picks up and most birds are nesting when the presumed peak in arthropod abundance occurs. Then fruit volume peaks just after juveniles have fledged and are searching for easy sources of food, and while adults are undergoing flight feather molt.

Thus the timing of both breeding and molt are ultimately set by the onset of the wet season rains. This hypothesis is supported by Wikelski et al. (2000) who found that gonad growth in the Spotted Antbird (*Hylophylax naevioides*) in Panama was spurred by increasing rainfall.

Migratory individuals in at least one partially migratory species are known to molt earlier and more synchronously than sedentary conspecifics (Munro et al. 2006). Completely migratory temperate populations of Stonechats also molt more quickly than nonmigratory tropical populations (Helm and Gwinner 1999, 2001). Our results are consistent with theory, and with these other studies, in suggesting that migratory individuals have a shorter molt window than nonmigratory individuals. In all cases, the presumed mechanism is that migratory individuals must increase the speed of molt in order to minimize the overlap of molt and migration. Interestingly, our results suggest that there is some cost associated with overlapping molt and migration even when the migration is over a very short distance. The entire elevational range of many Andean species, including most elevational migrants, is often only a few kilometers wide. Birds do not need to undertake the extreme physiological changes required of long-distance migrants (e.g., Piersma et al. 1999), yet there may be a different set of physiological constraints imposed by elevational migration. Changes in temperature and oxygen partial pressure along an elevational gradient can have great physiological and ecological effects on species through various mechanisms including metabolism, oxygen transport, and flight mechanics (Altshuler 2006, Altshuler and Dudley 2006). Species with broad elevational distributions show a high phenotypic plasticity in the expression of genes controlling compensation for thermal and hypoxic stress (Cheviron et al. 2008). Elevational migrants would not only require a similar capacity for acclimation, but would make use of it regularly. It is unclear what physiological changes an elevational migrant might undergo before migrating in order to prepare itself for the changes in environmental conditions it would encounter *en route*.

The timing of molt seems to vary little between elevations. Molt at high, middle, and low elevations is rare during the dry season and picks up gradually through the beginning of the wet season, presumably as birds finish breeding. The only large difference is in Mar when middle elevations apparently have much lower percentage of molt than high and low elevations. As previously mentioned, there is no variation in fruit abundance, temperature, or other climatic variables that appears to explain the mid-elevation decrease in molt activity. One possible explanation is that the percentage of birds molting is affected by seasonal changes in the abundance of elevational migrants at middle elevations. Middle elevations are more likely than higher elevations to receive an influx of elevational migrants because most elevational migrants move downslope after breeding (Merkord 2010 Chapter 4). We know that at least some elevational migrants have left their high-elevation breeding sites by Mar (Merkord 2010 Chapters 2, 4). Assuming that these elevational migrants molt earlier than nonmigrants, the percentage of birds molting in Mar would be higher at higher elevations, which by that time are composed primarily of slower-molting sedentary individuals. Likewise, middle elevations whose bird populations are augmented by early-molting migrants would show a lower percentage of molt in Mar. By this logic, lower elevations should also see a lower percentage of molting birds in Mar because of an influx of elevational migrants, but in fact, we observed a higher percentage of molt in Mar at lower elevations compared to middle elevations. This could be explained if there were less migration between middle and lower elevations than between higher and middle elevations. Unfortunately this hypothesis cannot be fully tested yet. While data suggest an influx of elevational migrants from higher elevations into a mixed-species flock at 1400 m (here defined as middle elevations; Merkord 2010 Chapter 2), data is lacking on the extent of movement between middle and lower elevations.

The differences between feeding guilds in the timing of molt are noticeable. The frequency of flight feather molt in frugivores and omnivores was quite low during the dry season and the first half of the wet season. This frequency increased dramatically by Feb, particularly in frugivores. Insectivores, on the other hand, and to a lesser degree nectarivores, appear to initiate molt earlier with the result being a longer window of molt and a less pronounced Feb–Mar peak. This contrasting pattern between insectivores and frugivores-insectivores is similar to that found by Marini and Durães (2001)in the Brazilian cerrado. Furthermore, this scenario fits in nicely with the overall patterns of resource abundance we noted above. If arthropod abundance peaks early in the breeding season it would make sense for insectivores to speed up their molt, possibly overlapping with breeding to a greater extent, to take advantage of the abundant arthropod resources. On the other hand, frugivores and omnivores, which also consume much fruit, may be best served by delaying molt until the peak of fruit abundance because fruits have a lower protein to calorie ratio than arthropods (Moermond and Denslow 1985).

Overall, the timing of molt at our Peruvian study site was similar to that found in areas with similar seasonal weather patterns in southern Brazil, and peaked as expected following the early wet season pulse in breeding activity. There was little apparent difference in molt timing between high and low elevation birds, except that perhaps middle elevation birds finish molting sooner than high or low elevation birds. If real, this difference may result in part from life history tradeoffs associated with migratory status or diet specialization. The question of whether high elevation birds live fast- or slow-paced lives compared to lower elevation birds is still quite relevant, but may require a broader approach that incorporates multiple life history parameters, including those associated with breeding, molt, *and* migration. We encourage the collection and publication of data on the natural history of tropical species, and suggest that tropical elevational gradients will provide an excellent laboratory for unraveling the causes of variation in avian life histories.

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Table 1. Mist netting effort (net hours) and number of individuals scored for flight feather molt in each month.

Month	***Net Hours***	***Number of Individuals Scored***
Jan	0	0
Feb	456	153
Mar	1024	159
Apr	0	0
May	0	0
Jun	713	158
Jul	4027	861
Aug	2346	652
Sep	1705	564
Oct	1662	337
Nov	560	99
Dec	0	0
Total	12493	2983

Table 2. Correlation between the frequency of flight feather molt and rainfall, temperature, photosynthetically active radiation, fruit volume, and fruit number. Cross correlation analysis allows flight feather molt to be correlated with other data series assuming there may be a lag time, measured in months. The results show the lag that yields the highest correlation. For example, molt frequency is best correlated with the current month's rainfall and the previous month's temperature. Correlations whose 95% confidence intervals do not overlap zero are denoted with an asterisk (*).

	r	*Lag*
Rainfall	0.92 *	0
Temperature	0.66 *	1
PAR	0.37	
Fruit Volume	0.66 *	1
Fruit Number	0.71 *	-4

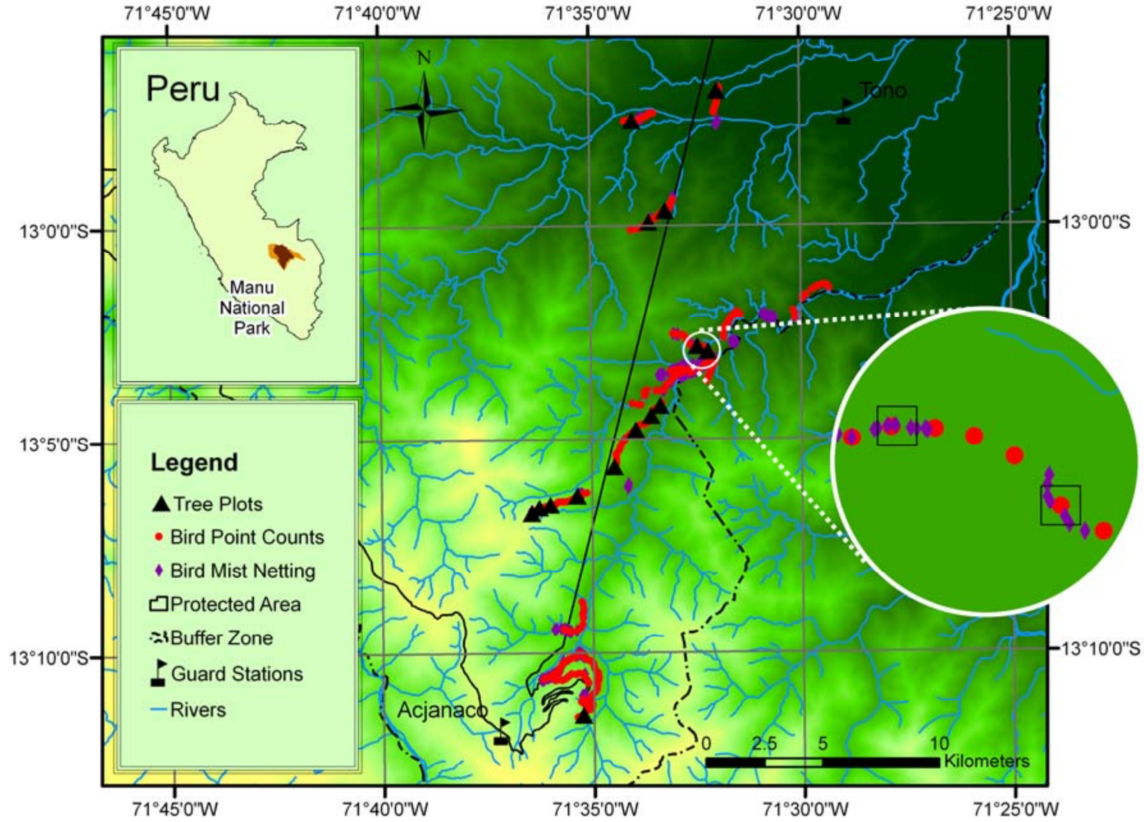

Figure 1. Map of sampling locations in Manu National Park, Cusco Region, Peru. Sites ranged from 900-3400 m a.s.l. Net sites are marked with purple diamonds.

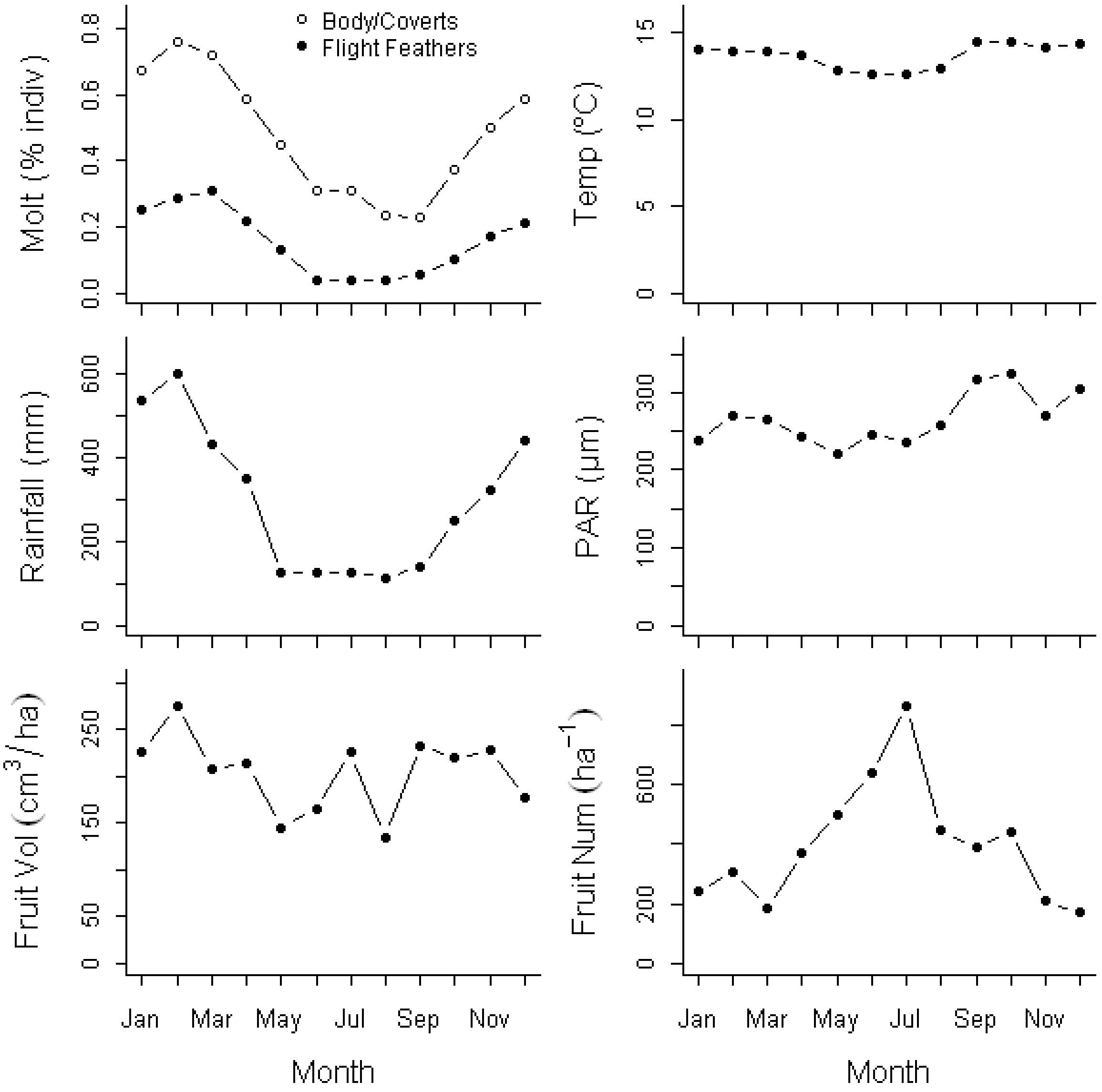

Figure 2. Monthly frequency of flight feather molt, frequency of body or covert molt, mean temperature, total rainfall, mean photosynthetically active radiation, mean seed mass in fruit fall traps, and mean number of seeds in fruit fall traps. Molt data for Dec-Jan and Apr-May are interpolated.

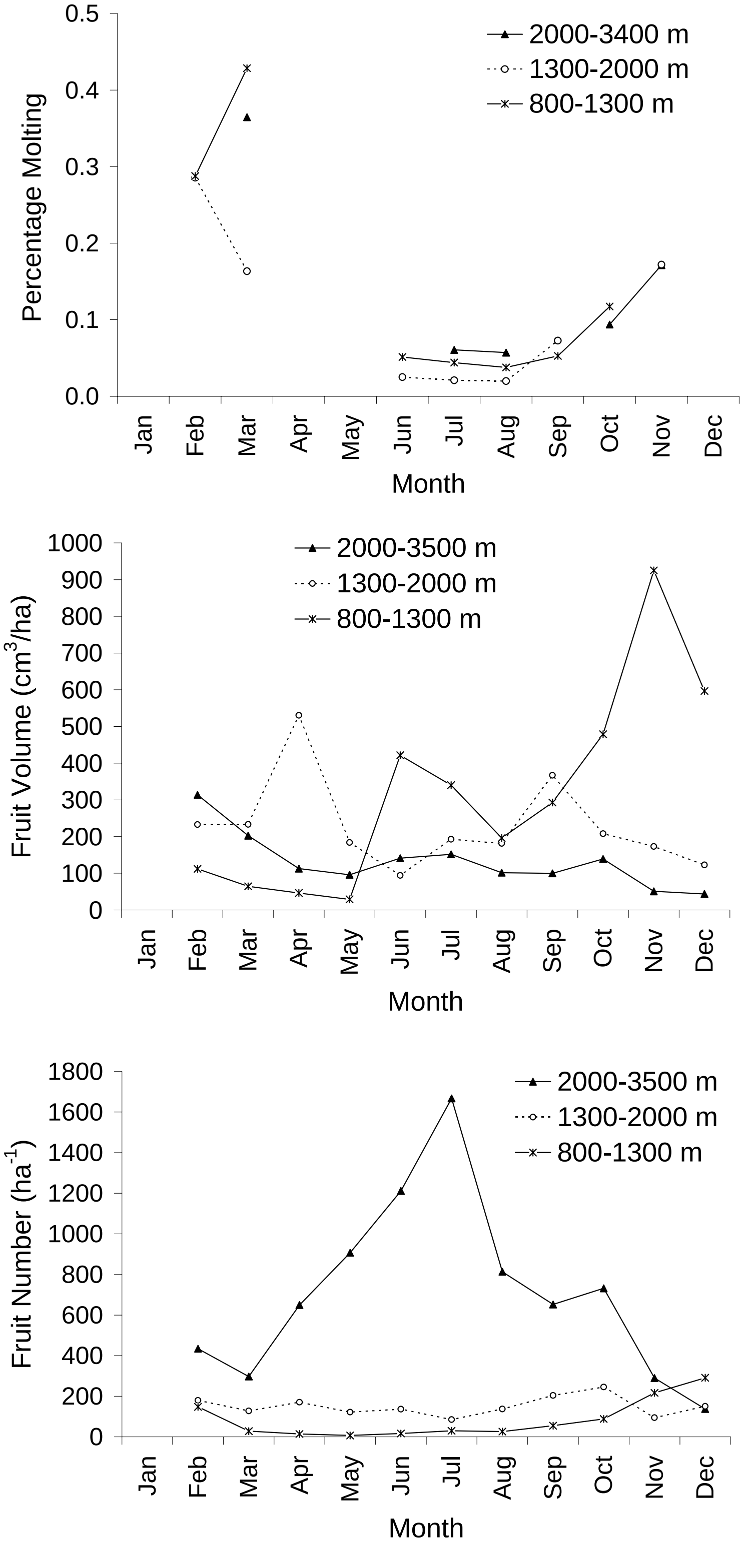

Figure 3. Monthly frequency of flight feather molt, mean seed mass in fruit fall traps, and mean number of seeds in fruit fall traps in three elevational zones

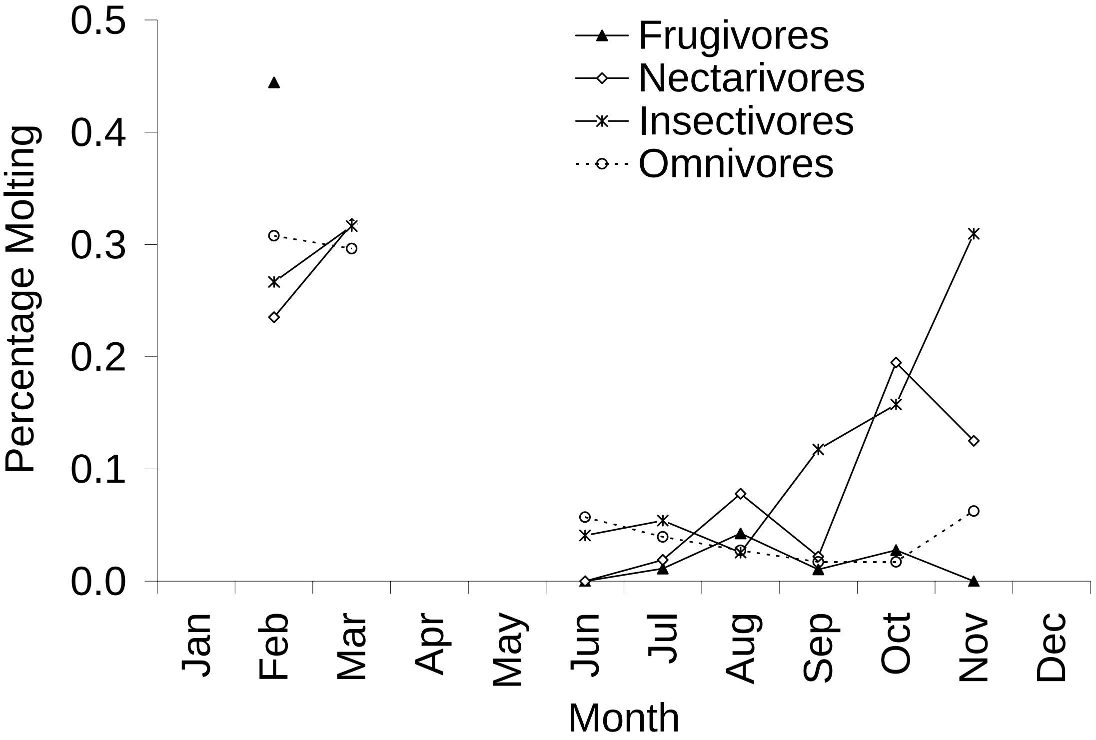

Figure 4. Monthly flight feather molt frequency among major foraging guilds.

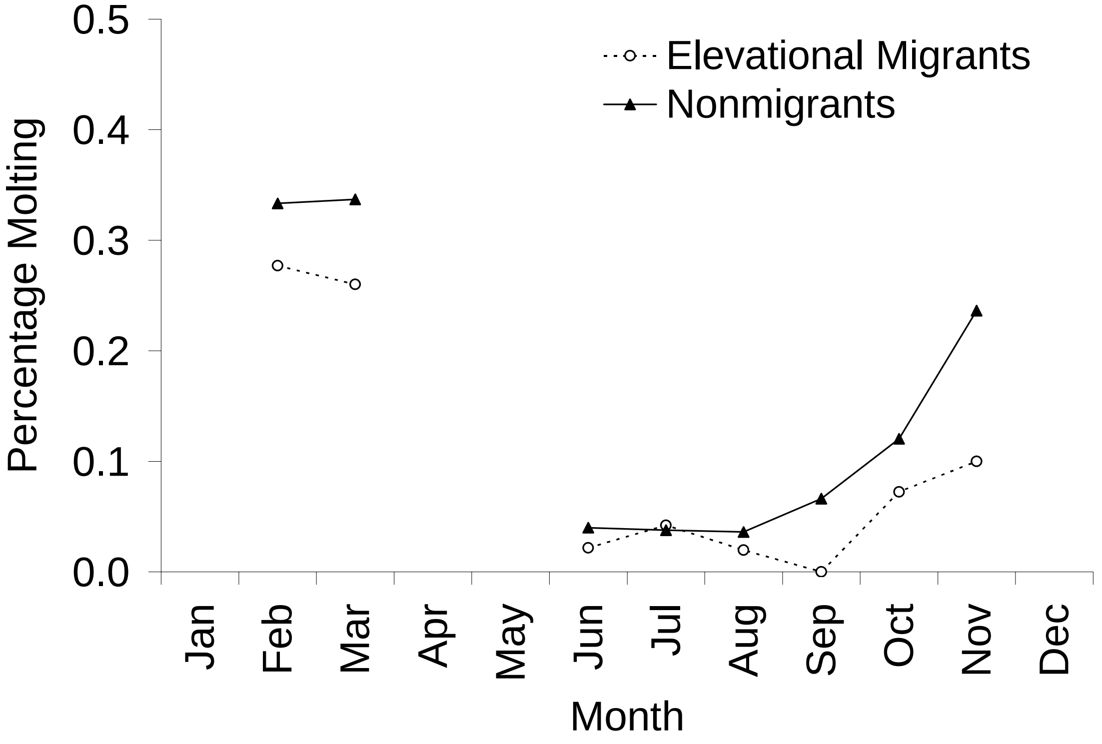

Figure 5. Monthly frequency of flight feather molt among elevational migrants and nonmigrants.

CHAPTER 2

COMPOSITION AND DYNAMICS OF A MEGA-DIVERSE MIXED-SPECIES FLOCK IN A TROPICAL MONTANE FOREST

Christopher L. Merkord

ABSTRACT

Mixed-species bird flocks are a common phenomenon throughout the world, reaching their highest diversity and size in the tropics, where flocks often defend permanent territories from neighboring flocks. I present notes on the composition of one particularly large and diverse mixed-species flock from a middle elevation site on the eastern slope of the Andes in Manu National Park, Peru. Through a combination of mist netting, color banding, resighting, behavioral observations, and point counts I thoroughly documented the composition of the flock. The primary nuclear species were 6 species of tanagers and bush-tanagers (*Tangara*, *Chlorochrysa*, *Chlorospingus*; at least 72 individuals). In addition, I classified another 52 species (311 individuals) as regular flock associates, 49 species (267 individuals) as occasional flock associates, and 5 species (9 individuals) as accidental flock associates. There was little distinction between canopy and understory components of the flock, and the entire flock operated under a dynamic fission-fusion process, with subflocks splitting and rejoining the main flock often. I deemed 17 species full or partial elevational migrants, including the two most abundant species, *Diglossa glauca* and *Mionectes striaticollis*. Seven individuals of six species originally captured in the mixed species flock were recaptured at a nearby ridge,

suggesting the possibility that a subflock of elevational migrants may have left the main flock and completed part of their upslope migration as a cohesive group.

INTRODUCTION

The aggregation of individual animals into monospecific groups is a widespread phenomenon across a diverse range of taxa and ecosystems (Parrish and Edelstein-Keshet 1999, Sumpter 2006). Fitness benefits of group formation have been attributed to factors including predation risk, foraging efficiency, mate choice, physiological regulation, and transportation cost (Krause and Ruxton 2002). These potential fitness benefits are just as applicable to polyspecific groups as monospecific. Among polyspecific, or mixed-species, foraging flocks of birds, reduced predation risk and increased foraging efficiency appear to be the factors driving flock participation (Morse 1977, Diamond 1981, Jullien and Clobert 2000). Recent studies, including both empirical evidence and individual-based models, suggest that reduction in predation risk is the more important of these two factors in both mono- and polyspecific foraging flocks (Dolby and Grubb 2000, Hart and Freed 2005, Wood and Ackland 2007).

Mixed-species flocks are highly variable in their composition and structure, although several geographic trends are apparent. Flocks in temperate latitudes are generally smaller, less diverse, and less stable than those in the tropics. The reduced size and diversity of temperate flocks may to some extent be a reflection of latitudinal trends in productivity and species diversity.

Temperate and subtropical mixed-species flocks are common during the nonbreeding season, but largely dissolve as breeding commences (Morse 1970, Bell 1980). Some flocks occupy a specific home range during the nonbreeding season and have a stable membership (e.g. insectivore flocks; Morse 1970), while others are more transitory in nature, forming and dissolving over the course of hours or days and defending no particular territory (e.g. granivorous sparrows and finches; Cody 1971). During migratory periods large, transient mixed-species flocks can be common in temperate forests (Rodewald and Brittingham 2002).

The largest and most diverse flocks are generally found in tropical forests, where mixed-species flocks can be composed of up to 60 species and 180 individuals (Munn 1985, Gram 1998). Flock territories are often permanent, and the flock territory is often defended from neighboring flocks by individuals of core flock species (Munn and Terborgh 1979, Jullien and Thiollay 1998), although some flocks do not exhibit strong territoriality (Hart and Freed 2003). Even when mixed-species flock territories are maintained throughout the year, participation in flocks varies seasonally as migrants leave the area and individuals spend less time participating in the flock during the breeding season, resulting in pronounced seasonal variation in flock size (Thomson and Ferguson 2007). In at least some areas, separate canopy and understory flocks exist independently of each other, rarely interacting despite their overlapping territories (Munn 1985).

The effect of elevation on mixed-species flock composition and structure is rather poorly known. In many areas, observers have noted that higher elevation flocks are smaller and less diverse than at lower elevations (Moynihan 1962, Macdonald and Henderson 1977). There may also be some tendency for montane flocks to be less stable, splitting and reforming in a fission-fusion process (Hart and Freed 2003). In some cases, flocks do not appear to hold permanent territories, and may disband completely during the breeding season (Hart and Freed 2003). Information is needed on tropical montane mixed-species flocks in more areas to begin to elucidate patterns related to elevation.

Here I describe the composition and structure of a mixed-species flock at a middle elevation site on the moist eastern slope of the Andes. I present data on core flock members, flock area, flock movements, and seasonal dynamics of flock membership. In particular, I discuss the seasonal presence of elevational migrants in the flock, and the offer comments on variation in flock characteristics along an elevational gradient.

METHODS

Study Site

The study site is located near the confluence of the San Pedro and Kosñipata rivers, in the buffer zone of Manu National Park (NP), Cusco, Peru (Fig. 1). Most work was conducted on the grounds of the Cock-of-the-Rock Lodge and adjacent tourist lodges in an area known locally as “San Pedro,” located at approx. km 152 on the Cusco-Pilcopata Highway, The climate is moderately seasonal, with monthly precipitation ranging from 117–802 mm and average monthly temperature ranging from 16.1–19.7 °C (Fig. 2). At 1360 to 1500 m a.s.l., the study site consists primarily of humid evergreen forest, although the presence of the rivers, lodges, and unpaved road creates a mosaic of forest, forest edge, *Guadua* and *Chusquea* bamboo, and thick scrubby vegetation. Forest canopy height varies from 10 m on steep exposed ridges to 40 m in the alluvial Kosñipata River valley, with a few large emergent trees over 60 m tall. The forest generally has a thick understory, except in the tallest closed-canopy forest along the Kosñipata at about 1370 m. Most of the lower Kosñipata valley, including the study site, has been selectively logged in the past 40 years, so the forest undoubtedly differs in floristics and physiognomy from its natural state. Near the lodge buildings, trees of the family Melastomataceae and non-native flowering shrubs have been planted to attract birds.

Mixed-species flocks are common in the area, and flock home ranges usually abut, leaving little area completely unused by a flock (*pers. obs.*). Our notes focus on the mixed-species flock whose range encompassed our field station, hereafter referred to as the "San Pedro flock". Portions of this flock's home range encompass several hundred m of the "highway" and several km of walking trails maintained by the Cock-of-the-Rock Lodge, allowing unprecedented opportunities to view and follow the flock in a region known for its unforgivingly steep terrain.

Mist Netting

The present study was conducted as part of a larger initiative to document the distribution and movements of birds in the Kosñipata Valley and surrounding areas. As part of this larger study, my field assistants and I captured birds in the San Pedro area with mist nets from June–August 2005 (826 net hrs; 6–12 m nets, 34 mm mesh). Nets were located at ground level throughout the entire flock area, although notes were not taken on whether captured birds were associating with the flock at the time of capture. I collected morphological measurements, molt data, and feather samples, and marked all birds except hummingbirds with numbered aluminum leg bands.

The following year I made a more concerted effort to capture members of the mixed-species flock. I located mist nets at 21 locations in areas frequently used by the flock, but subject to sufficient human disturbance that few birds used the area except when the flock was passing (Fig. 3). I placed mist nets either at ground level or up to 10 m above ground using a combination of long aluminum net poles or simple string-pulley systems using available branches as "pulleys." I opened the nets on 19 days between

June 27 and July 23, 2006 (961 net hrs), using no more than 6 net locations on any given day. Again I marked each individual with an aluminum band; on individuals I suspected of participating in the mixed-species flock at least occasionally, I also placed colored celluloid leg bands in a unique color combination. In addition to data collected in 2005, my assistants also collected blood samples and ectoparasites from some individuals. I repeated this sampling method on a later visit in February and March 2007 (5 days, 219 net hrs) using the 6 previously used net locations most successful at capturing flock members.

Flock Observations

After the primary netting period in 2006, I began to make more detailed observations, including the resighting of color-banded birds. While observations were primarily made by myself, my notes were augmented significantly by several field assistants and colleagues. Observations were made using one of two methods: we either followed the flock for as long as possible, often using available trails, or we remained at one of several excellent vantage points for a given amount of time. When possible, I standardized effort at the vantage points by dividing observation periods into 15 minute intervals. In all cases I recorded the location of the mixed-species flock or component thereof, the direction of movement of the flock, which species were present, which individuals were present (when color-band combinations could be read), and which individuals were associating with the flock. These detailed field observations were made from 16 July–24 October 2006, 13 February–31 March 2007, and 18 June-3 September 2007. I calculated the home range of the San Pedro flock by drawing the minimum convex polygon around flock locations that could be confirmed as the San Pedro flock or a component thereof by the presence of color-banded individuals. During the June–August dry seasons of 2004–2006 I also made general observations of flocks in the San Pedro area, recording the number of individuals of each species present in the flock. Observations were retroactively assigned to the San Pedro flock and neighboring flocks based on their location, under the assumption that flock home range remained stable from 2004-2007. General observations and detailed observations together totaled approx. 700 observer hours.

Species Characterization

Presence in the flock area. I classified each species as a year-round resident, elevational migrant, latitudinal migrant, or occasional or irregular visitor within the flock area based on a combination of my own observations and published information. Species listed as latitudinal migrants by Walker et al. (2006) I assigned each to that category, while species meeting one of the following criteria I classified as elevational migrants: 1) the species showed was marked seasonal variation in abundance as measured by the maximum number of individuals seen each month during standardized 15-min flock observations; 2) the species occurred occasionally in the flock, was rarely observed within the elevational range of the flock (approx. 1300–1500 m a.s.l.), and never showed signs of breeding anywhere within that elevational range, based on mist-netting and point count data (described in Merkord 2010 Chapters 3 and 4); 3) banded individuals were recaptured or resighted outside the home range of the San Pedro flock or neighboring flocks; or 4) the species was categorized as an elevational migrant by Merkord (2010 Chapter 4). Occasional or irregular visitors to the flock area were those species that occurred fewer than 3 times within the flock, whose apparent rarity was not suspected of being caused simply by low detectability, and for which data on breeding range is sufficiently lacking that we could not classify it as an elevational migrant. The remaining species comprised the resident category.

Flocking propensity. Farley et al. (2008) provide a useful review of the great variety of terminology used to describe participation in mixed-species bird flocks. Many description schemes, including those of Farley et al., rely on detailed knowledge of the movement patterns of individual birds, unbiased estimates of the percentage of time individuals spend associated with a flock, or observations of birds both within and without a flock. While I recorded notes on the subject, my behavioral observations lack sufficient detail and sample size to estimate flock propensity empirically, in part because of the large number of individuals participating in the San Pedro flock and the difficulty of following the flock throughout its entire home range. Instead, based on my impression of its flocking propensity, I place each species into one of the following four categories modified slightly from Farley et al. (2008): regular associates, occasional associates, accidental associates, and non-joiners.

Regular associates are those species I observed to associate with the flock whenever the opportunity presented itself. For species whose home range roughly coincided with the flock, individuals were almost always associated with the flock. For species whose home range was much smaller than that of the flock, individuals joined the flock only while it passed through their home range. Occasional associates are those species I observed to associate with the flock sometimes, but were often seen by themselves outside of the flock. Accidental associates are those species which do not appear to associate with the flock, but were observed in close proximity when the flock passed near their location. More detailed individual observations may indicate that some of the accidental flock associates do indeed alter their foraging or vigilance behavior to take advantage of the presence of the flock. In addition, I identify the apparent nuclear species of the San Pedro flock, those which contribute to the flock's cohesion (Moynihan 1962).

Number of individuals. I do not divide the species into low- and high-density species as others have (Munn 1985, Farley et al. 2008), but instead provide a conservative estimate of the number of individuals present in the flock's home range. This estimate is derived from the sum of the number of banded individuals captured or observed inside the flock home range and the minimum number of non-banded individuals seen at any given time.

RESULTS

Flock Home Range and Movements

The San Pedro flock used an area of about 15.4 ha (Fig. 1). At least three neighboring flocks had home ranges abutting the San Pedro flock, all identified by unbanded individuals of species that were mostly banded in the San Pedro flock. Topographic features including rivers and ridges at least partially defined the borders of the area used by the flock. Interestingly, the flock was quite willing to cross the Rio San Pedro, but never crossed the Río Kosñipata, despite the fact that both gaps were approximately the same width (30-40 m). The northern boundary of the flock home range was less well defined, but may have coincided with large open areas on the alluvial floor of the Río San Pedro valley. On two occasions I observed the San Pedro flock near the border of its home range and simultaneously could hear a neighboring flock < 100 m on the other side of the border. During one such event, I noted a single bird fly from the San Pedro flock across the San Pedro river to join the neighboring flock. The rest of the San Pedro flock turned and followed the river, which marked the edge of its home range. While I never observed direct territorial interactions with congeners in neighboring flocks, I suspect that the flock exhibited mixed species territoriality much like flocks in the lowlands of Manu National Park (Munn and Terborgh 1979).

Each day at dawn the flock coalesced in the same area in the northeastern portion of the flock home range, a pattern also noted in some understory flocks (Jullien and Thiollay 1998). Coalescence was initiated by loud dawn vocalizations of two species. In the predawn darkness several individuals of *Tangara chilensis* would perch atop the tallest trees, singing their simple, repetitive rising and falling dawn song. Several minutes later, one or more pairs of *Chlorospingus flavigularis* would begin their loud chattering calls in the understory nearby. During the next 30 minutes the number of birds vocalizing in the vicinity increased dramatically, dominated by the two species previously mentioned and by intraspecific interaction calls of several other species of tanagers (*Chlorochrysa*, *Tangara*) and frequent songs of two flycatchers, *Leptopogon superciliaris* and *Phylloscartes ophthalmicus*. It is likely that at least some of these vocalizations stimulate flock formation in some way, especially given that many of these species act as nuclear species in the flock throughout the day.

Flock movements varied after coalescence. Sometimes the flock formed a dense, tight association of individuals with perhaps as many as 200 individuals condensed into an area of approx. 0.1 ha, while at other times the flock was more diffuse, spread over 1 ha or more. Based on my general observations, the flock's rate of movement increased the more tightly packed it was (Morse 1970, contra Powell 1979). When the flock was tightly packed, it was relatively easy to define its location and movement parameters, but in its diffuse state such a task was considerably more difficult. Polyspecific, and occasionally monospecific, groups of individuals, which I call "subflocks," regularly split off from the main flock. These subflocks may have been individuals that preferred to move more quickly or slowly than other flock members. Subflocks would sometimes rejoin the main flock within minutes, or other times remain separate for undetermined periods of time. It was unclear whether certain individuals or species preferred the company of other individuals or species, but this would be a fruitful avenue for future work. Such was the proclivity for subflocks to form that often it was impossible to determine where the main body of "the flock" (if the term was even appropriate at those times) was to be found, particularly during the mid-afternoon lull in flocking activity. Resighting of banded birds failed to suggest that subflocks held smaller territories or home ranges than the flock as a whole.

For the most part, species traditionally assigned to "canopy" or "understory" guilds foraged together, often side-by-side in the same foraging group. Although species showed general preferences for foraging height, it was not uncommon to have "canopy" tanagers feeding near ground level, or "understory" furnariids and flycatchers feeding in the highest branches. Only in the southeastern half of the flock home range along the Kosñipata River, where the canopy height is greatest, did we ever see subflocks composed strictly of understory insectivores. Even in this portion of the flock home range, however, we still regularly observed groups composed of both "canopy" and "understory" birds, with individuals distributed, based on their autecological characteristics, more or less evenly from the forest floor to the upper canopy as the foraging group moved through the forest.

Flock Composition

I observed or collected observations of up to 111 species of birds participating in the San Pedro mixed species flock (Appendix 1). The 58 species classified as regular flock attendants were represented by at least 386 individuals, while the 45 species classified as occasional flock associates were represented by 252 individuals (Table 1). Because I was unable to categorize the flocking behavior of each individual captured, it is possible that not every individual reported here actually participated in the mixed species flock. However, I suspect that the majority of occasional associates, and almost every regular associate did participate at some point during their presence in the flock area. Another 8 species comprising 24 individuals were classified as accidental flock associates: they were observed within the flock, but I was uncertain whether their presence was merely accidental or not. Several species present in the flock home range that may in fact participate in the flock to some degree, including *Pyriglena leuconota*, *Henicorhina leucophrys*, *Thryothorus genibarbis*, *Cyphorhinus thoracicus*, and *Catharus dryas*, are not on my list because I never observed them to associate with the flock, and indeed most observations of these species were of stationary singing individuals.

Of the 111 species observed in the flock, I classified 63 (57%) as year-round residents within the flock home range (Table 1). Another 27 species (24%) were classified as elevational migrants, although at least 9 year-round residents and at least 7 occasional or irregular visitors may turn out to be elevational migrants with more study, bringing the potential total to 43 (39%). Latitudinal migrants comprised only 4 species (2%), including 2 Nearctic-Neotropical migrants and 2 South American austral migrants. A final 17 species (15%) were present only occasionally in the flock home range. When the number of individuals is considered instead of the number of species, year-round residents increase to 63% of the flock members, elevational migrants increase to 30%, and occasional or irregular visitors decrease to only 5% of flock members (Table 1), primarily because occasional or irregular visitors were often represented by only one or two individuals.

Seasonal Turnover

The abundance of most species in the mixed species flock remained fairly constant from month to month. For example, 2 species of *Tangara* and a *Chlorospingus* were observed every month of the year during which I made standardized 15-min flock observations, with fairly constant numbers observed from month to month (Fig. 3a). In contrast, the abundance of several species appeared to fluctuate seasonally. For three species of tanagers in particular, the maximum number of individuals seen during any single 15-min observation period varied substantially between months (Fig. 3b). The number of *Tangara punctata* and *Diglossa glauca* peaked in March near the end of the heavy rainy season at 7 and 5 individuals, respectively. By the middle of the dry season in June, numbers of *T. punctata* had declined somewhat, while numbers of *D. glauca* remained high. Both species decreased in abundance throughout the end of the dry season and the beginning of the rainy season. By October, the peak of the breeding season, none were observed in the San Pedro flock. Another tanager, *Tangara nigroviridis*, was absent from the flock in February but started appearing by March. Numbers peaked in July at 8 individuals and declined rapidly until, again, none were seen in October.

Emigration Events

Seven individuals of six species originally captured and color-banded in the mixed-species flock in San Pedro later moved to two sites along a ridge east of their original capture location (Table 2, Fig. 4). The individuals included *Chiroxiphia boliviana*, *Mionectes striaticollis* (2 individuals), *Zimmerius bolivianus*, *Turdus ignobilis*, *Chlorochrysa calliparaea*, and *Diglossa glauca*. These individuals were all color-banded in San Pedro between June 28 and July 8, 2006. On July 30, on a ridge at 1500 m a.s.l. and 1.0 km to the northeast of the edge of the flock home range, five individuals (*C. boliviana*, *M. striaticollis* #1, *Z. bolivianus*, *T. ignobilis*, and *C. calliparaea*) were captured in three adjacent nets. Then on August 9, three individuals (the same *C. boliviana*, *M. striaticollis* #2, and *D. glauca*) were recaptured at another site at about 1780 m a.s.l. on the same ridge, 800 m from the first recapture site and 900 m north of the edge of the flock home range. At both ridge sites, the recaptured color-banded birds comprised only a handful of the birds caught. Of the birds recaptured at the two ridge sites, only the *C. calliparaea* was seen again. That bird was resighted in the mixed-species flock at San Pedro on July 4 and 6, 2007.

