

AVIAN LIFE HISTORY DIVERSIFICATION ALONG AN ANDEAN ELEVATION
GRADIENT: A NESTING PERSPECTIVE

By

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To my mom who always invested in my education and supported my dreams and adventures to study birds in Colombia and other countries, and Rosario's unconditional support despite my long trips to the field

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Abstract of Dissertation Presented to the Graduate School
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Many tropical birds have life history traits such as small clutches and long incubation periods that characterize as a “slow pace of life” and presumably maximize fitness in the face of a relatively benign climate and intense biotic constraints on reproduction -- namely, nest predation and competition. Nest mortality plays an important selective role in shaping avian life history traits, ecology and the composition of communities. Nest predation is the most common type of nest failure; thus, nest predators directly influence avian reproductive success. To evaluate these ideas I examine three perspectives: 1) if variation in nest predation rates and predator frequency could act as ecological factors influencing species turnover patterns along an Andean elevational gradient. 2) If interspecific shifts in life-history traits of tanagers along a tropical elevation gradient are promote by changes in abiotic factors with elevation. 3) If tropical bird species evolving under relatively stable climates make similar investment decisions within elevation bands, but to differ considerably among elevation bands. To evaluate these ideas I study nesting behavior, success and predation on an elevation gradient (350-3100m) in the Manu National Park, Cusco and

Madre de Dios, Peru, between 2007 and 2011. I found that: 1) Nest predation rates decreased non-linear with an abrupt decrease between 1100–1350m, the zone in which predation by snakes and primates declined steeply. In general, community turnover was highest between zones in which nest predation rates and composition of the predator community changed the most. 2) Six of the 13-tanager species had a clutch size of one egg that was associated with longer incubation and nestling periods, lower nestling growth, and colder climates. 3) Incubation period increase with elevation and incubation strategies varied considerable among species within elevation band. These results suggest that nesting birds decision in the elevation gradient vary accordingly with changes in abiotic and biotic factors, which relative importance change with elevation. Dramatic shifts in nest predator communities and nest predation rates can explain variation in nesting success of species, and the slow pace of life in tanagers in the high Andes results from cold temperatures.

CHAPTER 1 INTRODUCTORY REMARKS

One of the key goals of life-history studies is to understand how biotic (e. g., predation) and abiotic (e. g., temperature) factors affect behavior and reproductive effort of an organism throughout its life (Reznick & Endler 1982; Stearns 1992; Roff 2002). Variation in the number of eggs among populations of oviparous species, for example, has been linked to differences in parental care (Stearns 1992; Roff 2002). Oviparous species such as birds, which invest greatly in parental care, tend to produce fewer eggs than similar taxa with less parental care. Although increasing investment in parental care typically accelerates embryonic development, it is costly for the parents and may constrain future reproduction. In particular, parental care entails trade-offs between self-maintenance behaviors (e. g., foraging) and embryonic development. These trade-offs are exacerbated when nesting oviparous species encounter environments with harsh biotic and abiotic factors such as high predation and cold temperatures that increase reproductive and parental care costs (Ghalambor & Martin 2002; Lima 2002, 2009).

Although it is generally accepted that investment decisions vary in contrasting environments (Berven 1982a, b; Baur & Raboud 1988; Badyaev 1997; Rohr 1997; Hancock *et al.* 1998; Badyaev & Ghalambor 2001), there is controversy about the proximate mechanisms that promote this variation (Badyaev & Ghalambor 2001; Ricklefs & Wikelski 2002; Martin 2004). One such controversy concerns the hypothesized mechanisms underlying the small clutch sizes and long incubation periods observed in many tropical birds. These traits have been generalized as latitudinal changes in the “pace of life”. In this context, tropical birds share many traits associated with a low pace of life: lower feeding rates and slower nestling growth (Skutch 1949;

Martin *et al.* 2011), lower adult mortality (Gill & Haggerty 2012) and lower metabolic rates (Wikelski *et al.* 2003; Wiersma *et al.* 2007). Alexander Skutch, for example, hypothesized that high biotic constraints, in particular high rates of nest predation, would select for smaller clutches and the reduced parental investment per nesting attempt associated with the slow pace of life (see also, (Martin *et al.* 2006; Martin *et al.* 2007; Martin *et al.* 2011). Yet, high rates of nest predation do not explain the longer incubation periods in species with small clutch sizes (Skutch 1985; Ricklefs & Wikelski 2002; Robinson *et al.* 2010; Roper *et al.* 2010). To date, most studies of these traits (e. g., small clutches, long incubation and nestling period) have involved latitudinal comparisons that might be confounded by multiple other factors that vary with latitude (e.g., productivity, day length, phylogenetic structure, seasonality; (Ricklefs & Wikelski 2002; Martin 2004; Robinson *et al.* 2010). One possible way to control for many of these variables (e. g., climate, nest predation pressure, productivity, phylogenetic structure) is to focus on variation in life-history traits in contrasting environments within the tropics, especially in environments that vary predictably in rates of nest predation and in abiotic variables such as temperature. Therefore, in my thesis I decided to exploit the variation in these selective pressures along an elevation gradient within the Neotropics by exploring how nesting strategies, particularly incubation, responds to these contrasting environments.

Tropical mountains have great promise as a place to uncover the mechanisms responsible for the slow pace of life observed in the reproductive behavior of tropical birds (Ricklefs & Wikelski 2002) because nest predation and ambient temperature change in a predictable way. The proportion of nests depredated (Skutch 1985; Boyle

2008) and ambient temperature (Janzen 1967; Ghalambor *et al.* 2006) decrease linearly with elevation, which makes it possible to test if changes in investment in eggs and incubation are associated with nest predation, ambient temperature, or both. Overall, bird species that nest in areas with high nest predation have smaller clutches and eggs (Martin *et al.* 2006), increase the proportion of the day they spend on the nest incubating the eggs (Ghalambor & Martin 2002) and have shorter incubation periods (Martin *et al.* 2007). In contrast, species that nest in colder climates have smaller clutches (Badyaev & Ghalambor 2001; Lu *et al.* 2010), increase their foraging trips (Conway & Martin 2000a), and have longer incubation periods (Lu *et al.* 2010). Therefore I predicted that bird species should change incubation investment decisions throughout tropical elevation gradients. I predicted that bird species nesting at high and low elevation would have smaller clutches and eggs compared with birds nesting at middle elevations, but that incubation constancy should be similar across the gradient. To test these predictions I used data from 84 species for which I had incubation period data along this 2750-m Andean elevation gradient in southeastern Peru.