Four other birds captured in the area of the mixed-species flock at San Pedro were recaptured or resighted elsewhere. A *Diglossa glauca* was first captured on July 31, 2005 at 1659 m on a ridge overlooking San Pedro, 450 horizontal m from the edge of the flock home range. The bird was recaptured and color-banded on July 8 in the mixed-species flock in San Pedro, 265 vertical m from its original capture location.

A male *Ramphocelus carbo* was captured and color-banded in San Pedro on July 7, 2006; it was resighted in almost the same location on August 10. On October 30 the bird was recaptured at a site at 1316 m a.s.l., 1.1 km from the edge of the flock boundary and 1.4 km from the original capture site. The recapture site is close to the Kosñipata River, and a direct route from one site to the other follows the riparian corridor, suggesting the corridor as a likely path of movement.

A *Platyrinchus mystaceus* was originally captured on October 28, 2006, at 1357 m a.s.l. in riparian habitat on the south side of the river, within the home range of a mixed-species flock adjacent to the San Pedro flock. The bird was recaptured in San Pedro on March 30, 2007 by C. Witt during a separate ornithological study, and again by us on July 12 in thick *Guadua* bamboo at a site 2.1 km to the northeast of the flock home range (1275 m a.s.l.). All three sites are close to the river, again suggesting the riparian corridor as a possible movement path.

Finally, I observed the resident pair of *Tangara xanthocephala* in the San Pedro flock feeding a fledgling in June and July 2006, and I captured and color-banded the juvenile in July. Although the parents were observed in the San Pedro flock several times in 2007, the color-banded bird was not. In July 2007, other observers reported seeing the color-banded bird in an adjacent mixed-species flock, one in which I had not previously noted any *T. xanthocephala*, suggesting that the bird had dispersed and filled an unoccupied slot in the neighboring flock.

DISCUSSION

Flock Home Range and Movements

In some aspects, the San Pedro mixed species flock was quite similar to other such flocks in the neighboring lowlands of Manu National Park (Munn and Terborgh 1979, Munn 1985) and throughout the neotropics (Powell 1979, Jullien and Thiollay 1998). For example, I suspect the San Pedro flock defends a mixed species territorial boundary, much like other rainforest flocks (Munn and Terborgh 1979, Jullien and Thiollay 1998). The flock maintained stable, well-defined home range boundaries, and only on one occasion did I see an unidentified individual in the San Pedro flock fly across the boundary to join a neighboring flock.

The approximate size of the San Pedro flock's home range, 15.4 ha, is significantly larger than territories found in the lowland rainforest of Amazonian Peru and Brazil (8 and 8.5 ha, respectively; Munn and Terborgh 1979, Develey and Stouffer 2001), but falls on the upper end of the 3.2–14.3 ha range for flocks studied by Jullien and Thiollay (1998) in the lowland rainforest of French Guiana. Jullien and Thiollay found that home range size varied based on vegetation density rather than flock size or species composition. The flocks that had home ranges over 14 ha in size were those with less than 5% cover of dense forest, much less than occurred in the San Pedro flock's home range. In many montane flock territories, it would be conceivable to have 100 % of the area covered by dense forest types, due to the vegetation structure created by steep topography. Thus the tight correlation between vegetation density and flock home range size is probably different in montane areas. Still, the relatively high percentage of tall, mature forest and anthropogenic open areas in the San Pedro flock's home range probably inflate its home range size above that of an average montane mixed species flock in the area. Jullien and Thiollay (1998) also found that 8.5–62.5% of each flock's territory overlapped with that of a neighboring flock. Lacking sufficient data on surrounding flocks, I can only speculate that such overlap would fall on the low end of that spectrum for the San Pedro flock.

The lack of differentiation between canopy and understory components of the San Pedro flock is similar to that found in other some other montane flocks (Stotz 1993, Poulsen 1996). Moynihan's (1962 p. 77) findings were similar, and he notes that birds in "montane bush flocks" were often scattered vertically through many levels of vegetation, unlike the canopy flocks of the lowlands. As Poulsen (1996) commented, this phenomenon appears to be correlated with physiognomic characteristics of the forest, including decreased canopy height and decreased canopy cover. I suspect that as elevation increases, the level of canopy-understory differentiation decreases. Near my study area there is certainly no distinction at all between canopy and understory flock members in flocks above 2500 m a.s.l., even in pockets of relatively tall forest (>20 m; *pers. obs.*), while in the lowlands there is almost complete separation of the two flock types (Munn 1985). The San Pedro flock appears to lie somewhere on the cline from complete separation to complete lack of separation, although perhaps falling closer to the latter.

Another interesting facet of the San Pedro flock was the complex process of fission and fusion that resulted as subflocks joined or left the main body of the flock. It may be that this process is somewhat illusionary, and that the subflocks only appear to split away but actually remain fairly close to each other, at least as far as bird sensory abilities are concerned. This cannot explain the entire situation however, because there was still a high degree of clumping of individuals regardless of whether all the “clumps” were moving in the same general direction or not. Other authors have not described the movements of individuals within mixed species flocks with enough detail for me to ascertain whether the fission-fusion model is the norm, or if it only applies to certain types of flocks. However, special note is made of the relative instability of mixed species flocks in some montane areas (Stotz 1993, Poulsen 1996), again suggesting that the dynamics of montane flocks may differ from their lowland counterparts. Flock size (i.e. number of individuals) may be one of the deciding factor in whether or how often a flock splits because the larger a flock, the less it needs to stay together to reap the benefits of flocking. A more detailed study of flock movements might be able to confirm this hypothesis by correlating the propensity of the main flock to spawn subflocks with the natural seasonal variation in flock size.

Seasonal Turnover

Tropical mixed species flocks have long been known to accommodate latitudinal migrants as either transient migrants or residents during the nonbreeding season (Powell 1980, Gram 1998). In many cases the ecology of migrant species in mixed flocks is even better known than that of resident species. This study demonstrates that elevational migrants may also play an important role in mixed species flocks. In fact, elevational migrants in the San Pedro flock outnumbered latitudinal migrants by 7 to 1 (although admittedly there was a seasonal bias in observer effort). No latitudinal migrants were nuclear flock species, or even regular flock associates. Elevational migrants, by contrast, included two nuclear species and 18 regular flock associates. Three of the most abundant species in the San Pedro flock (*Diglossa glauca*, *Tangara nigroviridis*, and *Tangara punctata*) were apparent elevational migrants, constituting almost 13% of all flock participants and 22% of all regular flock associates. Another species that is certainly at least partially migratory, *Mionectes striaticollis*, tied *D. glauca* as the most abundant species in the flock at 54 individuals. The exodus of elevational migrants from the mixed species flock that occurs from July through October undoubtedly affects the remaining flock members in ways as yet undetermined. My results contrast with those of other studies that have found nonresidents to play minor roles in seasonal variation in mixed species flock size (Powell 1979). I know of few studies that discuss the presence of elevational migrants in mixed species flocks (e.g. Chen and Hsieh 2002), but the situation may be more common than currently appreciated given that such a large percentage of species are known both to join mixed species flocks and to make elevational migrations.

Polyspecific Migration

The dispersal events or daily movements I documented to and from the San Pedro flock home range were not unexpected, and while the apparent elevational migration of a *Diglossa glauca* is interesting, it is in line with other data suggesting that the species is a seasonal elevational migrant in the study region. More interesting was the apparent emigration of a cohesive polyspecific group of birds from the San Pedro flock home range.

It is almost certain that the birds recaptured on a nearby ridge were traveling as a mixed species flock because the captures occurred so close together in space and time. While it is possible that the birds were traveling with the main body of the San Pedro flock on some large excursion from its home range, I offer four reasons why this is unlikely. First, I never observed the complete absence of the main body of the San Pedro flock from the San Pedro area. Second, I often watched the San Pedro flock, or one of its many subflocks, approach and stop at the northeastern boundary of the flock home range without crossing. Third, less than 50 m from this home range boundary I regularly observed the passage of the neighboring flock.

Any subflock that left the San Pedro flock home range would have had to cross this flock's territory and at least one other to reach either of the two ridge recaptures sites. And fourth, none of the most likely territorial member species of the flock, those represented in the flock territory by only one mated pair, were captured at the ridge sites.

Given that the group of birds in question did not represent the main San Pedro flock, I can condense the explanations for their capture at the ridge sites into a seasonal movement hypothesis and a daily movement hypothesis. According to the daily movement hypothesis, the observed movements may have been part of the regular movements, within its normal home range, of a mixed species flock separate from the San Pedro flock. This scenario, similar to that of the mixed flocks of tanagers in the lowlands in Manu, which occupy larger home ranges than sympatric canopy flocks, which in turn occupy larger home ranges than sympatric understory flocks (Munn 1985), seems unlikely to explain the present observations, however, because only one of the six species (*Chlorochrysa calliparaea*) might be considered a fast-moving, far-flying canopy species in the sense of *Tangara chilensis*, *Dacnis* spp., or *Cyanerpes* spp. The recaptured species are either understory or relatively slow-moving canopy species. Alternatively, the recaptured birds could represent one or two subflocks of the San Pedro flock that made occasional to regular forays outside of the flock home range. This explanation would seem to suffer the same flaws as the previous one with regards to the movement behavior of the species involved.

The seasonal movement hypothesis, on the other hand, posits that all 7 birds in question, and possibly others not recaptured, departed from the San Pedro flock home range together and slowly made their way along a path that took them to the first ridge recapture site, then climbed along the ridge to reach the second recapture site. Presumably at various stages of the trip individual birds dropped out of the subflock to establish breeding territories, although at least three of the birds were still together by the time they reached the second ridge site. All six species involved are either known elevational migrants themselves, are closely related to other elevationally migratory species, or show patterns of occurrence in the San Pedro flock consistent with elevational migration. At least 13 species of *Turdus*, including *T. ignobilis*, are known or suspected of making seasonal elevational movements (Ornelas and Arizmendi 1995, Hilty 1997, Gómez de Silva G. et al. 1999, Blake and Loiselle 2000, Tellería et al. 2001, Strewe and Navarro 2003). I present data in this manuscript suggesting that *Diglossa glauca* is an elevational migrant, a conclusion that is supported by other data including mist net- and point count-based density estimates (Merkord, *unpubl. data*) and by the presence of elevational migration elsewhere in the genus (Stiles 1985, Hilty 1997). I also observed a dry season abundance of *Mionectes striaticollis* consistent with a pattern of seasonal elevational movement, perhaps not surprising given that two of its congeners, *M. olivaceus* and *M. oleagineus*, are both known elevational migrants (Blake and Loiselle 2000). Field observations in Bolivia suggest that *Chiroxiphia boliviana* may be an elevational migrant there (M. Foster, *pers. comm.*), and a number of other manakins undertake elevational migrations (Ridgely and Gwynne 1992, Willis and Schuchmann 1993, Blake and Loiselle 2000). Few data exist on the ecology of *Zimmerius bolivianus*, but at least one other member of the genus may be a partial elevational migrant (Gómez de Silva G. et al. 1999). Finally, while no seasonal movements have been documented in *Chlorochrysa*, the status of *C. calliparaea* as an elevational migrant would not be surprising, given that it shares many characteristics with *Tangara punctata* and *T. nigroviridis*, two other probable elevational migrants in the San Pedro flock: they are all nuclear species within the flock, they occur in relatively large numbers in the flock, and they sometimes form monospecific groups.

Taken as a whole, the probable migratory status of the constituent species in the recaptured subflock suggest that the subflock could easily have been composed solely of elevationally migratory species, consistent with the seasonal movement hypothesis. While it is not uncommon for mixed species flocks of birds to migrate together (Rodewald and Brittingham 2002), these associations form during migration. The possibility of a polyspecific group of terrestrial forest birds sharing the same nonbreeding season home range and then migrating as a group towards a breeding area, even if they do not share a final destination, would be intriguing and certainly requires more study. At the very least, my observations suggest that complex interspecific and inter-individual relationships dictate individual movement patterns of birds in mixed species flocks.

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Table 1. Number of species (and number of individuals) in the mixed species flock, grouped by flocking propensity and residency status. Number of individuals is calculated assuming all individuals of a species exhibit the same residency status and flocking propensity, which may not be accurate for many species.

		Flocking propensity			***Total***	
		Regular associate	***Occasional associate***	***Accidental associate***		
Residency status	***Year-round resident***	31 (202)	29 (211)	3 (7)	63 (420)	57% (63%)
	Elevational migrant	16 (161)	8 (32)	3 (5)	27 (198)	24% (30%)
	Latitudinal migrant	1 (1)	2 (2)	1 (11)	4 (14)	4% (2%)
	Occasional or irregular visitor	10 (22)	6 (7)	1 (1)	17 (30)	15% (5%)
	Total	58 (386)	45 (252)	8 (24)	111 (662)	
		52% (58%)	41% (38%)	7% (4%)		

Table 2. Apparent elevational migrants captured in the San Pedro flock and recaptured at two sites on a nearby ridge (approx. 1500 m a.s.l. and 1780 m a.s.l.). All dates are 2006 unless otherwise noted.

Individual	***Date***	***Location***	***Elevation (m a.s.l.)***
Chiroxiphia boliviana	Jul 8	San Pedro	1398
	Jul 30	Ridge 1	1497
	Aug 9	Ridge 2	1763
Mionectes striaticollis 1	Jun 28	San Pedro	1407
	Jul 30	Ridge 1	1497
Mionectes striaticollis 2	Jul 7	San Pedro	1393
	Aug 9	Ridge 2	1802
Zimmerius bolivianus	Jul 1	San Pedro	1399
	Jul 30	Ridge 1	1497
Turdus ignobilis	Jul 23	San Pedro	1398
	Jul 30	Ridge 1	1505
Chlorochrysa calliparaea	Jul 8	San Pedro	1394
	Jul 30	Ridge 1	1521
	Sep 6	San Pedro	1410
	Mar 24, 2007 (R)	San Pedro	1410
	Jul 4, 2007 (R)	San Pedro	1410
	Jul 6, 2007 (R)	San Pedro	1400
Diglossa glauca	Jul 6	San Pedro	1394
	Aug 9	Ridge 2	1763

R = Indicates resighting of color-banded bird.

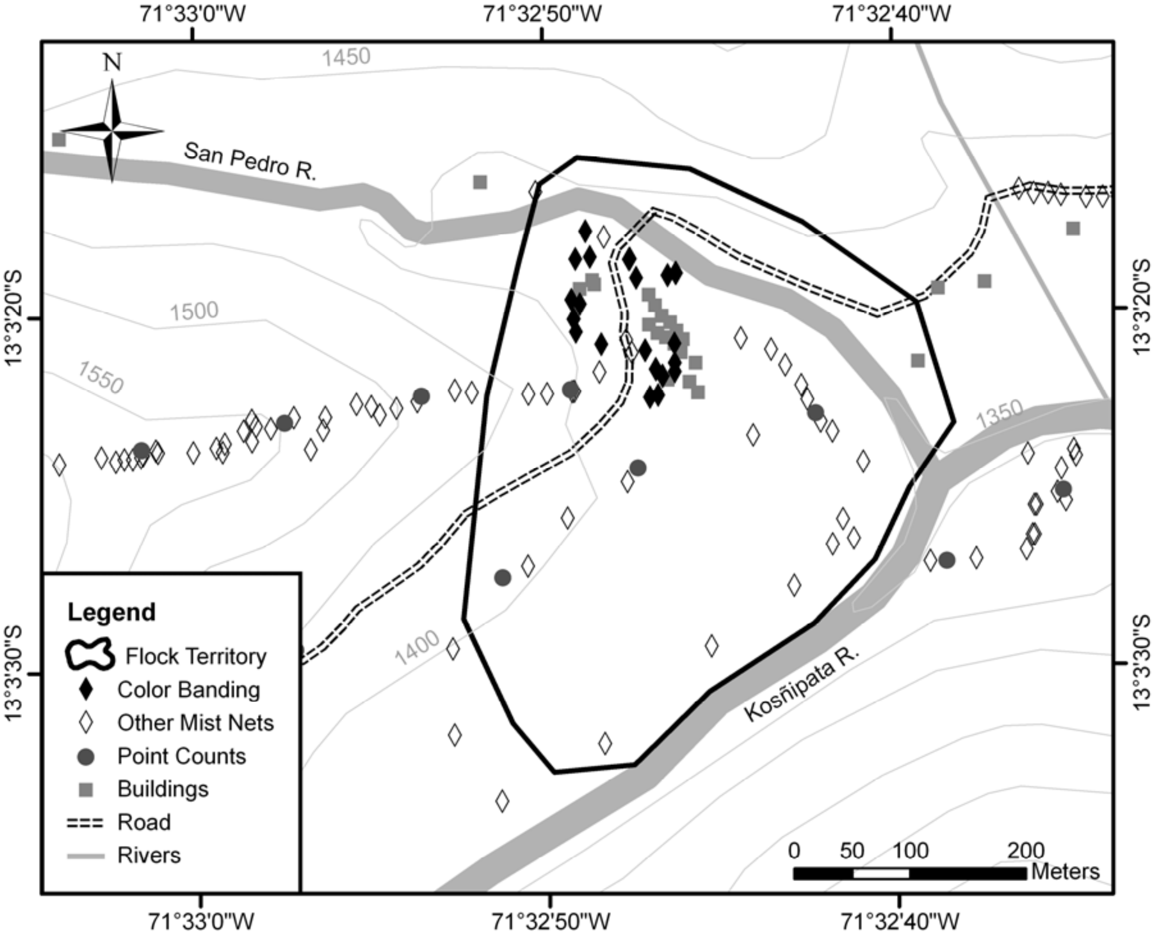

Figure 1. Territory of the mixed species flock around San Pedro on the Manu Road, Cusco, Peru.

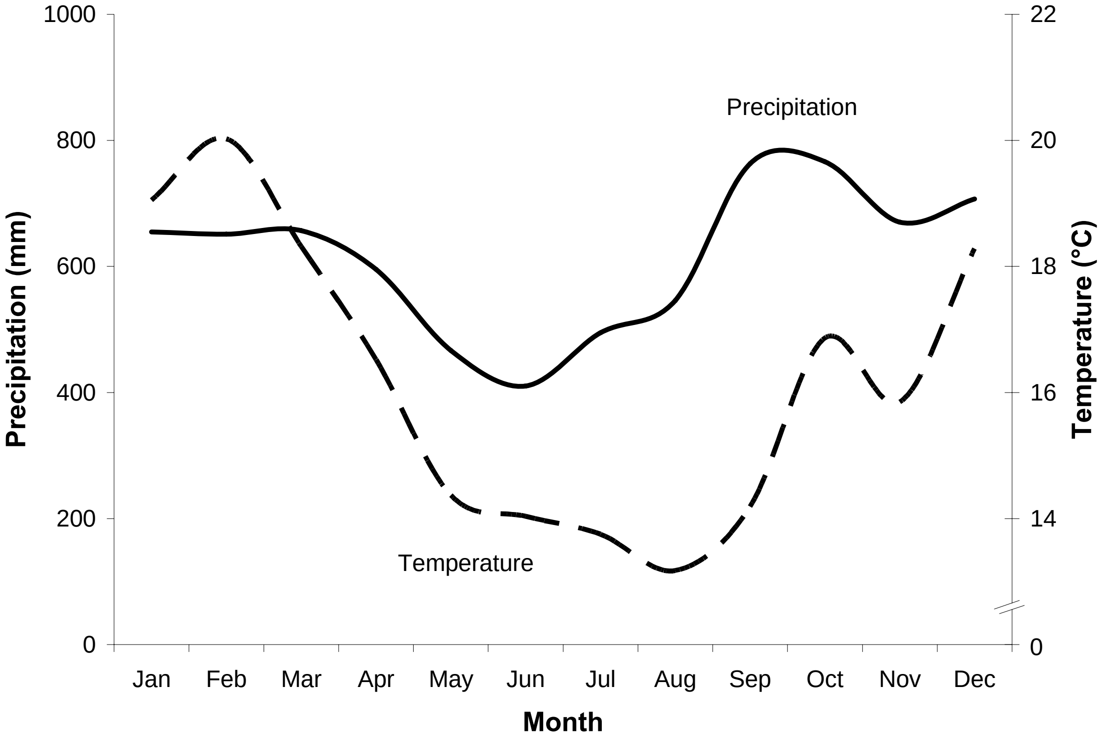

Figure 2. Average monthly precipitation and temperature recorded July 2007-July 2008 by a HOBO Micro Station mounted above the tree canopy near the study site (1500 m a.s.l.). Unpublished data courtesy of M. R. Silman.

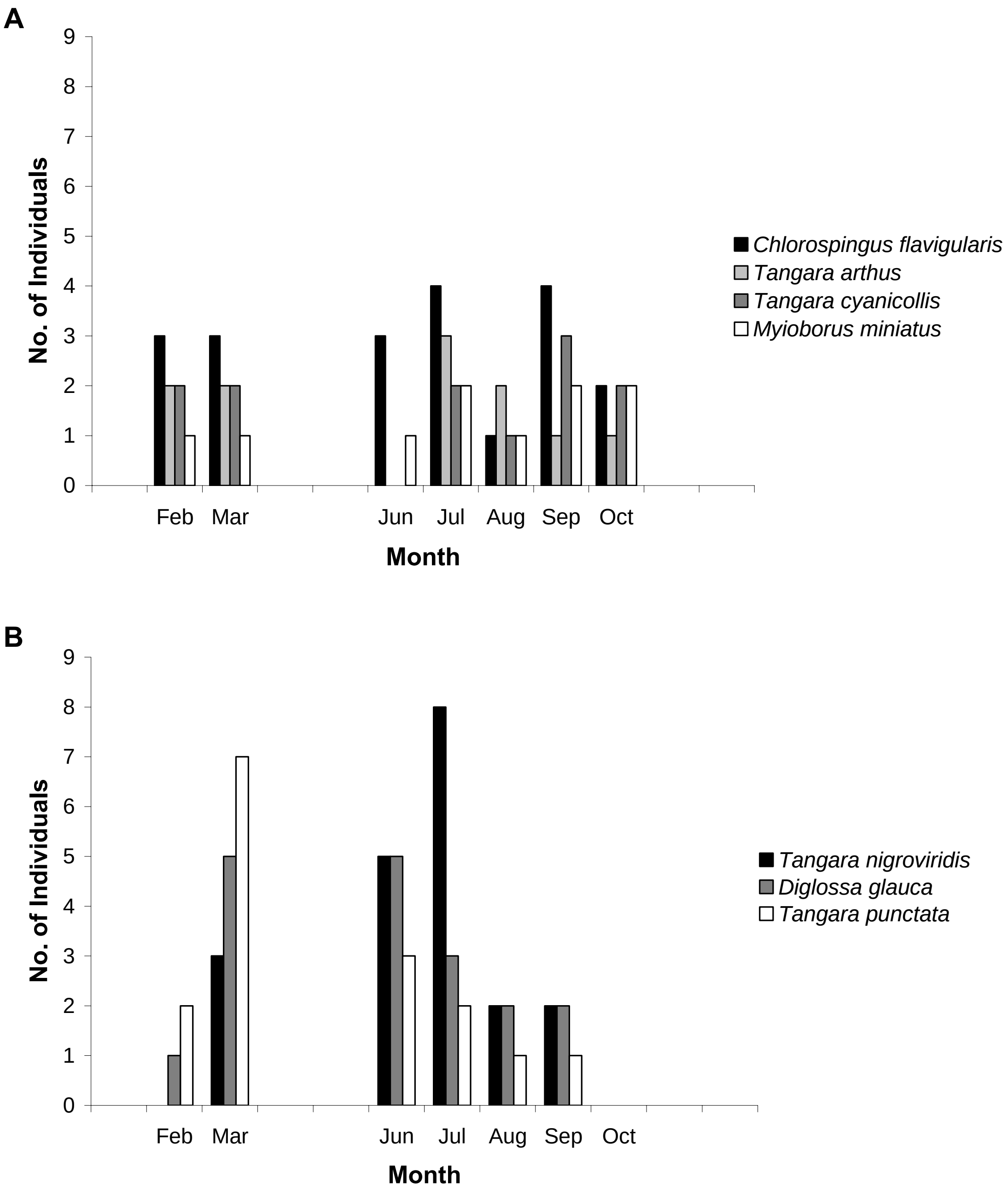

Figure 3. Maximum number of individuals seen during 15 minute observation periods in each month, for 4 species of presumed year-round residents (A) and three species of presumed elevational migrants (B). Data were collected February-March and June-October only.

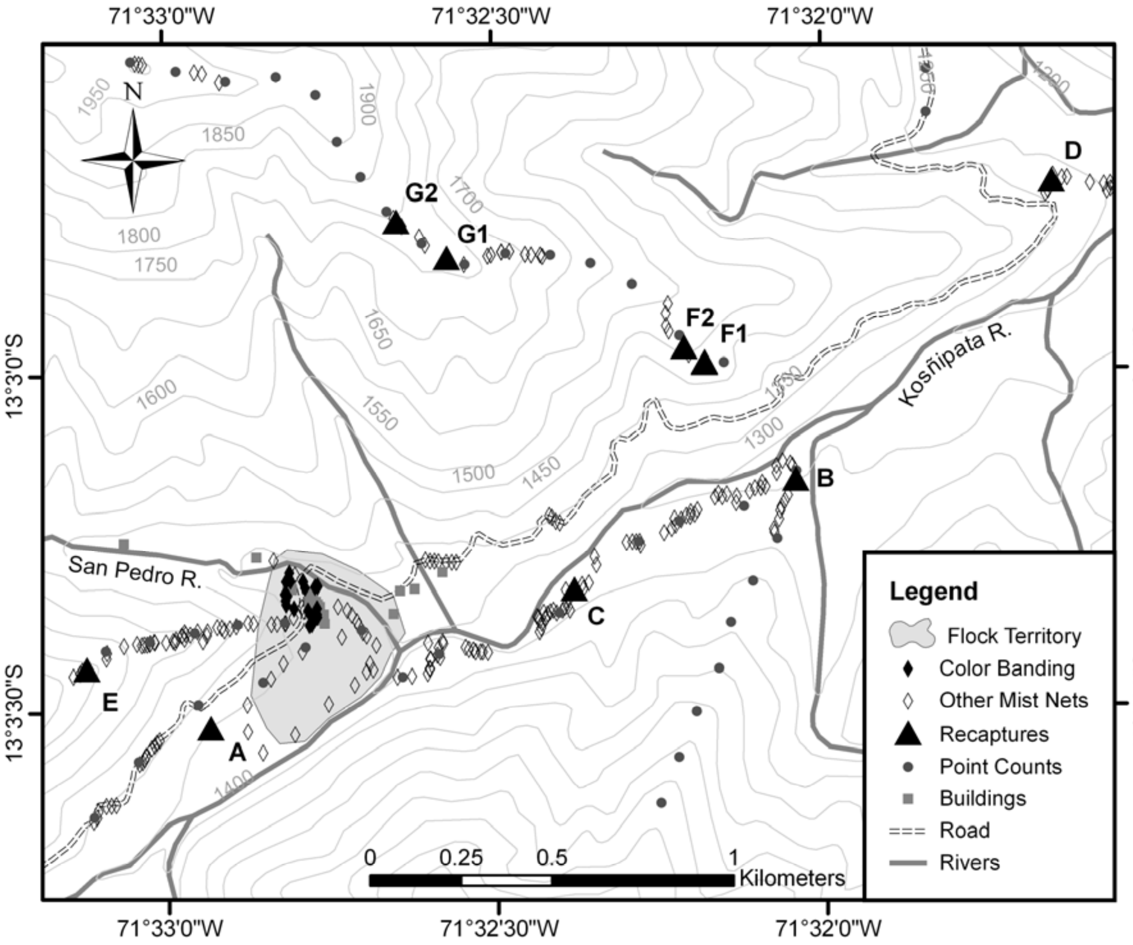

Figure 4. Recaptures of birds captured within the flock territory. Movements include presumed dispersal of a *Tangara xanthocephala* (A) and *Ramphocelus carbo* (B), possible daily movements of a *Platyrinchus mystaceus* (C, D), presumed elevational migration of a *Diglossa glauca* (E), and presumed elevational migration of a group consisting of *Chiroxiphia boliviana*, *Mionectes striaticollis*, *Zimmerius bolivianus*, *Turdus ignobilis*, *Chlorochrysa calliparaea*, and *Diglossa glauca* (F, G).

CHAPTER 3

POINT COUNTS SUGGEST PARTIAL ELEVATIONAL MIGRATION IN BIRDS ON THE EASTERN SLOPE OF THE ANDES

Christopher L. Merkord, Jill E. Jankowski, Frank R. Thompson, III, John Faaborg

ABSTRACT

Elevational migration of birds appears to be common throughout the world, but is poorly documented, especially in tropical montane regions. We used distance sampling to estimate bird density during breeding and nonbreeding seasons along a 2.7 km elevational gradient on the moist eastern slope of the Andes in Cusco, Peru. We compared distributions, using weighted mean elevations of occurrence and season-elevation interaction effects to identify potential elevational migrants. Of 50 species analyzed, nine show patterns consistent with elevational migrants, and another four are suggestive. The remaining 37 species show patterns consistent with a sedentary life history strategy. We discuss alternative hypotheses to explain the seasonal variation in density distributions, and offer comments on study design and the interpretation of our results. Effective conservation of tropical forests and their inhabitants relies on information about where species are located and how they interact. Our results fill in a critical information gap on elevational migration in the Andes and provide a method of quantifying distributions along environmental gradients

that can be applied to other taxa and gradients. Understanding the factors that affect the elevational distribution of organisms is particularly urgent as global climate change increasingly threatens montane biota.

INTRODUCTION

Naturalists have long studied the migrations of animals, and of birds in particular. Although much headway has been made in our understanding of avian migration, there is still much to learn (see Faaborg et al. 2009b for a New World review). Most treatises on the subject equate avian migration with the long distance movements of completely migratory populations from temperate breeding grounds to tropical or subtropical wintering grounds, glossing over other migratory schema (e.g. Wetmore 1926, Dorst 1962, Able 1999, Berthold 2001, Berthold et al. 2003, Greenberg and Marra 2005). This is partly due to a temperate bias in scientific inquiry in general (Short 1984), but also to the difficulty of detecting and describing very short-distance movements (Faaborg et al. 2009a). A growing number of ecologists have advocated widening our general understanding of bird migration to include a broader variety of migratory systems including elevational, intratropical, and South American austral migration (Levey 1994, Joseph 1997, Jahn et al. 2004, Dingle and Drake 2007, Faaborg et al. 2009b). If this goal is to be accomplished before anthropogenic climate change and habitat loss irreparably alter remaining natural systems, holes in our knowledge of the ecology and migratory status of a great many avian species will need to be filled quickly, necessitating efficient means of studying mega-diverse tropical avian communities, often in remote regions.

The case of elevational migration, the periodic movement of individuals along an elevational gradient, is particularly understudied, given that elevational migration probably occurs in mountains throughout the world (Grinnell and Miller 1944, Thiollay 1980, Stiles 1988, Johnson and Maclean 1994, Ornelas and Arizmendi 1995, Hilty 1997, Burgess and Mlingwa 2000, Kimura et al. 2001, Tellería et al. 2001, Dingle 2004) [replace this whole bunch by citing either Chapter 2 or upcoming review paper by Fraser and Merkord]. In temperate regions bird make elevational movements, at least in part, to avoid thermal extremes, either for physiological reasons or because foraging substrates or food resources are covered in snow or ice, or are otherwise reduced in availability (Osborne and Green 1992, Hahn et al. 2004, Morrissey et al. 2004). In the tropics, those same factors may explain facultative short-term elevational movements in response to severe weather (O'Neill and Parker 1978, Winker et al. 1997). The causes of regular seasonal elevational migration in the tropics, however, are less well understood. Proposed explanations include seasonal resource tracking (Loiselle and Blake 1991) and seasonal emigration from elevations with unpredictable food production (Boyle and Conway 2007), heavy predation risk (Boyle 2008a), or torrential, foraging-inhibiting rainfall (Boyle 2008b). Despite recent advances, there is little consensus on the proximate and ultimate mechanisms by which elevational migration evolves or is maintained, how elevational migration affects community dynamics, the degree to which populations are partially or completely migratory, or even which species are elevational migrants. Understanding the patterns and processes behind elevational migration is critical, both for understanding the evolution of migration (Levey and Stiles 1992, Boyle and Conway 2007), and for effectively conserving montane species (Stiles 1988, Powell and Bjork 1994b, a, Ornelas and Arizmendi 1995, Powell and Bjork 1995, Winker et al. 1997, Chaves-Campos et al. 2003, Powell and Bjork 2004).

Our understanding of elevational migration is limited by the degree to which the natural history of many tropical species is undescribed. It is particularly difficult to study elevational migration of birds in the moist tropics, due to heavy rains throughout much of the year, often steep topography, and a lack of civil and research infrastructure. Furthermore, tropical elevational gradients can be exceptionally diverse, making multi-species studies based on auditory or visual surveys more difficult. For example, over 1000 species have been observed along an elevational gradient in Manu National Park in Peru, with species richness ranging from over 100 near treeline (3400 m a.s.l.) to almost 600 at the base of the foothills (500 m a.s.l.; Walker et al. 2006).

A few successful studies on elevational migrants have focused on single species, using either radio-telemetry or capture-mark-recapture methods. Recovery of marked birds is a valuable tool for identifying migratory patterns, but inter-seasonal recaptures are rare enough that the method is impractical for short- or medium-term studies (ref). Radio-telemetry is useful for larger birds, and has been used to track elevational movements in bellbirds (*Procnias tricarunculatus*, 145–220 g, Powell and Bjork 2004), quetzals (*Pharomachrus mocinno*, ~200 g, Powell and Bjork 1994b), and umbrellabirds (Cephalopterus glabricollis, 320–450 g, Chaves-Campos et al. 2003) . Whereas radios with the requisite lifespan of several months can now conceivably be fit on birds as small as perhaps 50 g, this is still considerably larger than most tropical forest birds (Case et al. 1983). Even for larger species, the use of radio-telemetry on steep, variable, forested terrain with few roads would be difficult. Considering weight restrictions, access difficulties, and the high cost of radios, telemetry is not a viable option for the simultaneous study of many species. For community-wide studies of elevational migration, researchers must rely instead on population-level methods of studying elevational migration.

The general approach for population-level methods is to measure seasonal changes in bird abundance or occupancy (presence-absence) along an elevational gradient. Occupancy is by far the most commonly used metric for inferring migration. (e.g. Thiollay 1980, Stiles 1988). While estimates of species occupancy are easier to obtain than estimates of abundance, relying only on the former may miss detecting elevational migration in populations which are only partially migratory (i.e., some individuals do not migrate; Boyle 2008b), or when the elevational ranges during breeding and nonbreeding seasons overlap greatly. In these cases, data on relative abundance will be of more use in identifying migratory species. Abundance has also been shown to be more effective than occupancy at predicting species persistence, justifying the additional effort and cost of incorporating abundance estimates into conservation planning (Grouios and Manne 2009).

There are a number of factors to consider when interpreting studies on elevational migration based on changes in relative abundance, both during survey design and data analysis. The first is sampling density, which can be though of in spatial and temporal terms. Spatial sampling density along an elevational gradient increases as more sampling locations are added at different elevations; temporal sampling density increases as additional sampling periods are added throughout the annual cycle (e.g., from quarterly to monthly to weekly). Of the few relevant studies that exist on avian elevational migration, most have abundance data from only one (Hilty 1997) or a few (Loiselle and Blake 1991, Chaves-Campos 2003) sites, collected at intervals of 4–8 weeks.

The second factor affecting interpretation of abundance estimates is detection probability, or detectability, of the study organism. Abundance estimates depend not only on the abundance of an organism, but also its detectability (Toms et al. 2006, Buckland et al. 2008). Recent studies have called into question methods of assessing landbird abundance estimates that do not incorporate a measure of detectability (Confer et al. 2008). For an individual to be detected, it must first be available for detection. Mist netting surveys of birds and bats, for example, provide notoriously poor estimates of relative abundance partly because only individuals flying at net level are available for detection (Karr 1981, Remsen and Good 1996, Larsen et al. 2007). Abundance estimates from surveys based on auditory or visual cues are also affected when individuals do not vocalize or move into the open (Diefenbach et al. 2007). In humid tropical forests, where birds are more often heard than seen, individuals must generally be singing to be available for detection.

Given that a bird produces a cue for an observer to detect, there is still a chance that the observer will fail to detect the cue. Some factors affecting the probability of detection of birds during point counts include species, cue type, cue rate, habitat, season, time of day, weather, ambient noise, distance of the organism to the observer, and observer skill (Bibby and Buckland 1987, Blake 1992, Remsen and Good 1996, Buckland et al. 2001, Diefenbach et al. 2003, Buckland 2006, Alldredge et al. 2007c, Simons et al. 2007). Commonly used methods of adjusting abundance estimates to account for detection probability include distance sampling (Buckland et al. 2001, 2004), removal methods (Farnsworth et al. 2002), and time-of-detection methods (Alldredge et al. 2007a). With the advent of models to incorporate multiple covariates into detection probability (Marques et al. 2007), distance sampling is particularly appealing. Regardless of method, accounting for detectability can significantly improve abundance estimates over raw count data (Norvell et al. 2003), although care should be taken in choosing an appropriate method (Buckland et al. 2008, Thompson and La Sorte 2008). Only a few studies in tropical evergreen forests have incorporated detectability into abundance estimates (e.g., Lloyd 2004, Jankowski et al. 2009), but at least one study suggests that distance sampling offers relatively robust estimates in this habitat, despite the fact that most detections are aural and some assumptions of distance sampling are not always met (Gale et al. 2009).

Few studies have attempted to quantify temporal shifts in the *abundance* of a population along an environmental gradient, although many have looked for changed in *occurrence* along gradients (Tingley and Beissinger *in press*), including elevation (Wilson et al. 2005, Colwell et al. 2008, Lenoir et al. 2008, Moritz et al. 2008) and latitude (Parmesan et al. 1999, Thomas and Lennon 1999, Zuckerberg et al. 2009). Inferring spatial shifts from occurrence data is based on changes in occurrence at the ends of the gradient in question. Quantifying changes in occurrence at upper and lower ends of a species' elevational distribution is problematic, however, because one cannot distinguish patterns of migration in populations which are only partially migratory, and whose elevational ranges do not change between seasons. Of studies using abundance, Bergamini et al. (2009) compared the current and historic distributions of plant species along an elevational gradient using Wilcoxon signed rank tests to compare the number of records in 26 100-m elevational zones.

In the present study, our goal was to examine distributions of birds along an elevational gradient in the Andes in an attempt to document elevational migration. This study differs from previous studies on elevational migration in several ways. First, we specifically look for evidence of partial migration, using density rather than occupancy to infer movement at the population level. Second, we place more emphasis on spatial coverage of the elevational gradient, and less on temporal coverage of the annual cycle, in order to detect more fine-scale movements along the gradient. Third, we base abundance estimates on point counts rather than mist net captures. And fourth, we use modern distance sampling methods to make more robust estimates of abundance accounting for at least some of the factors affecting the detection probability of birds. Our results suggest that audio-visual surveys can be an efficient means of quantifying bird species distributions along environmental gradients and assessing elevational migration in diverse tropical montane communities in remote regions.

METHODS

Study Site

We conducted our study in eastern Cusco Department, Peru, in and around the valleys formed by the rivers Kosñipata and Tono (S12°56'46" to S13°11'31", W71°29'19" to W71°36'29"). The Kosñipata valley lies primarily in the buffer zone of the Manu National Park and Biosphere Reserve, while the Tono valley lies in the park's protected area. We established 23 transects between 805 and 3414 m elevation (Fig. 1). On each transect, we placed 6–14 points spaced 120–300 m from each other, for a total of 251 points. Many transects were located along existing but little-used trails, including those of the Trocha Union, Wayqecha Biological Station, and Cock-of-the-Rock Lodge. We cut additional trails wherever possible; at higher elevations steep topography restricted new trails to ridge tops. To fill in the remaining holes in our elevational gradient, we placed some transects along the Cusco-Pilcopata Highway, an unpaved road descending from the park entrance at Acjanaco to the town of Pilcopata. This road receives moderate traffic, sometimes as many as 10 vehicles per hour during peak use, but we rarely experienced this during morning surveys.

The principle habitat types ranged from tropical lowland evergreen forest at the lower elevations, through montane evergreen forest, to elfin forest at the higher elevations (habitat types taken from Stotz et al. 1996). Within these broad categories there was much variation in habitat due to aspect, slope, successional stage (landslides are common), and proximity to ridge or stream, creating a dynamic mosaic of habitats. *Guadua* spp. bamboo is common at elevations below 1500 m, while *Chusquea* spp. bamboo was common from there to treeline.

The climate varied by season and elevation (Fig. 2; M. R. Silman, unpublished data). Average daily temperatures along the elevational gradient ranged from 24.2 to 7.5°C, with a lapse rate of about 0.51°C per 100m. There was a cool period in May–Jul, with temperatures about 1.5°C cooler than the rest of the year. Rainfall also decreases with elevation, but with a less consistent pattern. The dry season from May–Aug received 0–200 mm per month, depending on elevation, while the peak of the wet season received 400–800 mm. Cloud base varied, but was generally several hundred meters higher during the dry season, while relative humidity and photosynthetically active radiation were also quite seasonal. Cold air masses called *friajes* periodically invaded from the south, especially from May to Aug, causing several days of heavy precipitation and cooler temperatures.

The flora and fauna of Manu National Park is better described than most sites in western Amazonia (Gentry 1990, Wilson and Sandoval 1996, MacQuarrie 1998, Patterson et al. 2006). Research at Cocha Cashu Biological Station (350 m) and other sites has led to a fairly well documented lowland avifauna (Terborgh et al. 1984, Robinson and Terborgh 1990, Servat 1996). Montane portions of the park, however, are not well studied, although an annotated checklist of birds of the park by Walker et al. (2006) lists elevational ranges for all species known to occur in the park at that time.

Data collection

We visited each point between 1 and 11 times (94% at least 4 times) from 2005 to 2008, from Jun through Nov. We conducted 1295 point counts, 779 during the breeding season, and 516 during the nonbreeding season (Fig. 3). Effort during both breeding and nonbreeding seasons covered the entire elevational gradient, but was not even throughout the gradient, with some elevations receiving less attention than others (Fig. 4), due primarily to weather- and transportation-related logistical constraints.

During each visit, a single observer (C. L. Merkord or J. E. Jankowski) conducted a 5 min survey, identifying and recording every bird seen or heard during the count. If a bird's location could be determined with reasonable surety, the observer used a laser range-finder to estimate the distance to the bird at the end of the third minute (the "snapshot" method, Buckland et al. 2001, Buckland 2006). Larger distances (i.e. > 100 m) were often rounded. To ensure species were identified correctly, we 1) compiled a library of published recordings of vocalizations of birds in the area, and continuously supplemented this library with an extensive set of field recordings of our own, 2) spent over one year each practicing identification of bird vocalizations, including three months in the field in 2005, 3) conducted a one-week field training course in 2006 to standardize field protocols, including distance estimation, and 4) recorded each point count with a field recorder and omnidirectional microphone so species identification could be double-checked later ; most recordings have been reviewed at least once for accuracy.

Data analysis

1. OVERVIEW

Our general approach for each species was to estimate its density along the elevational gradient during each of three seasons–dry, early wet, and late wet–and then make pairwise comparisons of those density distributions to look for upslope or downslope shifts. We divided the observed elevational range of each species into five equal-elevation zones and estimated density at two scales: elevational zones and sampling points. Given our three seasons, we were able to make three pairwise comparisons: dry to early wet, early wet to late wet, and late wet to dry. Our approach is similar to that adopted by Simon et al. (2002), who used only three elevational zones to infer seasonal movement in populations of birds a tropical Hawaiian rainforest.

2. DATA PREPARATION

Starting with our dataset of all point count observations, we filtered out those lacking a distance measurement, and hereafter refer only to the filtered dataset. Next we found the minimum and maximum elevation of observations for each species, subtracted the maximum from the minimum, divided the resulting range into five equal-elevation zones, and assigned each observation to a zone. Because elevational minima and maxima differed between species, this process resulted in different zone cutoff points for each species.

We then assigned each observation to a season (Fig. 5). Most species in the study area initiate breeding in Sep, at the start of the rainy season (e.g. Thryothorus genibarbis, Londoño 2009), a pattern common in tropical systems (Wikelski et al. 2000, Hau et al. 2008). Data from mist netting efforts in the study system confirm that the percentage of birds molting feathers, which usually follows breeding, increases gradually from Sep to Nov and peaks in Feb and Mar. There is scant evidence on the timing of post-breeding migration, but studies of a mixed species flock of birds at 1400 m a.s.l. indicate that the first elevational migrants may move downslope and take up nonbreeding season residency in the flock as early as Feb or Mar (Merkord 2010 Chapter 3). Certainly by Jun, the middle of the dry season, there are numerous species present at lower elevations that are absent during the breeding season (e.g. *Myiotheretes striaticollis*, *Thraupis cyanocephala*, *Tangara nigricollis*, *Diglossa glauca*; *pers. obs.*), indicating that for many species the drier months represent the period when most altitudinal migrants are as far from their breeding areas as they will get. Bird song and breeding activity reaches its nadir during the dry season, but begins to increase again during Aug (C. L. Merkord, *pers. obs.*), concurrent with increases in precipitation and temperature (Fig. 2). In temperate regions, the number of birds singing, volume of song, and song rate are correlated with the amount of breeding activity (Slagsvold 1977, Foerster et al. 2002). These relationships appears to hold true in the tropics as well (Stutchbury et al. 1998, Wikelski et al. 2000, Topp and Mennill 2008). Furthermore, both song and breeding activity are tied to the same physiological mechanisms (Ketterson et al. 1992, Hau 2001, Foerster et al. 2002, Moore et al. 2004). Altogether, we feel justified in determining *ad hoc* the approximate start of the breeding season based upon the onset of the rainy season, singing activity, and our observations of nesting activity.

We assigned observations from Feb–Apr to the late wet season and chose the dates of Aug 15–16 to represent the cutoff between the dry season and early wet season (Fig. 5). We recognize that there is both inter- and intra-specific variation in timing of breeding, and thus the timing of any pre-breeding altitudinal migration. Ideally, we would have restricted our surveys to widely separated, short-duration periods in each season, but such a study design would not have allowed for sufficient coverage of the elevational gradient. Even though species-specific cutoff dates would have improved our analyses, we do not have sufficient data on breeding phenology in various species to permit this.

3. DENSITY ESTIMATION

Valid estimates of the abundance of an organism must account for variation in detectability (Buckland et al. 2008, Thompson and La Sorte 2008). While cue-counting and removal estimates are viable options in some scenarios, the amount of effort required is not conducive to multi-species studies (Buckland 2006). Instead we opted for a distance sampling approach (Buckland et al. 2001, 2004). Distance sampling assumes that only a portion of the individuals are detected within a circular sampling plot centered on a point. The probability of detecting an individual can be expressed as a function $g(x)$ of the distance from the observer to the individual, with $g(x)$ declining from 1 at the point to zero at some distance from the point. If $g(x)$ can be estimated, it is possible to estimate the percentage of individuals present within the circular sampling plot that are actually detected. Marques et al. (2007) improved upon the distance sampling framework with a method for incorporating other variables affecting detectability as covariates in the detection function $g(x)$ (called multiple covariate distance sampling, or MCDS).

We used program Distance version 6.0 beta 2 (hereafter "Distance"; Thomas et al. 2010) to analyze our point count data, estimate the detection function $g(x)$, and provide density estimates for each species. Within Distance there are four data layer types: global, stratum, sample, and observation; we used a default global layer, no stratum layer, point count location as the sample layer, and observation as the observation layer. Within the sample layer, survey effort was defined as the number of visits to the point. We analyzed each species individually, using a three-step process: data exploration, model selection, and density estimation.

Data Exploration -. To determine which observations to include in the analyses, we first constructed a histogram of detection distances for each species (Fig. 6). Large outlying distances contribute little to density estimates but greatly increase the difficulty of modeling $g(x)$, requiring more model parameters. Buckland et al. (2001) suggest right truncating (excluding) the largest 10% of distances, as a rule of thumb, to facilitate model fitting. The down side to right truncation is that some observations are excluded, which can be problematic when a common detection function is used to estimate density in multiple strata, and some strata are composed primarily of truncated distances. We followed the 10% rule for most species, but in cases where the excluded observations were the only observations in a stratum, we manually set the truncation distance to include those detections. Only species with at least 40 detections after truncation were included in further analyses.

Problems in density estimation may also arise when distances are heaped, or grouped at round numbers, which can lead to reduced robustness of density estimates (Buckland et al. 2001). Heaping is usually due to rounding of distance estimates in the field. To check for evidence of heaping, we created a histogram of detection distances for each species (see Fig. 6 for example). If heaping appeared to be a problem, we grouped observations into distance bins, with cutpoints selected so that heaps fell at approximately the midpoint of each bin (Buckland et al. 2001). We then ran a plausible candidate model using both grouped and ungrouped data. If the density estimates showed little difference between the two analyses, we chose to keep the data ungrouped.

Model Selection -. We defined a set of candidate models to fit the detection function $g(x)$. Each model starts with a key function and series expansion to define the general shape of the detection function. Due to theoretical considerations, the two models best suited for MCDS are the half-normal key function with a hermit polynomial expansion, and hazard-rate model with a cosine expansion (Buckland et al. 2004). In addition to the key functions, we *a priori* chose 5 covariates (4 factor level, 1 continuous) which we suspected would affect detection probability. These covariates were:

1. Season (factor). To account for seasonal variation in cue rate or detection probability.
2. Observer (factor). To account for variation in detection probability between observers.
3. Time after sunrise (continuous). To account for temporal variation in detection probability.
4. Precipitation (factor). To account for the fact that even light rain lowered the detection probability of most species.
5. Year (factor). To account for a “learning effect” by the observer.

Habitat characteristics are also known to affect detection probability, either directly by affecting sound attenuation rates, or indirectly by affecting the timing of breeding or other factors associated with cue rate (refs). In our study area, elevation is the single biggest factor determining habitat characteristics. We chose not to use elevation as a covariate because our conceptual model relies on the assumption that detectability does not vary along the elevational gradient. Each of our 5 covariates represents a highly plausible hypothesis to explain variation in detection probability. Furthermore, there is no biological or statistical reason to suspect that any combination of these covariates would be more or less suitable as a candidate model. Thus it is reasonable to construct candidate models based on every combination of these covariates, as well as the two potential key functions, a process which results in a set of 64 candidate models. As a final step in the model definition process, we set the detection function to be estimated at the global level.

For each species, we first ran the two candidate models with no covariates (one for each key function), to determine which key best fit the observed distance data. We chose a model based on a combination of AIC scores, and goodness of fit *p*-values. We then ran each of the 31 covariate models based on that key. If neither key function received much more support than the other, we ran all 62 covariate models. We ranked these relying primarily on AIC scores and selected the best supported model. If two models received the same AIC score, we chose the one with the fewest covariates.

Density Estimation -. We estimated the density of each species at the level of elevational zones and individual survey points. To obtain the zone-level estimates, we post-stratified the data by season and elevational zone. With two seasons and five elevational zones, this effectively assigned each observation to one of 10 strata. We then used the species' global detection function to estimate the density of birds in each stratum, resulting in 10 density estimates for each species, one for each combination of elevational zone and season. To obtain the point-level estimates, we again used the species' global detection function to estimate bird density at each point, post-stratifying by season.

4. SEASONAL COMPARISONS

Using the point- and zone-level relative density estimates, we attempted to make three pairwise comparisons between seasons. For each seasonal comparison, we used a three-step approach to classify a species as an elevational migrant or nonmigrant. First, we found the weighted mean elevation of occurrence

w for each species in each season by taking the mean elevation e of the zone midpoints, weighted by the density d in that zone:

$$w = \frac{\sum_{i=1}^{5} d_i e_i}{\sum_{i=1}^{5} d_i}$$

Subtracting one weighted mean elevation from another, we found the mean shift in elevation of the population from one season to the next. Dividing this shift by the elevational range of the species (the difference between the maximum $e_{\max}$ and minimum $e_{\min}$ elevation of all observations included in the analysis), we can express the mean elevation shift s as a percentage:

$$s = \frac{w_1 - w_2}{e_{\max} - e_{\min}}$$

Second, we used a two-way analysis of variance to model how density varied with elevation, season, and an elevation-season interaction term, treating elevation as a continuous variable. Because the residuals of the point-level density estimates were overdispersed (as is typical of count data), we transformed the data prior to analysis using a square root transformation of the form:

$$X' = \sqrt{X} + \sqrt{X+1}$$

as suggested by Zar (1999) for data where $X \leq 2$. A significant interaction effect would indicate the pattern of densities across elevations differed between seasons. We considered a significant elevation-season interaction and a large shift (s > 5%) in mean elevation was taken as evidence of elevation migration, while a nonsignificant interaction term or a small shift (s < 5%) in mean elevation was taken as evidence of a lack of migration. Third, we scored the evidence for each species on a scale of 3 (strong evidence of elevational migration) to -3 (strong evidence of lack of elevational migration) using criteria explained in Table 1. These criteria base the assignment of migratory status on the assumption that the larger the shift in mean elevation between seasons, the more likely a species is to be migratory.

For each species we scored up to three pairwise comparisons of seasonal density distributions. A final score was derived for each species by comparing these seasonal comparison scores. If at least one score was positive, indicating migratory status, then we chose the largest positive value as the final score. If no positive scores were obtained then we chose the most negative score, indicating resident status. If no positive or negative scores were obtained the final score was set to 0, indicating uncertainty as to the species' migratory status.

RESULTS

We were able to assign "snapshot" distances to 9021 birds or groups of birds of 333 species, of which 93% were by sound only. After filtering out those species without at least 8 point counts per elevational zone per season, and those with fewer than 40 detections after truncation, we were left with 50 species for which we had sufficient data to fit a detection function in Distance. With a some notable exceptions, goodness-of-fit *p*-values were high for the best supported detection function for each species, and most included few or no covariates (Table 2). Probability of detection for the 50 species ranged from 0.06 to 0.73 (mean 0.35, median 0.32), and effective detection radius ranged from 9.9 m to 123.9 m (mean 54.6, median 48.0). Each of the 50 species analyzed here species showed a unique elevational distribution ranging in width from 592 m to 1903 m (1146 mean, 1099 median) before data truncation.

All three seasonal comparisons were performed for 29 species while only one seasonal comparison was performed for the other 21 species, for a total of 108 seasonal comparisons (Table 3). Twelve seasonal comparisons received positive scores, indicating that 9 species were migratory (Table 4). Another 79 species received negative scores, indicating that 38 species were nonmigratory. The other 17 seasonal comparisons failed to yield a non-zero score indicating uncertainty about the migratory status of the species during the two seasons being compared, resulting in a final score of 0 for three species.

Four species received the greatest support as elevational migrants: *Colibri thalassinus*, *Contopus fumigatus*, *Myadestes ralloides*, and *Myioborus miniatus* (Fig. 7); four more species received moderate support as elevational migrants: *Basileuterus signatus*, *Cacicus chrysonotus*, *Cyanocorax yncas*, *Scytalopus atratus* (Fig. 8); and one species received weak support: *Entomodestes leucotis* (Fig. 9; Table 4).

Three additional species could not be assigned a migratory status: *Chlorophonia cyanea*, *Chlorospingus ophthalmicus*, and *Parula pitiayumi* (Fig. 10; Table 4). Thirty-eight species were classified as nonmigratory, with one species (*Euphonia xanthogaster*; Fig. 10) receiving only weak support and the other 37 receiving strong support (Figures 11–19; Table 4).

DISCUSSION

Migratory Patterns

Our results clearly demonstrate seasonal variation in the elevational distribution of some species, and lack of seasonal variation for others. Some of the variation observed is consistent with that expected under a scenario of seasonal elevational migration. We view these results not as definitive proof of elevational migration, but as sufficient evidence to construct a hypothesis of elevational migration in these species, to be confirmed or refuted by species-specific studies.

Of the group of nine species that showed evidence consistent with elevational migration, 5 are known to make seasonal movements elsewhere within their geographical ranges, and another 3 have congeners that migrate. Two of the species we were unable to classify as migrants or residents also make seasonal movements elsewhere within their range, and the third species is likely to as well, based on its congeners. Even Euphonia xanthogaster, the single species we classified tentatively as sedentary, is likely to be an elevational migrant. That leaves only Scytalopus atratus as an unlikely migrant, which we discuss below. Overall, the species we classified as probable elevational migrants are some of the most likely species in our study area to move seasonally, lending support to our findings. Here we provide brief commentary on the nine species of likely migrants, three species of unknown migratory behavior, and one species showing weak evidence for nonmigratory status.

Colibri thalassinus. - Seasonal elevational movements in the species are not surprising at all, given that it is known to migrate elevationally throughout its range (Stiles 1985b, Ornelas and Arizmendi 1995, Strewe and Navarro 2003).

Contopus fumigatus. – Although Hilty (1997) found no evidence for migration in the species in Colombia, its status as an elevational migrant would not be surprising. Four members of the genus are latitudinal migrants and two, *Contopus lugubris and C. pertinax,* are elevational migrants (Stiles 1985a, Nocedal 1995, Arvin 2001).

Myadestes ralloides. Elevational migration in this would likewise not be surprising. Although seasonal movements have not been noted in *M. ralloides*, at least three other members of the genus, *M. melanops,* *M. occidentalis, M. unicolor*, make seasonal elevational or latitudinal movements elsewhere (Howell and Webb 1995, Blake and Loiselle 2000, Arvin 2001).

Myioborus miniatus. Several populations are known to make seasonal elevational movements in west, central, and southern Mexico (Binford 1989, Nocedal 1995, Gómez de Silva G. et al. 1999). Despite a lack of evidence for migration of Andean populations, elevational movements in our study area are not unexpected.

Basileuterus signatus. – Congeners *B. culicivorus* and *B. rufifrons* are known to migrate elevationally in Mexico and Costa Rica (Binford 1989, Arvin 2001). Otherwise the Andean members of the genus remain poorly studied.

Cacicus chrysonotus. – Jaramillo and Burke (1999) describe the species as sedentary, but say that it "may undergo minor elevational movements." Three other members of the genus are prone to elevational migration, seasonal wandering, or undescribed local movements (Stiles 1985a, Jaramillo and Burke 1999).

Cyanocorax yncas. – Elevational movements in this species are not surprising given that it is migratory at least in western Mexico (Ornelas and Arizmendi 1995), if not elsewhere.

Scytalopus atratus. - Of all the species whose seasonal distributions suggest elevational movements, perhaps the most surprising is *Scytalopus atratus*. Tapaculos are small, short-tailed and short-winged, and almost never fly more than a few meters at a time. To our knowledge, no members of the Rhinocryptidae engage in any kind of seasonal movement other than natal or adult dispersal. Thus, despite the evidence suggesting a strong difference between the breeding and nonbreeding season distribution of S. atratus, we are hesitant to suggest the species makes any seasonal movements. The species makes frequent use of the early successional roadside habitat created by the Cusco-Pilcopata highway. Although only a few of our transects followed the road, it is possible that biases introduced by the location of the transects influenced detectability of this species in such a way as to produce the seemingly different seasonal distributions. Other alternative explanations besides elevational movements are discussed in more detail later. It is worth noting that analysis of relative abundance data from point counts, which includes a larger sample size of observations for this species, indicated strong evidence for sedentariness in the species (Merkord 2010 Chapter 4).

Entomodestes leucotis. - The species is not known to be migratory, but the closely related *E. coracinus* is an elevational migrant in Colombia (Hilty 1997).

Chlorophonia cyanea. - Although the results from this analysis were ambiguous for *C. cyanea*, other evidence gathered during our field work suggests that the species is likely to be migratory in our study area (Merkord 2010 Chapter 4). Three other *Chlorophonia* spp. are known to be elevational or short distance migrants elsewhere in the Neotropics as well (Binford 1989, Hilty 1997, Gómez de Silva G. et al. 1999, Blake and Loiselle 2000).

Chlorospingus ophthalmicus. - In the Tuxtla range of eastern Mexico, *Chlorospingus ophthalmicus wetmorei* moves downslope in low numbers during the nonbreeding season, and occasionally severe weather can spark a mass exodus from higher elevations (Winker et al. 1997); other subspecies may move downslope during winter elsewhere in Mexico (Howell and Webb 1995). However, no elevational movements have been noted elsewhere within the species' Central or South American range (Stiles 1985a, Blake and Loiselle 2000). Studies have also failed to find evidence of elevational movements in other members of the genus, although many are poorly studied (Stiles 1985a, Hilty 1997). Our results appear to indicate upslope migration during the nonbreeding season in *C. ophthalmicus*, which would be quite interesting if true. While common in some hummingbirds (Stiles 1988), upslope movements are not the norm among elevational migrants (Stiles 1988, Loiselle and Blake 1991). A possible exception to this rule, although not an elevational migration in the strict two-way sense, can be found in some bird species breeding in western North America that move upslope after breeding, presumably to build up fat stores before beginning their long-distance migrations southward (Small 1994, Sogge et al. 1994, Pearson 1997).

Parula pitiayumi. - The northernmost populations in Mexico may make seasonal latitudinal movements (Binford 1989, Curson et al. 1994), but overall the species appears to be sedentary. We found no other evidence of migration within the species during the course of our field work.

Euphonia xanthogaster. – We found weak support for sedentariness in the species. However, the species appears to move upslope as high as 2000 m a.s.l. to breed during the early wet season, but we have no records of it occurring above 1500 m a.s.l. during the late wet season, and records above 1700 m a.s.l. are rare during the dry season. Merkord (2010 Chapter 4) classifies this species as an elevational migrant. At least five other species of Euphonia are elevational migrants (Binford 1989, Hilty 1997, Gómez de Silva G. et al. 1999, Blake and Loiselle 2000) so the status of this species as a migrant would not be surprising at all.

Nonmigratory Patterns

We present specific evidence to support a nonmigratory, or sedentary state in 38 of our study species. This differs from a number of studies on elevational migration, which tend to provide evidence supporting migration when it is found, but gloss over or do not present evidence supporting sedentariness.

Our information should be particularly useful for studies attempting to map character traits associated with migration onto species phylogenies. In such cases, data suggesting the absence of migration in a population is just as valuable as data suggesting its presence.

Although we present a lack of evidence for seasonal movements in most of the species we studied, this does not necessarily imply that all of these species are sedentary. It is quite possible that biases in our study design or survey methods create a false picture of the seasonal distributions of species. For instance, because the amplitude of the five elevational zones varied by species, depending on the total elevational range of the species, a species with a larger elevational range would need to migrate farther (vertically) in order to show the same migratory patterns as a narrowly-distributed species. Also, our surveys would not have detected silent individuals, such as juveniles, females, or non-singing males. Finally, our surveys may have failed to pick up small changes in density at the edge of a species distribution, such as would be expected if only a small percentage of individuals in a population were migratory. For example, mist netting surveys and flock observations in our study area suggest that at least a few individuals of *Zimmerius bolivianus*, *Chiroxiphia boliviana*, *Myioborus melanocephalus*, and *Diglossa cyanea* move to lower elevations during the dry nonbreeding season (Merkord 2010 Chapters 2, 4). These data impress the importance of using multiple survey methods when possible, and illustrate the potential pitfalls of using any survey method prone to detection biases to estimate animal abundance.

Interpretation and Alternative Hypotheses

Given that survey transects were not placed systematically or randomly, but were often placed with respect to topographical features such as ridges, it is likely that survey points were not placed randomly with respect to the distribution of individual birds. Thus our density estimates may not be representative of the elevational gradient as a whole. An ideal study design would remedy this, but given constraints imposed by the topography, such a design would be difficult to implement.

It is important not to generalize our results to say that the true density of individuals of a species varied in any given way. At most, we can only characterize the distributions of *sampled* individuals, which in our study were primarily singing birds. While we did detect some individuals using visual cues, the majority of detections were auditory, as is typical of surveys in tropical forests. For six of the species studied, auditory detections may have been of either males or females (*Pyrrhomyias cinnamomeus*, *Chlorornis riefferii, Cyanolyca viridicyanus, Cacicus chrysonotus, Heliangelus amethysticollis, Synallaxis azarae*). Two other species are known to engage in male-female duetting (*Thryothorus genibarbis* and *Henicorhina leucophrys*; Skutch 1940, Mann et al. 2009), and many of our detections of those species were of duetting pairs. For the other 21 species, the majority of auditory detections were of song, presumably given by males. Thus, for most species we were effectively quantifying only the number of singing males. Our interpretations should therefore only be taken to refer to potential elevational migration, or lack thereof, of the sampled subset of any given population.

Upon inspection, it is apparent that density estimates of our 50 species were lower, on average, during the nonbreeding season than during the breeding season (Figs. 7–14). We do not interpret these as differences in the true number of individuals present, but rather differences in the number of birds detected. Although many species sing during the nonbreeding season, many individuals may sing with reduced volume, reduced frequency, or not at all during this period. Thus when comparing the distribution of birds between seasons, it is more useful to compare the shapes of their density distribution curves than their magnitudes. For example, even though the densities of *Chiroxiphia boliviana* (Fig 11) were much lower during the nonbreeding season, the proportion of the total number of birds in each elevational zone was almost identical between seasons.

It is also apparent that most of the density distributions we present are unimodal in shape (Table 3; Figs. 7–19). This is unsurprising given that niche theory predicts that an organism's distribution along a given environmental gradient should be unimodal and approximately normal in shape (Hutchinson 1957, Brown 1984, but see Sagarin et al. 2006). The presence of varying amounts of skew and kurtosis in our modeled density distributions are a testament to the complex interactions determining the abundance of species. An elevational gradient is only a proxy for other environmental gradient such as oxygen, temperature, rainfall, vegetation structure, and floristics. The simultaneous effect of multiple environmental gradients on the abundance of an organism undoubtedly account for the shape of each species' density distribution curve. The apparent presence of several bimodal distributions in our study species warrants further study to determine if these distributions exist in fact, or are merely effects of noise, small sample size, or some form of sampling bias.

Although we interpret the season-elevation interaction effects on bird density as indicative of elevational migration, there are other potential explanations of those patterns. For example, it may be that we were actually noting a habitat-elevation interaction effect on bird density (a "habitat migration hypothesis" rather than an elevational migration hypothesis). As mentioned previously, our survey transects were not laid out in a systematic design, but were placed opportunistically, most often on ridges or roads. Ridge or roadside habitat may be different than other habitat at a given elevation. For instance, canopy height may be reduced on ridges, or the canopy broken along roadsides, altering local temperature or moisture conditions. Even small changes in habitat structure can impact the local occurrence of species, and Karr et al. (1982) have suggested some species may undertake seasonal movements to track ideal microclimates. Thus it is possible that birds in our study area may show a seasonal movement into or out of the more xeric ridge or roadside habitats. Variation in the direction or timing of such a seasonal movement due to elevation could yield results much like those we observed. An inter-seasonal, intra-elevational movement would be just as interesting as elevational migration in its own right. Nevertheless, we do not favor this interpretation of our data. We sampled primarily along an elevational gradient, not a within-elevation habitat gradient, and we believe the elevational migration hypothesis is a more parsimonious explanation of our results than the habitat migration hypothesis.

Another possible alternative explanation of our results, the "breeding timing hypothesis," is that the timing of breeding varies along the elevational gradient, and with it the likelihood that individuals are vocalizing, and thus available for detection. In many montane regions, nesting is initiated later at higher elevations, but usually only by a few weeks, even in areas with harsh winter conditions prohibiting early nesting at high elevations (Hahn et al. 2004). In our study area, increases in precipitation at the beginning of the rainy season do occur later at higher elevations (Fig. 1), so later nesting of birds at higher elevations might be expected. However, the months of Jun–Jul, which we assign to the “nonbreeding season”, are the driest months at all elevations, giving no reason to suspect that birds at high elevations are actually breeding during what we defined as the “nonbreeding season.” Nesting data from the study area (G. A. Londoño, *pers. comm.*) [confirm with Gustavo] suggests that breeding initiates at approximately the same time throughout the elevational gradient. There is also apparently little variation along the elevational gradient in the timing of molt, which usually follows breeding (Merkord 2010 Chapter 1, Fig. 4). Furthermore, for the breeding timing hypothesis to hold up, we would expect *apparent* seasonal changes in distribution of many species whose elevational ranges span a large portion of the elevational gradient. Instead, we found most species with large elevational distributions to show relatively similar density distributions between seasons. While the breeding timing hypothesis may explain a minority of the patterns suggestive of elevational migration, we do not believe it can adequately explain all of them.

Conclusions

Our findings provide insights into the ecology of some poorly-known Andean species, and establish a framework within which year-round resident birds of montane forests may be classified as either elevationally migratory or sedentary. Patterns of partial elevational migration in montane bird communities may be impossible to identify with presence-absence data alone, highlighting the usefulness of abundance data in studying species distributions. By creating estimates of density corrected for numerous biases in detection probability, we are able to identify several potentially migratory species, and several potentially sedentary species. It is important to note that migratory or sedentary patterns can be masked by confounding factors, including seasonal variation in cue rates and elevational variation in detection probability. That said, the current study provides the best information available to date on the seasonal distributions of dozens of Andean bird species.

The methods we used to identify elevational migrants could be used on a broader scale to fill in knowledge gaps in understudied communities throughout the tropics. Future studies attempting to document the abundance of tropical montane bird species should carefully consider the limitations of point- or transect-based surveys in estimating species abundances. Distance-based methods of correcting for detection biases require minimum numbers of detections, and are better suited for commonly detected species. For example, out of 333 species detected, we were only able to garner a sufficient number of detections for 50 species, about 15%. This percentage could be increased by combining species with similar detection probability functions using the MCDS engine in program Distance (Alldredge et al. 2007b). In additional, the methods used to identify seasonal changes in distribution could be employed on density or abundance estimates that are not corrected for variation in detection probability (see Merkord 2010 Chapter 4 for such an approach).

Accurate measurement of the abundance of organisms along an elevational gradient is crucial for determining how species are being affected by global climate change, and hence predicting how species will be affected in the future. Numerous studies have compared past and present species along elevational gradients to infer climate change-induced elevational range shifts (Wilson et al. 2005, Colwell et al. 2008, Lenoir et al. 2008, Moritz et al. 2008). This technique will only work with montane animals if appropriate attention is given to the possibility of elevational migration. Data from historic studies conducted primarily during one season should not be compared directly to present-day studies conducted during another season unless there is evidence that the species being compared are sedentary, lest spurious long-term shifts in elevational range be inferred.

Abundance estimates based on data such as ours are useful for other reasons as well. At least one study has predicted the susceptibility of species to climate change based on their elevational ranges of occurrence (Laurance et al. *In review*), assuming that both common and rare species will respond similarly. Incorporating abundance estimates into these models will provide a better indication of the likelihood of species persistence (Grouios and Manne 2009).

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Table 1. System used to score the weight of evidence for elevational migration by comparing the density estimates from point count data between two seasons.

Elevation-Season Interaction p-value	***Weighted Mean Elevation Shift***	***Score***
$p \leq 0.05$	$s \leq 0.15$	3
$p \leq 0.05$	$0.10 < s \leq 0.15$	2
$p \leq 0.05$	$0.05 < s \leq 0.10$	1
$p \leq 0.05$	$s \leq 0.05$	0
$0.05 < p \leq 0.10$		0
$0.10 < p$	$0.20 < s$	0
$0.10 < p$	$0.15 < s \leq 0.20$	-1
$0.10 < p$	$0.10 < s \leq 0.15$	-2
$0.10 < p$	$s \leq 0.10$	-3

Table 2. Best supported models estimating the detection probability function for each species. Number of observations are given after truncation. The two possible key functions are a hazard rate function with a cosine expansion (HR) and a half normal function with a hermite polynomial expansion (HN). Covariates included observer (O), precipitation (P), season (S), time of day (T), and year (Y). Goodness-of-fit p-values are given for chi-square (grouped distance data) and Kolmogorov-Smirnov (continuous distance data) tests. Estimated probability of detection (P), mean cluster size (CS), and effective detection radius (EDR) are each given with their coefficient of variation (CV). Scientific names follow Remsen et al. (Version April 14, 2010).

			Covariates					***# Parameters***				***Goodness-of-Fit p values***		***P***		***CS***		***EDR***	
Species	***# Obs***	***Key Func.***	***O***	***P***	***S***	***T***	***Y***	***Key***	***Adj***	***Cov***	***Total***	***Chi***	***K-S***	***Est.***	***CV***	***Est.***	***CV***	***Est.***	***CV***
Atlapetes melanolaemus	105	HR	O		S	T		2	0	4	6		1.00	0.12	0.21	1.30	0.06	23.3	0.11
Basileuterus bivittatus	158	HN				T	Y	1	0	2	3		0.83	0.35	0.07	1.23	0.03	55.1	0.04
Basileuterus coronatus	129	HN	O		S	T	Y	1	0	5	6		0.11	0.35	0.11	1.16	0.03	38.1	0.05
Basileuterus luteoviridis	51	HN						1	0	0	1		0.68	0.43	0.18	1.02	0.02	34.6	0.09
Basileuterus signatus	115	HR						2	0	0	2		0.64	0.24	0.13	1.03	0.02	56.8	0.07
Cacicus chrysonotus	61	HN						1	0	0	1	1.00		0.31	0.15	1.28	0.06	81.2	0.08
Chiroxiphia boliviana	185	HR				T		2	1	1	4	0.71		0.24	0.07	1.17	0.03	41.0	0.03
Chlorophonia cyanea	43	HR						2	0	0	2		0.71	0.73	0.14	1.07	0.04	33.3	0.07
Chlorornis riefferii	50	HR						2	0	0	2		0.88	0.24	0.28	1.18	0.05	29.6	0.14
Chlorospingus ophthalmicus	67	HR						2	0	0	2		0.91	0.15	0.30	1.22	0.07	34.8	0.15
Colibri thalassinus	38	HN				T		1	0	1	2		0.65	0.36	0.16	1.29	0.19	29.9	0.08
Contopus fumigatus	57	HR						2	0	0	2		0.80	0.36	0.22	1.00	0.00	84.0	0.11
Cranioleuca curtata	47	HR	O					2	0	1	3	0.87		0.49	0.11	1.02	0.02	59.5	0.06
Crypturellus obsoletus	69	HN	O		S	T		1	0	4	5	0.54		0.39	0.12	1.03	0.02	102.5	0.06
Cyanocorax yncas	42	HN	O		S			1	0	3	4		0.97	0.17	0.17	1.17	0.06	62.1	0.08
Cyanolyca viridicyanus	54	HR						2	0	0	2	0.80		0.22	0.36	1.52	0.08	51.1	0.18
Diglossa cyanea	230	HR	O			T	Y	2	0	4	6	0.27		0.33	0.07	1.07	0.02	45.9	0.03
Diglossa glauca	50	HR	O					2	0	1	3		0.22	0.65	0.09	1.06	0.03	32.2	0.05
Entomodestes leucotis	139	HR	O				Y	2	0	3	5	0.60		0.27	0.08	1.00	0.00	55.0	0.04
Euphonia xanthogaster	69	HR			S	T		2	0	3	5		0.25	0.45	0.10	1.03	0.02	26.2	0.05
Formicarius rufipectus	85	HN				T		1	0	1	2	0.85		0.44	0.10	1.00	0.00	112.7	0.05
Grallaria albigula	42	HR						2	0	0	2	0.95		0.46	0.17	1.00	0.00	111.4	0.09
Grallaria erythroleuca	235	HR						2	0	0	2	0.99		0.67	0.08	1.00	0.00	114.2	0.04
Heliangelus amethysticollis	64	HR	O					2	0	1	3	0.79		0.07	0.29	1.02	0.02	9.9	0.15
Hemispingus melanotis	43	HR						2	0	0	2		0.97	0.33	0.65	1.05	0.03	27.4	0.32

Species	***# Obs***	***Key Func.***	***Covariates***					***# Parameters***				***Goodness-of-Fit p values***		***P***		***CS***		***EDR***	
			O	***P***	***S***	***T***	***Y***	***Key***	***Adj***	***Cov***	***Total***	***Chi***	***K-S***	***Est.***	***CV***	***Est.***	***CV***	***Est.***	***CV***
Hemitriccus granadensis	104	HR						2	0	0	2		0.97	0.23	0.20	1.00	0.00	38.6	0.10
Henicorhina leucophrys	306	HR						2	2	0	4	0.93		0.14	0.16	1.02	0.01	44.1	0.08
Hypocnemis subflava	134	HR						2	0	0	2		0.98	0.42	0.18	1.12	0.03	58.6	0.09
Leptopogon superciliaris	43	HR						2	0	0	2		0.77	0.31	0.29	1.07	0.04	26.7	0.14
Lophotriccus pileatus	193	HR						2	0	0	2		0.51	0.40	0.16	1.01	0.01	41.9	0.08
Mecocerculus stictopterus	72	HN				T	Y	1	0	3	4		0.68	0.40	0.12	1.24	0.04	38.1	0.06
Myadestes ralloides	84	HR	O					2	0	1	3	0.8		0.58	0.08	1.00	0.00	102.4	0.04
Myioborus melanocephalus	303	HR			S	T	Y	2	0	5	7		0.69	0.31	0.06	1.03	0.01	47.0	0.03
Myioborus miniatus	224	HR	O	P	S	T	Y	2	0	6	8		0.98	0.41	0.06	1.04	0.01	52.7	0.03
Ochthoeca pulchella	49	HN				T	Y	1	0	3	4		0.89	0.50	0.27	1.02	0.02	27.6	0.13
Parula pitiayumi	48	HN				T	Y	1	0	2	3		0.81	0.33	0.20	1.00	0.00	46.2	0.10
Patagioenas plumbea	68	HN	O			T		1	0	2	3		0.59	0.32	0.14	1.03	0.02	107.4	0.07
Pharomachrus auriceps	32	HR					Y	2	0	1	3	1		0.70	0.11	1.00	0.00	138.3	0.06
Pheugopedius genibarbis	63	HR						2	0	0	2		0.96	0.37	0.21	1.08	0.03	54.4	0.10
Pipreola arcuata	44	HR				T		2	0	1	3		0.74	0.47	0.15	1.02	0.02	34.2	0.07
Psarocolius angustifrons	36	HR	O					2	0	1	3	0.8		0.09	0.32	1.72	0.18	45.8	0.16
Pyriglena leuconota	41	HN						1	0	0	1		0.64	0.65	0.23	1.15	0.05	61.1	0.11
Pyrrhomyias cinnamomeus	106	HR	O					2	0	1	3	0.8		0.31	0.09	1.08	0.03	46.0	0.04
Scytalopus atratus	109	HR						2	0	0	2	0.9		0.37	0.27	1.00	0.00	64.3	0.13
Scytalopus parvirostris	138	HN			S	T		1	0	3	4		0.73	0.22	0.08	1.01	0.01	55.7	0.04
Synallaxis azarae	214	HN						1	0	0	1	0.9		0.31	0.08	1.14	0.02	40.3	0.04
Troglodytes solstitialis	42	HN						1	0	0	1		0.43	0.47	0.22	1.14	0.05	24.6	0.11
Trogon personatus	108	HN	O					1	0	1	2	1		0.22	0.09	1.05	0.02	77.0	0.05
Turdus serranus	69	HN	O	P				1	0	2	3		0.9	0.22	0.20	1.00	0.00	93.6	0.10
Zimmerius bolivianus	44	HN			S	T		1	0	2	3		0.81	0.56	0.13	1.05	0.03	33.79	0.07

Table 3. Pairwise comparisons of density distributions for the dry season (DR), early wet season (EW), and late wet season (LW). Elevational minima and maxima are based on a dataset including only detections for which the distance to the bird could be measured. Scores indicate the weight of evidence for migratory status. Positive scores represent elevational migrants while negative scores represent residents. The greater the score, the larger the weight of evidence. Taxonomy follows Remsen et al. (Version April 14, 2010)

			Elevation (m a.s.l.)		***Season***		***Number of Detections***		***Weighted Mean Elevation (m a.s.l.)***					
Family	***Scientific Name***	***English Name***	***Min***	***Max***	***1***	***2***	***1***	***2***	***1***	***2***	***Elev. Shift (m)***	***Elev. Shift (%)***	***Season x Elevation Interaction* p-value**	**Score**
Tinamidae	*Crypturellus obsoletus*	Brown Tinamou	1055	2904	DR	EW	18	51	1980	1925	-54	-0.03	0.473	-3
Tinamidae	*Crypturellus obsoletus*	Brown Tinamou	1055	2904	EW	LW	51	19	1925	2082	157	0.08	0.151	-3
Tinamidae	*Crypturellus obsoletus*	Brown Tinamou	1055	2904	LW	DR	19	18	2082	1980	-103	-0.06	0.206	-3
Columbidae	*Patagioenas plumbea*	Plumbeous Pigeon	934	1950	DR	EW	9	55	1194	1453	259	0.25	0.077	0
Columbidae	*Patagioenas plumbea*	Plumbeous Pigeon	934	1950	EW	LW	55	4	1453	1523	70	0.07	0.424	-3
Columbidae	*Patagioenas plumbea*	Plumbeous Pigeon	934	1950	LW	DR	4	9	1523	1194	-330	-0.32	0.027	3
Trochilidae	*Colibri thalassinus*	Green Violetear	1486	2590	DR	EW	5	33	2215	1837	-377	-0.34	0.011	3
Trochilidae	*Heliangelus amethysticollis*	Amethyst-throated Sunangel	2324	3383	DR	EW	20	35	2844	2773	-71	-0.07	0.751	-3
Trogonidae	*Pharomachrus auriceps*	Golden-headed Quetzal	1950	3049	DR	EW	10	51	2426	2522	96	0.09	0.629	-3
Trogonidae	*Trogon personatus*	Masked Trogon	1578	3032	DR	EW	32	73	2414	2510	96	0.07	0.156	-3
Trogonidae	*Trogon personatus*	Masked Trogon	1578	3032	EW	LW	73	6	2510	2402	-109	-0.07	0.372	-3
Trogonidae	*Trogon personatus*	Masked Trogon	1578	3032	LW	DR	6	32	2402	2414	12	0.01	0.548	-3
Furnariidae	*Synallaxis azarae*	Azara's Spinetail	1224	2991	DR	EW	79	118	2362	2521	159	0.09	0.125	-3
Furnariidae	*Synallaxis azarae*	Azara's Spinetail	1224	2991	EW	LW	118	34	2521	2482	-39	-0.02	0.451	-3
Furnariidae	*Synallaxis azarae*	Azara's Spinetail	1224	2991	LW	DR	34	79	2482	2362	-121	-0.07	0.425	-3
Furnariidae	*Cranioleuca curtata*	Ash-browed Spinetail	968	1821	DR	EW	22	23	1289	1331	42	0.05	0.903	-3
Furnariidae	*Cranioleuca curtata*	Ash-browed Spinetail	968	1821	EW	LW	23	4	1331	1338	7	0.01	0.345	-3
Furnariidae	*Cranioleuca curtata*	Ash-browed Spinetail	968	1821	LW	DR	4	22	1338	1289	-49	-0.06	0.389	-3
Thamnophilidae	*Hypocnemis subflava*	Yellow-breasted Warbling-Antbird	805	1429	DR	EW	59	50	1122	1166	43	0.07	0.711	-3
Thamnophilidae	*Pyriglena leuconota*	White-backed Fire-eye	990	1948	DR	EW	9	27	1354	1444	90	0.09	0.512	-3
Thamnophilidae	*Pyriglena leuconota*	White-backed Fire-eye	990	1948	EW	LW	27	5	1444	1277	-167	-0.17	0.444	-1
Thamnophilidae	*Pyriglena leuconota*	White-backed Fire-eye	990	1948	LW	DR	5	9	1277	1354	77	0.08	0.915	-3
Formicariidae	*Formicarius rufipectus*	Rufous-breasted Antthrush	1139	2012	DR	EW	18	60	1411	1455	45	0.05	0.566	-3