Before I could test these predictions, however, I needed to know if indeed nest predation decreases linearly with elevation, as reported in previous studies (Skutch 1985; Boyle 2008). Those studies were based either on data from artificial nests baited with eggs (Boyle 2008) or on data from many widely scattered sites in Central America (Skutch 1985). A better test of the hypothesis that nest predation changes systematically with elevation would be based on observations of real nests along one elevation gradient. In the first chapter of my thesis, I estimated the daily nest predation rate from data on 1584 nests of 245 species along the Manu Road in Peru. To help

understand the mechanisms underlying any changes in nest predation with elevation, I used camera traps to document the identity of nest predators at four different elevation ranges (350-500 m, 700-1100 m, 1200-1600 m, and 2300-3100 m). I found that nest predation decreases with increased elevation, but it does not do so linearly, as previously suggested (Skutch 1985; Boyle 2008). I found that nest predation decreases dramatically between foothill and cloud forest bird communities (1100-1350 m). Furthermore, I found that this decrease in nest predation was associated with a dramatic decrease in nest predation by snakes -- from 46.4% in the lowlands to 20.8% in the cloud forest and 0%; forests from 2300-3100m. The majority of bird nests at all elevations were depredated during the day, therefore, selection for behaviors around the nest (e.g., number of trips to and from the nest) should be similar along the gradient.

In the second chapter I explored how the abrupt change in nest predation in the foothills and the linear decrease in ambient temperature over the entire gradient affected incubation time across 84 species. First, I evaluated whether daily nest predation rates among the 84 species followed the same general pattern that I documented for the sample from the entire community of 245 species. I found that nest predation decreased significantly in the cloud forest (1200-1600 m), but increased at higher elevations. In general, I found that changes in investment decisions were mainly associated with ambient temperature. Although the clutch size (the number of eggs produced per nesting attempt) was relatively constant along the gradient, egg mass increased with elevation. Similarly, egg temperature decreased with elevation, which supported the hypothesis that low temperatures constrain embryonic development

(Badyaev & Ghalambor 2001; Olson *et al.* 2006). Although incubation period did not vary significantly among bird communities, it had a tendency to increase with elevation.

In the third and final chapter I show that for one clade (tanagers) the "pace of life" varies substantially even within the tropics and document further clutch reduction among passerines at high elevations, an entirely new "pace of life" that is even slower than other tropical species (Martin 2004; Robinson *et al.* 2010). Of particular interest, I discovered that six species of mountain tanagers had one-egg clutches, thus decreasing their potential fitness and reproductive investment by 50% relative to species with the typical clutch size of two eggs, all else being equal. Based on a literature review for the monophyletic tanager clade, this is the first time one-egg clutches have been reported. Clutch size has a strong phylogenetic signal in this clade, but it is variable among species in the mountain tanager sub clade. Additionally, I found that tanager species with one-egg clutches inhabit higher elevations and had longer incubation and nestling periods than tanager species with two- and three-egg clutches. I also collected more detailed nesting data for 12 tanager species that nest in the elevation gradient. These data also showed that species with one-egg clutches inhabited high elevations and had longer nestling periods and slower nestling growth rates. Taken together, these results suggest that the combination of constant severe abiotic constraints (e. g., cold temperature) and high nest predation severely constrain tanager nesting and lead to an extremely slow pace of life; tropical tanagers living at high elevations are likely "making the best of a bad situation."

CHAPTER 2 CHANGES IN NEST PREDATION, PREDATOR IDENTITY AND BIRD COMMUNITY COMPOSITION ALONG AN ELEVATION GRADIENT IN THE ANDES

Introduction

Nest mortality is proposed to play an important role in avian ecology and community composition (Cresswell 1997; Martin *et al.* 2000; Lima 2009; Cresswell 2010; McKinnon *et al.* 2010). Predation is the most important type of nesting failure and, hence, the most important type of predator-prey interaction is likely with nest predators (Ricklefs 1969; Martin & Roper 1988). Experimental studies have demonstrated that birds use nest predator cues to choose among habitats, such that individuals exposed to habitats with different levels of predation risk prefer those habitats with lower risk (Fontaine & Martin 2006; Morosinotto *et al.* 2010; Parejo & Aviles 2011). Spatial variation in nest predation has also been used to explain the evolution of bird migration along large-scale (e.g., latitudinal) and small-scale (e.g., elevational) gradients (Boyle 2008; McKinnon *et al.* 2010). Taken together, these studies suggest that regional differences in avian life histories and reproductive success can be caused by spatial variation in nest predation (Matysioková *et al.* 2011).

Although nest predation rates vary across landscapes (Chalfoun *et al.* 2002; Martin *et al.* 2006; Matysioková *et al.* 2011), our understanding of the factors responsible for this variation is limited. Nest concealment, nest type, and parental behavior have been used to explain variation in nest predation, but results are rarely consistent among studies (Cresswell 1997; Fontaine *et al.* 2007; Matysioková *et al.* 2011). Variation in the identity and relative importance of nest predators is increasingly considered to be an important predictor of nesting success and an important explanatory factor in patterns of nest predation (Benson *et al.* 2010; Reidy & Thomson

2012). For example, one possible source of variation in predation rates is spatial variation in nest predator composition (Rodewald & Kearns 2011; Cox *et al.* 2012). Studies of forest bird communities, however, have not yet linked geographical variation in avian nest predation rates with variation in predator community composition. Understanding the relative importance of different nest predators and their activity patterns should improve our understanding of which life-history traits may allow bird species to thrive in different habitats or at particular locations along environmental gradients (Lima 2002). Habitats dominated by diurnal predators, for example, will impose very different selective regimes on avian life histories than those dominated by nocturnal predators (Carter *et al.* 2007; Reidy & Thomson 2012).