			Elevation (m a.s.l.)		***Season***		***Number of Detections***		***Weighted Mean Elevation (m a.s.l.)***		***Elev. Shift (m)***	***Elev. Shift (%)***	***Season x Elevation Interaction p-value***	***Score***
Family	***Scientific Name***	***English Name***	***Min***	***Max***	***1***	***2***	***1***	***2***	***1***	***2***				
Formicariidae	*Formicarius rufipectus*	Rufous-breasted Antthrush	1139	2012	EW	LW	60	6	1455	1605	149	0.17	0.067	0
Formicariidae	*Formicarius rufipectus*	Rufous-breasted Antthrush	1139	2012	LW	DR	6	18	1605	1411	-194	-0.22	0.067	0
Grallariidae	*Grallaria albigula*	White-throated Antpitta	1506	2554	DR	EW	6	32	1850	1827	-23	-0.02	0.283	-3
Grallariidae	*Grallaria albigula*	White-throated Antpitta	1506	2554	EW	LW	32	3	1827	1751	-76	-0.07	0.121	-3
Grallariidae	*Grallaria albigula*	White-throated Antpitta	1506	2554	LW	DR	3	6	1751	1850	100	0.1	0.356	-3
Grallariidae	*Grallaria erythroleuca*	Red-and-white Antpitta	1758	3049	DR	EW	59	160	2591	2597	6	0	0.983	-3
Grallariidae	*Grallaria erythroleuca*	Red-and-white Antpitta	1758	3049	EW	LW	160	57	2597	2656	60	0.05	0.091	0
Grallariidae	*Grallaria erythroleuca*	Red-and-white Antpitta	1758	3049	LW	DR	57	59	2656	2591	-66	-0.05	0.029	0
Rhinocryptidae	*Scytalopus parvirostris*	Trilling Tapaculo	2184	3414	DR	EW	44	88	2761	2710	-51	-0.04	0.778	-3
Rhinocryptidae	*Scytalopus atratus*	White-crowned Tapaculo	1059	2065	DR	EW	26	59	1485	1620	135	0.13	0.007	2
Rhinocryptidae	*Scytalopus atratus*	White-crowned Tapaculo	1059	2065	EW	LW	59	26	1620	1604	-16	-0.02	0.094	0
Rhinocryptidae	*Scytalopus atratus*	White-crowned Tapaculo	1059	2065	LW	DR	26	26	1604	1485	-119	-0.12	0.238	-2
Tyrannidae	*Mecocerculus stictopterus*	White-banded Tyrannulet	2324	3383	DR	EW	19	46	2820	2767	-53	-0.05	0.978	-3
Tyrannidae	*Zimmerius bolivianus*	Bolivian Tyrannulet	1373	2826	DR	EW	10	34	2221	2117	-104	-0.07	0.898	-3
Tyrannidae	*Leptopogon superciliaris*	Slaty-capped Flycatcher	866	1709	DR	EW	12	26	1360	1425	65	0.08	0.781	-3
Tyrannidae	*Leptopogon superciliaris*	Slaty-capped Flycatcher	866	1709	EW	LW	26	5	1425	1321	-104	-0.12	0.253	-2
Tyrannidae	*Leptopogon superciliaris*	Slaty-capped Flycatcher	866	1709	LW	DR	5	12	1321	1360	39	0.05	0.181	-3
Tyrannidae	*Lophotriccus pileatus*	Scale-crested Pygmy-Tyrant	983	1758	DR	EW	69	102	1276	1389	113	0.15	0.43	-2
Tyrannidae	*Lophotriccus pileatus*	Scale-crested Pygmy-Tyrant	983	1758	EW	LW	102	22	1389	1370	-18	-0.02	0.809	-3
Tyrannidae	*Lophotriccus pileatus*	Scale-crested Pygmy-Tyrant	983	1758	LW	DR	22	69	1370	1276	-94	-0.12	0.22	-2
Tyrannidae	*Hemitriccus granadensis*	Black-throated Tody-Tyrant	2305	3101	DR	EW	34	68	2769	2733	-35	-0.04	0.975	-3
Tyrannidae	*Pyrrhomyias cinnamomeus*	Cinnamon Flycatcher	1198	3101	DR	EW	23	66	2135	2186	51	0.03	0.695	-3
Tyrannidae	*Pyrrhomyias cinnamomeus*	Cinnamon Flycatcher	1198	3101	EW	LW	66	13	2186	2268	82	0.04	0.891	-3
Tyrannidae	*Pyrrhomyias cinnamomeus*	Cinnamon Flycatcher	1198	3101	LW	DR	13	23	2268	2135	-134	-0.07	0.771	-3
Tyrannidae	*Contopus fumigatus*	Smoke-colored Pewee	1450	3049	DR	EW	15	36	2335	2676	341	0.21	0.002	3
Tyrannidae	*Contopus fumigatus*	Smoke-colored Pewee	1450	3049	EW	LW	36	6	2676	2090	-586	-0.37	0.001	3
Tyrannidae	*Contopus fumigatus*	Smoke-colored Pewee	1450	3049	LW	DR	6	15	2090	2335	245	0.15	0.569	-2
Tyrannidae	*Ochthoeca pulchella*	Golden-browed Chat-Tyrant	2324	3101	DR	EW	16	32	2713	2703	-9	-0.01	0.972	-3
Cotingidae	*Pipreola arcuata*	Barred Fruiteater	1821	3215	DR	EW	14	21	2677	2717	40	0.03	0.464	-3

			Elevation (m a.s.l.)		Season		Number of Detections		Weighted Mean Elevation (m a.s.l.)					
Family	***Scientific Name***	***English Name***	***Min***	***Max***	***1***	***2***	***1***	***2***	***1***	***2***	***Elev. Shift (m)***	***Elev. Shift (%)***	***Season x Elevation Interaction* p-*value***	***Score***
Cotingidae	*Pipreola arcuata*	Barred Fruiteater	1821	3215	EW	LW	21	9	2717	2546	-171	-0.12	0.181	-2
Cotingidae	*Pipreola arcuata*	Barred Fruiteater	1821	3215	LW	DR	9	14	2546	2677	131	0.09	0.443	-3
Pipridae	*Chiroxiphia boliviana*	Yungas Manakin	983	2033	DR	EW	28	149	1541	1498	-43	-0.04	0.512	-3
Pipridae	*Chiroxiphia boliviana*	Yungas Manakin	983	2033	EW	LW	149	8	1498	1460	-39	-0.04	0.327	-3
Pipridae	*Chiroxiphia boliviana*	Yungas Manakin	983	2033	LW	DR	8	28	1460	1541	81	0.08	0.479	-3
Corvidae	*Cyanolyca viridicyanus*	White-collared Jay	2292	3032	DR	EW	18	34	2595	2662	67	0.09	0.973	-3
Corvidae	*Cyanolyca viridicyanus*	White-collared Jay	2292	3032	EW	LW	34	17	2662	2539	-123	-0.17	0.824	-1
Corvidae	*Cyanolyca viridicyanus*	White-collared Jay	2292	3032	LW	DR	17	18	2539	2595	56	0.08	0.722	-3
Corvidae	*Cyanocorax yncas*	Green Jay	1190	2012	DR	EW	17	18	1664	1782	118	0.14	0.057	0
Corvidae	*Cyanocorax yncas*	Green Jay	1190	2012	EW	LW	18	7	1782	1683	-99	-0.12	0.048	2
Corvidae	*Cyanocorax yncas*	Green Jay	1190	2012	LW	DR	7	17	1683	1664	-20	-0.02	0.698	-3
Troglodytidae	*Troglodytes solstitialis*	Mountain Wren	2305	3215	DR	EW	12	28	2695	2690	-5	-0.01	0.733	-3
Troglodytidae	*Pheugopedius genibarbis*	Moustached Wren	805	1496	DR	EW	31	19	1184	1223	39	0.06	0.923	-3
Troglodytidae	*Henicorhina leucophrys*	Gray-breasted Wood-Wren	1190	2787	DR	EW	72	173	1586	1707	121	0.08	0.595	-3
Troglodytidae	*Henicorhina leucophrys*	Gray-breasted Wood-Wren	1190	2787	EW	LW	173	61	1707	1736	29	0.02	0.057	0
Troglodytidae	*Henicorhina leucophrys*	Gray-breasted Wood-Wren	1190	2787	LW	DR	61	72	1736	1586	-150	-0.09	0.067	0
Turdidae	*Myadestes ralloides*	Andean Solitaire	1193	2828	DR	EW	20	59	1896	2221	325	0.2	0.03	3
Turdidae	*Myadestes ralloides*	Andean Solitaire	1193	2828	EW	LW	59	5	2221	1422	-799	-0.49	0.055	0
Turdidae	*Myadestes ralloides*	Andean Solitaire	1193	2828	LW	DR	5	20	1422	1896	474	0.29	0.769	0
Turdidae	*Entomodestes leucotis*	White-eared Solitaire	1640	2781	DR	EW	28	106	2100	1997	-104	-0.09	0.001	1
Turdidae	*Turdus serranus*	Glossy-black Thrush	1852	3342	DR	EW	7	61	2597	2607	10	0.01	0.628	-3
Thraupidae	*Hemispingus melanotis*	Black-eared Hemispingus	1193	2319	DR	EW	15	25	1545	1583	38	0.03	0.775	-3
Thraupidae	*Hemispingus melanotis*	Black-eared Hemispingus	1193	2319	EW	LW	25	3	1583	1756	173	0.15	0.558	-2
Thraupidae	*Hemispingus melanotis*	Black-eared Hemispingus	1193	2319	LW	DR	3	15	1756	1545	-211	-0.19	0.259	-1
Thraupidae	*Chlorornis riefferii*	Grass-green Tanager	2292	3215	DR	EW	17	31	2763	2744	-19	-0.02	0.236	-3
Thraupidae	*Diglossa glauca*	Deep-blue Flowerpiercer	1535	2154	EW	LW	39	5	1863	1869	7	0.01	0.194	-3
Thraupidae	*Diglossa cyanea*	Masked Flowerpiercer	2109	3342	DR	EW	63	128	2774	2726	-49	-0.04	0.475	-3
Incertae Sedis	*Chlorospingus ophthalmicus*	Common Bush-Tanager	1193	2561	DR	EW	11	55	2196	1905	-291	-0.21	0.79	0
Emberizidae	*Atlapetes melanolaemus*	Black-faced Brush-Finch	1450	3215	DR	EW	31	65	2544	2430	-115	-0.07	0.87	-3

			Elevation (m a.s.l.)		Season		Number of Detections		Weighted Mean Elevation (m a.s.l.)					
Family	***Scientific Name***	***English Name***	***Min***	***Max***	***1***	***2***	***1***	***2***	***1***	***2***	***Elev. Shift (m)***	***Elev. Shift (%)***	***Season x Elevation Interaction* p*-value***	***Score***
Emberizidae	*Atlapetes melanolaemus*	Black-faced Brush-Finch	1450	3215	EW	LW	65	9	2430	2477	47	0.03	0.998	-3
Emberizidae	*Atlapetes melanolaemus*	Black-faced Brush-Finch	1450	3215	LW	DR	9	31	2477	2544	67	0.04	0.856	-3
Parulidae	*Parula pitiayumi*	Tropical Parula	1059	1651	EW	LW	28	5	1368	1237	-131	-0.22	0.598	0
Parulidae	*Myioborus miniatus*	Slate-throated Redstart	829	2012	DR	EW	65	128	1281	1478	197	0.17	0.005	3
Parulidae	*Myioborus miniatus*	Slate-throated Redstart	829	2012	EW	LW	128	31	1478	1344	-134	-0.11	0.008	2
Parulidae	*Myioborus miniatus*	Slate-throated Redstart	829	2012	LW	DR	31	65	1344	1281	-63	-0.05	0.976	-3
Parulidae	*Myioborus melanocephalus*	Spectacled Redstart	1973	3159	DR	EW	87	139	2579	2551	-28	-0.02	0.171	-3
Parulidae	*Myioborus melanocephalus*	Spectacled Redstart	1973	3159	EW	LW	139	77	2551	2517	-34	-0.03	0.443	-3
Parulidae	*Myioborus melanocephalus*	Spectacled Redstart	1973	3159	LW	DR	77	87	2517	2579	62	0.05	0.715	-3
Parulidae	*Basileuterus bivittatus*	Two-banded Warbler	893	1591	DR	EW	68	58	1118	1189	71	0.1	0.113	-3
Parulidae	*Basileuterus bivittatus*	Two-banded Warbler	893	1591	EW	LW	58	32	1189	1202	12	0.02	0.464	-3
Parulidae	*Basileuterus bivittatus*	Two-banded Warbler	893	1591	LW	DR	32	68	1202	1118	-84	-0.12	0.477	-2
Parulidae	*Basileuterus luteoviridis*	Citrine Warbler	2305	3215	DR	EW	12	25	2563	2651	88	0.1	0.868	-3
Parulidae	*Basileuterus signatus*	Pale-legged Warbler	1462	2981	DR	EW	34	58	2265	2489	224	0.15	0.009	2
Parulidae	*Basileuterus signatus*	Pale-legged Warbler	1462	2981	EW	LW	58	23	2489	2440	-49	-0.03	0.523	-3
Parulidae	*Basileuterus signatus*	Pale-legged Warbler	1462	2981	LW	DR	23	34	2440	2265	-175	-0.12	0.055	0
Parulidae	*Basileuterus coronatus*	Russet-crowned Warbler	1334	2335	DR	EW	32	80	1601	1589	-12	-0.01	0.258	-3
Parulidae	*Basileuterus coronatus*	Russet-crowned Warbler	1334	2335	EW	LW	80	17	1589	1540	-49	-0.05	0.149	-3
Parulidae	*Basileuterus coronatus*	Russet-crowned Warbler	1334	2335	LW	DR	17	32	1540	1601	61	0.06	0.615	-3
Icteridae	*Psarocolius angustifrons*	Russet-backed Oropendola	805	2065	DR	EW	12	19	979	1254	275	0.22	0.338	0
Icteridae	*Psarocolius angustifrons*	Russet-backed Oropendola	805	2065	EW	LW	19	6	1254	1325	71	0.06	0.559	-3
Icteridae	*Psarocolius angustifrons*	Russet-backed Oropendola	805	2065	LW	DR	6	12	1325	979	-346	-0.27	0.109	0
Icteridae	*Cacicus chrysonotus*	Mountain Cacique	2184	3101	DR	EW	20	44	2642	2763	121	0.13	0.034	2
Icteridae	*Cacicus chrysonotus*	Mountain Cacique	2184	3101	EW	LW	44	9	2763	2699	-64	-0.07	0.15	-3
Icteridae	*Cacicus chrysonotus*	Mountain Cacique	2184	3101	LW	DR	9	20	2699	2642	-56	-0.06	0.683	-3
Fringillidae	*Euphonia xanthogaster*	Orange-bellied Euphonia	837	1965	DR	EW	15	52	1175	1388	213	0.19	0.12	-1
Fringillidae	*Chlorophonia cyanea*	Blue-naped Chlorophonia	1059	2010	DR	EW	6	36	1154	1484	330	0.35	0.298	0

Table 4. Summary of pairwise comparisons of density distributions for the dry season (DR), early wet season (EW), and late wet season (LW). Missing scores represent seasonal comparisons with insufficient effort or number of detections. Each species is assigned a combined score based on the scores from the three pairwise seasonal comparisons. Scores indicate the weight of evidence for migratory status. Positive scores represent elevational migrants (EM) while negative scores represent residents (R). The greater the score, the larger the weight of evidence. Species are ranked by combined score. Taxonomy follows Remsen et al. (Version April 14, 2010)

Scientific Name	***Scores from Seasonal Comparisons***			***Combined Score***	***Migratory Status***
	DR-EW	***EW-LW***	***LW-DR***		
Colibri thalassinus	3			3	EM
Contopus fumigatus	3	3	-2	3	EM
Myadestes ralloides	3	0	0	3	EM
Myioborus miniatus	3	2	-3	3	EM
Patagioenas plumbea	0	-3	3	3	EM
Basileuterus signatus	2	-3	0	2	EM
Cacicus chrysonotus	2	-3	-3	2	EM
Cyanocorax yncas	0	2	-3	2	EM
Scytalopus atratus	2	0	-2	2	EM
Entomodestes leucotis	1			1	EM
Chlorophonia cyanea	0			0	?
Chlorospingus ophthalmicus	0			0	?
Parula pitiayumi		0		0	?
Euphonia xanthogaster	-1			-1	R
Atlapetes melanolaemus	-3	-3	-3	-3	R
Basileuterus bivittatus	-3	-3	-2	-3	R
Basileuterus coronatus	-3	-3	-3	-3	R
Basileuterus luteoviridis	-3			-3	R
Chiroxiphia boliviana	-3	-3	-3	-3	R
Chlorornis riefferii	-3			-3	R
Cranioleuca curtata	-3	-3	-3	-3	R
Crypturellus obsoletus	-3	-3	-3	-3	R
Cyanolyca viridicyanus	-3	-1	-3	-3	R
Diglossa cyanea	-3			-3	R
Diglossa glauca		-3		-3	R
Formicarius rufipectus	-3	0	0	-3	R
Grallaria albigula	-3	-3	-3	-3	R
Grallaria erythroleuca	-3	0	0	-3	R
Heliangelus amethysticollis	-3			-3	R
Hemispingus melanotis	-3	-2	-1	-3	R
Hemitriccus granadensis	-3			-3	R
Henicorhina leucophrys	-3	0	0	-3	R
Hypocnemis subflava	-3			-3	R
Leptopogon superciliaris	-3	-2	-3	-3	R
Lophotriccus pileatus	-2	-3	-2	-3	R
Mecocerculus stictopterus	-3			-3	R
Myioborus melanocephalus	-3	-3	-3	-3	R

Scientific Name	***Scores from Seasonal Comparisons***			***Combined Score***	***Migratory Status***
	DR-EW	***EW-LW***	***LW-DR***		
Ochthoeca pulchella	-3			-3	R
Pharomachrus auriceps	-3			-3	R
Pheugopedius genibarbis	-3			-3	R
Pipreola arcuata	-3	-2	-3	-3	R
Psarocolius angustifrons	0	-3	0	-3	R
Pyriglena leuconota	-3	-1	-3	-3	R
Pyrrhomyias cinnamomeus	-3	-3	-3	-3	R
Scytalopus parvirostris	-3			-3	R
Synallaxis azarae	-3	-3	-3	-3	R
Troglodytes solstitialis	-3			-3	R
Trogon personatus	-3	-3	-3	-3	R
Turdus serranus	-3			-3	R
Zimmerius bolivianus	-3			-3	R

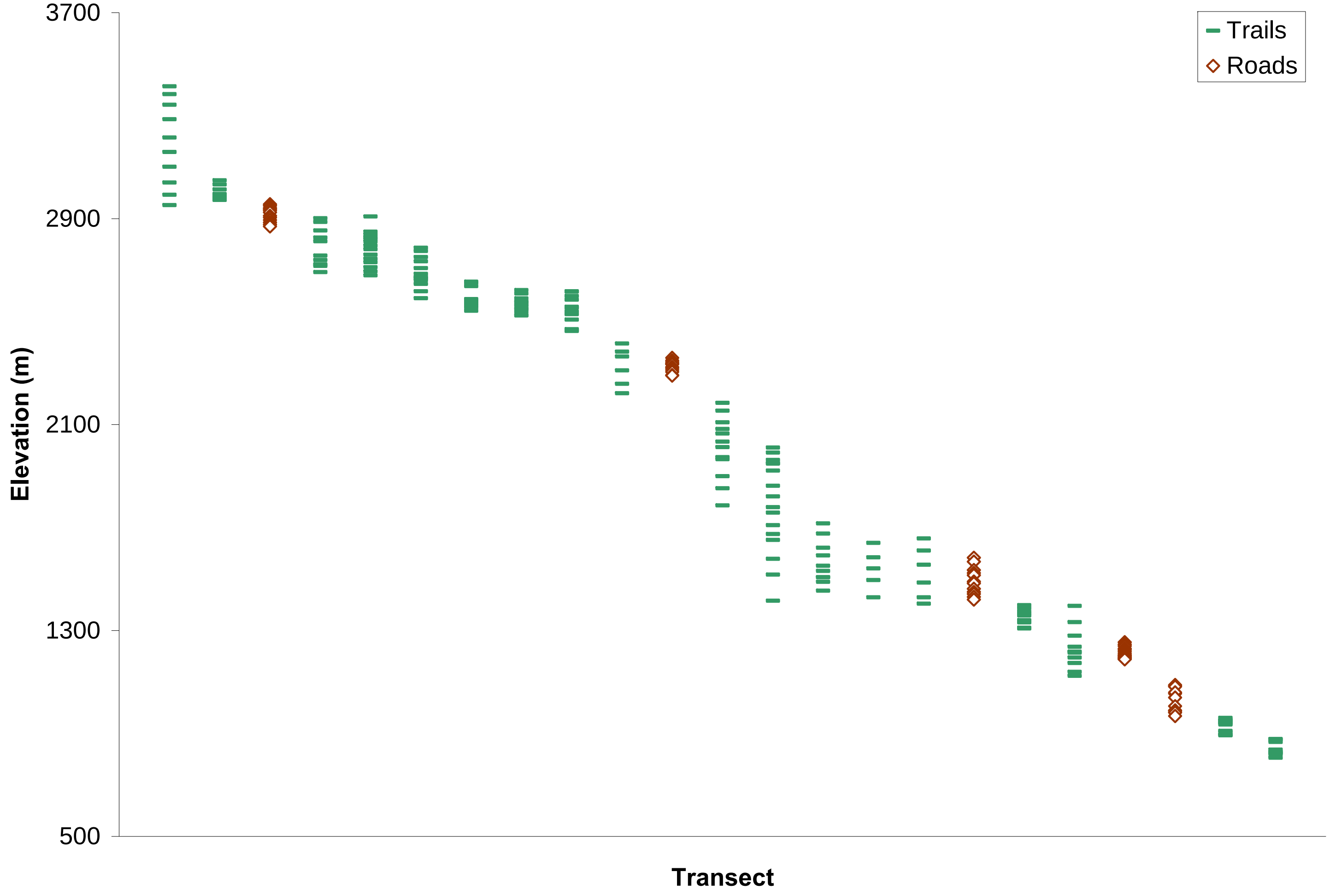

Figure 1. Spatial coverage of the elevational gradient. Columns represent survey transects and dashes represent survey points.

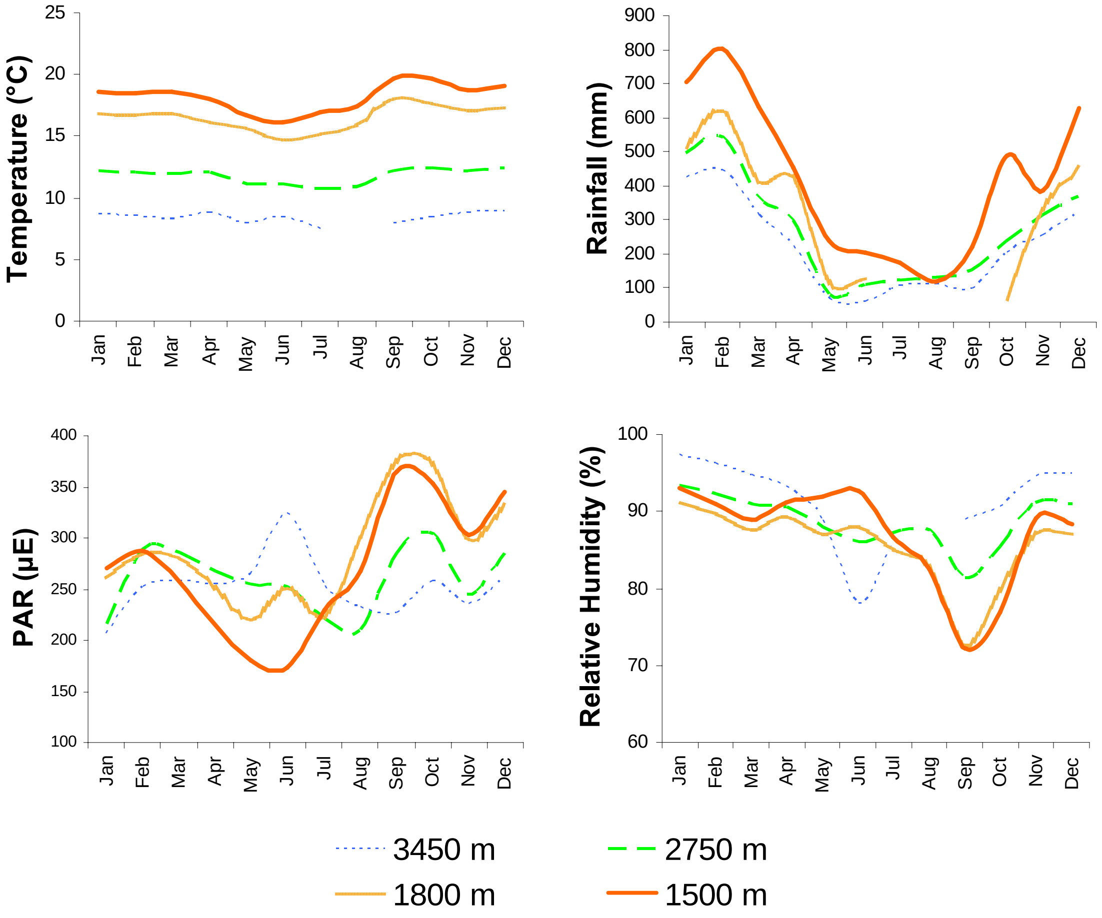

Figure 2. Monthly averages of four climatic variables (temperature, rainfall, photosynthetically active radiation and relative humidity) at four sites in the Kosñipata Valley, Cusco, Perú, recorded Jul 2007-Jul 2008 by HOBO Micro Stations mounted above the tree canopy. Unpublished data courtesy of M. R. Silman.

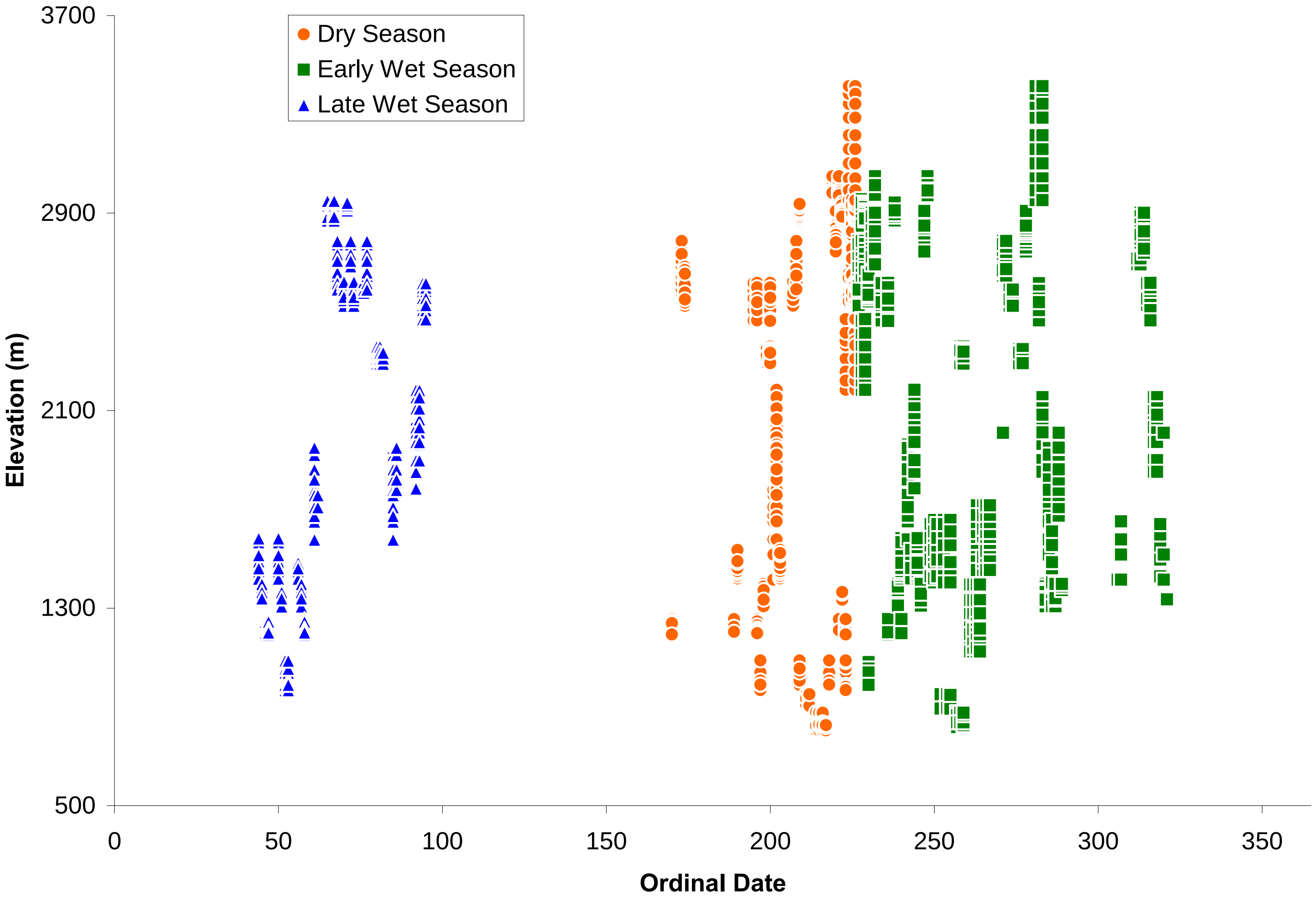

Figure 3. Seasonal distribution of point counts along the elevational gradient. Symbols represent point counts, plotted according to their elevation and the julian date on which they were conducted. Multiple visits to the same survey point on the same ordinal date are not depicted here, but see Fig. 4 for distribution of effort along the gradient.

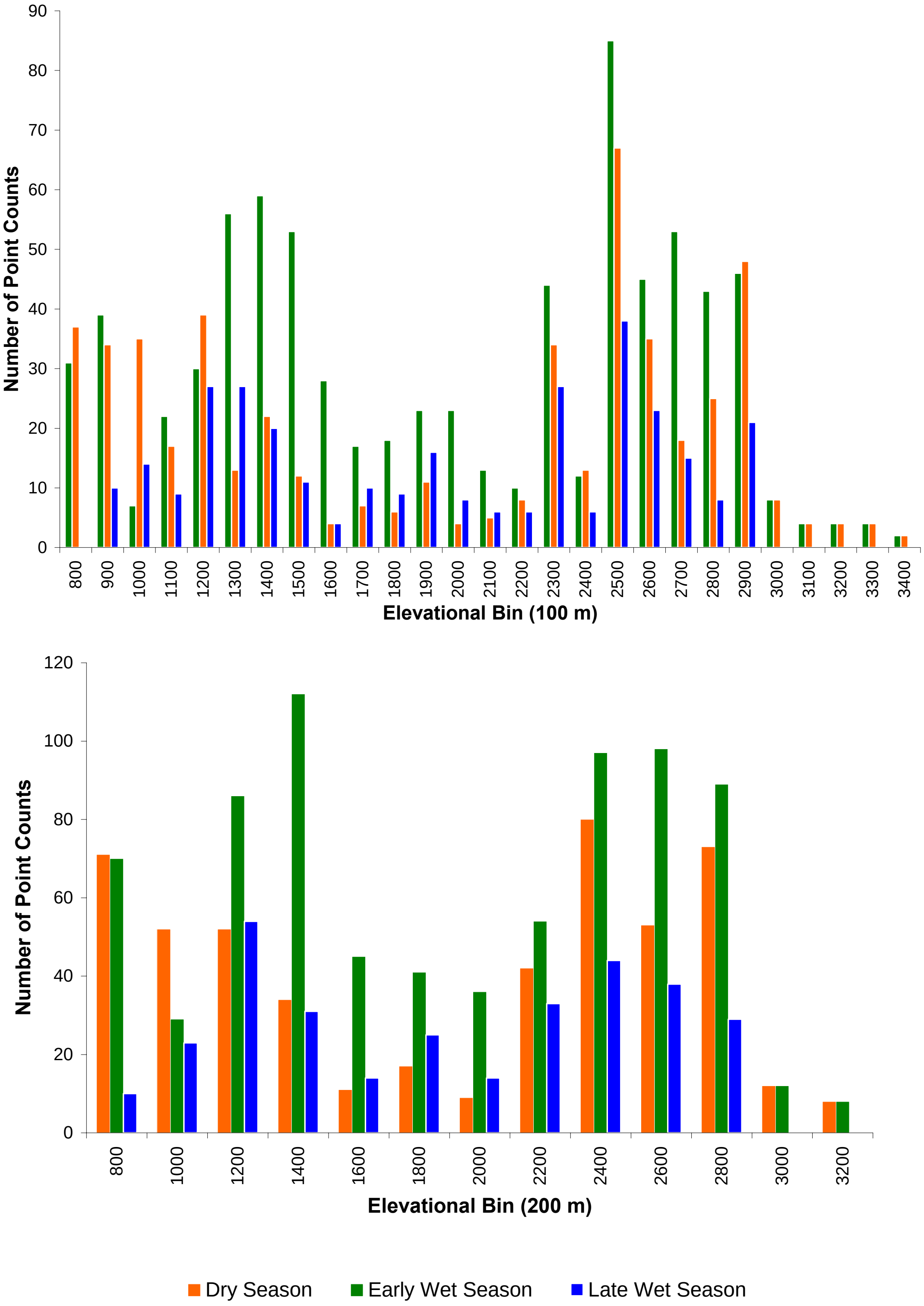

Figure 4. Histogram of the number of point counts conducted in each 100 m (a) and 200 m (b) bin along the elevational gradient.

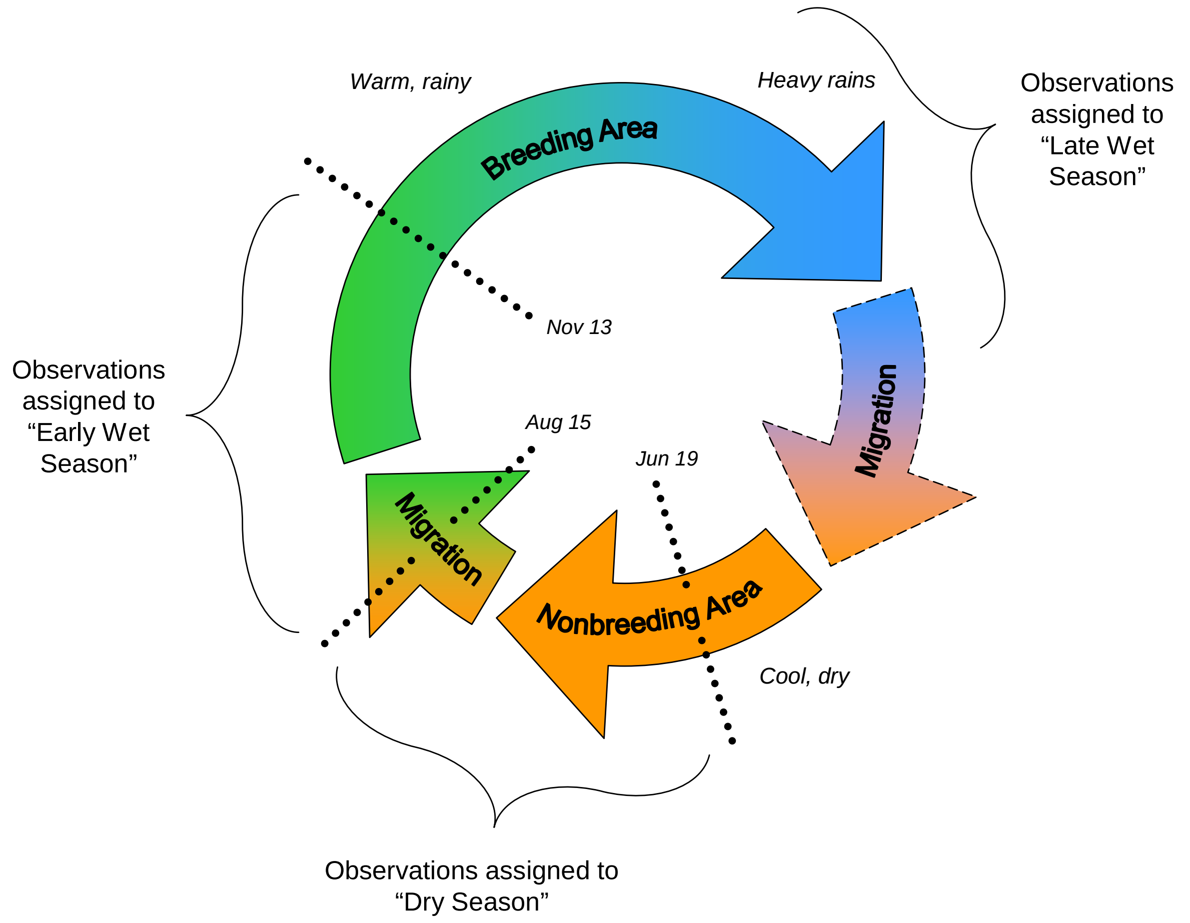

Figure 5. Schematic diagram illustrating the seasonal movements of an altitudinal migrant, and our method of assigning observations to breeding and nonbreeding seasons. The dashed migration period indicates that the timing is uncertain.

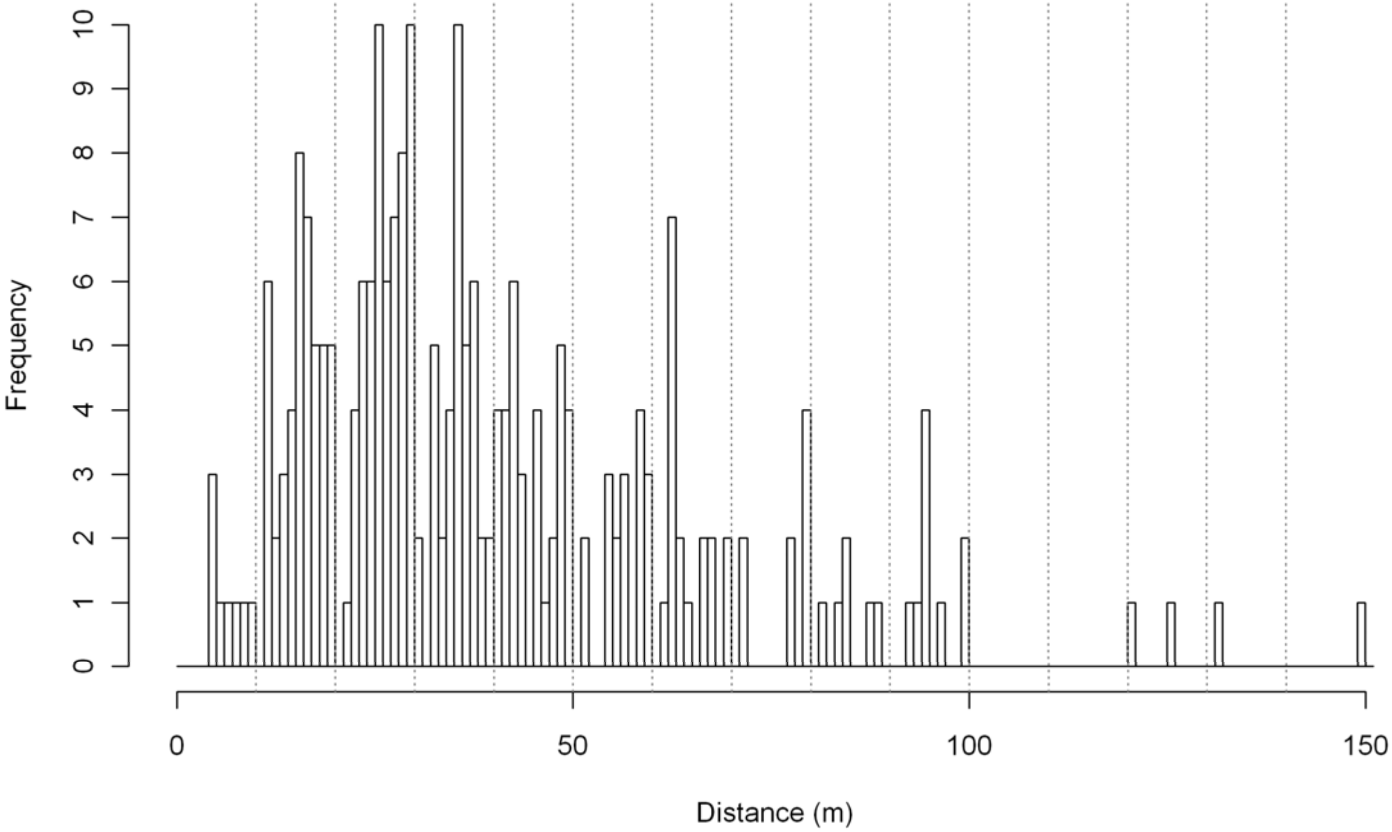

Figure 6. Histogram of detection distances for the Spectacled Redstart (*Myioborus miniatus*).

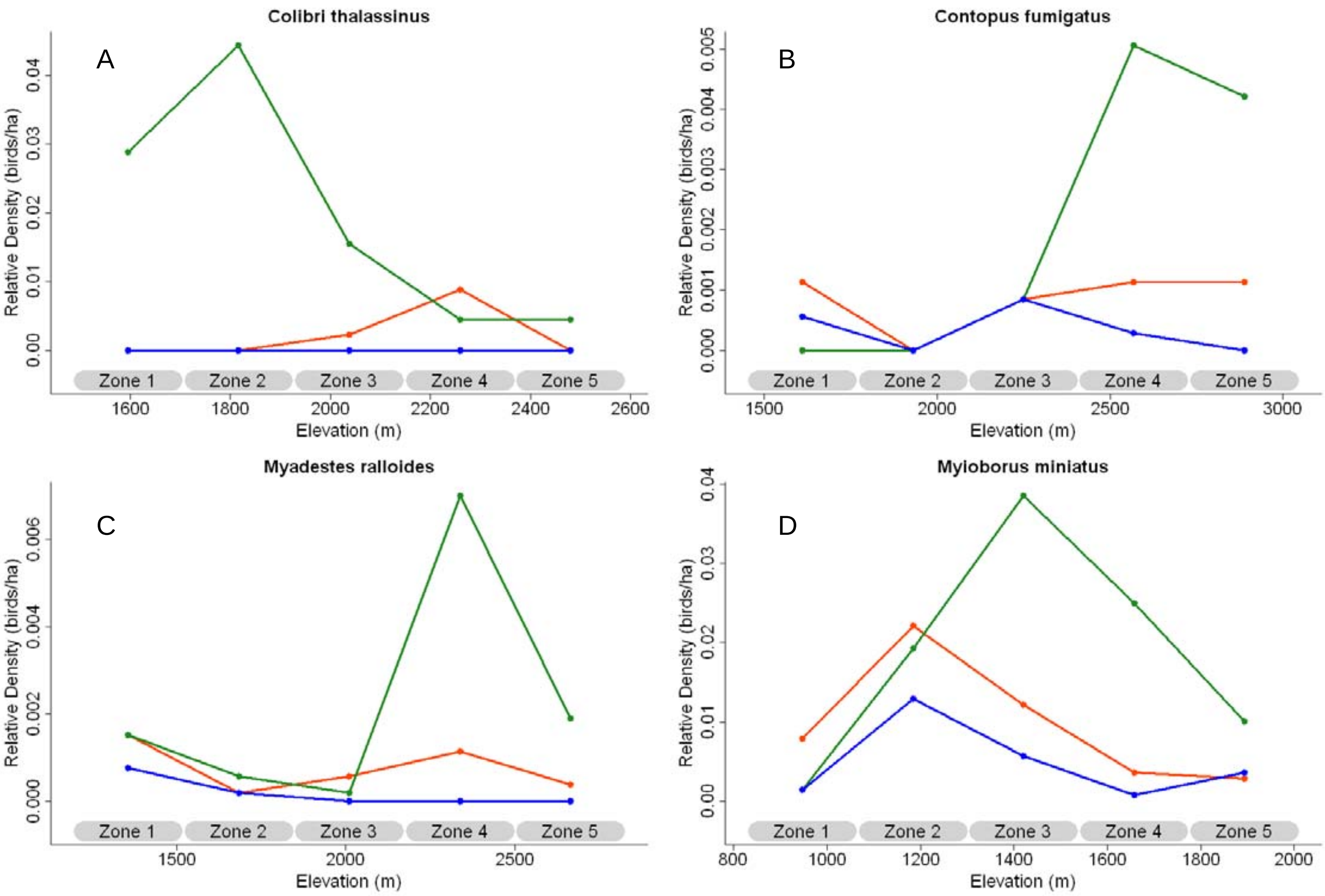

Figure 7. Distributions of four species exhibiting strong evidence of being elevational migrants: a) *Colibri thalassinus*, b) *Contopus fumigatus*, c) *Myadestes ralloides*, and d) *Myioborus miniatus* during the dry season (orange line), early wet season (green line), and late wet season (blue line).

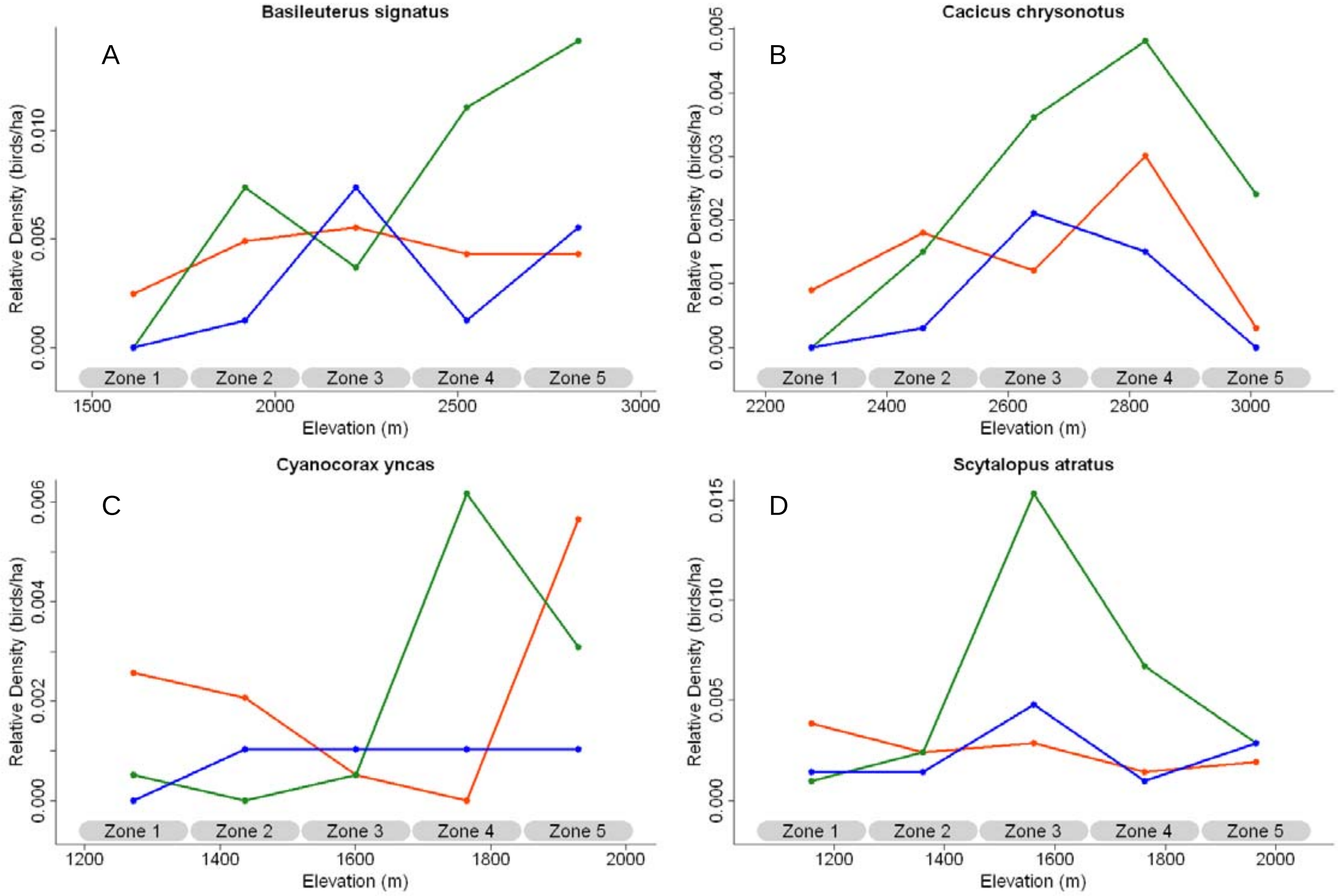

Figure 8. Distributions of four species exhibiting moderate evidence of being elevational migrants: a) *Basileuterus signatus*, b) *Cacicus chrysonotus*, c) *Cyanocorax yncas*, and d) *Scytalopus atratus* during the dry season (orange line), early wet season (green line), and late wet season (blue line).

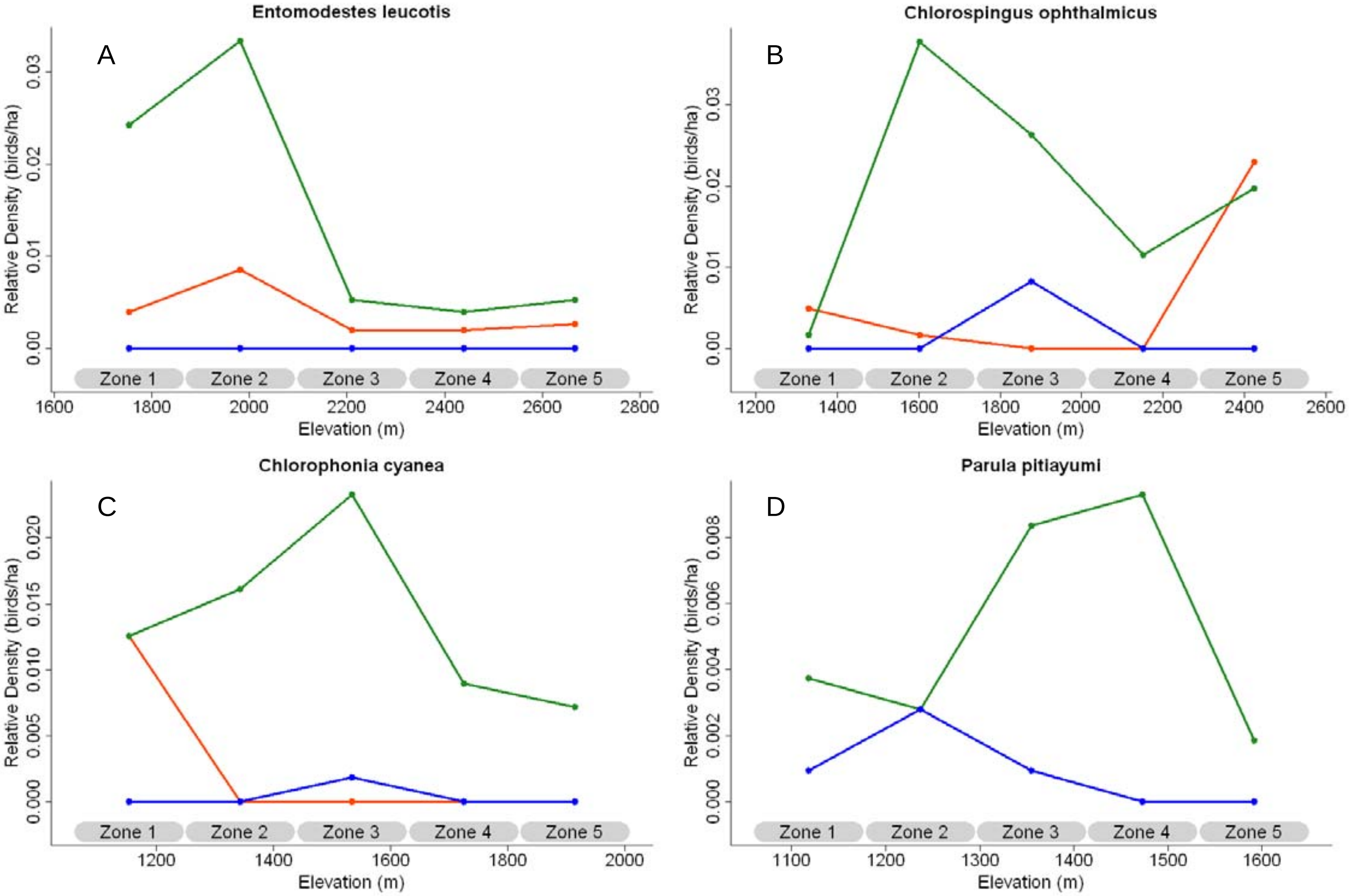

Figure 9. Distributions of one species exhibiting weak evidence of being an elevational migrants: a) *Entomodestes leucotis*, and three species for which the data were not conclusive enough to classify them as migratory or nonmigratory: b) *Chlorospingus ophthalmicus*, c) *Chlorophonia cyanea*, and d) *Parula pitiayumi* during the dry season (orange line), early wet season (green line), and late wet season (blue line).

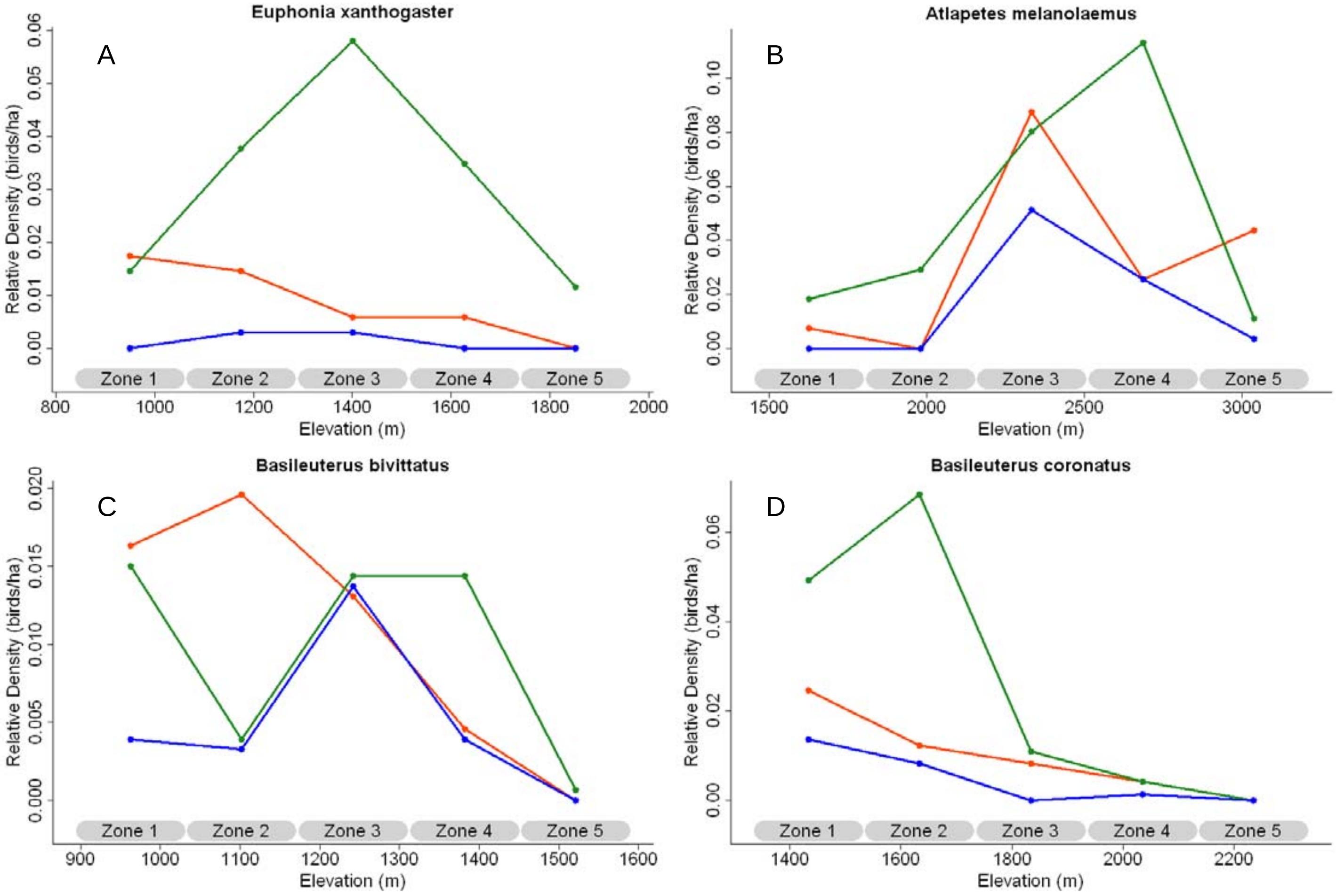

Figure 10. Distributions of one species exhibiting weak evidence of being a nonmigrant: a) *Euphonia xanthogaster*, and three example species showing strong evidence of a nonmigratory status: b) *Atlapetes melanolaemus*, c) *Basileuterus bivittatus*, and d) *Basileuterus coronatus* during the dry season (orange line), early wet season (green line), and late wet season (blue line).

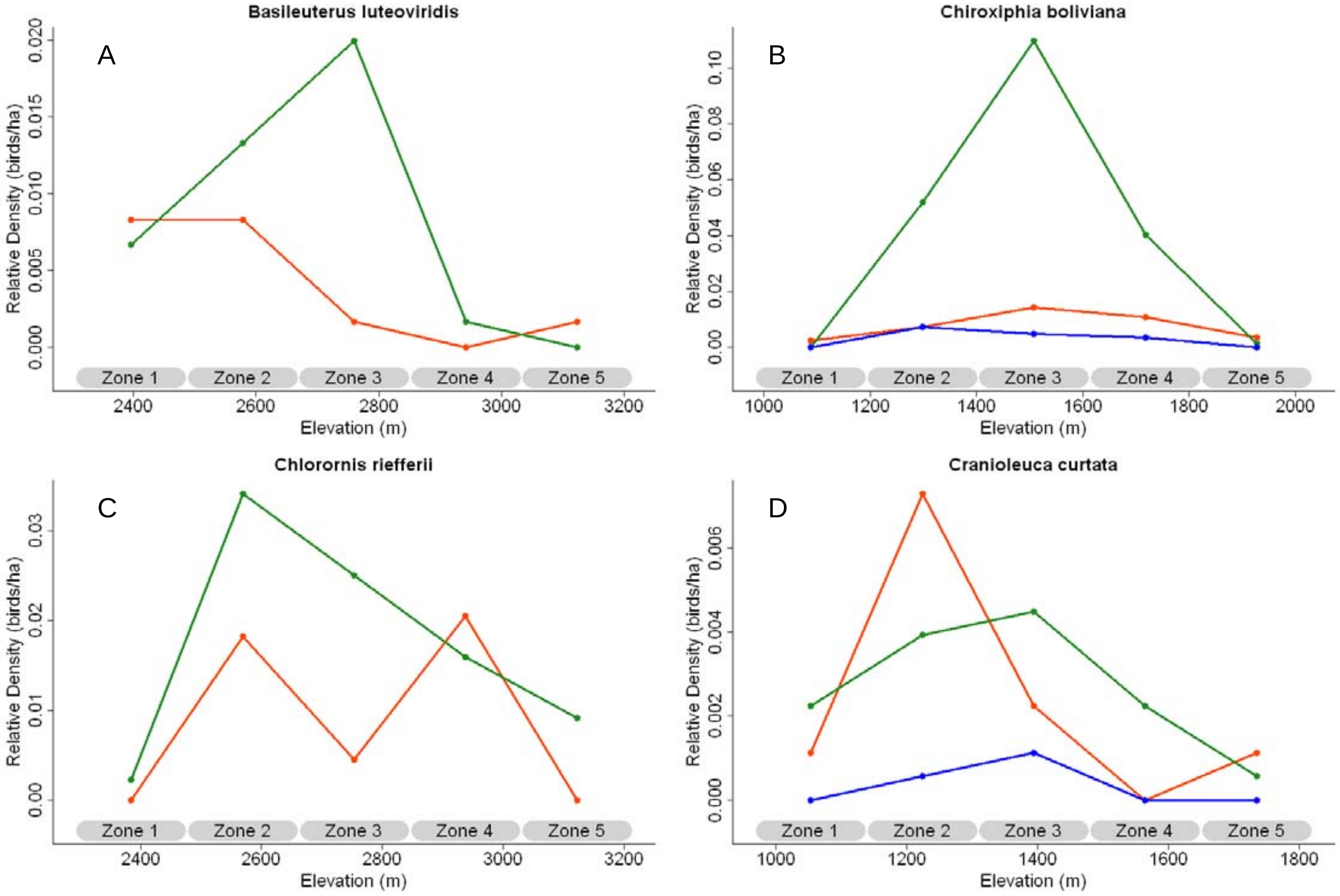

Figure 11. Distributions of four species exhibiting strong evidence of being elevational migrants: a) *Basileuterus luteoviridis*, b) *Chiroxiphia boliviana*, c) *Chlorornis riefferii*, and d) *Cranioleuca curtata* during the dry season (orange line), early wet season (green line), and late wet season (blue line).

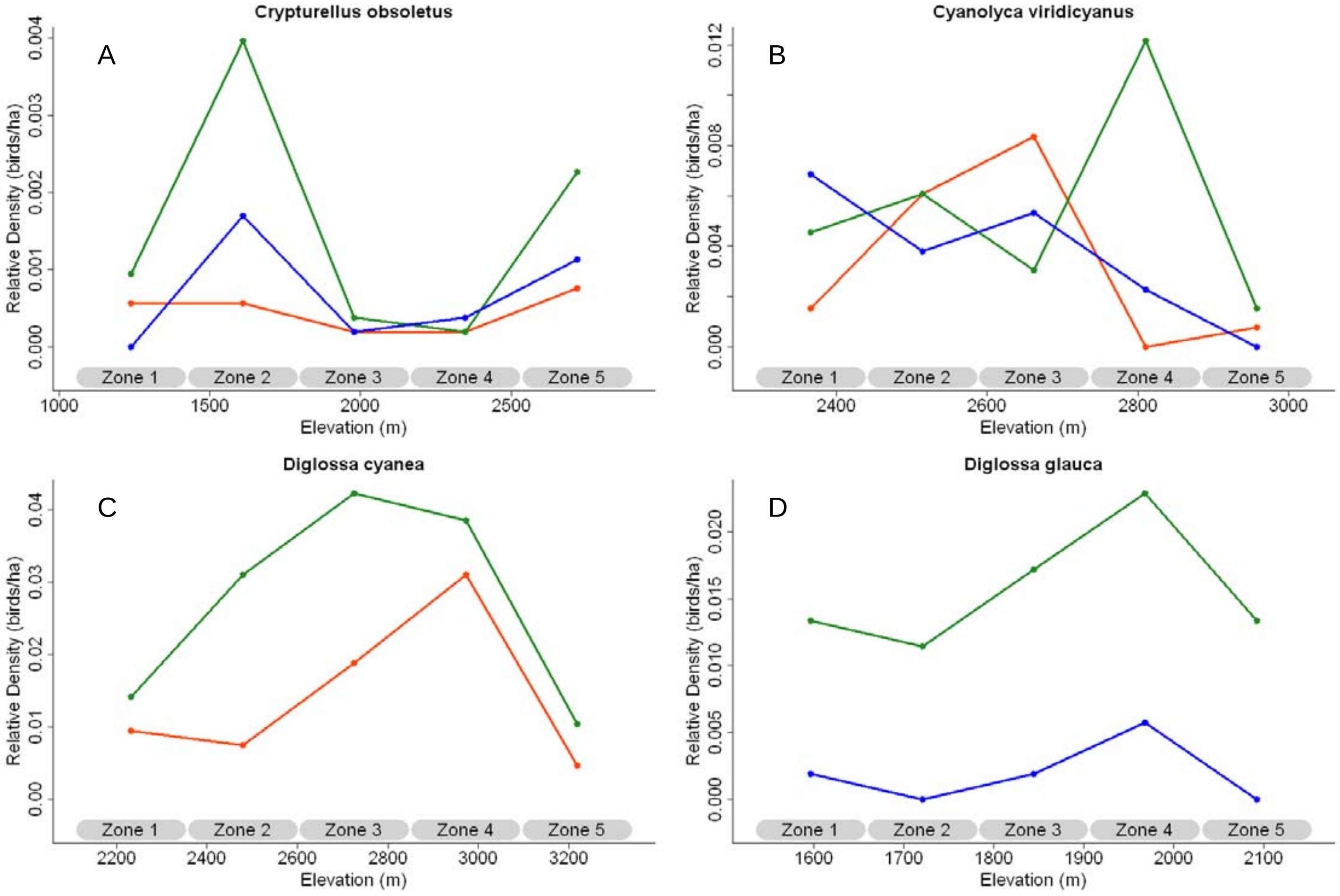

Figure 12. Distributions of four species exhibiting strong evidence of being elevational migrants: a) *Crypturellus obsoletus*, b) *Cyanolyca viridicyanus*, c) *Diglossa cyanea*, and d) *Diglossa glauca* during the dry season (orange line), early wet season (green line), and late wet season (blue line).

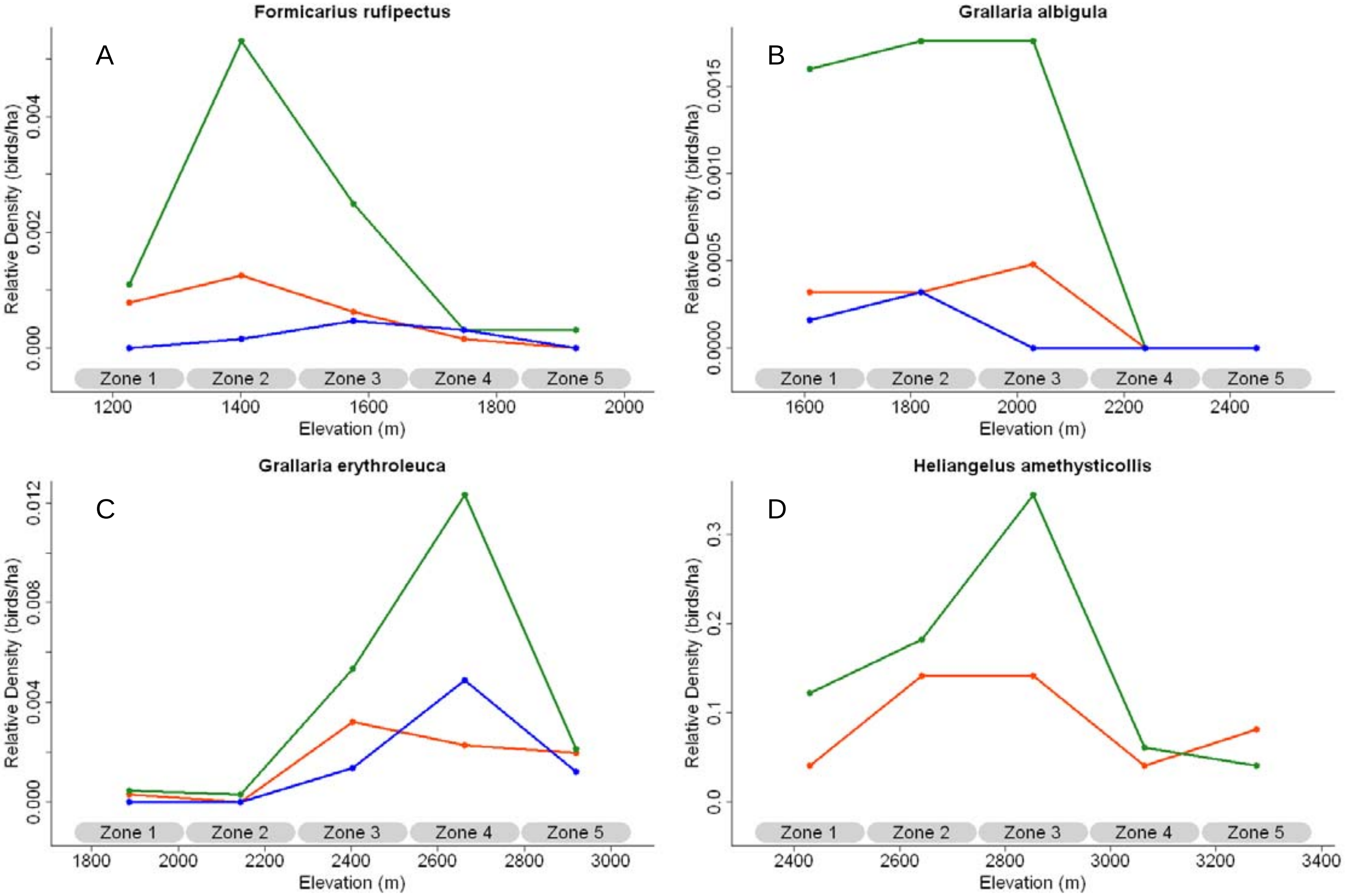

Figure 13. Distributions of four species exhibiting strong evidence of being elevational migrants: a) *Formicarius rufipectus*, b) *Grallaria albigula*, c) *Grallaria erythroleuca*, and d) *Heliangelus amethysticollis* during the dry season (orange line), early wet season (green line), and late wet season (blue line).

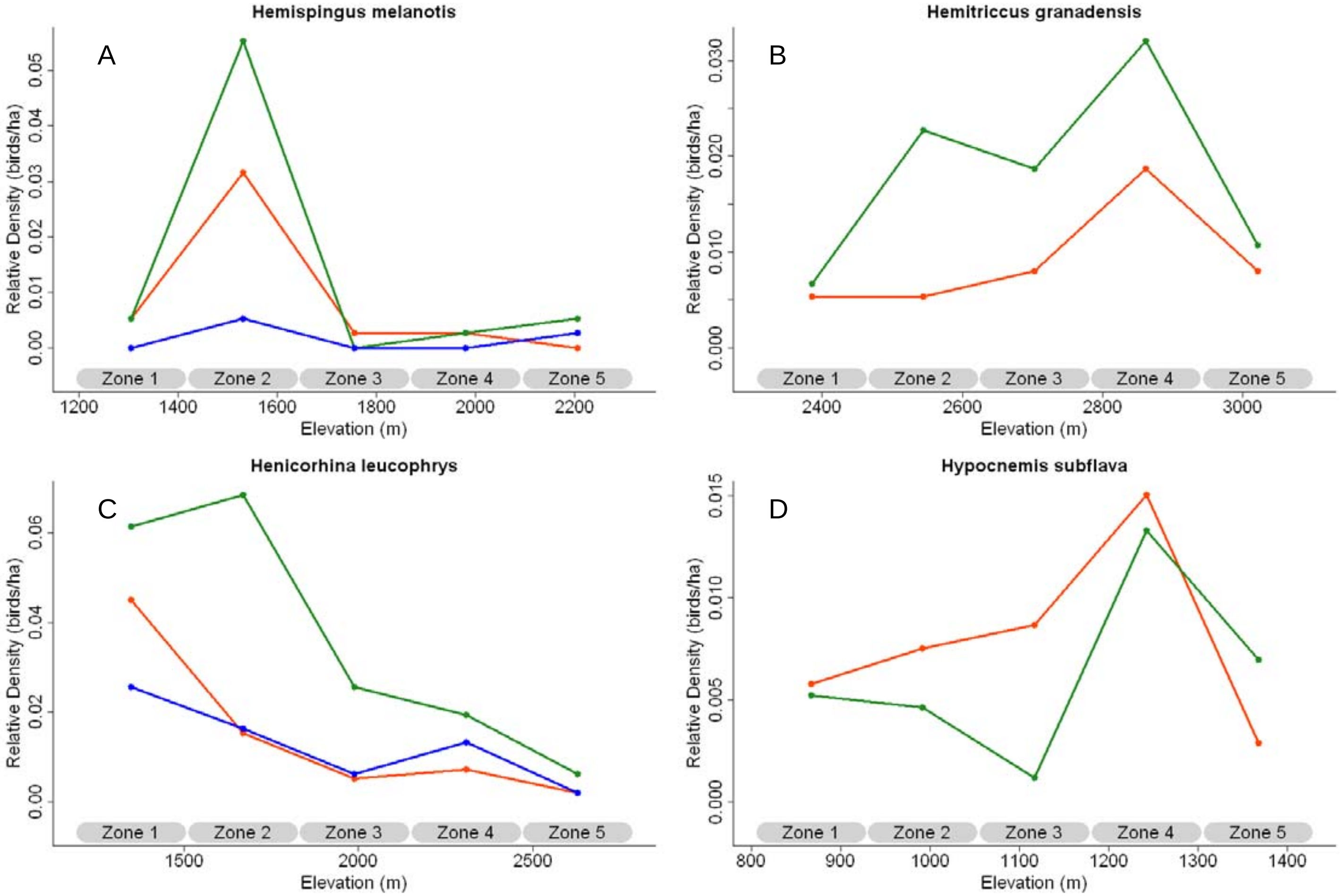

Figure 14. Distributions of four species exhibiting strong evidence of being elevational migrants: a) *Hemispingus melanotis*, b) *Hemitriccus granadensis*, c) *Henicorhina leucophrys*, and d) *Hypocnemis subflava* during the dry season (orange line), early wet season (green line), and late wet season (blue line).

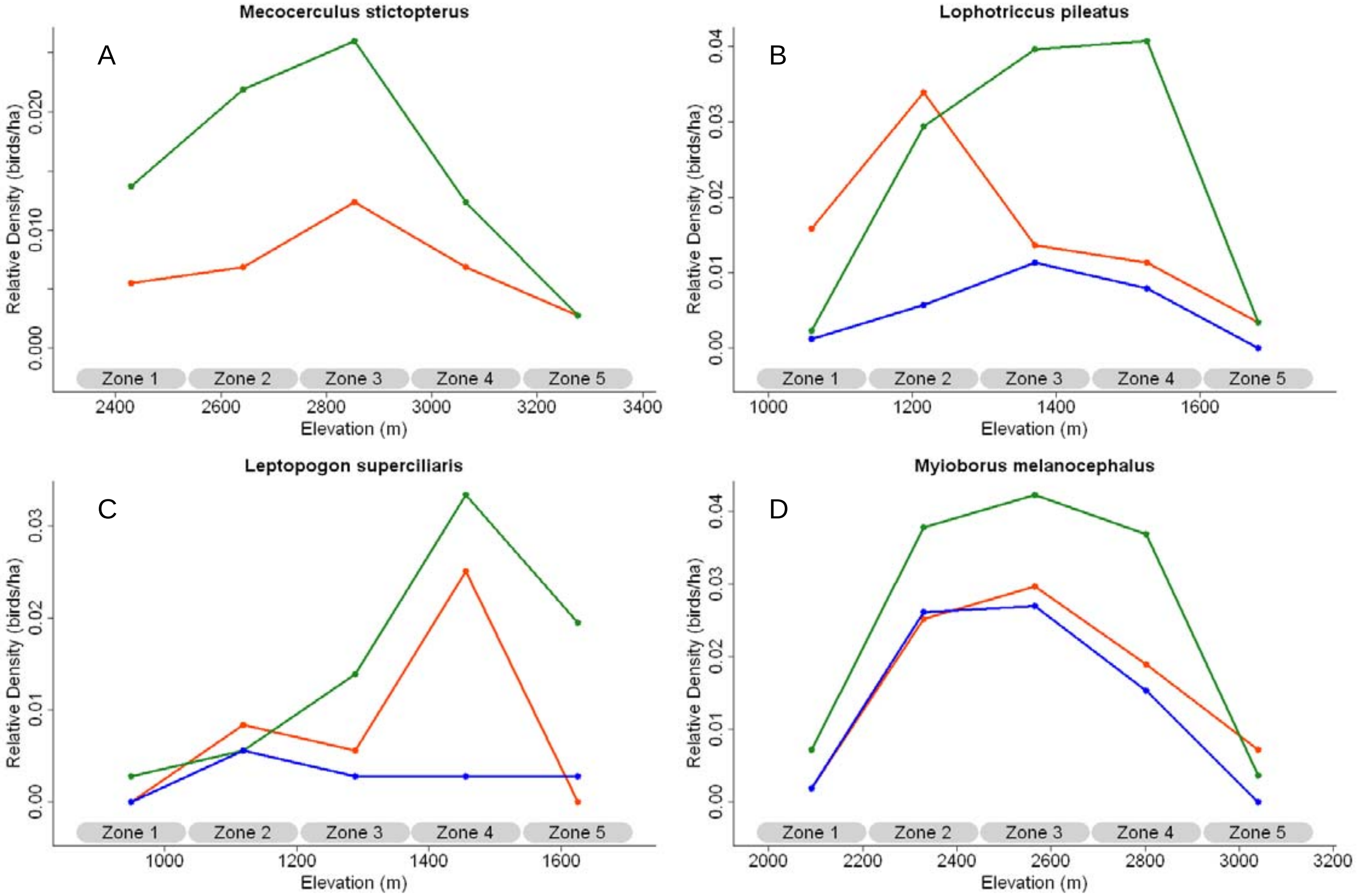

Figure 15. Distributions of four species exhibiting strong evidence of being elevational migrants: a) *Mecocerculus stictopterus*, b) *Lophotriccus pileatus*, c) *Leptopogon superciliaris*, and d) *Myioborus melanocephalus* during the dry season (orange line), early wet season (green line), and late wet season (blue line).

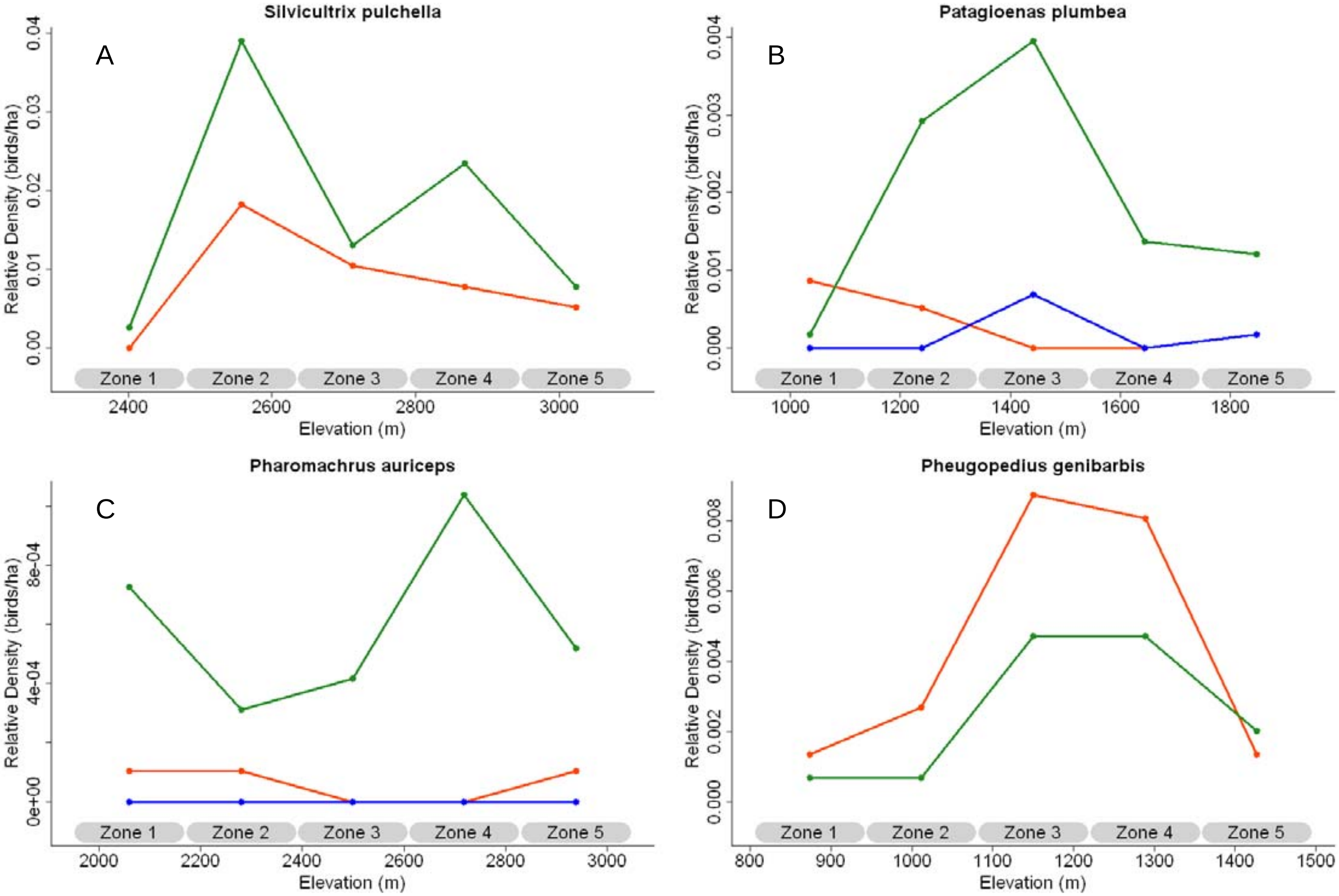

Figure 16. Distributions of four species exhibiting strong evidence of being elevational migrants: a) *Ochthoeca (Silvicultrix) pulchella*, b) *Patagioenas plumbea*, c) *Pharomachrus auriceps*, and d) *Pheugopedius genibarbis* during the dry season (orange line), early wet season (green line), and late wet season (blue line).