While the high avian community turnover found along tropical elevational gradients has been partially linked to biotic factors such as competition and vegetation structure (Jankowski *et al.* 2012), other biotic factors such as nest predation may also influence species elevational distributions and could have far-reaching effects across montane species. Evidence from both artificial nests (Boyle 2008) and from studies of actual nests from widely scattered sites at different elevations (Skutch 1985) shows that nest predation varies with elevation in the Neotropics. If there is substantial variation in actual nest predation rates with elevation, as these studies have suggested, then I may also expect nest predation to be an important driver of changing species composition with elevation, potentially reinforcing the elevational range limits of multiple species. In addition to changes in the rate of nest predation with elevation, shifts in the predator community may also be critical determinants of nesting success of species at different elevations and may also underlie patterns of species turnover.

Here I report patterns of nest predation along a large-scale elevational gradient (350-3100m) in the eastern Andes of Peru (Walker *et al.* 2006), a diverse region characterized by high avian species turnover (Patternson *et al.* 1998; Jankowski *et al.* 2012). Specifically, I sought to answer four questions: (1) Do overall rates of nest predation vary with elevation? (2) Does taxonomic composition of nest predators vary with elevation? (3) Do daily activity patterns of predators and the timing of nest predation (nocturnal vs. diurnal) vary with elevation? (4) Do abrupt shifts in nest predation along the gradient correspond with abrupt shifts in bird species composition? If variation in nest predation rate is one of the mechanisms underlying shifts in the composition of bird communities along this gradient, then I predicted that there will be substantial bird community turnover in zones where there are dramatic changes in nest predation rates (e. g., between 1000-1500 m) (Terborgh 1971; Rahbek 1977; Patternson *et al.* 1998; Herzog *et al.* 2005; Jankowski *et al.* 2012).

Methods

Study site: This study was conducted along an elevational gradient in the southeastern Andes of Peru in the Manu Biosphere Reserve between 2008 and 2011, during the height of the breeding season each year (August to December). Data collection took place at four stations distributed along this gradient (Table 1). The low elevation station, Pantiacolla, is located in the buffer zone of Manu National Park between the Pantiacolla ridge and the Alto Madre de Dios River. The site features lowland tropical rainforest, with a combination of high canopy floodplain and *terra firme* habitat. The second station, Tono, is found in the Andean foothills near the Tono River inside Manu National Park. This site contains typical premontane forest with rolling hills and outlying ridges, where forest canopy is slightly shorter than lowland forest. The mid-

elevation station, San Pedro, is found within the Kcosñipata Valley near the intersection of the San Pedro and Kcosñipata Rivers. This site contains lower montane cloud forest, with a high density of mosses and epiphytes and an average canopy height half that of foothill forest. The high elevation station is at the Centro de Investigación Wayqecha near forest treeline and harbors the last low canopy cloud forest moving upslope before *puna* grassland becomes dominant at higher elevations. The San Pedro and Wayqecha stations are found along the Manu road, which descends along the eastern slope of the Andes down to the foothills (Patternson *et al.* 1998; Jankowski *et al.* 2012).

Nest search: To address whether nest predation varies with elevation, I searched for and monitored nests along the gradient following protocols approved by the University of Florida IACUC. Nest searching teams were assembled at each station, where an average of nine (Pantiacolla), seven (Tono), seven (San Pedro) and five (Wayqecha) people searched for nests for ten hours a day, six days a week from mid-August until mid-December. At all stations, each team member was assigned to different 5-10 ha plots, where they searched for and monitored nests throughout the season. To cover additional elevations, I conducted weekly nest searches between 1500 and 3000 m along the Manu Road. I used two techniques to monitor nests, depending on nesting stage: (1) During the incubation period I positioned a thermal sensor inside the nest connected to a U12 4-channel Hobo data logger (Onset Computer Corporation, MA, USA <http://www.onsetcomp.com>) that recorded nest temperature every minute, allowing us to continuously monitor incubation activity. Thermistors registered arrivals and departures of birds, consistently recording abrupt changes in temperature (<1.5 °C). (2) For nests with eggs or young, I deployed motion

cameras (Rapidfire professional; Reconyx, Inc. WI, USA; between 10 and 27 per station) placed on tripods 0.5 to 1m from the nest and covered with vegetation to reduce disturbance and conspicuousness. Cameras were programmed to take ten photos when camera sensors detected movement at the nest. Once a camera or data logger was set, it was removed either after a predation event, when eggs hatched (only nests with data loggers), or when the nestlings left the nest (only nests with cameras). These techniques allowed us to continuously monitor more than 90% of encountered nests. Nests with nestlings were visited daily and some were continuously monitored with motion cameras based on camera availability. Nests with data loggers and cameras were visited every six days to download data and replace batteries, and nests without data loggers or cameras were visited every three days, except those along the road, which were visited weekly. Daily nest survival probability did not vary among nets monitoring techniques: nest with camera traps (0.95; CI 95% = 0.94-0.96, n = 122), data loggers (0.96; CI 95% = 0.95-0.96, n = 558), camera trap and data logger (0.96; CI 95% = 0.95-0.97, n = 182) and traditional three to four day monitoring (0.93; CI 95% = 0.92-0.93, n = 721).

To reduce disturbance and decrease the impact created by unfamiliar objects around the nest, I covered the data loggers, cables, and camera traps with vegetation (e.g., dry leaves, moss). Also, to reduce disturbance and avoid nest abandonment, I avoided revisiting nests during the laying period, when birds are more prone to abandon their nest; eggs were not measured and monitoring equipment was not put in place until 2-3 days after clutch completion in most nests.

Data analyses: To estimate daily nest predation rate, I used a nest survival model constructed using the program MARK (Rotella 2007). This model allowed us to estimate daily nest survival probability using the number of exposure days to calculate probability of survival. I used all nests with known fate (depredated or successful), regardless of monitoring technique (n = 1584). Variables in the model included: (1) the first date an active nest was encountered; (2) the last date the nest was checked and eggs or nestlings were present; (3) the last date the nest was checked; (4) the fate of the nest (0 = successful, 1 = depredated); and (5) the nest location within continuous elevational bands of 250m, between 350 and 3100 m (i.e., 350-600m, 600-850m, etc.). The gradient was divided into 250m bands because it was the minimum range with adequate sample size that would not affect nest daily survival probabilities.

I examined the change in taxonomic composition of nest predators with elevation using photos provided by cameras to identify predators. I tested for significant variation with elevation in the proportion of these broad taxonomic groups (i.e., birds, mammals, and reptiles) using a Chi-squared test.