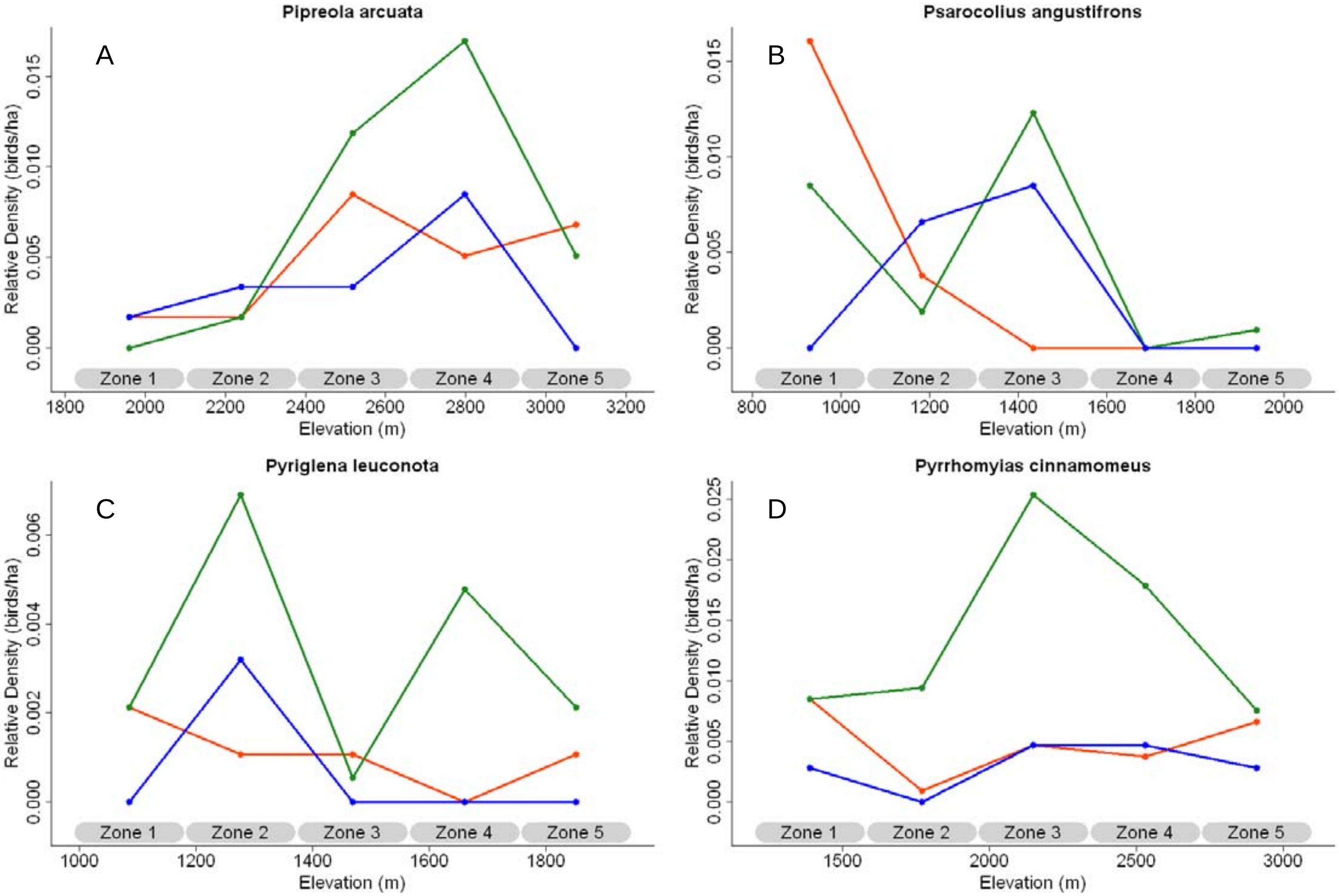

Figure 17. Distributions of four species exhibiting strong evidence of being elevational migrants: a) *Pipreola arcuata*, b) *Psarocolius angustifrons*, c) *Pyriglena leuconota*, and d) *Pyrrhomyias cinnamomeus* during the dry season (orange line), early wet season (green line), and late wet season (blue line).

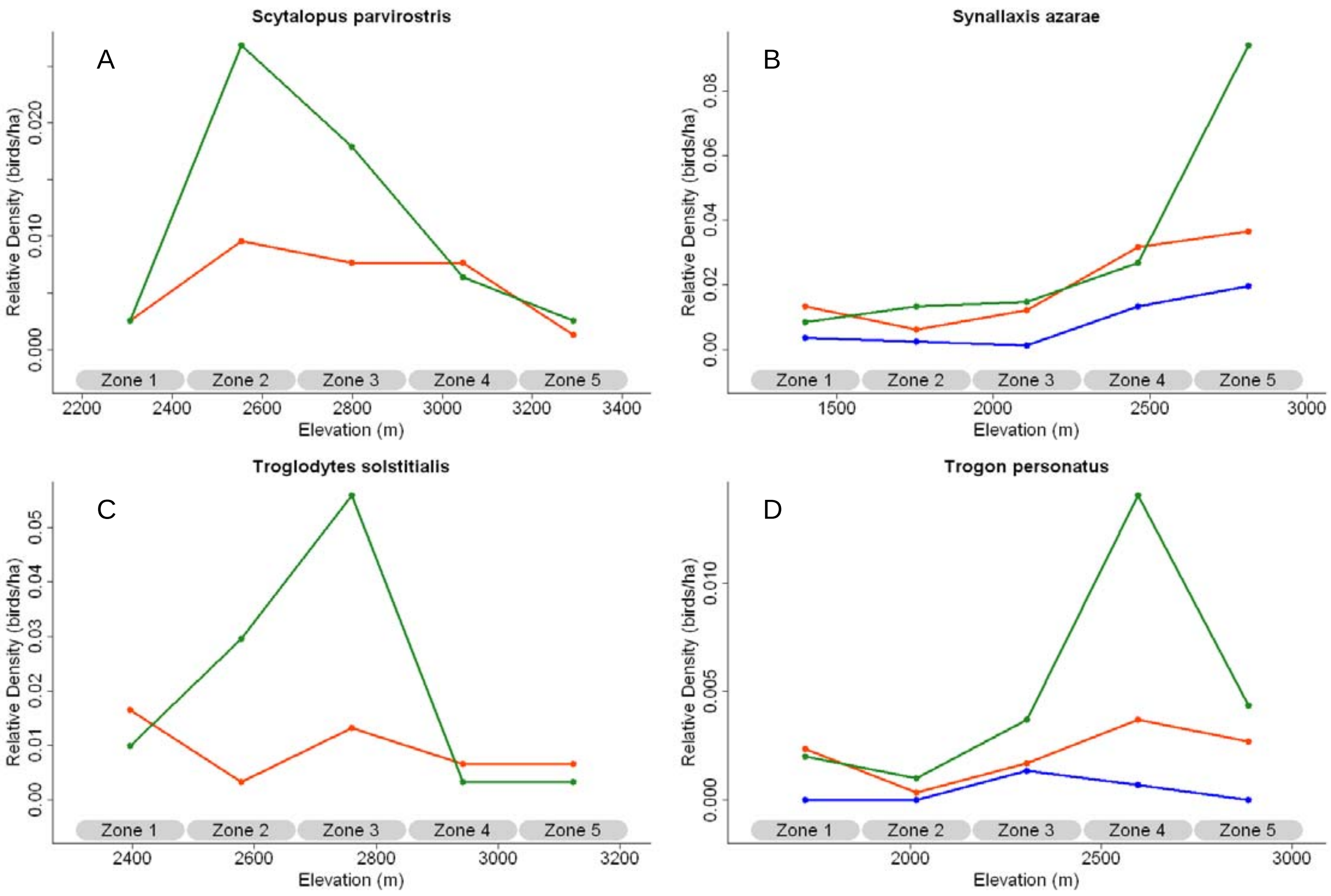

Figure 18. Distributions of four species exhibiting strong evidence of being elevational migrants: a) *Scytalopus parvirostris*, b) *Synallaxis azarae*, c) *Troglodytes solstitialis*, and d) *Trogon personatus* during the dry season (orange line), early wet season (green line), and late wet season (blue line).

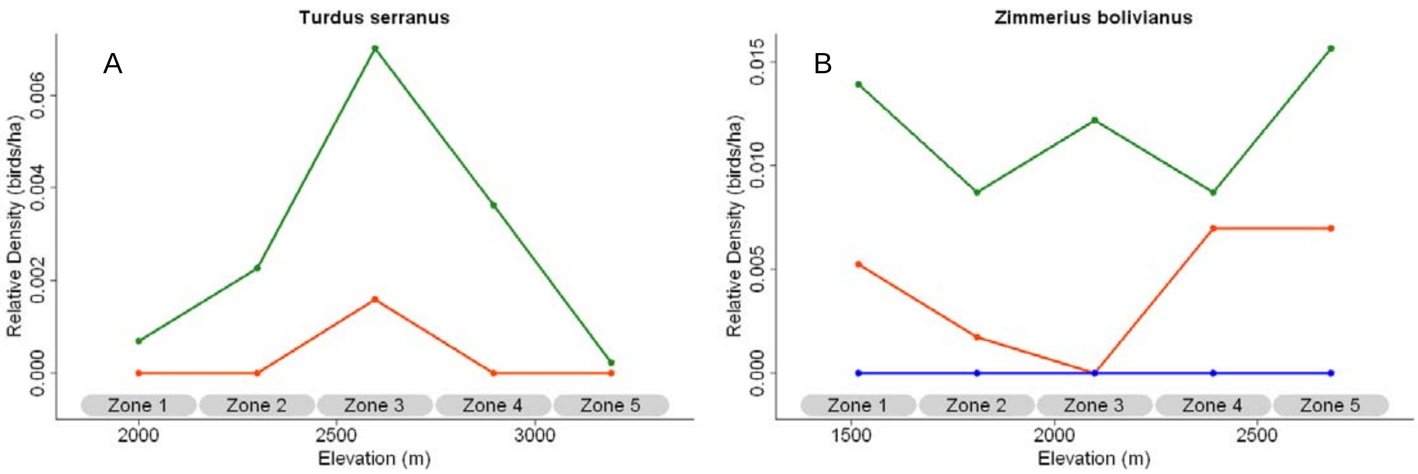

Figure 19. Distributions of two species exhibiting strong evidence of being elevational migrants: a) *Turdus serranus*, and b) *Zimmerius bolivianus* during the dry season (orange line), early wet season (green line), and late wet season (blue line).

CHAPTER 4

ELEVATIONAL MIGRATION OF BIRDS IN THE ANDES: PATTERNS, PROCESSES, AND A PLEA

Christopher L. Merkord, Jill E. Jankowski

ABSTRACT

The distribution of species and individuals along environmental gradients is a central question in biogeography, from both ecological and conservation perspectives. Our understanding of factors affecting species distributions at a global scale is hindered by a lack of information on many tropical species. Simply describing the distribution of many species along environmental gradients is complicated when individuals perform regular two-way migrations along the gradient, as is the case with elevationally migratory insects, birds, and mammals. While elevational migration is known to be widespread in birds, in the Neotropics the phenomenon has only been studied in detail along elevational gradients in Central America. Here we provide the first community-level assessment of avian elevational migration in South America. We used point counts, mist netting, and focal observations of a mid-elevation mixed species flock to document patterns of avian elevational migration along a 2.7 km elevational gradient in southeastern Peru. We scored each species as migratory or resident based on a combination of analyses from each dataset. Sufficient data were obtained to assign 234 species a residency status. Of these, 55 (24%) were classified as elevational migrants and 169 (76%) as residents. Included as elevational migrants are four species which may, in fact, undergo latitudinal or trans-Andean movements. We conducted a meta-analysis of studies describing the

migratory status of birds at other Neotropical sites and compared those results to our Peruvian study site. The percentage of latitudinal migrant species in Neotropical bird communities decreases from north to south while the percentage of elevational migrant species, the percentage of resident nonmigratory species, and the ratio of elevational migrants to residents all increase from north to south. These results fill in a large gap in our knowledge of the seasonal movements of birds in South America. Additional studies in the Atlantic Forest of Brazil, the Guiana Shield, and on both slopes of the Andes, including temperate latitudes, are urgently needed to determine how patterns of elevational migration vary within South America. Description of the broad patterns of migration and distribution along elevational gradients is a necessary precursor to asking targeted questions about the proximate and ultimate causes of these distributional patterns.

INTRODUCTION

Elevational gradients represent excellent natural laboratories to test a variety of biogeographic questions on the distribution of species and individuals along environmental gradients (Whittaker 1967), the relative role of abiotic and biotic interactions in shaping communities (Terborgh 1971, Jankowski et al. *In review*), and the role of mountains as barriers to dispersal and gene flow (Janzen 1967, Ghalambor et al. 2006, Graham et al. 2009). In diverse tropical ecosystems, however, basic information on the distribution and natural history of many species is often lacking. This is the case even in birds, one of the most well-studied taxa on the planet. Complete species inventories of tropical montane sites are not uncommon (Blake and Loiselle 2000, Herzog et al. 2005, Walker et al. 2006, Jankowski et al. 2009), but data on the elevational distributions of species are often imprecise, coarsely sampled, or lacking. Such data are of vital importance, not only for addressing basic ecological questions, but also for predicting how species may respond to climate change (Laurance et al. *In review*).

The study of species distributions along environmental gradients is made all the more complicated when species are migratory. Along elevational gradients, this movement is known as altitudinal or elevational migration, and has been documented in diverse taxa including butterflies, birds, bats, and ungulates (Loiselle and Blake 1991, Timm and LaVal 2000, Haber and Stevenson 2004, Igota et al. 2004). Elevational migration in birds is widespread, occurring on all continents except Antarctica (Thiollay 1980, Hilty 1997, Burgess and Mlingwa 2000, Tellería et al. 2001, Dingle 2004). However, most references to elevational migration in the literature are either anecdotal or pertain to one or a few species. Community-wide assessments of elevational migration are restricted primarily to the Neotropics, at sites in Mexico (Ornelas and Arizmendi 1995, Gómez de Silva G. et al. 1999, Arvin 2001), Costa Rica (Loiselle and Blake 1991), and Colombia (Hilty 1997). The only country-wide assessment of elevational migration has been provided for Costa Rica (Stiles 1985a). Together, these studies paint a broad picture of elevational migration in the northern Neotropics, confirming that such seasonal movements are widespread among taxa and across geographic regions. The percentage of species in any given montane community that show seasonal elevational movements ranges from 5 to 35 % in Mexico alone, depending on latitude and the length of the elevational gradient sampled.

Very little is known about elevational migration, except that it is widespread (Faaborg et al. 2010b). The direction and timing of elevational movements remain unknown for most taxa, with some notable exceptions. Detailed work has been conducted on several species of Costa Rican hummingbirds (Stiles 1985b) and manakins (Rosselli 1994, Blake and Loiselle 2002, Boyle 2008b, Boyle 2010, Boyle et al. 2010), and radio-tracking studies of the Resplendent Quetzal (*Pharomachrus mocinno*) and Three-wattled Bellbird (*Procnias tricarunculatus*) demonstrate that both exhibit complicated multidirectional movements in Costa Rica (Powell and Bjork 1995, 2004). It is likely that many other species of “elevational” migrants also exhibit complex seasonal movements at local or regional scales within the Neotropics.

The cues and causes of elevational migration are also poorly known. Studies have shown conflicting evidence that seasonal tracking of food resources can explain both the uphill and downhill movements of elevational migrations (Boyle 2010). Predation and competition may play some role in driving migration (Boyle 2006, 2008a), and the extensive use of mixed-species flocks by elevational migrants in Peru suggests that mutualistic interactions may also facilitate migration (Merkord 2010 Chapter 2). Recent work on White-ruffed Manakins (*Corapipo altera*) in Costa Rica has shed considerable light on the proximate and ultimate causes of migration in the species and supports a novel hypothesis that severe storms at higher elevations reduce foraging opportunities sufficiently to reward downslope movement in some birds (Boyle et al. 2010). While this ‘limited foraging opportunities’ hypothesis may be supported for

White-ruffed Manakins, different physiological and life history tradeoffs may be important for other species. Detailed studies are much needed to gain a broad understanding of the variety of causes of elevational migration, though such studies cannot be accomplished without first documenting underlying movement patterns of individuals and species in bird communities, groundwork in this case laid by numerous studies in Costa Rica (Stiles 1988, Loiselle and Blake 1991, Blake and Loiselle 2000).

Detailed studies on elevational migration beyond Central America would allow us to synthesize general migratory patterns and processes across a much broader geographic spectrum. The lone South American study, by Hilty (1997) in the western cordillera of Colombia, was conducted at only one site (950–1050 m a.s.l.). Hilty found evidence suggesting that many species were seasonal visitors to his study site and inferred that about 23% of species are elevational or local migrants, while 68% are sedentary residents. While a first for the Andes, Hilty's findings beg several questions. Did the seasonal appearance and disappearance of individuals at his study site represent variation in detectability, movements between habitats, or actual elevational migration? What is the direction and distance traveled by migrants? Which species are complete migrants (at the population level), which are partial migrants, and among partial migrants, what percentage of individuals actually migrate? And finally, how does the extent of elevational migration in Andean bird communities vary with latitude? The percentage of resident species is higher in Colombia compared to Central American sites. Does this trend continue southward until almost all species are sedentary? Terborgh's (1971, 1977) pioneering work in the Cordillera Vilcabamba in southeastern Peru described the elevational distributions of hundreds of species, but he made no mention of seasonal movements in the bird community. One of the most complete avifaunal lists of any Neotropical region documents the elevational distributions of all bird species known from Manu National Park, Peru, on the eastern slope of the Andes (Walker et al. 2006). Of the 1006 species listed, 3% are vagrants to the area, 6% are latitudinal migrants, and the rest are classified as "residents." While the term "resident" may be true in that they are present year-round within Manu, this classification masks any variation in migratory tendency among species.

We documented the extent of elevational migration in a bird community in the central Andes along a 2.7 km elevational gradient in Manu National Park, southeastern Peru. We use a combination of approaches to assess as many species as possible, including point counts, mist netting, and focal observations of a mid-elevation mixed-species flocks. We use modern distance-sampling techniques to estimate bird densities when possible. Rather than simply labeling each species as migratory or nonmigratory, as is done in most studies, we provide a cumulative estimate across datasets of the weight of evidence for a species being migratory or resident. This study fills in a gap in our understanding of the dynamics of avian bird communities in the New World by providing the first quantitative community-level assessment of elevational migration in the Andes and in South America south of the equator.

METHODS

Study Site

We studied an elevational gradient on the eastern slope of the Andes in Manu National Park, Cusco Department, Peru, from 750–3450 m a.s.l. Habitats ranged from humid lowland rainforest to humid montane forest to humid elfin forest (MacQuarrie 1998). The climate was seasonal, with a short but pronounced dry season from May–Aug and a cloud base that ranges from 1400–2000 m a.s.l. depending on season and time of day (C. L. Merkord, *pers. obs.*). Over 1000 species of birds have been documented from Manu National Park, including lowland habitats. Unlike most Neotropical sites, the elevational distributions of many species in Manu are known (Walker et al. 2006), although their seasonal movements are not. Breeding in most species coincides with the onset of the rains in Aug–Sep, and nests are common from Sep–Dec (Merkord 2010 Chapters 1, 3).

Data Collection

We collected data on the seasonal distribution of bird species using mist netting, point counts, detailed observations of a color-banded mixed-species flock at 1400 m a.s.l., casual observations of mixed-species flocks along the gradient, and incidental observations. Mist netting and point counts are each subject to biases in detecting species, and great care should be taken in interpreting relative abundance estimates based on either method, particularly for diverse bird communities in structurally complex forests (Remsen and Good 1996). Individual-based methods of tracking birds such as radio-telemetry or band recaptures are more reliable but are expensive and result in small sample sizes or cannot be employed on many species simultaneously. By using a combination of methods, we hope both to survey the maximum number of species possible and to control for misleading evidence of migratory status imposed by the limitations of one method or another.

POINT COUNTS

Point counts were conducted at 249 points on 23 transects from 805–3414 m a.s.l. Most points were visited 2-4 times per season, but due to weather and logistical constraints, many were not, particularly during the late wet season when rain was abundant. Observers recorded the distance to individuals using the snapshot method (Buckland 2006) for use in estimating detection probabilities and relative densities. Additional details about the location of survey points and field methodologies used can be found in Jankowski et al. (*In review*) and Merkord (2010 Chapter 3).

MIST NETTING

Mist netting was conducted at 47 netting sites from 795–3387 m a.s.l. At each site, we used 6–22 nets (6–12 m long, 30–36 mm mesh) to capture birds for approx. 2.5 days, depending on weather. We placed a numbered aluminum band on each individual except hummingbirds and very large species. Additional details of netting protocols are given in Merkord (2010 Chapter 1). Six sites (950–2023 m a.s.l.) were sampled during both the dry and early wet seasons, allowing for direct comparisons of relative abundance between seasons at those sites. Three sites (2023–2538 m a.s.l.) were sampled during both the early wet and late wet seasons, and another three sites (1397–2023 m a.s.l.) were sampled during both the late wet and dry seasons.

FLOCK OBSERVATIONS

Detailed observations of a mixed species flock at 1400 m a.s.l. were made, primarily by CLM, during all three seasons. These observations included standardized methods for estimating the number of individuals in the flock, extensive ground and canopy mist netting within the flock territory (823 net hours), color banding of hundreds of individuals, and approx. 700 observer hrs of observations of the behavior and movements of flock members. A complete description of the methods employed and the results of these efforts are provided in Merkord (2010 Chapter 2). In addition, we kept records whenever possible of the composition of mixed species flocks encountered anywhere along the elevational gradient. We recorded the species present, number of individuals, latitude, longitude, and elevation. These records enhance our understanding of the distribution of many species that are not readily sampled using mist nets or point counts.

INCIDENTAL OBSERVATIONS

When possible, we recorded incidental observations of birds outside of the standard sampling protocols described above. This category included birds observed while walking to or between point counts or while mist netting, as well as those observed while working or traveling in the study area. Like the flock observations, these incidental observations often provided useful information on the distribution of otherwise under-sampled species.

Data Analysis

The strength of inference about migratory status can vary greatly depending on the quality and quantity of data, which in turn vary depending on observer effort and limitations of each method. In addition to categorizing each species as migratory, sedentary, or unknown based on the data collected, we score the strength of available evidence in an attempt to transparently depict our current understanding of each species' migratory status and to highlight the many unresolved questions. We scored each species separately for each of four analyses based on point counts, mist netting, flock observations, and incidental observations. Our scoring system ranged from 3 to -3, with larger positive values indicating greater support for elevational migration, and larger negative values indicating greater support for lack of migration (Table 1). We then averaged scores across analyses for each species to produce a final species assessment of residency status. Assignment of each species as migratory or nonmigratory is based on this average score, with positive values indicating probable migrants and negative values indicating probable nonmigrants. Zeros reflect uncertainty, or contradictory evidence, and are applied to species for which we cannot assign a migratory status.

Ideally, we would have collected abundance information at all points along the elevational gradient every day of the year over multiple years. Lacking the means to do this, we combined data across years and grouped observations into one of three discreet periods: dry season (Jun-15 Aug), early wet season (15 Aug-Nov), and late wet season (Feb–Apr; Merkord 2010 Chapter 3). Our general approach with mist netting and point count data was to estimate the relative abundance of each species along the elevational gradient during each of these three seasons and then to make pairwise comparisons of those three distributions. Considering that it is possible for a species to show an upslope shift during one pairwise seasonal comparison, no distributional shift in distribution in the next pairwise comparison, and a downslope shift in the final comparison, it follows that inferring at least one distributional shift can be done with fewer comparisons than inferring a complete lack of distributional shifts. We consider this in the scoring of seasonal comparisons of distributional data, as outlined below. For community-level analyses, we assigned each species to a foraging guild using published sources and personal data (Merkord 2010 Chapter 1).

POINT COUNTS

The analysis of count-based data to identify elevational migration in birds has not been addressed sufficiently in the published literature, so we use here the methods outlined in Merkord (2010 Chapter 3). The probability of detecting individuals can vary by observer, season, time of day, etc., potentially biasing density estimates. We used the multiple covariate distance sampling engine in program Distance (Thomas et al. 2010) to generate relative abundance estimates after correcting for variation in detection probability associated with time of day, season, precipitation, observer, and year as a way to account for experience, i.e. a learning effect. In this analysis, we included only observations for which a distance could be estimated at a 'snapshot' moment (Buckland 2006) exactly 3 min after the start of each point count. We divided the observed elevational range of each species into five equal elevation zones, and analyzed data for those species for which at least 8 point counts were conducted in each elevational zone in each season. At this point our methods diverged from Merkord (2010 Chapter 3). If dividing the range of the species into 5 elevational zones resulted in zones in which fewer than 8 counts were conducted, we attempted to divide the range into four zones, then three, then two. Species with fewer than 8 counts in each season in each of two elevational zones were excluded from this analysis. For each species in the analysis, we modeled a global detection probability and estimated density at the point level (post-stratifying by season), and at the zone level (post-stratifying by season and zone).

Using the point- and zone-level relative density estimates, we attempted to make three pairwise comparisons between seasons. For each seasonal comparison, we used a three-step approach to classify a species as an elevational migrant or nonmigrant (see Merkord 2010 Chapter 3 for details and equations). Briefly, we first compared the weighted mean elevation of occurrence in each season. Then, we used a two-way analysis of variance to model how density varied with elevation, season, and an elevation-season interaction term. A significant elevation-season interaction and a large shift ($s > 5\%$) in mean elevation was taken as evidence of elevation migration, while a nonsignificant interaction term or a small shift ($s \leq 5\%$) in mean elevation was taken as evidence of a lack of migration. Third, we scored the evidence for each species using criteria explained in Merkord (2010 Chapter 3 Table 1). If only one seasonal comparison could be made using a given number of elevational zones (due to constraints imposed by insufficient effort), then the other two seasonal comparisons were attempted using fewer elevational zones. Thus for each species we scored up to three pairwise comparisons of seasonal density distributions. A combined score was derived for each species by comparing these seasonal comparison scores. If at least one score was positive, indicating migratory status, then we chose the largest positive value as the combined score. If no positive score was obtained then we chose the most negative score, indicating resident status. If no positive or negative score was obtained, the combined score was set to 0, indicating uncertainty about the species' migratory status.

Recognizing that many species would not meet the effort or sample size requirements imposed by distance-based estimation of relative densities, we also opted to analyze each species using relative abundance estimates based on the mean number of birds seen at each point. All observations were included in this analysis, regardless of whether a snapshot distance could be estimated. Relative abundance at the point level was estimated by dividing the total number of individuals detected at each point by the number of visits to the point. Density estimates at the elevational zone level were calculated by averaging the point-level density estimates of all points within each zone. The minimum and maximum elevation for each species, and thus the zone widths, varied somewhat between this analysis and the distance-based analysis because many more observations were included in this analysis. We only included in this analysis those species for which we had surveyed at least 8 points within each elevational zone within each season, and for which we had at least 10 observations in each season. Thus, like in the distance-based analysis, species might be limited to only one or two seasonal comparisons, or excluded all together. After estimating density at the point and zone level, we analyzed and scored the data using the same weighted mean elevation shift and ANOVA analyses outlined above for the distance-based density estimates.

MIST NETTING

We calculated the relative abundance of each species at each site as the number of birds captured per net hour. Each of the three seasonal comparisons was scored separately for each species present at two or more sites during each of the two seasons being compared. We established a scoring procedure by which to assign each seasonal comparison a score from 3 to -3 using criteria explained in Table 2. If any seasonal comparison yielded a positive score (migratory), we assigned the species a final score equal to the largest positive score among the seasonal comparisons, unless there was one positive score and two negative scores, in which case we assigned the species a score of zero (equivocal). If there were only negative scores for a species, we assigned the species a final score equal to the largest negative score among the seasonal comparisons. For negative scores (nonmigratory), we applied a penalty by adding 1 to the score if only one seasonal comparison could be made, to account for the possibility that a lack of migration between two seasons is not sufficient to infer a lack of migration throughout the year. If a species scored only zeros, it was assigned a final score of zero. The net result of our scoring system is a fairly conservative approach whereby most species are likely to be scored as equivocal unless the evidence for or against a migratory status is compelling.

FLOCK OBSERVATIONS

The residency status of species participating in the mixed-species flock described by Merkord (2010 Chapter 2) was converted to the 3 to -3 scoring system in the following manner. Species for which repeated standardized sampling of flock membership revealed pronounced seasonal changes (category 1) received a score of 3. Species that occurred only occasionally in the flock, were rarely observed within the elevational range of the flock (approx. 1300–1500 m a.s.l.), and never showed signs of breeding anywhere within that elevational range (category 2) received a score of 1.5. Species for which band recaptures suggested seasonal movements (category 3) also received a score of 1.5. A nonmigratory score of -3 was given only to species for which band recaptures and resightings suggested that individuals remained within the flock territory year-round. Species lacking such detailed recapture data, but that were nonetheless considered year-round residents, were given a score of -1.5. Species of occasional or irregular status, and suspected year-round residents that were observed fewer than 5 times, received a score of 0.

INCIDENTAL OBSERVATIONS

To gain a different perspective on the distribution of each species, we combined all records of occurrence—point counts, mist net captures, and all other observations including flock observations and incidental sightings—and plotted presence and absence on an elevation x date scatterplot. A benefit to this approach is that "date" is treated as a continuous variable rather than pooling all observations into three meaningful but still somewhat artificial seasons. We visually inspected these plots and scored each species using integer scores from 3 to -3. The downsides to this approach are that our incidental observations are useful for determining species presence, but less useful for determining absence, and that our scoring system was necessarily more subjective. We did not attempt to score species with fewer than 10 observations, and in general gave lower scores (closer to zero) to species with smaller samples sizes.

Meta-analysis

We combed through the literature to find lists of local or regional avifaunas within the Neotropics that included information on the migratory status of most species. We excluded all species classified as vagrant to the area, and included only landbird species, defined here as members of the orders Tinamiformes, Galliformes, Cathartiformes, Accipitriformes, Falconiformes, Columbiformes, Psittaciformes, Cuculiformes, Strigiformes, Caprimulgiformes, Apodiformes, Trogoniformes, Coraciiformes, Piciformes, and Passeriformes. Each species was assigned to one or more of the following categories: latitudinal migrants, elevational migrants, and residents (nonmigrants). Species classified as local and short-distance migrants were classified as elevational migrants. Species classified as members of two migratory status categories were divided as half a species for each category. We then counted the number and calculated the percentage of species in each category.

RESULTS

Field Work

During the course of our field work, we observed 465 species along the elevational gradient from 750 to 3450 m a.s.l. (Appendix 2). All but three species were known to occur in Manu National Park, and of the remaining species, all but six were among the 733 known to occur within the specified elevational range within Manu National Park (Walker et al. 2006). Two species are South American austral latitudinal migrants, and four are North American boreal latitudinal migrants; the remaining 456 species are categorized as "resident" by Walker et al. (2006), as presumably would be the 3 species not listed therein. We detected 386 species on point counts, captured 278 species in mist nets, and detected 121 species while studying the mixed-species flock (Merkord 2010 Chapter 2). Sixty-nine species were detected only on point counts, 28 only by mist netting, 3 only during flock observations, and 33 only as incidental observations. Of the "resident" species (i.e. those not austral or boreal migrants), we were able to assign a non-zero score, signifying evidence of a migratory or nonmigratory status, to 234 species (51 and 78 using distance-based and relative abundance-based analysis of point count data, respectively, 31 using mist net data, 86 using flock observations, and 211 using a combination of all four datasets).

We scored 55 (22.9%) species as elevational migrants and 179 (74.6%) species as residents, and observed 6 (2.5%) species of latitudinal migrants (Appendix 2). Assuming these results are accurate, the most conservative measure of the percentage of migratory species within our study area would be 7.5% (55 elevational migrants / 736 possible species). Walker et al. (2006) classify 29 species in our study area as latitudinal migrants. If we assume that the remaining 707 species have the same ratio of elevational migrants to residents as the species we scored, which is perhaps a more reasonable assumption than the previous conservative one, then the percentage of elevational migrants in the community is 22.0%. If we classify 3 of our potential elevational migrants as latitudinal migrants (see below), the percentage drops to 20.7%, and would likely drop further if we extended our elevational coverage even 200 m lower into Amazonia as more strictly lowland taxa were included.

The frequency of species in each of five foraging guilds varies between elevational migrants and residents (Fisher's exact test, $p < 0.0003$; Table 3, Fig. 3). Elevational migrant species are comprised of more frugivores, granivores, nectarivores, and omnivores and fewer insectivores than residents. Most noticeably, the proportion of insectivores among migrants (25%) is significantly lower than the proportion among residents (54%; $p < 0.0004$). Almost half of all granivores and nectarivores for which we could assign a residency status are elevational migrants, while only a quarter of frugivores and omnivores are migrants, and only one out of every 8 insectivores is a migrant (Table 3). Elevational migration appears to be less associated with insectivory and more associated with granivory and nectarivory, with frugivores and omnivores falling somewhere in the middle. Our results agree with similar findings in Costa Rica (Stiles 1983, Boyle 2006), and together these patterns suggest that diet is an important correlate of migratory tendency.

Most elevational migrants moved upslope from the dry season to the early wet season (n=38; Appendix 2). Two species that moved upslope are conspicuous lowland psittacids, Military Macaw (*Ara militaris*) and Chestnut-fronted Macaw (*Ara severus*). This seasonal variation is similar to that found in three other species of *Ara* in lowland Manu (Renton 2002), and may represent either nomadic movements, tracking of preferred food resources, or migration. Another 10 species of migrants are lowland or lower montane species whose upslope movements may be due seasonal resource tracking as in the previous group, or they may represent individuals moving upslope to breed. Nest predation is high at our low elevation study sites, primarily due to snake depredations (G. Londoño, *unpubl. data*), so lowland species may benefit from reduced nest predation simply by moving upslope a few hundred meters (Boyle 2008a). The remaining 24 species that move upslope from the dry to early wet seasons are montane. Within this group some species appear to be more migratory than others. For example, movements of Streak-necked Flycatchers (*Mionectes striaticollis*) (Fig. 1) and Dusky-green Oropendolas (*Psarocolius atrovirens*) certainly involve large portions of the population, while in other species only a few individuals stray to lower elevations during the late wet and dry season.

A few elevational migrants (n=11) move downslope from the dry to the early wet season. Six of these are primarily lowland or lower montane species that extended their ranges upwards during the dry season, perhaps in a post-breeding habitat shift. One is a hummingbird, the Green Violetear (*Colibri coruscans*; Fig. 2), which is known to migrate elevationally elsewhere within its range (Stiles 1985b, Ornelas and Arizmendi 1995, Strewe and Navarro 2003). Four are highland species whose movement patterns are poorly known. The final species is the White-crested Elaenia (*Elaenia albiceps*). Although we did not identify the elaenias to subspecies, the occurrence of White-crested Elaenia in our study area from Jul to Nov is consistent with that expected of the race *modesta*, which breeds on the Pacific slope from Dec to Feb (Fjeldså and Krabbe 1990) and migrates east across the Andes to spend the non-breeding season on the eastern slopes (Schulenberg 2009).

Two other species apparently did not move between the dry and early wet season, but perhaps move during the late wet season. The Chiguanco Thrush (*Turdus chiguanco*) was found from 1800–3000 m a.s.l. during the dry and early wet season, but was completely absent during the late wet season, except for a single individual noted in the paramo at 3500 m a.s.l. We never observed singing birds, indicating that the species may not breed in our study area. Nesting records from May to Jul in the intermontane valleys of Cusco and neighboring regions (Fjeldså and Krabbe 1990) indicate that the presence of Chiguanco Thrush in our study area may represent post-breeding dispersal. The second species is the Slaty Finch (*Haplospiza rustica*), whose dependence on seeding bamboo results in complex seasonal or nomadic movements (Sánchez 2005). We heard singing birds from 2300–2700 m a.s.l. from Aug to Oct, but during Feb and Mar, the late wet season, the only individuals we observed were captured in mist nets at 1100 and 1700 m a.s.l.

Seasonal patterns of occurrence in three species classified as elevational migrants may actually represent latitudinal rather than elevational movements. These include the Barred Parakeet (*Bolborhynchus lineola*), which was found only during the early wet season, the Chestnut-collared Swift (*Streptoprocne rutila*), which was found only during the early wet and late wet seasons, and the Blue-and-white Swallow (*Pygochelidon cyanoleuca*), which was found only during the late wet and dry seasons. Others have noted apparent seasonal fluctuations in the occurrence of the parakeet elsewhere in the Andes (Fjeldså and Krabbe 1990, Hilty 1997), but a comprehensive assessment of its seasonal movements has not been done. We observed the Chestnut-collared Swift in large numbers in Feb, Mar, Aug, and Sep, and in low numbers in June and Jul, but never in Oct and Nov. At his Colombian site, Hilty (1997) noted the species in Feb–May and Oct–Dec, and suggested that it is an elevational migrant. In Manu, the lack of records from the lowlands (Terborgh et al. 1984), combined with our results, suggests that the species leaves the park completely for portions of the year. The Blue-and-white Swallow was present Feb to Aug, and absent thereafter. While its absence may be due to birds of the "resident" nominate race migrating downslope during the early wet season, it is perhaps more likely that we were observing birds of the austral migrant race *patagonica*, which migrate south in Sep and Oct to breed. Unfortunately we did not identify the swallows in our study area to subspecies.

Meta-analysis

We found three regions in the Neotropics for which the migratory status of all landbirds has been described: Tamaulipas, Mexico (Arvin 2001), Oaxaca, Mexico (Binford 1989), and Costa Rica (Stiles 1985a). The only South American location with an extensive avifaunal survey including migratory status for most species is from Valle de Cauca, Colombia (Hilty 1997). Although the Colombian study only surveyed birds within a narrow elevational range at one site (950–1050 m a.s.l.), it is the only such dataset from the Andes. Given that the site is from middle elevations, it is still perhaps more representative of the entire elevational gradient than a strictly lowland or highland site would be. Combining the results of these studies with our own, we now have a community-level characterization of five regions from approx. 23°N to 13°S latitude.

Comparing the percentage of species of latitudinal migrants, elevational migrants, and residents from the five regions revealed three general patterns (Table 4). First, the relative contribution of latitudinal migrants to local avifaunas decreased drastically from 45% in northern Mexico (Tamaulipas) to less than 4% in Peru. Second, the percentage of resident species and elevational migrants generally increased from north to south, from 6% and 49%, respectively, in northern Mexico to 22% and 72% in Peru. While this trend was fairly constant for elevational migrants, the percentage of residents did not vary greatly between southern Mexico (Oaxaca), Costa Rica, and Colombia. At a glance, it appeared that Colombia had more elevational migrants than Peru, but this may have been an artifact of the smaller elevational range surveyed in Colombia. For example, when we restricted our dataset to only those species observed within a heavily-studied 100-m elevational zone at middle elevations (1350–1450 m a.s.l.), the percentage of elevational migrants was actually higher in Peru (28%) than in Colombia (23%; Table 4), supporting the north-south trend rather than an "equatorial-peak". Third, the ratio of elevational migrants to residents increased from north to south. Even though the percentage of both residents and elevation migrants increased from north to south at the expense of latitudinal migrants, elevational migrants outpaced residents in their rate of increase. As with the previous two trends, it is clear that this pattern is one of a north-to-south increase rather than a peak at low latitudes.

DISCUSSION

Each of our methods of determining the distribution and abundance of species along the elevational gradient is subject to biases. Point counts work well for species that vocalize often, but not well for those that vocalize rarely or are seasonally silent. Mist nets provide some estimate of the occurrence and abundance of non-vocalizing birds, but are biased towards small understory species that move frequently. Flock observations were very useful for determining occurrence and in many cases abundance at one site, but could not be widely applied given our time constraints. We believe the use of multiple datasets and analytical methods increased the robustness of our inferences about the migratory status of species. Yet there are areas where our approach needs to be improved.

In most if not all cases, it seems that the elevational range of elevational migrants overlaps between seasons. This pattern indicates either that species are completely migratory (all individuals move) over very short distances or that they are partially migratory, with individual variation in migratory behavior. Partial migration has proven to be the case in the White-ruffed Manakin (Boyle et al. 2010), one of the best studied elevational migrants. The prospect of partial migration presents an interesting dilemma. The key question is how to be sure that an observed pattern consistent with elevational migration does in fact indicate migration. In other words, what differences are biologically significant versus statistically significant, a problem that has long plagued biologists (Johnson 1999). We suggest that follow-up studies use individual-based methods (e.g., radio- or GPS-tracking) to determine if particular species are indeed migratory, and to what extent. The results from these studies can be compared with our results here to determine the biological significance of the patterns we have described statistically and the appropriate cutoffs for classifying species as migratory or nonmigratory. A further note of caution should be given concerning the interpretation of our results. It is possible that we may have documented movements other than elevational migration, such as dispersal, nomadism, or movements between habitats within an elevation. Again, the only way to address these concerns is with detailed follow-up studies.

Despite the caveats mentioned above, our results suggest that seasonal elevational migration is a prominent characteristic of the avian community in Manu National Park. These finding are the first of their kind for a large elevational transect in the Andes or anywhere else in South America. Furthermore, we show that elevational migration is not simply correlated with distance from the equator. Our southern hemisphere site (Peru, 13°S) had considerably more elevational migrants than similar latitudes in the northern hemisphere (Costa Rica, 8–11°N). Rather, elevational migration becomes increasingly common from north to south, at least as far south as Peru. Our results also concur with other studies that latitudinal migrants show the opposite trend, decreasing numbers from north to south (Pearson 1980, Mönkkönen and Forsman 2005). Presumably at some point the percentage of latitudinal migrants would begin to increase again as one nears the south temperate zone, but this increase would likely occur further south in the southern hemisphere given that South American austral migrants comprise a smaller proportion of the southern hemisphere avifauna than boreal migrants do in the northern hemisphere, and that austral migrants tend to migrate shorter distances than boreal migrants (Jahn et al. 2004). Costa Rican sites support a large percentage of elevational migrants, but they also support many Nearctic-Neotropical latitudinal migrants for seven months of the year. Competitive interactions between latitudinal migrants, elevational or local migrants, and residents may result in differing life-history tradeoffs between species in Central America, where latitudinal migrants are common, and those in the Andes where latitudinal migrants are rare. Also, mixed-species flocks at our middle elevation study sites are the largest known flocks in the world, and the most abundant members of those flocks are elevational migrants (Merkord 2010 Chapter 2). If there is any interaction between flocking propensity and migratory propensity, then the mutualistic interspecific interactions occurring in flocks may play a role in structuring avian communities, and this role may vary regionally depending on the size of mixed-species flock.

The Andes harbor many endemic species restricted to habitats above treeline such as paramo, puna, and *Polylepis* forests. Although our sampling stopped at treeline, seasonal migration across treeline appears to be uncommon, consistent with the traditional view that most high-elevation species are not migratory. However, recent research by R. Gibbons (*unpubl. data*) in the high Andes of Peru suggests that many “resident” species may actually undertake seasonal movements of their own, all occurring above treeline. Clearly there is much to learn about the seasonal movements of birds in the Andes.

This brings us to our plea to field biologists to increase efforts to understand the patterns of bird movements in South America. Faaborg et al. (2010a) point out that even in North America, where migrant ecology is comparatively well-studied, we often lack sufficient information to manage migratory landbird populations. Their conclusion that “replication of comprehensive studies is needed for multiple species across a range of areas” applies 10-fold for elevational, local, and austral migrants in South America. Increasing the quantity of studies on the movement of South American birds, as well as the spatial and temporal scope of such studies, is necessary to manage biodiversity at appropriate local, regional, and continental scales. Effective conservation strategies are especially needed for montane ecosystems, which are expected to be disproportionately affected by climate change (Williams et al. 2007, Laurance et al. *In review*).

The study of elevational migration also offers the possibility to address key questions regarding the distribution of species along environmental gradients. Species-specific studies in Costa Rica are beginning to unravel the ultimate factors involved in elevational migration there, which will inevitably lead to a better understanding of the evolution of migration, dispersal, and other animal movements. These movements (or lack thereof) play a huge role in our understanding of avian biogeography, because they serve as mechanisms for species range expansion and contraction and create opportunities for speciation. There is currently very little information on seasonal movements of birds along elevational gradients in the Guiana Shield, the Atlantic Forest, or the southern Andes, although recent findings indicate that elevational and longitudinal migration systems may exist within the Atlantic Forest (Areta and Bodrati 2010). We urgently need 1) replication of studies along multiple elevational transects throughout South America, including both the dry western and moist eastern slopes of the Andes, and 2) more species-specific studies of the proximate and ultimate causes of migration, especially in partially migratory species. With effort, we can begin to piece together a more comprehensive picture of avian migration within the Neotropics.

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Table 1. System used to score the weight of evidence for elevational migration. Positive numbers indicate evidence of migratory status, negative numbers indicate evidence of nonmigratory status.

Migratory Status	***Strength of evidence***	***Score***
Migratory	Strong	3
Migratory	Moderate	2
Migratory	Weak	1
Unknown	Equivocal	0
Nonmigratory	Weak	-1
Nonmigratory	Moderate	-2
Nonmigratory	Strong	-3

Table 2. System used to score the weight of evidence for elevational migration by comparing the relative abundance estimates from mist netting data between two seasons.

Criterion	*Score*	*Condition*
A. Threshold shift[1]	1	If the relative abundance in one or more zone shifts from high to low or low to high
	-1	If the relative abundance in NO zone shifts from high to low or low to high
B. Matching threshold shift[2]	1	If criterion A scored 1, and if there was a matching threshold shift in the opposite direction at another site
	-1	If criterion A scored 1, and if there was NO matching threshold shift in the opposite direction at another site
	0	If criterion A scored -1
C. Lowest elevation[3]	1	If the lowest site in which the species occurred changed from one season to the next
	-1	If the lowest site in which the species occurred DID NOT change from one season to the next
D. Highest elevation	1	If the highest site in which the species occurred changed from one season to the next
	-1	If the highest site in which the species occurred DID NOT change from one season to the next
E. Directions contradictory	TRUE	If the threshold shifts suggest migration in one direction, but the changes in the elevation of highest or lowest occurrence suggest migration in the other direction, ignore other scores and score a zero
	FALSE	If the condition is not met, do not score this criterion
Total Score	If criterion E was met, then total 0 for this seasonal comparison. Otherwise, total the sum of scores from criteria A-D.	

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[1] An abundance threshold was set as the average relative abundance of all species at all sites. Abundances above this threshold were categorized as “high”, and abundances below this threshold as “low.”

[2] Because the three sites near 1350 m a.s.l. were close to each other, they could not simultaneously qualify for a threshold shift and a matching threshold shift by themselves.

[3] Likewise, changes in occurrence at these three sites alone was not considered a shift in the elevation of lowest or highest occurrence.

Table 3. Number of elevational migrant and resident species in each foraging guild.

Foraging Guild	***Number of Elevational Migrant Species***	***Number of Resident Species***	***Total***
Frugivore	6	17	23
Granivore	8	9	17
Insectivore	14	97	111
Nectarivore	9	12	21
Omnivore	17	44	61
Raptor	1		1
Total	55	179	234

Table 4. Percentage of species of resident, elevational migrant, and latitudinal migrant landbird species in five Neotropical regions. Vagrant species are not included. Lists from Mexico and Costa Rica represent fairly complete elevational gradients, while the Colombian list is from one site only, spanning about 100 m elevation. Results from the current study in Cusco region, Peru are given in three ways: 1) the actual number of species for which a migratory status could be determined, 2) the total number of species within the surveyed elevational range, using published information on the number of latitudinal migrants (Walker et al. 2006) and extrapolating the ratio of elevational migrants to residents from the observed data, and 3) a subset comprising species observed within a 100-m middle elevation zone of intense study similar to that in the Colombian study.

Location	***Elevational Range***	***Number of Species***	***Percentage of species***			***Ratio of Elevational Migrants to Residents***	***Source***
			Latitudinal Migrants	***Elevational Migrants***	***Residents***		
Tamaulipas, Mexico	100-2150 m	309	45.1	6.0	48.9	0.12	Arvin (2001)
Oaxaca, Mexico	0-3300 m	548	24.4	8.4	67.2	0.12	Binford (1989)
Costa Rica	0-3800 m	451	20.6	14.9	64.5	0.23	Stiles (1985a)
Valle de Cauca, Colombia	950-1050 m	256	8.6	23.4	68.0	0.34	Hilty (1997)
Cusco, Peru (actual)	750-3450 m	240	2.5	22.9	74.6	0.31	
Cusco, Peru (extrapolated)	750-3450 m	736	3.9	22.0	71.6	0.31	
Cusco, Peru (100 m range)	1350-1450 m	153	2.0	27.5	70.6	0.39	

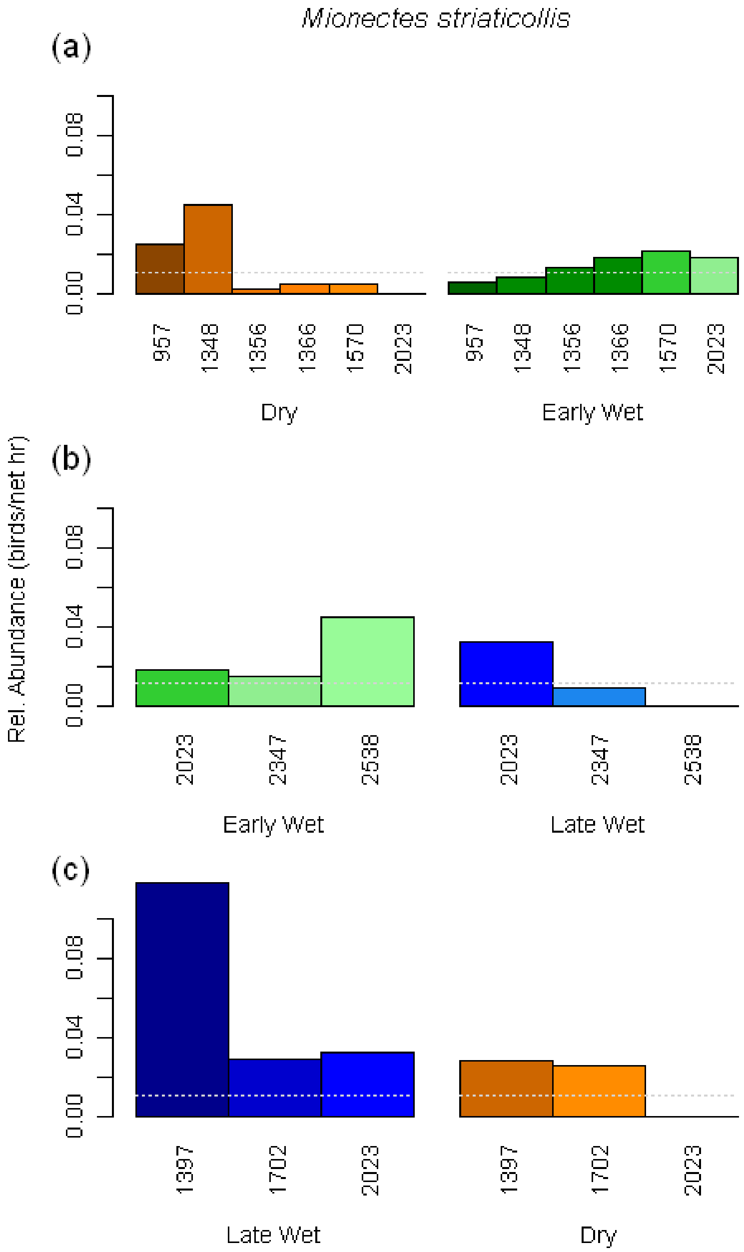

Figure 1. Example of netting data showing strong evidence of elevational migration in the Streak-necked Flycatcher (*Mionectes striaticollis*). Sites sampled during each of two seasons are plotted side-by-side. Numbers on the x-axis are the average elevation of each group of nets in m a.s.l. The horizontal dotted line indicates the abundance threshold used to score evidence for or against migration (see Methods). Note the upslope shift in occurrence and relative abundance from the dry season to the early wet season (a), and a subsequent downward shift from the early wet seasons to late wet season (b). The abundance of birds may shift downslope from the late wet season to dry season (c), but without having sampled during the late wet season at our 950 m study site, it is impossible to say for certain.

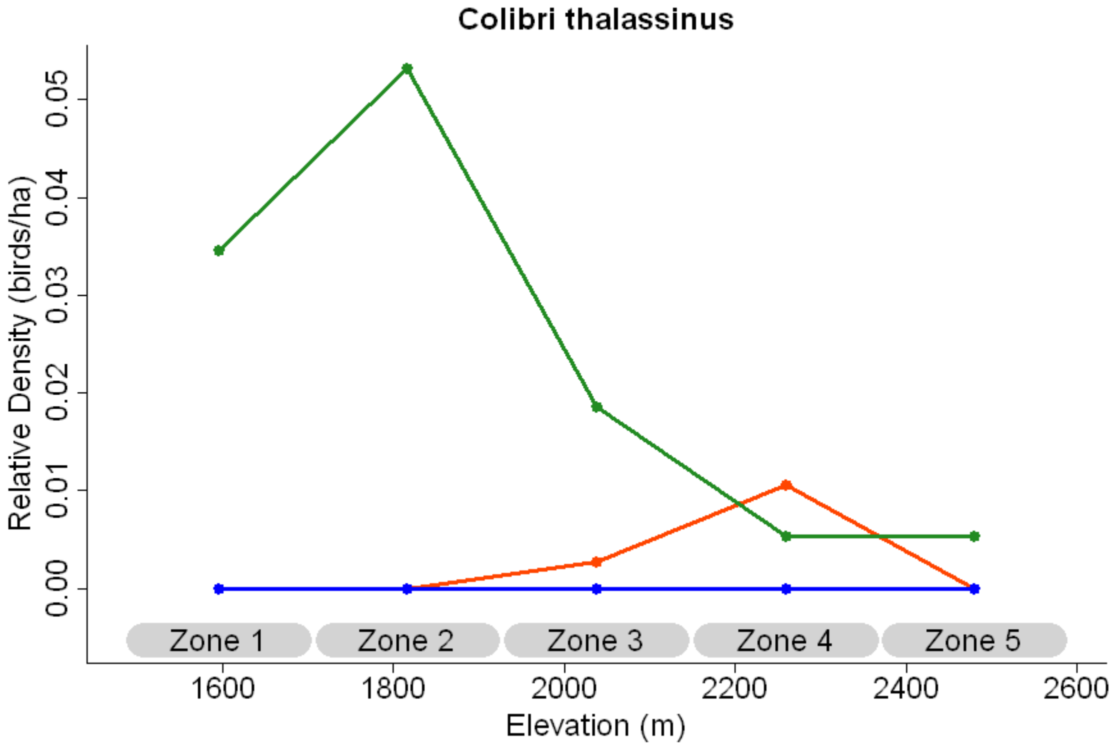

Figure 2. Example of point count data showing strong evidence of elevational migration in the Green Violetears (*Colibri thalassinus*) during the dry season (orange line), early wet season (green line), and late wet season (blue line). Relative density was estimated using distance-based methods. The species was never detected during the late wet season.

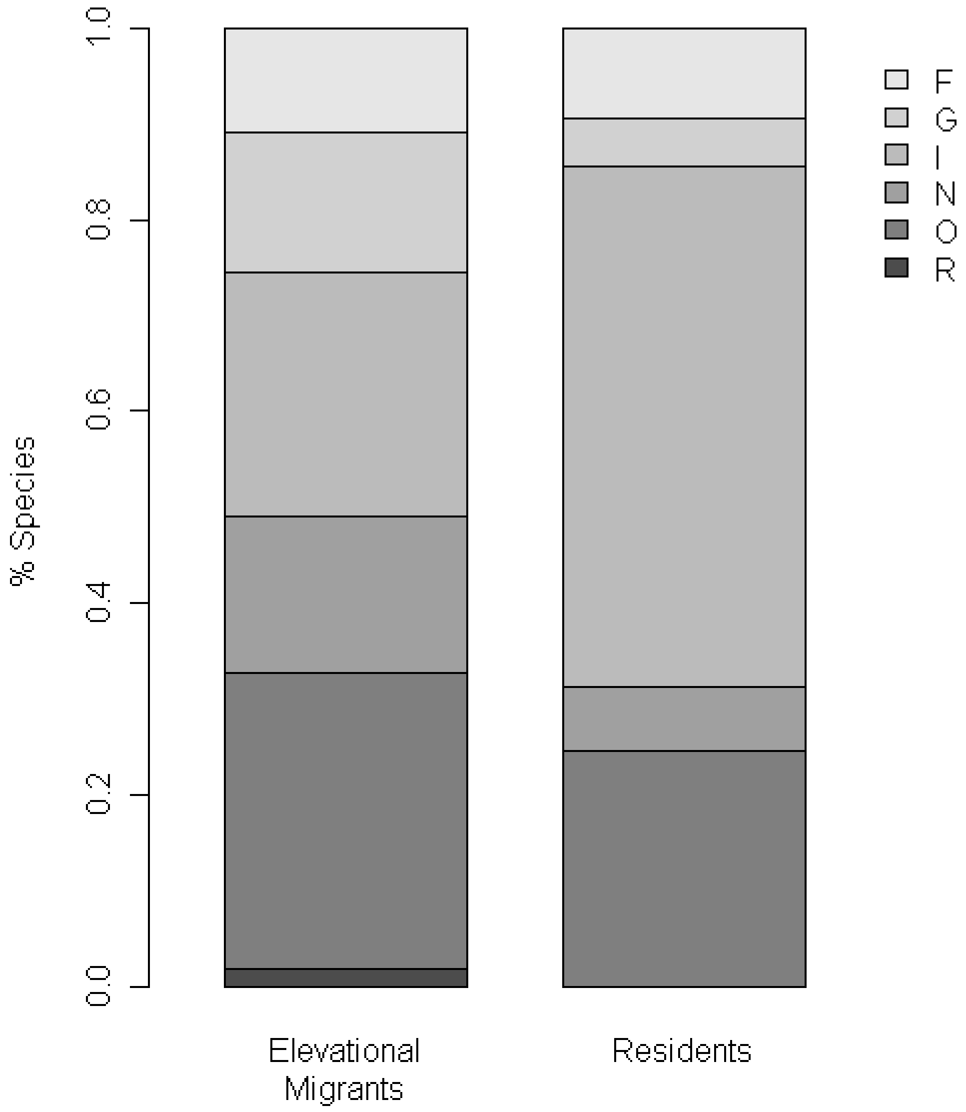

Figure 3. Percentage of species in each foraging guild for elevational migrants and residents. Guilds are frugivores (F), granivores (G), insectivores (I), nectarivores (N), omnivores (O), and raptors (R).

Appendix 1. Species participating in a mixed-species flock near San Pedro, Kosñipata Valley, Cusco Region, Peru, elevation 1360-1500 m a.s.l.

Residency status is given as year-round resident (Y), elevational migrant (E), boreal latitudinal migrant (B), South American austral latitudinal migrant (A), and occasional/irregular visitor (O). Data suggesting status as elevational migrant is based on monthly variation in abundance (1), apparent lack of breeding at the elevation of the flock (2), recaptures of banded birds (3), and results from Merkord (2010 Chapter 4). Flock propensity is given as regular flock associate (R), occasional flock associate (O), and accidental/non-joiner (A). Nuclear species and specie which also form monospecific groups are also noted. Taxonomy follows Remsen et al. (Version April 14, 2010).

Scientific name	***English name***	***Residency status***	***Elevational Migrant Data***	***Flocking propensity***	***Number of Individuals***	***Nuclear species***	***Mono-specific groups***
Cuculidae							
Piaya cayana	Squirrel Cuckoo	Y		O	2		
Trogonidae							
Pharomachrus auriceps	Golden-headed Quetzal	E?	2	O	1		
Pharomachrus antisianus	Crested Quetzal	E?	2	O	1		
Trogon personatus	Masked Trogon	O		O	2		
Galbulidae							
Galbula cyanescens	Bluish-fronted Jacamar	Y		O?	N		
Bucconidae							
Malacoptila fulvogularis	Black-streaked Puffbird	O/Y?		R?	1		
Capitonidae							
Eubucco versicolor	Versicolored Barbet	Y		R	3		
Picidae							
Colaptes rubiginosus	Golden-olive Woodpecker	Y?		O	1		
Campephilus haematogaster	Crimson-bellied Woodpecker	O		A	1		
Furnariidae							
Synallaxis azarae	Azara's Spinetail	Y		O	3		

Scientific name	***English name***	***Residency status***	***Elevational Migrant Data***	***Flocking propensity***	***Number of Individuals***	***Nuclear species***	***Mono-specific groups***
Cranioleuca curtata	Ash-browed Spinetail	Y		R	2		
Premnoplex brunnescens	Spotted Barbtail	Y?		R	22		
Anabacerthia striaticollis	Montane Foliage-gleaner	Y		R	10		
Thripadectes melanorhynchus	Black-billed Treehunter	Y		O	7		
Xenops rutilans	Streaked Xenops	O		R?	1		
Xiphorhynchus triangularis	Olive-backed Woodcreeper	Y		R	7		
Thamnophilidae							
Thamnophilus palliatus	Chestnut-backed Antshrike	Y		O	2		
Epinecrophylla ornata	Ornate Antwren	Y?		O	3		M
Myrmotherula longicauda	Stripe-chested Antwren	Y		O	2		
Myrmotherula schisticolor	Slaty Antwren	Y?		O	10		M
Hypocnemis subflava	Yellow-breasted Warbling-Antbird	Y		A	3		
Terenura sharpei	Yellow-rumped Antwren	Y?		R	N		
Tyrannidae							
Phyllomyias cinereiceps	Ashy-headed Tyrannulet	Y/O?		R?	1		
Elaenia pallatangae	Sierran Elaenia	E?	2	R?	1		
Zimmerius bolivianus	Bolivian Tyrannulet	Y, E?	3	R	7		
Phylloscartes poecilotis	Variegated Bristle-Tyrant	E	2, 4	R?	1		
Phylloscartes ophthalmicus	Marble-faced Bristle-Tyrant	Y		R	6		
Phylloscartes parkeri	Cinnamon-faced Tyrannulet	Y?		R	2		
Mionectes striaticollis	Streak-necked Flycatcher	E, Y?	1, 2, 3, 4	R	54		
Mionectes olivaceus	Olive-striped Flycatcher	E	2, 4	O?	2		
Leptopogon superciliaris	Slaty-capped Flycatcher	Y		R	11		
Lophotriccus pileatus	Scale-crested Pygmy-Tyrant	Y		O	9		
Rhynchocyclus fulvipectus	Fulvous-breasted Flatbill	Y?		O?	2		
Tolmomyias sulphurescens	Yellow-olive Flycatcher	O?		O?	1		
Platyrinchus mystaceus	White-throated Spadebill	O		O?	1		
Myiophobus inornatus	Unadorned Flycatcher	E?	2	R?	N		
Pyrrhomyias cinnamomeus	Cinnamon Flycatcher	O		O	1		
Lathrotriccus euleri	Euler's Flycatcher	O?		R?	2		

Scientific name	***English name***	***Residency status***	***Elevational Migrant Data***	***Flocking propensity***	***Number of Individuals***	***Nuclear species***	***Mono-specific groups***
Contopus fumigatus	Smoke-colored Pewee	E	2, 4	O	1		
Contopus sordidulus/virens	Wood-Pewee sp.	B		O	1		
Myiotheretes striaticollis	Streak-throated Bush-Tyrant	E	2, 4	A	1		
Legatus leucophaius	Piratic Flycatcher	O		O	1		
Myiozetetes similis	Social Flycatcher	Y?		O	2		
Conopias cinchoneti	Lemon-browed Flycatcher	Y		O	8		M
Myiodynastes chrysocephalus	Golden-crowned Flycatcher	Y, E?	4	O	2		
Myiodynastes maculatus	Streaked Flycatcher	O		O	1		
Tyrannus melancholicus	Tropical Kingbird	Y		O	4		
Myiarchus tuberculifer	Dusky-capped Flycatcher	E?	2	R	2		
Pipridae							
Machaeropterus pyrocephalus	Fiery-capped Manakin	Y?		O	3		M
Lepidothrix coeruleocapilla	Cerulean-capped Manakin	Y?		O	1		
Chiroxiphia boliviana	Yungas Manakin	Y, E?	3	O	12		M
Vireonidae							
Vireo leucophrys	Brown-capped Vireo	Y		R	2		
Vireo olivaceus	Red-eyed Vireo	O		R?	1		
Vireo flavoviridis	Yellow-green Vireo	A		R?	1		
Corvidae							
Cyanocorax yncas	Green Jay	Y		O	5		M
Troglodytidae							
Odontorchilus branickii	Gray-mantled Wren	Y		R	2		
Turdidae							
Myadestes ralloides	Andean Solitaire	Y/E?	4	O	26		
Catharus ustulatus	Swainson's Thrush	B		O	1		
Entomodestes leucotis	White-eared Solitaire	E	2, 4	O	3		
Turdus hauxwelli	Hauxwell's Thrush	Y?		A?	2		
Turdus ignobilis	Black-billed Thrush	Y?, E?	3	O?	4		
Turdus nigriceps	Slaty Thrush	A		A?	11		
Thraupidae							

Scientific name	English name	Residency status	Elevational Migrant Data	Flocking propensity	Number of Individuals	Nuclear species	Mono-specific groups
Cissopis leverianus	Magpie Tanager	Y?		O	N		
Creurgops dentatus	Slaty Tanager	E	2, 4	R	N		
Hemispingus melanotis	Black-eared Hemispingus	E, Y?	1, 3	O	12		M
Thlypopsis ruficeps	Rust-and-yellow Tanager	E	2, 4	R?	1		M
Trichothraupis melanops	Black-goggled Tanager	Y?		R	10		
Ramphocelus carbo	Silver-beaked Tanager	Y		O	26		M
Thraupis episcopus	Blue-gray Tanager	Y		R	6		M
Thraupis palmarum	Palm Tanager	E?	2	R	2		M
Thraupis cyanocephala	Blue-capped Tanager	E	2	R	2		M
Anisognathus somptuosus	Blue-winged Mountain-Tanager	E	2, 4	R?	1		
Iridosornis analis	Yellow-throated Tanager	Y		R	6		
Pipraeidea melanonota	Fawn-breasted Tanager	E	2, 4	R	3		M
Chlorochrysa calliparaea	Orange-eared Tanager	Y, E?	3	R	13	N	M
Tangara ruficervix	Golden-naped Tanager	O		R	4		M
Tangara cyanicollis	Blue-necked Tanager	Y		R	7		M
Tangara xanthogastra	Yellow-bellied Tanager	O		R	2		
Tangara punctata	Spotted Tanager	E?	1	R	14	N	M
Tangara nigroviridis	Beryl-spangled Tanager	E	1, 4	R	17	N	M
Tangara chilensis	Paradise Tanager	Y		R	10	N	M
Tangara gyrola	Bay-headed Tanager	Y?		R	2		
Tangara chrysotis	Golden-eared Tanager	Y?		R	3		
Tangara xanthocephala	Saffron-crowned Tanager	Y?		R	3		
Tangara parzudakii	Flame-faced Tanager	Y/E?	2	R	1		
Tangara arthus	Golden Tanager	Y		R	6	N	M
Dacnis cayana	Blue Dacnis	Y?		R	3		M
Cyanerpes caeruleus	Purple Honeycreeper	O		R	2		M
Chlorophanes spiza	Green Honeycreeper	O		R	1		
Iridophanes pulcherrimus	Golden-collared Honeycreeper	Y?		R	2		
Diglossa glauca	Deep-blue Flowerpiercer	E	1, 3, 4	R	54		M
Diglossa caerulescens	Bluish Flowerpiercer	E	2, 4	R?	3		

Scientific name	***English name***	***Residency status***	***Elevational Migrant Data***	***Flocking propensity***	***Number of Individuals***	***Nuclear species***	***Mono-specific groups***
Diglossa cyanea	Masked Flowerpiercer	E	2	R?	2		
Incertae Sedis							
Chlorospingus ophthalmicus	Common Bush-Tanager	E	2	R?	3		M
Chlorospingus parvirostris	Short-billed Bush-Tanager	O		R?	7		M
Chlorospingus flavigularis	Yellow-throated Bush-Tanager	Y		R	12	N	M
Coereba flaveola	Bananaquit	Y		O	5		
Saltator maximus	Buff-throated Saltator	Y		O	6		
Emberizidae							
Ammodramus aurifrons	Yellow-browed Sparrow	Y?		O	4		
Sporophila luctuosa	Black-and-white Seedeater	E?	2	A	3		M
Sporophila castaneiventris	Chestnut-bellied Seedeater	E?	2	A	1		M
Arremon brunneinucha	Chestnut-capped Brush-Finch	Y?		A	2		
Atlapetes melanolaemus	Black-faced Brush-Finch	Y		O	4		
Cardinalidae							
Piranga flava	Hepatic Tanager	O		R?	1		
Pheucticus aureoventris	Black-backed Grosbeak	E?	2	O	2		
Parulidae							
Parula pitiayumi	Tropical Parula	Y?		R	3		
Myioborus miniatus	Slate-throated Redstart	Y, E?	4	R	12		M
Myioborus melanocephalus	Spectacled Redstart	E	2	R?	1		M
Basileuterus bivittatus	Two-banded Warbler	Y		O	7		
Basileuterus coronatus	Russet-crowned Warbler	Y		O	12		
Basileuterus tristriatus	Three-striped Warbler	Y		O	9		
Icteridae							
Psarocolius angustifrons	Russet-backed Oropendola	Y		O	30		M
Psarocolius atrovirens	Dusky-green Oropendola	E, Y?	1, 4	O	10		M
Fringillidae							
Euphonia mesochrysa	Bronze-green Euphonia	Y		R	4		
Euphonia xanthogaster	Orange-bellied Euphonia	Y?, E?	4	R	21		
Chlorophonia cyanea	Blue-naped Chlorophonia	Y/E?	4	R	3		

Appendix 2. Migratory status of species detected during point counts, mist netting, flock observations, and incidental observations from 750-3450 m a.s.l. in Manu National Park, Cusco Region, Peru.

Published elevational minima and maxima are taken from Walker et al .(2006). Three species not previously known to occur in the park do not have published elevational ranges. Observed elevational minima and maxima include only our own observations. Foraging guild classifications follow Merkord (2010 Chapter 1): frugivores (F), granivores (G), insectivores (I), nectarivores (N), and omnivores (O). Migratory status codes: resident (R), elevational migrant (E), boreal latitudinal migrant (B), and South American austral latitudinal migrant (A). Classification of boreal and austral migrants follows Walker et al.(2006). For elevational migrants the direction of migration is given for each of three seasonal transitions: dry season to early wet season (D-E), early wet season to late wet season (E-L), and late wet season to dry season (L-D). The possible directions are up (u), down (d), and unknown (-). Scores are given for each type of migratory analysis: distance-based point counts (PC D), relative abundance-based point counts (PC RA), mist netting data (N), mixed-species flock observations (F), and the analysis of a combined dataset using all observations (C). All scores range from 3 (strong evidence of migration) to -3 (strong evidence of lack of migration). If not otherwise marked, all scores were zero, indicating equivocal results or lack of data. The weighted mean elevation (w), used to assign the migratory status, is given for each species. Taxonomy follows Remsen et al. (Version April 14, 2010).

		Published Elevation		***Observed Elevation***				***Seasonal Transition***			***Analysis Scores***					
Scientific Name	***English Name***	***Min***	***Max***	***Min***	***Max***	***Diet***	***Migr. Stat.***	***DR-EW***	***EW-LW***	***LW-DR***	***PC D***	***PC RA***	***N***	***F***	***C***	***w***
Tinamidae																
Nothocercus nigrocapillus	Hooded Tinamou	1600	3200	1852	2973	G										
Tinamus tao	Gray Tinamou	250	1300	805	960	G	R								-2	-0.18
Tinamus osgoodi	Black Tinamou	900	1350	983	1720	G	R								-1	-0.09
Tinamus guttatus	White-throated Tinamou	250	1100	934	951	G	R								-1	-0.09
Crypturellus soui	Little Tinamou	250	1500	818	1430	G										
Crypturellus obsoletus	Brown Tinamou	450	2200	1006	3013	G	R				-3	-3			-3	-1.91
Anatidae																
Merganetta armata	Torrent Duck	1400	2200	1460	1460	A										
Cracidae																

		Published Elevation		Observed Elevation				Seasonal Transition			Analysis Scores					
Scientific Name	**English Name**	**Min**	**Max**	**Min**	**Max**	**Diet**	**Migr. Stat.**	**DR-EW**	**EW-LW**	**LW-DR**	**PC D**	**PC RA**	**N**	**F**	**C**	**w**
Penelope montagnii	Andean Guan	900	3200	1440	3049	F	R					-2			1	-0.27
Penelope jacquacu	Spix's Guan	250	1500	829	1236	F										
Aburria aburri	Wattled Guan	650	1600	1330	1948	F										
Ortalis guttata	Speckled Chachalaca	250	1600	600	1410	F										
Mitu tuberosum	Razor-billed Curassow	250	1000	950	950	G										
Odontophoridae																
Odontophorus speciosus	Rufous-breasted Wood-Quail	1000	2100	1081	1950	G	R								-1	-0.09
Odontophorus balliviani	Stripe-faced Wood-Quail	800	3100	1390	2937	G										
Odontophorus stellatus	Starred Wood-Quail	250	1050	893	909	G										
Cathartidae																
Cathartes aura	Turkey Vulture	250	2700	1375	1375	C										
Accipitridae																
Elanoides forficatus	Swallow-tailed Kite	250	2000	818	1184	R										
Ictinia plumbea	Plumbeous Kite	250	1450	1380	1380	R										
Accipiter collaris	Semicollared Hawk	1100	2500	1380	1380	R										
Accipiter striatus	Sharp-shinned Hawk	900	3500	2010	2591	R										
Harpyhaliaetus solitarius	Solitary Eagle	700	2100	1184	2900	R										
Buteo magnirostris	Roadside Hawk	250	2500	550	1385	R										
Buteo platypterus	Broad-winged Hawk	250	3000	2937	2937	R	B									
Spizaetus isidori	Black-and-chestnut Eagle	900	3600	1230	1400	R										
Falconidae																
Herpetotheres cachinnans	Laughing Falcon	250	1000	600	750	R										
Micrastur ruficollis	Barred Forest-Falcon	250	2000	823	2154	R										
Micrastur gilvicollis	Lined Forest-Falcon	250	1000	983	983	R										
Ibycter americanus	Red-throated Caracara	250	1250	895	895	R										
Phalcoboenus megalopterus	Mountain Caracara	2850	3500	3200	3515	R										
Eurypygidae																
Eurypyga helias	Sunbittern	250	1600	1130	1130	A										
Scolopacidae																
Gallinago jamesoni	Andean Snipe	2700	3550	2920	2940	A										
Columbidae																
Claravis mondetoura	Maroon-chested Ground-Dove	1900	2500	2319	2673	G										
Patagioenas fasciata	Band-tailed Pigeon	1200	3500	1370	3530	F	E	d	d	u					1	0.09
Patagioenas plumbea	Plumbeous Pigeon	250	1800	818	1991	F	E	u	n	d		3			2	0.73
Patagioenas subvinacea	Ruddy Pigeon	250	1550	805	1236	F										
Leptotila rufaxilla	Gray-fronted Dove	250	1250	797	985	G										
Geotrygon frenata	White-throated Quail-Dove	700	2850	1130	3040	F										
Geotrygon montana	Ruddy Quail-Dove	250	1200	877	1489	F										
Psittacidae																
Ara ararauna	Blue-and-yellow Macaw	250	1000	829	829	G										

		Published Elevation		Observed Elevation				Seasonal Transition			Analysis Scores					
Scientific Name	**English Name**	**Min**	**Max**	**Min**	**Max**	**Diet**	**Migr. Stat.**	**DR-EW**	**EW-LW**	**LW-DR**	**PC D**	**PC RA**	**N**	**F**	**C**	**w**
Ara militaris	Military Macaw	600	1500	600	1716	G	E	u	d	u					3	0.27
Ara chloropterus	Red-and-green Macaw	250	1050	550	1390	G										
Ara severus	Chestnut-fronted Macaw	250	1200	718	1236	G	E	u	d	u					2	0.18
Primolius couloni	Blue-headed Macaw	250	1300	1039	1039	G										
Aratinga mitrata	Mitred Parakeet	2000	3200	1621	3414	G	R					-2			2	-0.18
Aratinga leucophthalma	White-eyed Parakeet	250	1650	805	1390	G	E	d	u	d					1	0.09
Bolborhynchus lineola	Barred Parakeet	1100	2550	1551	3383	G	E	?	?	?					3	0.27
Bolborhynchus orbygnesius	Andean Parakeet	2500	3500	2956	2956	G										
Nannopsittaca dachilleae	Amazonian Parrotlet	250	1050	1088	1088	G										
Touit huetii	Scarlet-shouldered Parrotlet	300	1300	989	1084	G										
Pionus menstruus	Blue-headed Parrot	250	1250	718	2383	G	R					-3			1	-0.45
Pionus tumultuosus	Speckle-faced Parrot	1100	3000	1430	3032	G	R								-1	-0.09
Amazona mercenaria	Scaly-naped Parrot	1100	3100	826	2942	G	R					-3			2	-0.36
Amazona farinosa	Mealy Parrot	250	1200	818	1350	G	E	d	-	u					1	0.09
Cuculidae																
Piaya cayana	Squirrel Cuckoo	250	2800	550	1779	I	R							-3	-1	-0.64
Dromococcyx pavoninus	Pavonine Cuckoo	250	900	1039	1454	I										
Strigidae																
Megascops ingens	Rufescent Screech-Owl	1000	2100	1330	1390	R										
Megascops albogularis	White-throated Screech-Owl	2500	3250	2530	2720	R										
Ciccaba huhula	Black-banded Owl	250	500	1949	1949	R										
Ciccaba albitarsis	Rufous-banded Owl	1900	3200	2908	2908	R										
Glaucidium bolivianum	Yungas Pygmy-Owl	1500	3500	2312	3414	R	E	d	d	u		2			-2	0.18
Caprimulgidae																
Lurocalis rufiventris	Rufous-bellied Nighthawk	1500	3450	1410	2575	I										
Caprimulgus longirostris	Band-winged Nightjar	1700	3500	2870	2870	I										
Uropsalis segmentata	Swallow-tailed Nightjar	2000	3500	2600	2920	I										
Uropsalis lyra	Lyre-tailed Nightjar	1300	2800	1715	2350	I										
Apodidae																
Streptoprocne rutila	Chestnut-collared Swift	250	3000	1198	2774	I	E	?	?	?					2	0.18
Streptoprocne zonaris	White-collared Swift	250	4000	1039	2609	I										
Chaetura cinereiventris	Gray-rumped Swift	250	1450	1400	1400	I										
Trochilidae																
Eutoxeres condamini	Buff-tailed Sicklebill	450	1950	942	2350	N	R						-2		1	-0.27
Threnetes leucurus	Pale-tailed Barbthroat	250	1200	797	1250	N										
Phaethornis ruber	Reddish Hermit	250	1400	805	990	N	R								-2	-0.18
Phaethornis stuarti	White-browed Hermit	450	450	951	951	N										
Phaethornis hispidus	White-bearded Hermit	250	1400	797	837	N										
Phaethornis guy	Green Hermit	550	1600	942	1691	N	E	u	-	d			2		1	0.45
Phaethornis superciliosus	Long-tailed Hermit	250	1350	893	1202	N										

		Published Elevation		Observed Elevation				Seasonal Transition			Analysis Scores					
Scientific Name	**English Name**	***Min***	***Max***	***Min***	***Max***	***Diet***	***Migr. Stat.***	***DR-EW***	***EW-LW***	***LW-DR***	***PC D***	***PC RA***	***N***	***F***	***C***	***w***
Doryfera ludovicae	Green-fronted Lancebill	800	1900	956	1574	N	R						-1		1	-0.09
Schistes geoffroyi	Wedge-billed Hummingbird	800	1900	797	1954	N	R						-1			-0.18
Colibri thalassinus	Green Violetear	1000	2850	1141	2901	N	E	d	d	u	3				2	1.27
Colibri coruscans	Sparkling Violetear	400	3500	1136	2992	N	E	u	d	n					1	0.09
Heliothryx auritus	Black-eared Fairy	250	1100	1129	1400	N										
Heliangelus amethysticollis	Amethyst-throated Sunangel	1950	3500	2305	3383	N	R				-3	-3			-3	-1.91
Discosura popelairii	Wire-crested Thorntail	500	1500	1202	1390	N										
Phlogophilus harterti	Peruvian Piedtail	750	1500	893	1545	N	R								-1	-0.09
Adelomyia melanogenys	Speckled Hummingbird	1000	2800	938	2870	N	E	u	d	d			1		1	0.27
Aglaiocercus kingi	Long-tailed Sylph	1200	2200	1224	2510	N	E	u	d	n					2	0.18
Lesbia nuna	Green-tailed Trainbearer	3000	3500	2685	2911	N										
Chalcostigma ruficeps	Rufous-capped Thornbill	1800	2700	2184	3101	N	R								-2	-0.18
Metallura tyrianthina	Tyrian Metaltail	1900	3500	2319	3530	N	R					-2			2	-0.18
Haplophaedia assimilis	Buff-thighed Puffleg	1500	2200	1141	2544	N										
Aglaeactis cupripennis	Shining Sunbeam	2500	3350	2924	2991	N										
Aglaeactis castelnaudii	White-tufted Sunbeam	2500	3500	2911	2937	N										
Coeligena coeligena	Bronzy Inca	1000	2400	1129	2937	N	E	u	-	-			3		1	0.64
Coeligena torquata	Collared Inca	2000	3000	2312	2887	N										
Coeligena violifer	Violet-throated Starfrontlet	1900	3350	2465	3550	N										
Boissonneaua matthewsii	Chestnut-breasted Coronet	1900	2900	1645	2972	N	E	u	n	d					1	0.09
Ocreatus underwoodii	Booted Racket-tail	1000	1850	956	2184	N	R					-3	2		-2	-0.36
Heliodoxa schreibersii	Black-throated Brilliant	600	1250	1100	1501	N										
Heliodoxa aurescens	Gould's Jewelfront	250	1050	1133	1133	N										
Heliodoxa rubinoides	Fawn-breasted Brilliant	1500	2200	1400	2324	N	E	u	-	-					1	0.09
Heliodoxa leadbeateri	Violet-fronted Brilliant	900	2000	1088	2154	N	R						-2			-0.36
Chaetocercus mulsant	White-bellied Woodstar	900	3000	1407	2781	N										
Chlorostilbon mellisugus	Blue-tailed Emerald	250	900	1203	1203	N										
Campylopterus largipennis	Gray-breasted Sabrewing	250	1300	879	1202	N										
Thalurania furcata	Fork-tailed Woodnymph	250	1400	866	1350	N	E	u	d	n					2	0.18
Taphrospilus hypostictus	Many-spotted Hummingbird	750	1500	1133	1434	N										
Amazilia chionogaster	White-bellied Hummingbird	1100	3400	797	797	N										
Amazilia viridicauda	Green-and-white Hummingbird	1500	2500	1498	1498	N										
Chrysuronia oenone	Golden-tailed Sapphire	250	1550	1100	1202	N										
Trogonidae																
Pharomachrus auriceps	Golden-headed Quetzal	1300	2800	1360	3049	O	R				-3	-3		1.5	2	-1.18
Pharomachrus antisianus	Crested Quetzal	1000	2100	1239	2338	O	E	u	-	-				1.5		0.27
Trogon melanurus	Black-tailed Trogon	250	1000	826	878	O	R								-2	-0.18
Trogon viridis	Green-backed Trogon	250	750	866	878	O										
Trogon violaceus	Violaceous Trogon	250	800	805	876	O										
Trogon curucui	Blue-crowned Trogon	250	1500	878	904	O										