To examine whether the time at which nest predation occurred (day vs. night) varied with elevation, I noted the time of nest predation (n = 505 nests). Daytime was defined as hours between 06:00 and 18:00 and nighttime between 18:01 and 05:59. Time of nest predation was usually obvious for nests with camera traps. For nests with data loggers, a predation event was marked by prolonged departures of incubating adults that broke the normal cycle of incubation. Although less direct than the use of cameras, the accuracy of this technique has been independently validated (Libsch *et al.* 2008).

To address whether changes in nest predation corresponded with areas of high turnover in bird species along the elevational gradient, I compared daily nest predation risk with data on species turnover from elevational zones between 850-3100m (as sufficient lowland species distribution data are not yet available). For daily nest predation risk, I estimated daily nest predation probability for the nine 250 m elevational zones between 850 and 3100 m. Species turnover data come from a large number of point count surveys (n=940) conducted during the early avian breeding seasons (July-November) of 2006-2009 at 235 survey sites (see Jankowski *et al.* 2012 for more details on survey methods). Species detected during any visit to the survey site were considered present. Survey sites within 250 m elevational zones were combined to create a site-species presence-absence matrix for 367 bird species and nine 250-m elevational zones. Differences in species composition between elevational segments were calculated using Simpson's dissimilarity index (Lennon *et al.* 2001) (to create a dissimilarity matrix. I used a generalized dissimilarity model (GDM; which allows for nonlinear relationships between predictor and response matrices (Ferrier *et al.* 2007) to determine the variation in bird dissimilarity among zones explained by differences in daily nest predation risk.

Results

Daily nest predation was estimated for 1584 nests from 245 bird species and predator identity was documented in 136 cases. Additionally, the time of day when nest predation occurred was recorded for 505 nests.

Daily nest predation rates: Community-wide nest predation rates decreased nonlinearly with elevation (Figure 2-1). Daily nest predation rates were high at low elevations (7.1%; 350-600m), reached a peak at foothill elevations (9.8%; 850-1100m),

abruptly decreased to 3.8% above 1350m, and remained fairly constant at higher elevations (1.3-4.7%). Hence, daily nest predation in the foothills was 1.4 times greater than in the lowlands and 2-3 times greater than elevations above the foothills.

Taxonomic composition of predator communities: All taxonomic groups were recorded as nest predators at all elevations, with the exception of reptiles and invertebrates, which were never recorded predating nests at high elevations (Figure 2-2). Overall, reptiles and mammals were the most frequent nest predators (37.8% and 38.5% of all predation events, respectively), followed by birds (16.9%) and invertebrates (6.7%). The relative importance of each predator type changed with elevation ($X^2 = 58.3$, $df = 6$, $P < 0.0001$, $n = 138$; Figure 2). Reptiles were the most frequent predators recorded at the two lower stations, comprising 39.4% of predation events in the lowlands (350-600m) and 46.4% of predation events in the foothills (750-1100m). The frequency of reptile predation events decreased abruptly to 20.8% above 1250m where only one nocturnal species of snake was recorded between 1250 and 1600m (*Oxyrhopus petola*; Appendix 1). Within the reptile category, snakes were responsible for 95.7% of predation events, and among snakes, one species, *Pseustes sulphureus*, was responsible for 78.3% of predation events. The frequency of nest predation by mammals decreased by 83.3% from the lowlands to the foothills (750-1100m) and then increased by 76.5% at higher elevations (Figure 2-2). Among mammalian predators, marsupials and primates were detected with the same frequency and together accounted for 72% of all mammalian predation events. Primates accounted for 65% of mammalian nest predation events between 350-600m and 35% between 1250-1600m, but I did not document any primate nest predation event in the foothills between 750-

1100m. In contrast, marsupials accounted for 30% of the mammalian predation events between 350-550m, 20% between 750-1100m, and 45% between 1250-1600m. Nest predation frequency by birds was low below 1600m, but birds were the most frequent nest predators, along with mammals, at higher elevations (Figure 2-2). Among birds, most (92%) predation events between 350-1100m were by toucans. At high elevations (2500-3000m), 66% of bird predation events were by one species, *Turdus fuscater*. Invertebrate nest predation was the rarest type of nest loss at all elevations, except between 1250-1600m; ants accounted for 70% of all invertebrate predation events.

Timing of nest predation: Overall, 331 predation events occurred during the day and 174 occurred at night (Figure 2-3a). Nocturnal and diurnal predation events varied among predator taxa. Birds and reptiles depredated nests mainly during the day: 91.7% and 73.3% of bird and reptile predation events, respectively, occurred during daylight hours (Figure 2-3a,c). In contrast, mammals tended to depredate nests during the night (56.4%; Figure 2-3b). Diurnal nest predation did not change significantly with elevation among birds ($R^2 = 0.09$, $P = 0.17$) or among snakes ($R^2 = 0.001$, $P = 0.80$; Figure 2-3a,c), but mammalian nest predation was exclusively nocturnal at high elevations ($R^2 = 0.12$, $P = 0.009$; Figure 2-3b). As elevation increased, nest predator communities became dominated by a few nocturnal mammals and diurnal birds (e.g., *Turdus fuscater*).

Nest predation and bird species turnover: Along the elevational gradient, I found that abrupt increases in rates of nest predation occurred at the same two elevational zones where the composition of bird species changed most dramatically (Figure 2-4). When comparing the bird species composition of adjacent elevational

zones, I found the highest species turnover between the elevational zones of 850-1100m and 1100-1350m where approximately 60% of bird species were replaced. This shift in bird species composition was associated with a 2.2% increase in daily nest predation compared with the lowlands and a 6.0% increase compared to most elevations above the foothills (Figure 2-4). Similarly, the second largest shift in bird species composition occurred between the elevational zones of 1850-2100 and 2100-2350m, where roughly 50% of bird species were replaced. At this elevation, I observed a 3.4% increase and 1.6% decrease in daily nest predation compared to elevations immediately below and above this elevation, respectively (Figure 2-4). Across the entire gradient, differences in nest predation rates alone explained 29.8% of the variation in compositional dissimilarity of species among elevational zones, and were positive ($R^2 = 0.33$, $P = 0.08$).

Discussion

Although nesting success increased with elevation, it did not do so in a linear fashion, as previously suggested (Skutch 1985; Boyle 2008). The daily rate of nest predation I recorded at low elevations, 7%, is near the upper end of the range of daily nest predation values reported for tropical forest birds (0.038—0.083) (Robinson *et al.* 2000; Martin *et al.* 2006). In contrast, the rate of daily nest predation of 0.098 in the foothills is among the highest rates recorded for a tropical bird community.

Furthermore, this nest predation rate in the foothills is even higher than those recorded from small forest fragments thought to be population sinks for nesting songbirds in North America (Robinson *et al.* 1995). Above 1350m, nest predation rates abruptly declined from 9.8% to 3.8%, beginning to approach those more typical of temperate and cloud forest habitats (~0.038; Martin *et al.* 2006).

I found support for my prediction that nest predation rates and frequency of nest predators change most abruptly in zones of high bird species turnover. My analysis of species turnover found that the abrupt increase in nest predation between 850-1350m coincided with the largest peak in bird species turnover along the gradient. Likewise, an increase in nest predation between 1850-2350 coincided with a smaller peak in species turnover along the gradient. High species turnover in foothill elevations (i.e., between 1000-1500m) has been reported along other tropical mountains (Rahbek 1977; Herzog *et al.* 2005); however, the abiotic (e.g., temperature, precipitation) and biotic (e.g., competition, vegetation structure) factors considered in these studies have not provided a mechanism for why so many lowland bird species disappear above this elevational band, or, alternatively, why so many highland bird species do not extend their ranges downslope into a thermally benign foothill environment. Physiological limitations have been proposed as a mechanism to explain the narrow distribution of birds on elevational gradients (Janzen 1967; Ghalambor *et al.* 2006), and competition has been proposed for setting the lower and upper distributions of species (Terborgh 1971; Remsen & Graves 1995). There are no data available, however, on avian physiology for species on tropical mountains to test the former hypothesis, and interspecific competition may explain some congener replacements but not community-wide turnover patterns (Terborgh 1971; Jankowski *et al.* 2010). I propose that high nest predation pressure below cloud-forest elevations at least partially explains why many montane tropical species have not extended their ranges downslope to warmer and more productive sites. The extraordinarily high nest predation found in the foothills in combination with lower temperatures compared to lowland habitats may also truncate the upper

distribution of lowland birds. Rahbek (1997) demonstrated that the high peak in bird species richness observed in the foothills of tropical mountains is mainly driven by the overlap of elevational ranges limits between highland and lowland communities (see also Herzog *et al.* 2005) and proposed that foothill tropical bird communities may be marginal populations that are poorly adapted to local conditions. My results support this hypothesis and provide a plausible mechanism—high rates of nest predation may make foothills suboptimal habitat for most birds. Thus, despite the high species richness observed in the foothills of tropical mountains, this elevational zone may represent a sink habitat, where lowland and highland nesting birds may not be able to cope with local conditions, specifically, a combination of cooler temperatures (relative to lowland thermal regimes) and high nest predation.

The abrupt decrease in rates of nest predation above the Andean foothills was coincident with a shift in the relative frequency of common nest predators at lower elevations. The loss of diurnal snakes and mammals likely played a role in the community-wide decrease in predation rates from the foothills to cloud forest. Snake predation frequency increased in the foothills where mammalian nest predation frequency decreased, which made snakes by far the most important predators in this zone. Among snakes the species most frequently observed depredating nests in the lowlands was *Pseustes poecilonotus* (83%), which has been reported as a common nest predator in other lowland tropical forests (Robinson *et al.* 2005; Tarwater 2008). Given how frequently *P. sulphureus* preyed on nests below 1100 m and its complete absence as a nest predator above 1200 m, the elevational distribution of this single

species may be largely responsible for the overall drop in nest predation above 1200 m the Andean foothills.

Both diurnal and nocturnal predation events were recorded at all elevations and were observed in all taxonomic groups of predators, but the frequency of diurnal predation decreased with elevation, primarily because snakes and diurnal mammals became increasingly rare at higher elevations. Because many of the life history and behavioral traits associated with reducing nest predation rates (e.g., number of foraging trips, active mobbing of nest predators) are only affected by diurnal nest predators, this reduction of diurnal nest predation at high elevations may relax selection on these traits. Nocturnal nest predation, however, is not trivial anywhere on the gradient. The combination of nocturnal and diurnal predation could favor diverse nesting strategies across bird species, depending on the suite of common predators and differences in nest searching strategies among those predators. For example, bird species whose nests are more likely to be depredated by common diurnal predators (i.e., snakes, primates and birds) may show a reduced number of foraging trips (Fontaine *et al.* 2007), but I would not expect similar traits for species that are depredated mainly by nocturnal mammals. It is likely that species nesting at low elevations and in the foothills require a suite of adaptations that enable them to cope with extreme levels of nest predation; such characteristics could include short nesting cycles (Badyaev & Ghalambor 2001; Lu *et al.* 2010) and minimizing the number of trips to the nest (with correspondingly long incubation bouts; Badyaev and Ghalambor 2001). Such high selection pressures imposed by predation may be strongest for common species if nest predation is density-dependent (Martin & Roper 1988), with the result that rare species, with low population

densities, have an advantage in these environments (Martin & Roper 1988). Species nesting at higher elevations, which encounter cooler environments, should be expected to have longer nesting cycles and make more frequent trips to and from the nest (Badyaev 1997; Conway & Martin 2000a; Lu *et al.* 2010), but these are traits that would make them less able to cope with high levels of nest predation at lower elevations, especially those in the foothills. A comparison of life history traits of species nesting above and below this transition zone would shed light on the potential for this abrupt shift in nest predation rates to act as a habitat filter (Reznick & Endler 1982).

Although the incremental increase in nest predation observed in the second zone of species turnover from 1850-2350m seems small relative to the changes in the foothill region, it may impose a strong selection pressure in nesting traits above this elevation compared to the foothills. Birds nesting in cold temperatures can increase energy expenditure up to three times basal metabolic rate (Williams 1996), and the low productivity of these environments (Salinas *et al.* 2011) may not supply enough food to compensate for harsh weather conditions (Moreno 1989). Thus, I propose that middle elevations (cloud forest) can serve as a refuge for nesting birds, because nesting birds encounter moderate temperatures, high productivity and low nest predation at this elevation. In contrast, birds nesting at high elevation encounter an increase in nest predation, low temperature and productivity, and birds nesting at lower elevations encounter high productivity but also high nest predation.