		Published Elevation		Observed Elevation				Seasonal Transition			Analysis Scores					
Scientific Name	**English Name**	**Min**	**Max**	**Min**	**Max**	**Diet**	**Migr. Stat.**	**DR-EW**	**EW-LW**	**LW-DR**	**PC D**	**PC RA**	**N**	**F**	**C**	**w**
Trogon collaris	Collared Trogon	250	1050	866	1489	O	E	u	-	-					1	0.09
Trogon personatus	Masked Trogon	1100	3500	1230	3032	O	R				-3	1			-2	-1.09
Alcedinidae																
Megaceryle torquata	Ringed Kingfisher	250	1000	800	800	P										
Chloroceryle aenea	American Pygmy Kingfisher	250	500	956	956	P										
Momotidae																
Baryphthengus martii	Rufous Motmot	250	1600	892	1621	I										
Momotus aequatorialis	Andean Motmot	1000	2400	1309	1820	I										
Galbulidae																
Galbula cyanescens	Bluish-fronted Jacamar	250	1450	600	1425	I	R							-3		-0.55
Bucconidae																
Bucco macrodactylus	Chestnut-capped Puffbird	250	1000	780	780	I										
Malacoptila fulvogularis	Black-streaked Puffbird	900	1950	1213	1852	I	R								-2	-0.18
Micromonacha lanceolata	Lanceolated Monklet	500	1500	1139	1852	I										
Nonnula ruficapilla	Rufous-capped Nunlet	250	1250	949	949	I										
Capitonidae																
Capito auratus	Gilded Barbet	250	1350	950	950	O										
Eubucco versicolor	Versicolored Barbet	750	2100	1193	2130	O	R							-3		-0.55
Ramphastidae																
Ramphastos tucanus	White-throated Toucan	250	800	818	876	F										
Aulacorhynchus prasinus	Emerald Toucanet	250	1500	826	1429	F										
Aulacorhynchus derbianus	Chestnut-tipped Toucanet	800	1550	990	1852	F	R								-1	-0.09
Aulacorhynchus coeruleicinctis	Blue-banded Toucanet	1300	2700	1059	2937	F	R					-3			2	-0.36
Andigena hypoglauca	Gray-breasted Mountain-Toucan	1450	3500	1840	3159	F	E	u	n	d					1	0.09
Selenidera reinwardtii	Golden-collared Toucanet	250	1050	826	1682	F										
Pteroglossus azara	Ivory-billed Aracari	250	1200	950	950	F										
Pteroglossus beauharnaesii	Curl-crested Aracari	250	800	948	951	F										
Picidae																
Picumnus aurifrons	Bar-breasted Piculet	250	1250	837	837	I										
Melanerpes cruentatus	Yellow-tufted Woodpecker	250	1200	550	909	O										
Colaptes rubiginosus	Golden-olive Woodpecker	750	2000	1055	2010	I	R				-3			-1.5	-2	-1.55
Colaptes rivolii	Crimson-mantled Woodpecker	1500	3350	1230	3000	I	R					-3			-2	-0.73
Colaptes rupicola	Andean Flicker	3000	3500	2870	2870	I										
Dryocopus lineatus	Lineated Woodpecker	250	1550	934	1224	I	R								-1	-0.09
Campephilus haematogaster	Crimson-bellied Woodpecker	1450	2000	1360	2578	I										
Campephilus rubricollis	Red-necked Woodpecker	300	650	878	878	I										
Campephilus melanoleucos	Crimson-crested Woodpecker	250	1400	893	1217	I										
Furnariidae																
Sclerurus mexicanus	Tawny-throated Leaftosser	250	1100	956	956	I										
Furnarius leucopus	Pale-legged Hornero	250	1100	797	1230	I										

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Scientific Name	***English Name***	***Min***	***Max***	***Min***	***Max***	***Diet***	***Migr. Stat.***	***DR-EW***	***EW-LW***	***LW-DR***	***PC D***	***PC RA***	***N***	***F***	***C***	***w***
Schizoeaca helleri	Puna Thistletail	2700	3500	2904	3414	I	R								-1	-0.09
Synallaxis azarae	Azara's Spinetail	1000	3000	1193	3049	I	R				-3			-3	-2	-1.82
Synallaxis cabanisi	Cabanis's Spinetail	250	1500	797	1396	I	R								-1	-0.09
Synallaxis gujanensis	Plain-crowned Spinetail	250	1300	718	990	I										
Cranioleuca marcapatae	Marcapata Spinetail	2350	3500	2512	2789	I										
Cranioleuca curtata	Ash-browed Spinetail	700	1600	968	1821	I	R				-3	-2		-3		-2.00
Premnornis guttuligera	Rusty-winged Barbtail	1300	2500	1709	2456	I										
Premnoplex brunnescens	Spotted Barbtail	900	2100	1059	2130	I	R						-2	-1.5	-2	-0.82
Margarornis squamiger	Pearled Treerunner	1900	3500	1962	3342	I	R								-2	-0.18
Pseudocolaptes boissonneautii	Streaked Tuftedcheek	2000	3500	1716	3159	I	R					-3			-2	-0.73
Anabacerthia striaticollis	Montane Foliage-gleaner	1000	2000	1039	1899	I	R					3	-2	-3	-3	-0.64
Syndactyla rufosuperciliata	Buff-browed Foliage-gleaner	1000	1950	1279	2016	I	R								-2	-0.18
Simoxenops ucayalae	Peruvian Recurvebill	250	1300	942	1308	I										
Ancistrops strigilatus	Chestnut-winged Hookbill	250	1100	826	878	I	R								-1	-0.09
Hyloctistes subulatus	Striped Woodhaunter	250	1300	800	1129	I										
Philydor ruficaudatum	Rufous-tailed Foliage-gleaner	250	900	1202	1202	I										
Philydor erythrocercum	Rufous-rumped Foliage-gleaner	250	1600	878	878	I										
Philydor erythropterum	Chestnut-winged Foliage-gleaner	250	900	892	951	I										
Philydor rufum	Buff-fronted Foliage-gleaner	250	1000	1100	1100	I										
Anabazenops dorsalis	Dusky-cheeked Foliage-gleaner	250	1350	805	1236	I	R					-2			-2	-0.55
Thripadectes melanorhynchus	Black-billed Treehunter	900	1600	956	1562	I	R							-3	-2	-0.73
Thripadectes holostictus	Striped Treehunter	1500	2500	1355	2349	I	R								-2	-0.18
Thripadectes scrutator	Rufous-backed Treehunter	2300	3200	2305	2569	I										
Automolus ochrolaemus	Buff-throated Foliage-gleaner	250	1400	805	1250	I										
Automolus rubiginosus	Ruddy Foliage-gleaner	250	1400	956	1279	I										
Automolus rufipileatus	Chestnut-crowned Foliage-gleaner	250	1000	797	989	I	R								-1	-0.09
Lochmias nematura	Sharp-tailed Streamcreeper	500	2850	818	2290	I	R								-1	-0.09
Xenops minutus	Plain Xenops	250	1500	818	1279	I										
Xenops rutilans	Streaked Xenops	500	1600	1198	1410	I										
Dendrocincla tyrannina	Tyrannine Woodcreeper	2100	3150	2319	3011	I										
Dendrocincla fuliginosa	Plain-brown Woodcreeper	250	1200	800	1454	I										
Glyphorynchus spirurus	Wedge-billed Woodcreeper	250	1400	800	1496	I										
Dendrexetastes rufigula	Cinnamon-throated Woodcreeper	250	1100	948	1395	I										
Xiphocolaptes promeropirhynchus	Strong-billed Woodcreeper	500	2500	876	3049	I	R					-3			-2	-0.73
Dendrocolaptes certhia	Amazonian Barred-Woodcreeper	250	800	951	1217	I										
Dendrocolaptes picumnus	Black-banded Woodcreeper	250	1350	805	1515	I										
Xiphorhynchus obsoletus	Striped Woodcreeper	250	500	800	800	I										
Xiphorhynchus ocellatus	Ocellated Woodcreeper	250	1350	956	1496	I										
Xiphorhynchus guttatus	Buff-throated Woodcreeper	250	850	866	1115	I										
Xiphorhynchus triangularis	Olive-backed Woodcreeper	1100	2400	1115	2033	I	R						-1	-3	-1	-0.82

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Scientific Name	***English Name***	***Min***	***Max***	***Min***	***Max***	***Diet***	***Migr. Stat.***	***DR-EW***	***EW-LW***	***LW-DR***	***PC D***	***PC RA***	***N***	***F***	***C***	***w***
Lepidocolaptes lacrymiger	Montane Woodcreeper	2000	3200	2200	2795	I										
Campylorhamphus pucherani	Greater Scythebill	2100	3000	797	2542	I										
Campylorhamphus trochilirostris	Red-billed Scythebill	250	1500	800	1429	I	R								-2	-0.18
Thamnophilidae																
Cymbilaimus lineatus	Fasciated Antshrike	250	950	950	950	I										
Cymbilaimus sanctaemariae	Bamboo Antshrike	250	1450	823	1279	I	R								-2	-0.18
Thamnophilus palliatus	Chestnut-backed Antshrike	500	1600	989	1531	I	R							-3	-2	-0.73
Thamnophilus schistaceus	Plain-winged Antshrike	250	1400	805	1236	I	R								-1	-0.09
Thamnophilus caerulescens	Variable Antshrike	1250	2000	1507	2154	I	R						-1		-1	-0.27
Thamnophilus unicolor	Uniform Antshrike	1250	2000	1490	1523	I										
Thamnophilus aethiops	White-shouldered Antshrike	250	950	826	879	I										
Dysithamnus mentalis	Plain Antvireo	600	1600	818	1691	I	R					-2			-1	-0.45
Thamnomanes schistogynus	Bluish-slate Antshrike	250	1400	805	1217	I	R								-2	-0.18
Epinecrophylla spodionota	Foothill Antwren	700	1350	823	1501	I	R								-2	-0.18
Epinecrophylla ornata	Ornate Antwren	250	1500	805	1429	I	R							-1.5	-2	-0.45
Epinecrophylla erythrura	Rufous-tailed Antwren	250	900	879	879	I										
Myrmotherula brachyura	Pygmy Antwren	250	1300	826	1236	I										
Myrmotherula longicauda	Stripe-chested Antwren	500	1550	837	1429	I	R					-2		-3	-1	-1.00
Myrmotherula axillaris	White-flanked Antwren	250	1400	1502	1502	I										
Myrmotherula schisticolor	Slaty Antwren	1100	1950	989	1852	I	R							-1.5	-1	-0.36
Myrmotherula menetriesii	Gray Antwren	250	1100	904	909	I										
Herpsilochmus axillaris	Yellow-breasted Antwren	750	1600	1055	1531	I	R								-1	-0.09
Microrhopias quixensis	Dot-winged Antwren	250	1350	550	1279	I										
Drymophila caudata	Long-tailed Antbird	2100	2100	1442	2952	I	R								-1	-0.09
Hypocnemis subflava	Yellow-breasted Warbling-Antbird	250	1600	805	1429	I	R				-3	-3		-3	-3	-2.45
Terenura sharpei	Yellow-rumped Antwren	1000	1550	934	1651	I	R							-1.5		-0.27
Cercomacra cinerascens	Gray Antbird	250	1000	823	823	I										
Cercomacra serva	Black Antbird	250	1550	800	1567	I	R								-2	-0.18
Cercomacra manu	Manu Antbird	250	1350	805	942	I	R								-2	-0.18
Pyriglena leuconota	White-backed Fire-eye	500	1850	948	2010	I	R				-3	-2			-2	-1.64
Myrmoborus leucophrys	White-browed Antbird	250	1350	800	1088	I	R				-3	-3			-2	-1.82
Myrmoborus myotherinus	Black-faced Antbird	250	1250	818	990	I	R								-2	-0.18
Percnostola lophotes	White-lined Antbird	250	1350	805	1335	I										
Schistocichla brunneiceps	Brownish-headed Antbird	250	1400	818	1341	I										
Myrmeciza hemimelaena	Chestnut-tailed Antbird	250	1550	805	1395	I	R				-3	2			-1	-0.82
Myrmeciza atrothorax	Black-throated Antbird	250	1000	805	990	I										
Myrmeciza goeldii	Goeldi's Antbird	250	800	805	942	I	R								-1	-0.09
Rhegmatorhina melanosticta	Hairy-crested Antbird	250	1200	871	956	I										
Hylophylax naevius	Spot-backed Antbird	250	1200	805	1283	I	R					-3			-2	-0.73
Phlegopsis nigromaculata	Black-spotted Bare-eye	250	1250	934	950	I										

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Scientific Name	**English Name**	**Min**	**Max**	**Min**	**Max**	**Diet**	**Migr. Stat.**	**DR-EW**	**EW-LW**	**LW-DR**	**PC D**	**PC RA**	**N**	**F**	**C**	**w**
Formicariidae																
Formicarius analis	Black-faced Antthrush	250	1150	805	1006	I	R								-2	-0.18
Formicarius rufipectus	Rufous-breasted Antthrush	1100	1700	1139	2012	I	R				-3	-3			2	-1.45
Chamaeza campanisona	Short-tailed Antthrush	1100	1600	1124	2561	I										
Chamaeza mollissima	Barred Antthrush	1900	3100	1962	2995	I	R					-3			-2	-0.73
Grallariidae																
Grallaria squamigera	Undulated Antpitta	2350	3500	2465	3414	I										
Grallaria guatimalensis	Scaled Antpitta	700	1600	1173	1716	I	R								-1	-0.09
Grallaria albigula	White-throated Antpitta	1150	2100	1474	2554	I	R				-3				-2	-1.27
Grallaria erythroleuca	Red-and-white Antpitta	2100	3000	1758	3049	I	R				-3	-3			-2	-1.82
Grallaria rufula	Rufous Antpitta	1800	3500	2739	3414	I	R								-2	-0.18
Myrmothera campanisona	Thrush-like Antpitta	250	1200	893	1334	I										
Grallaricula flavirostris	Ochre-breasted Antpitta	800	2200	1640	1980	I										
Grallaricula ferrugineipectus	Rusty-breasted Antpitta	2600	3250	2456	2995	I	R								-1	-0.09
Conopophagidae																
Conopophaga ardesiaca	Slaty Gnateater	850	1650	1088	1718	I	R						-1		-2	-0.36
Rhinocryptidae																
Liosceles thoracicus	Rusty-belted Tapaculo	250	1100	818	1084	I	R								-2	-0.18
Scytalopus parvirostris	Trilling Tapaculo	2100	3450	2033	3414	I	R				-3	-3			-2	-1.82
Scytalopus atratus	White-crowned Tapaculo	1000	2200	1059	2065	I	R				2	-3			-3	-0.09
Scytalopus schulenbergi	Diademed Tapaculo	2800	3350	3414	3414	I										
Tyrannidae																
Phyllomyias burmeisteri	Rough-legged Tyrannulet	750	1600	1431	1431	I										
Phyllomyias cinereiceps	Ashy-headed Tyrannulet	1300	2700	1373	1517	I										
Phyllomyias plumbeiceps	Plumbeous-crowned Tyrannulet	-	-	1578	1578	I										
Elaenia albiceps	White-crested Elaenia	500	3250	2561	3000	I	E	d	-	-					1	0.09
Elaenia pallatangae	Sierran Elaenia	1100	3250	1410	3049	F	R					-3		1.5		-0.27
Mecocerculus stictopterus	White-banded Tyrannulet	2400	3350	2292	3383	I	R				-3	-3			-3	-1.91
Mecocerculus leucophrys	White-throated Tyrannulet	1800	3500	2305	3070	I	R								-1	-0.09
Anairetes parulus	Tufted Tit-Tyrant	2500	3450	2870	3500	I										
Serpophaga cinerea	Torrent Tyrannulet	600	3000	1357	1400	I										
Pseudotriccus simplex	Hazel-fronted Pygmy-Tyrant	1100	1900	1960	1960	I										
Pseudotriccus ruficeps	Rufous-headed Pygmy-Tyrant	-	-	2452	3377	I	E	d	n	u					1	0.09
Corythopis torquatus	Ringed Antpipit	250	1050	948	975	I	R								-2	-0.18
Zimmerius bolivianus	Bolivian Tyrannulet	1000	2600	1193	2901	O	R				-3	-3		1.5	-1	-1.45
Zimmerius cinereicapilla	Red-billed Tyrannulet	550	1300	1006	1006	O										
Phylloscartes poecilotis	Variegated Bristle-Tyrant	1500	2300	1375	2367	I	E	u	-	-				1.5	1	0.36
Phylloscartes ophthalmicus	Marble-faced Bristle-Tyrant	750	1800	1055	1651	I	R					-3		-3	-2	-1.27
Phylloscartes orbitalis	Spectacled Bristle-Tyrant	500	1250	941	1198	I										
Phylloscartes ventralis	Mottle-cheeked Tyrannulet	1000	1650	1541	2023	I										

Scientific Name	English Name	Published Elevation Min	Published Elevation Max	Observed Elevation Min	Observed Elevation Max	Diet	Migr. Stat.	Seasonal Transition DR-EW	Seasonal Transition EW-LW	Seasonal Transition LW-DR	Analysis Scores PC D	Analysis Scores PC RA	Analysis Scores N	Analysis Scores F	Analysis Scores C	w
Phylloscartes parkeri	Cinnamon-faced Tyrannulet	650	1550	983	1400	I	R							-1.5	-2	-0.45
Mionectes striaticollis	Streak-necked Flycatcher	550	2750	800	3377	O	E	u	d	-			3	3	1	1.18
Mionectes olivaceus	Olive-striped Flycatcher	250	1400	600	1712	O	E	u	-	-			2	1.5		0.64
Mionectes oleagineus	Ochre-bellied Flycatcher	250	1350	800	1134	O										
Leptopogon amaurocephalus	Sepia-capped Flycatcher	250	1100	797	950	I										
Leptopogon superciliaris	Slaty-capped Flycatcher	600	1800	866	1716	I	R				-3	-3	-1	-3	-2	-2.55
Leptopogon taczanowskii	Inca Flycatcher	1850	2750	2130	2350	I										
Myiotriccus ornatus	Ornate Flycatcher	500	1500	818	1202	I	R								-2	-0.18
Myiornis ecaudatus	Short-tailed Pygmy-Tyrant	250	800	876	878	I										
Lophotriccus pileatus	Scale-crested Pygmy-Tyrant	800	1800	956	1821	I	R				-2	-3	-1		2	-1.27
Hemitriccus flammulatus	Flammulated Pygmy-Tyrant	250	850	866	951	I	R								-1	-0.09
Hemitriccus granadensis	Black-throated Tody-Tyrant	2600	3000	2258	3215	I	R				-3	-3			-1	-1.73
Poecilotriccus albifacies	White-cheeked Tody-Flycatcher	250	1050	823	823	I										
Poecilotriccus plumbeiceps	Ochre-faced Tody-Flycatcher	1600	2150	1610	2065	I	R								-2	-0.18
Poecilotriccus pulchellus	Black-backed Tody-Flycatcher	600	1500	990	990	I										
Rhynchocyclus fulvipectus	Fulvous-breasted Flatbill	1000	2000	1124	1665	I	R							-1.5	-1	-0.36
Tolmomyias assimilis	Yellow-margined Flycatcher	250	1000	1224	1224	I										
Tolmomyias flaviventris	Yellow-breasted Flycatcher	250	1500	968	1324	I	E	d	u	n					2	0.18
Platyrinchus mystaceus	White-throated Spadebill	800	1800	1244	1781	I										
Myiophobus inornatus	Unadorned Flycatcher	1000	2150	1529	2130	I	E	u	-	-				1.5	-1	0.18
Myiophobus pulcher	Handsome Flycatcher	1500	2600	2620	3070	I										
Myiophobus ochraceiventris	Ochraceous-breasted Flycatcher	2200	3400	2324	3215	I	R								-1	-0.09
Myiophobus fasciatus	Bran-colored Flycatcher	250	1450	1220	1220	I	A									
Myiobius villosus	Tawny-breasted Flycatcher	650	1350	880	1544	I										
Terenotriccus erythrurus	Ruddy-tailed Flycatcher	250	950	837	975	I										
Pyrrhomyias cinnamomeus	Cinnamon Flycatcher	900	2850	1006	3101	I	R				-3	-3				-1.64
Lathrotriccus euleri	Euler's Flycatcher	250	1500	800	1716	I										
Contopus fumigatus	Smoke-colored Pewee	1000	2800	1081	3101	I	E	u	d	d	3	1		1.5	3	1.82
Contopus sordidulus	Western Wood-Pewee	600	1400	1217	1255	I	B									
Mitrephanes olivaceus	Olive Flycatcher	1550	2100	1682	1718	I										
Sayornis nigricans	Black Phoebe	600	2000	550	1700	I										
Knipolegus aterrimus	White-winged Black-Tyrant	1250	3500	2685	2937	I										
Muscisaxicola fluviatilis	Little Ground-Tyrant	250	1600	718	1600	I										
Myiotheretes striaticollis	Streak-throated Bush-Tyrant	1300	3500	1059	3032	I	E	u	-	-				1.5		0.27
Myiotheretes fuscorufus	Rufous-bellied Bush-Tyrant	2350	3400	2617	2932	I										
Cnemarchus erythropygius	Red-rumped Bush-Tyrant	3250	3350	2524	2524	I										
Ochthoeca pulchella	Golden-browed Chat-Tyrant	3200	3500	3000	3377	I										
Ochthoeca pulchella	Golden-browed Chat-Tyrant	2200	3250	2021	3101	I	R				-3	-3				-1.64
Ochthoeca cinnamomeiventris	Slaty-backed Chat-Tyrant	1500	2800	2290	3001	I	R								-1	-0.09
Ochthoeca rufipectoralis	Rufous-breasted Chat-Tyrant	2500	3450	2339	3377	I	R								-2	-0.18

		Published Elevation		Observed Elevation				Seasonal Transition			Analysis Scores					
Scientific Name	English Name	Min	Max	Min	Max	Diet	Migr. Stat.	DR-EW	EW-LW	LW-DR	PC D	PC RA	N	F	C	w
Colonia colonus	Long-tailed Tyrant	300	1300	775	1230	I										
Legatus leucophaius	Piratic Flycatcher	250	1200	1410	1410	O										
Myiozetetes similis	Social Flycatcher	250	1500	550	1410	I	R							-1.5		-0.27
Myiozetetes granadensis	Gray-capped Flycatcher	250	1300	718	1230	I										
Conopias cinchoneti	Lemon-browed Flycatcher	900	1950	968	1500	I	R					3		-3	-3	-0.27
Myiodynastes chrysocephalus	Golden-crowned Flycatcher	600	2750	989	2734	I	E	u	d	d		2			2	0.55
Myiodynastes maculatus	Streaked Flycatcher	250	1500	1388	1388	I										
Tyrannus melancholicus	Tropical Kingbird	250	2600	600	2723	I	R							-3	-2	-0.73
Rhytipterna simplex	Grayish Mourner	250	1400	866	878	I										
Myiarchus tuberculifer	Dusky-capped Flycatcher	250	3250	990	3215	O	R					-3		1.5	1	-0.18
Myiarchus ferox	Short-crested Flycatcher	250	1100	990	990	O										
Ramphotrigon megacephalum	Large-headed Flatbill	250	1200	805	951	I										
Ramphotrigon fuscicauda	Dusky-tailed Flatbill	250	1050	934	951	I										
Attila spadiceus	Bright-rumped Attila	250	1250	1124	1173	I										
Cotingidae																
Pipreola intermedia	Band-tailed Fruiteater	1500	2900	1459	3101	F	R					-3			2	-0.36
Pipreola arcuata	Barred Fruiteater	2600	3400	1821	3215	F	R				-3	-3			-1	-1.73
Pipreola pulchra	Masked Fruiteater	-	-	1976	1976	F										
Pipreola frontalis	Scarlet-breasted Fruiteater	1000	1500	1780	1780	F										
Ampelion rubrocristatus	Red-crested Cotinga	2500	3450	2685	2924	F										
Ampelion rufaxilla	Chestnut-crested Cotinga	1600	2850	2721	2721	F										
Rupicola peruvianus	Andean Cock-of-the-rock	650	2550	866	2591	F	R					-3			-2	-0.73
Cephalopterus ornatus	Amazonian Umbrellabird	250	1650	1307	1583	F										
Pipridae																
Tyranneutes stolzmanni	Dwarf Tyrant-Manakin	250	800	866	866	F										
Machaeropterus pyrocephalus	Fiery-capped Manakin	250	1350	818	1429	F	R							-1.5	-2	-0.45
Lepidothrix coeruleocapilla	Cerulean-capped Manakin	800	1600	797	1709	F	R							-1.5	1	-0.18
Manacus manacus	White-bearded Manakin	450	950	950	975	F										
Chiroxiphia boliviana	Yungas Manakin	950	2000	956	2033	F	R				-3	-3	1	1.5	1	-1.09
Pipra fasciicauda	Band-tailed Manakin	250	1000	800	1055	F	R								-1	-0.09
Pipra chloromeros	Round-tailed Manakin	250	1400	797	950	F										
Tityridae																
Tityra semifasciata	Masked Tityra	250	1500	991	991	O										
Schiffornis turdina	Thrush-like Schiffornis	250	1400	818	946	F	R								-1	-0.09
Pachyramphus versicolor	Barred Becard	1500	2600	1523	3101	F	E	u	-	d					1	0.09
Family *Incertae Sedis*																
Piprites chloris	Wing-barred Piprites	250	1050	956	956	I										
Vireonidae																
Vireo leucophrys	Brown-capped Vireo	1300	2500	1310	2312	I	R							-3	2	-0.36
Vireo olivaceus	Red-eyed Vireo	250	1900	550	1390	I										

		Published Elevation		Observed Elevation				Seasonal Transition			Analysis Scores					
Scientific Name	**English Name**	**Min**	**Max**	**Min**	**Max**	**Diet**	**Migr. Stat.**	**DR-EW**	**EW-LW**	**LW-DR**	**PC D**	**PC RA**	**N**	**F**	**C**	**w**
Vireo flavoviridis	Yellow-green Vireo	250	900	1410	1410	I	B									
Hylophilus hypoxanthus	Dusky-capped Greenlet	250	1100	826	878	O	R								-1	-0.09
Hylophilus ochraceiceps	Tawny-crowned Greenlet	250	1050	800	1139	O	R								-1	-0.09
Corvidae																
Cyanolyca viridicyanus	White-collared Jay	1850	3000	2290	3101	O	R				-3				1	-1.00
Cyanocorax violaceus	Violaceous Jay	250	1400	718	1255	O	R								-2	-0.18
Cyanocorax yncas	Green Jay	1150	2200	1188	2065	O	R							-3	-3	-0.82
Hirundinidae																
Pygochelidon cyanoleuca	Blue-and-white Swallow	250	3450	1193	1810	I	E	?	?	?					2	0.18
Orochelidon flavipes	Pale-footed Swallow	1500	3500	2557	2557	I										
Atticora fasciata	White-banded Swallow	250	800	550	805	I										
Stelgidopteryx ruficollis	Southern Rough-winged Swallow	250	1600	550	1400	I										
Troglodytidae																
Microcerculus marginatus	Scaly-breasted Wren	250	1250	800	1390	I	R					-3			-2	-0.73
Odontorchilus branickii	Gray-mantled Wren	750	1800	1198	1578	I	R							-3	-1	-0.64
Troglodytes aedon	House Wren	250	3500	2734	3500	I										
Troglodytes solstitialis	Mountain Wren	1850	3400	1851	3235	I	R				-3	-3			-2	-1.82
Campylorhynchus turdinus	Thrush-like Wren	250	1050	823	1332	I										
Pheugopedius genibarbis	Moustached Wren	250	1500	797	1510	I	R				-3	-3			-3	-1.91
Cinnycerthia fulva	Fulvous Wren	2100	3000	1962	3286	I	R								-2	-0.18
Henicorhina leucophrys	Gray-breasted Wood-Wren	1000	2850	1130	2790	I	R				-3	-3	-3		-2	-2.36
Cyphorhinus thoracicus	Chestnut-breasted Wren	800	1600	981	1591	I	R					-1	-1		-2	-0.55
Polioptilidae																
Microbates cinereiventris	Half-collared Gnatwren	450	1000	1210	1210	I										
Cinclidae																
Cinclus leucocephalus	White-capped Dipper	950	2850	858	1460	A										
Turdidae																
Myadestes ralloides	Andean Solitaire	750	2900	797	2828	O	E	u	d	u	3	1	-3		3	1.00
Catharus dryas	Spotted Nightingale-Thrush	750	1500	1124	1398	O	R						-1		-2	-0.36
Catharus ustulatus	Swainson's Thrush	250	3500	1129	2016	O	B									
Entomodestes leucotis	White-eared Solitaire	1300	2900	1139	2781	O	E	u	-	-	1	-3	-1	1.5	2	0.09
Turdus leucops	Pale-eyed Thrush	850	2600	1124	1950	O										
Turdus hauxwelli	Hauxwell's Thrush	250	800	1193	1496	O	R							-1.5		-0.27
Turdus ignobilis	Black-billed Thrush	250	1500	550	1640	O	R							-1.5		-0.27
Turdus nigriceps	Slaty Thrush	250	1850	1204	1851	O	A									
Turdus fuscater	Great Thrush	2500	3500	2673	3500	O	R					-3			-2	-0.73
Turdus chiguanco	Chiguanco Thrush	1300	3500	1800	3520	O	E	n	u	d					1	0.09
Turdus serranus	Glossy-black Thrush	1400	3200	1550	3342	O	R				-3				1	-1.00
Thraupidae																
Cissopis leverianus	Magpie Tanager	250	1600	550	1400	O	R							-1.5	1	-0.18

Scientific Name	English Name	Published Elevation		Observed Elevation		Diet	Migr. Stat.	Seasonal Transition			Analysis Scores					w
		Min	Max	Min	Max			DR-EW	EW-LW	LW-DR	PC D	PC RA	N	F	C	
Creurgops dentatus	Slaty Tanager	1100	2500	1390	2324	I	E	u	-	-				1.5	1	0.36
Hemispingus atropileus	Black-capped Hemispingus	2600	3500	1950	3000	I	R								-1	-0.09
Hemispingus superciliaris	Superciliaried Hemispingus	2500	3000	2324	2870	I	R								-2	-0.18
Hemispingus frontalis	Oleaginous Hemispingus	1500	2500	1870	3242	I										
Hemispingus melanotis	Black-eared Hemispingus	1100	2200	1134	2319	I	R				-3	-3	2	3	2	-0.55
Hemispingus xanthophthalmus	Drab Hemispingus	2200	3250	2650	2781	I										
Hemispingus trifasciatus	Three-striped Hemispingus	3000	3500	3342	3414	I										
Cnemoscopus rubrirostris	Gray-hooded Bush Tanager	1400	2500	1815	2811	I	R								-1	-0.09
Thlypopsis ruficeps	Rust-and-yellow Tanager	1500	3500	1390	2994	I	E	u	-	-				1.5	2	0.45
Trichothraupis melanops	Black-goggled Tanager	1000	1650	1115	1559	O	R						1	-1.5	-1	-0.18
Lanio versicolor	White-winged Shrike-Tanager	250	1000	818	956	O	R								-2	-0.18
Ramphocelus carbo	Silver-beaked Tanager	250	1600	550	1552	O	R							-3	-2	-0.73
Thraupis episcopus	Blue-gray Tanager	250	1600	550	1462	O	R							-3	-1	-0.64
Thraupis palmarum	Palm Tanager	250	1600	990	1410	O	E	u	-	-				1.5		0.27
Thraupis cyanocephala	Blue-capped Tanager	1500	3000	1335	3032	F	R					-3		1.5	1	-0.18
Thraupis bonariensis	Blue-and-yellow Tanager	1000	3500	2660	2815	F										
Buthraupis montana	Hooded Mountain-Tanager	2500	3250	2312	3215	F	R				-3	-3			-2	-1.82
Anisognathus igniventris	Scarlet-bellied Mountain-Tanager	2600	3400	2525	3383	F	R					-3			-2	-0.73
Anisognathus somptuosus	Blue-winged Mountain-Tanager	1600	3000	1375	2470	F	R					-3		1.5	1	-0.18
Chlorornis riefferii	Grass-green Tanager	2100	3200	2292	3215	O	R				-3	-3			-1	-1.73
Dubusia taeniata	Buff-breasted Mountain-Tanager	1900	3200	2305	2305	O										
Delothraupis castaneoventris	Chestnut-bellied Mountain-Tanager	2600	3500	2305	3520	I										
Iridosornis analis	Yellow-throated Tanager	1000	2200	1055	2154	O	R							-3	1	-0.45
Iridosornis jelskii	Golden-collared Tanager	2200	3500	2309	3377	O	R								-1	-0.09
Pipraeidea melanonota	Fawn-breasted Tanager	450	3000	1217	2338	O	E	u	-	-				1.5		0.27
Chlorochrysa calliparaea	Orange-eared Tanager	1000	2200	1059	1779	O	R								-2	-0.18
Tangara ruficervix	Golden-naped Tanager	1000	2100	1395	1400	O										
Tangara cyanicollis	Blue-necked Tanager	500	2000	780	1500	O	R							-3	1	-0.45
Tangara xanthogastra	Yellow-bellied Tanager	250	1300	879	1400	O										
Tangara punctata	Spotted Tanager	600	2000	1059	1763	O	E	u	d	-				3		0.55
Tangara vassorii	Blue-and-black Tanager	1900	3250	1712	3032	O										
Tangara nigroviridis	Beryl-spangled Tanager	1500	2500	1220	2319	O	E	u	d	d				3	2	0.73
Tangara chilensis	Paradise Tanager	250	1600	818	1921	O	R					2		-3	-1	-0.27
Tangara gyrola	Bay-headed Tanager	250	1500	1124	1500	O	R							-1.5	-1	-0.36
Tangara chrysotis	Golden-eared Tanager	850	1600	1290	2115	O	R							-1.5	1	-0.18
Tangara xanthocephala	Saffron-crowned Tanager	1000	2500	1230	2240	O	R							-1.5	1	-0.18
Tangara parzudakii	Flame-faced Tanager	1550	2000	1375	1980	O										
Tangara schrankii	Green-and-gold Tanager	250	1100	826	956	O										
Tangara arthus	Golden Tanager	600	1800	1059	1659	O	R							-3	-2	-0.73
Tersina viridis	Swallow Tanager	250	1450	860	860	O										

		Published Elevation		Observed Elevation				Seasonal Transition			Analysis Scores					
Scientific Name	**English Name**	**Min**	**Max**	**Min**	**Max**	**Diet**	**Migr. Stat.**	**DR-EW**	**EW-LW**	**LW-DR**	**PC D**	**PC RA**	**N**	**F**	**C**	**w**
Dacnis cayana	Blue Dacnis	250	1550	718	1405	O	R							-1.5		-0.27
Cyanerpes caeruleus	Purple Honeycreeper	250	1400	1124	1400	O										
Chlorophanes spiza	Green Honeycreeper	250	1200	718	1430	O										
Iridophanes pulcherrimus	Golden-collared Honeycreeper	1100	1800	1390	1521	O	R							-1.5		-0.27
Hemithraupis flavicollis	Yellow-backed Tanager	250	700	826	826	I										
Conirostrum sitticolor	Blue-backed Conebill	2300	3350	2305	2790	I										
Conirostrum albifrons	Capped Conebill	1200	3000	2130	2789	I										
Diglossa mystacalis	Moustached Flowerpiercer	2600	3500	2789	3560	N	R								-2	-0.18
Diglossa brunneiventris	Black-throated Flowerpiercer	2600	3500	2518	3560	N	R								-1	-0.09
Diglossa glauca	Deep-blue Flowerpiercer	1000	2300	1141	2154	O	E	u	d	d	2		-2	3	2	1.09
Diglossa caerulescens	Bluish Flowerpiercer	1600	2700	1399	2310	O	E	u	-	-				1.5	2	0.45
Diglossa cyanea	Masked Flowerpiercer	1500	3500	1394	3515	O	R				-3	1		1.5	1	-0.55
Catamblyrhynchus diadema	Plushcap	2000	3250	2324	2981	I										
Family *Incertae Sedis*																
Chlorospingus ophthalmicus	Common Bush-Tanager	1000	2400	1193	2561	O	E	u	-	d			1	1.5	2	0.64
Chlorospingus parvirostris	Short-billed Bush-Tanager	1100	2600	1129	2400	O										
Chlorospingus flavigularis	Yellow-throated Bush-Tanager	800	1600	1095	2350	O	R							-3	-2	-0.73
Coereba flaveola	Bananaquit	250	1500	550	1442	O	R							-3	1	-0.45
Saltator grossus	Slate-colored Grosbeak	250	1000	805	1006	O										
Saltator maximus	Buff-throated Saltator	250	1500	797	2507	O	R							-3	-2	-0.73
Saltator coerulescens	Grayish Saltator	250	900	800	800	O										
Emberizidae																
Zonotrichia capensis	Rufous-collared Sparrow	2500	3500	2900	3515	O										
Ammodramus aurifrons	Yellow-browed Sparrow	250	1600	690	1552	O								-1.5	3	
Haplospiza rustica	Slaty Finch	950	3200	1134	2820	G	E	n	d	u					1	0.09
Sporophila schistacea	Slate-colored Seedeater	250	1200	805	1230	G										
Sporophila luctuosa	Black-and-white Seedeater	300	2000	1136	1408	G	E	d	u	-				1.5		0.27
Sporophila castaneiventris	Chestnut-bellied Seedeater	250	1450	830	1390	G	E	d	-	-				1.5		0.27
Oryzoborus angolensis	Chestnut-bellied Seed-Finch	250	1500	941	1324	G										
Arremon taciturnus	Pectoral Sparrow	250	1000	800	989	O	R								-2	-0.18
Arremon brunneinucha	Chestnut-capped Brush-Finch	1300	2150	1367	2109	O	R							-1.5	-2	-0.45
Arremon torquatus	Stripe-headed Brush-Finch	2500	3250	2539	3032	O	R								-2	-0.18
Arremon castaneiceps	Olive Finch	900	1800	1349	1349	O										
Atlapetes melanolaemus	Black-faced Brush-Finch	1400	3200	1330	3231	O	R				-3	-3	-2	-3	-3	-2.82
Cardinalidae																
Piranga flava	Hepatic Tanager	800	2000	1173	1410	O										
Piranga leucoptera	White-winged Tanager	900	1800	1124	1415	O										
Chlorothraupis carmioli	Carmiol's Tanager	450	1250	800	960	O	R								-2	-0.18
Pheucticus aureoventris	Black-backed Grosbeak	600	3250	1210	1400	O	E	?	-	-				1.5		0.27
Cyanocompsa cyanoides	Blue-black Grosbeak	250	1400	797	1213	O										

		Published Elevation		***Observed Elevation***				***Seasonal Transition***			***Analysis Scores***					
Scientific Name	***English Name***	***Min***	***Max***	***Min***	***Max***	***Diet***	***Migr. Stat.***	***DR-EW***	***EW-LW***	***LW-DR***	***PC D***	***PC RA***	***N***	***F***	***C***	***w***
Parulidae																
Parula pitiayumi	Tropical Parula	700	1500	1059	1660	I	R				-3	-3		-1.5	1	-1.82
Myioborus miniatus	Slate-throated Redstart	550	2100	818	2012	I	E	u	d	n	3		-3		-2	0.36
Myioborus melanocephalus	Spectacled Redstart	1600	3350	1390	3383	I	R				-3	-3		1.5	2	-1.18
Basileuterus bivittatus	Two-banded Warbler	750	1500	893	1591	I	R				-3	-3		-3	-3	-2.45
Basileuterus chrysogaster	Golden-bellied Warbler	250	1200	800	1239	I	R				-3	-3			-3	-1.91
Basileuterus luteoviridis	Citrine Warbler	2150	3400	1815	3215	I	R				-2	-3			1	-1.18
Basileuterus signatus	Pale-legged Warbler	1700	2900	1462	2999	I	E	u	d	d	2	-3			3	0.45
Basileuterus coronatus	Russet-crowned Warbler	1100	2550	1330	2460	I	R				-3	-3		-3	-2	-2.36
Basileuterus tristriatus	Three-striped Warbler	1100	2100	1193	2200	I	R				-1	-2	-1	-3		-1.45
Phaeothlypis fulvicauda	Buff-rumped Warbler	250	1500	750	1255	I										
Icteridae																
Psarocolius angustifrons	Russet-backed Oropendola	250	1900	805	2083	O	R					-3		-3	-2	-1.27
Psarocolius atrovirens	Dusky-green Oropendola	1000	2700	983	2750	O	E	u	n	d		3		3	2	1.27
Psarocolius decumanus	Crested Oropendola	250	1300	740	1320	O	E	d	-	-		2			-1	0.27
Psarocolius bifasciatus	Olive Oropendola	250	800	876	970	O	R								-1	-0.09
Cacicus chrysonotus	Mountain Cacique	2300	3250	2010	3342	O					2	-3			-2	
Cacicus cela	Yellow-rumped Cacique	250	1050	718	934	O										
Amblycercus holosericeus	Yellow-billed Cacique	2600	3300	2456	2887	O										
Fringillidae																
Carduelis magellanica	Hooded Siskin	400	3500	990	1523	F										
Euphonia mesochrysa	Bronze-green Euphonia	600	1800	970	1678	F	R							-3		-0.55
Euphonia xanthogaster	Orange-bellied Euphonia	250	2100	797	2130	F	E	u	d	n	-1	3	-1		3	0.27
Chlorophonia cyanea	Blue-naped Chlorophonia	250	1900	876	2115	F	E	u	d	n					3	0.27

VITA

Christopher L. Merkord was born and raised in central Texas. He earned his bachelor’s degree in 2002 from Texas A&M University, majoring in Wildlife & Fisheries Sciences, with an emphasis in Vertebrate Zoology, and his Ph.D. in 2010 from the University of Missouri in Biological Sciences, with an emphasis in Ecology & Evolutionary Biology. He is married to Marissa Ahlering and is living happily in North Dakota.