Additionally, Boyle (2008) hypothesized that species inhabiting low elevations with high nest predation rates could increase fitness by moving upslope to breed, seeking refuge from predation. A previous study of elevation migration at this site,

however, did not find frequent migration from elevations with high nest predation to elevations with low nest predation (Merkord 2010). I hypothesize that the extra time and energy of nesting in colder climates at high elevations would require more time for development, resulting in longer nesting periods with increasingly colder thermal regimes (Badyaev 1997; Lu *et al.* 2010), and this could counteract presumed benefits of having lower daily predation rates at high elevations. While I agree with Boyle (2008) that birds could benefit from moving upslope to breed, for elevational gradients with strong nonlinear changes in daily predation rates, such as Manu, I would expect that this benefit would only be realized for species moving from the lowlands, especially from the foothills, to lower cloud forest (1500-2000m) where thermal regimes are moderate and predation rates are low. These movements, however, are uncommon at my study site (Merkord 2010).

Conclusion: My study revealed that changes in the relative importance of different nest predators and their activity patterns likely contribute to variation in nesting success along an elevational gradient. Furthermore, my work suggests that this variation may limit the elevational distributions of some tropical bird species, with community-wide implications. Nest predation seems especially likely to contribute to changes in bird species composition in the foothills of tropical mountains, and possibly within upper cloud forest. I view this study as a first step towards evaluating the hypothesis that nest predation contributes to species turnover and life history evolution along Neotropical montane gradients, and propose that nest predation is a critical factor both promoting and maintaining the high beta diversity and extraordinary regional diversity found in the Andes (Rahbek & Graves 2001). The next steps for testing this

hypothesis will require data on life-history traits as potential adaptations to nest predation, such as egg and clutch mass, incubation and nestling periods and behaviors during nesting, consideration of abiotic factors that change along the gradient (i.e., temperature, rainfall and productivity) and biotic factors such as interspecific competition. Understanding the interactions and relative importance of these factors will provide a more complete picture of the ecological mechanisms that promote species turnover along tropical elevational gradients.

Table 2-1. Site characteristics for stations found along the Manu elevational gradient, including geographic coordinates, elevational range, average mean monthly temperature and average canopy height of the forest, \pm SD.

Site	Lat/Long Coordinates	Elevation (m)	Avg Mean Monthly Temperature (C)	Avg Canopy Height (m)
Pantiacolla	12°65'59.5" S 71°23'18.3" W	350-500	23.7 \pm 1.8	27 \pm 2.4
Tono	12°57'58.2" S 71°34'05.3" W	750-1100	22.4 \pm 0.9	20 \pm 4.8
San Pedro	13°39'19.4" S 71°32'48.50" W	1100-1600	18.3 \pm 2.1	13 \pm 3.9
Wayqecha	13°10'30.1" S 71°35'14" W	2300-3100	11.9 \pm 2.5	9.4 \pm 4.2

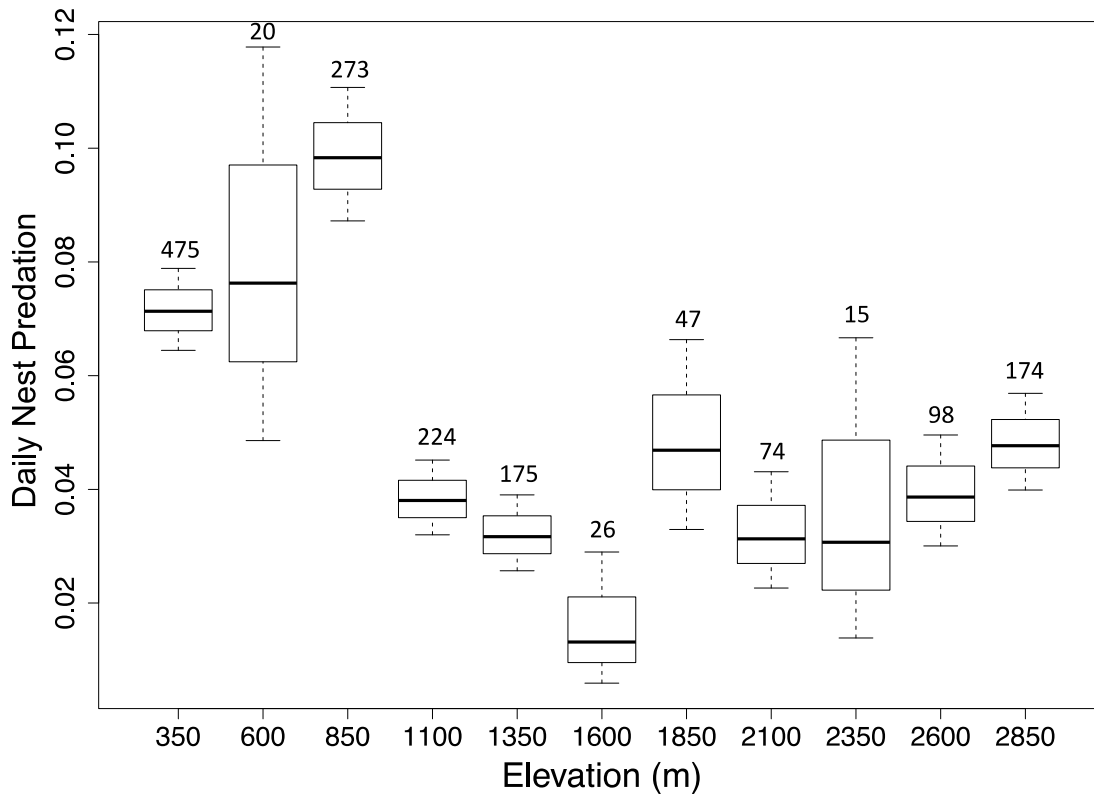


Figure 2-1. Daily nest predation rates along an Andean elevational gradient between 350-3100m. Boxes represent 75% of data for each band, and bars show 95% confident intervals. The numbers above boxes show the number of nests included in the analysis for each elevational band.

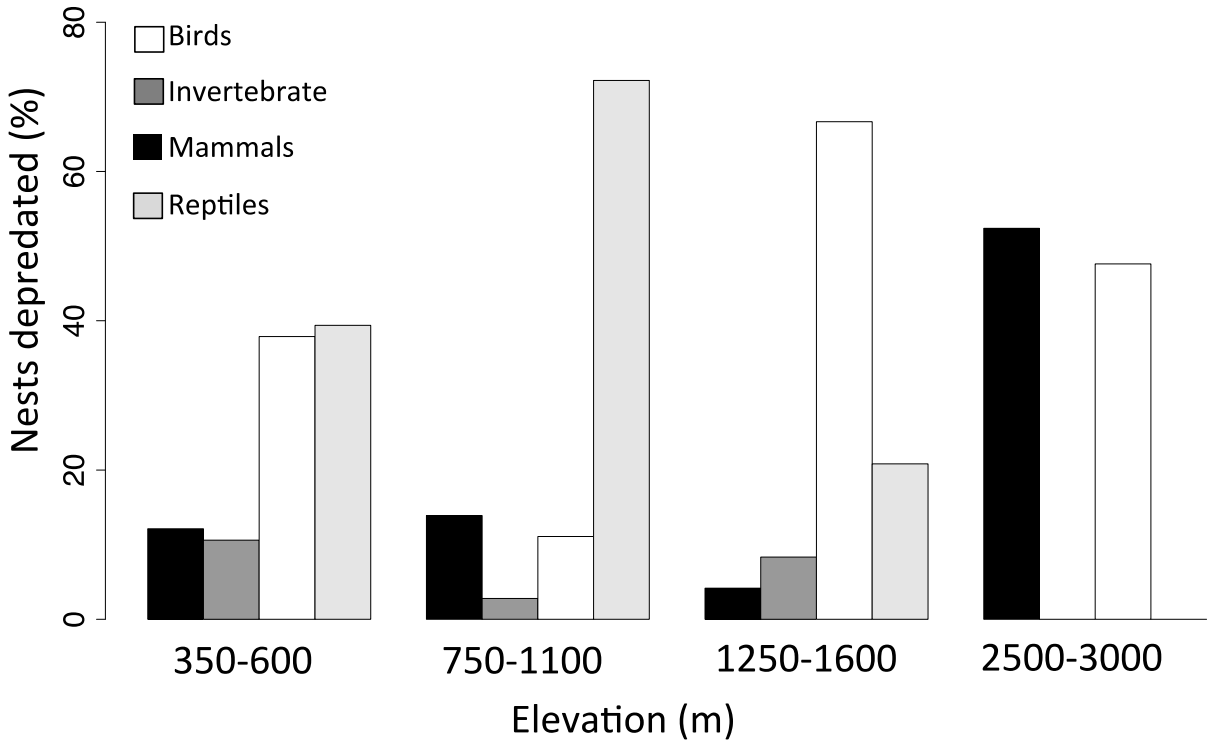


Figure 2-2. Percentage of nests depredated by different predators at four stations distributed along the 2750-m elevational gradient.

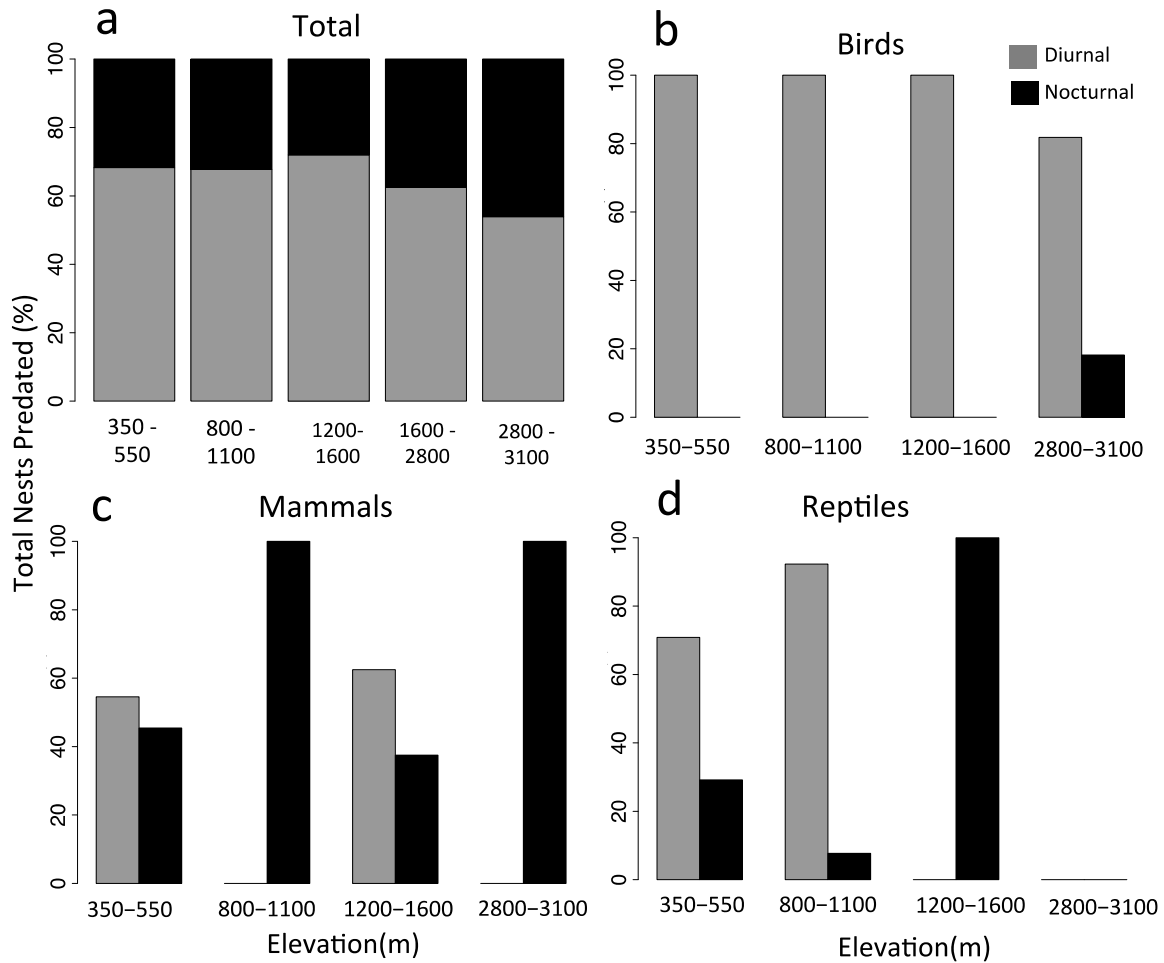


Figure 2-3. Percent of diurnal (gray bars) and nocturnal (black bars) nest predation events distributed along the elevational gradient for a) all the nests for which the time of predation is known, obtained from data logger and camera trap records (n= 505) and percent of diurnal and nocturnal nest predation events where predator identity, recorded exclusively with camera traps, is known for b) birds, c) mammals, and d) reptiles.

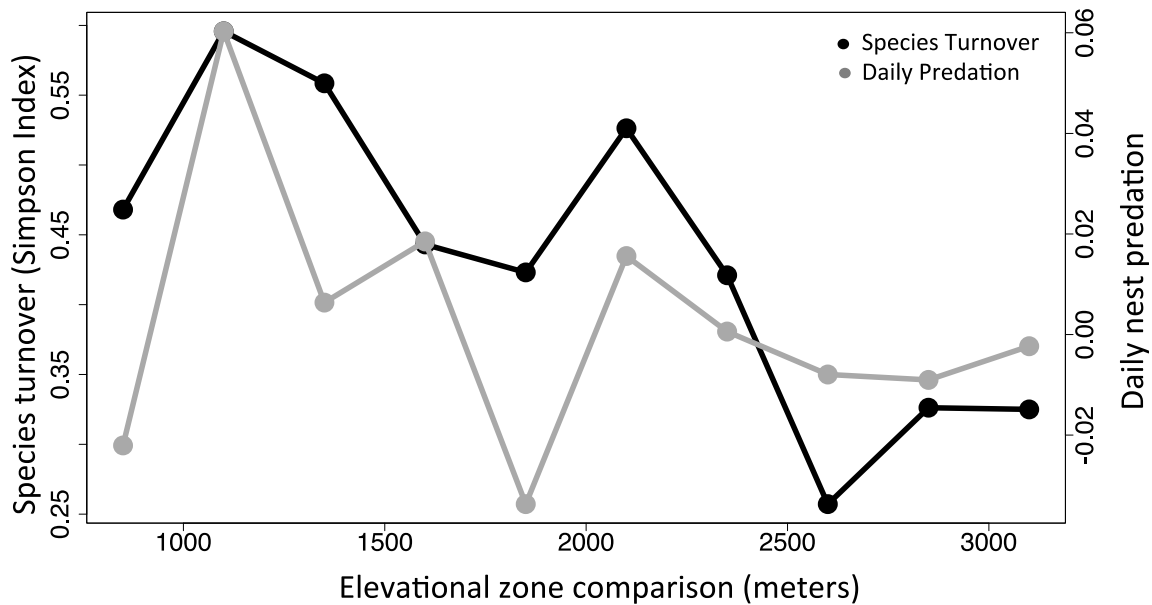


Figure 2-4. Dissimilarity values for bird species composition (Simpson's Dissimilarity Index; black line) and differences in daily nest predation (gray line) along the elevational gradient between 850 and 3100m. Simpson's Dissimilarity Index compares bird species composition of two adjacent 250-m elevational zones so that peaks in species turnover with elevation can be identified. Daily nest predation is estimated for each 250-m elevational zone, and differences in daily nest predation between adjacent elevational zones allow peaks in daily nest predation change to be identified. The x-axis (Elevational Zone Comparisons) indicates the elevation of the lower of the two adjacent zones compared.

CHAPTER 3
EFFECTS OF BIOTIC AND ABIOTIC FACTORS ON AVIAN CLUTCH INVESTMENT
AND INCUBATION BEHAVIOR ALONG A TROPICAL ELEVATION GRADIENT

Introduction

Food resources and parental care provided to the embryo will affect the survival of progeny (Stearns 1992; Reznick *et al.* 1996; Roff 2002); therefore, decisions made during the reproductive period affect other life-history components. Most oviparous organisms can produce hundreds or even millions of eggs because their offspring require minimal parental care. In most birds, however, eggs require extensive parental care and they would not hatch without precise temperature regulation provided by the attendant adults (Turner 2002; Williams 2012). Egg care, therefore, involves a tradeoff between self-maintenance and reproductive investment, which ultimately could limit clutch size (Lack 1968; Clutton-Brock 1991). Tradeoffs in investment decisions are usually related to variation in nest predation risk and ambient temperature (Conway & Martin 2000b). Birds living in the tropics, for example, have been hypothesized to reduce investment in each clutch in favor of increased adult survival in the face of severe nest predation rates and a benign climate (Ricklefs & Wikelski 2002; Roper *et al.* 2010). Many tropical birds, however, also have relatively long incubation periods, a trait that would increase vulnerability to nest predation (Tieleman *et al.* 2004; Martin *et al.* 2007). Before I can resolve this paradox, I need studies of birds from the same region in which nest predation and other potential selective factors such as ambient temperature and nest predation vary so that I can associate investment decisions with these factors.

Tropical elevation gradients offer an opportunity to test the relative contributions of nest predation rates and ambient temperature to investment decisions. Along elevation gradients, bird species with similar evolutionary histories have been evolving

under different biotic and abiotic conditions, but have experienced relatively stable climates (Brumfield & Edwards 2007). Ambient temperature decreases steadily with elevation, whereas nest predation rates decrease abruptly at the border between lower elevations and cloud forest (Jankowski *et al.* 2013); Chapter 1). Under these conditions I might expect species to make similar reproductive investment decisions within elevation bands, but to differ considerably among elevation bands if predation is an important factor in the evolution of nesting behavior. Neotropical elevation gradients, at least those on the mainland, also contain the world's most diverse regional bird communities (Stotz *et al.* 1996), which provides an opportunity to search for repeated patterns of responses to similar and different biotic and abiotic conditions.

Investment decisions during nesting periods can be partitioned into egg and nestling stages. The egg is a closed system in which all the food resources are fixed from the beginning and the transformation rate of these resources to form the embryo depends largely on the amount of heat – energy – transferred by the incubating parent (Brua 2002; Deeming 2002b). In contrast, nestling growth relies mainly on quantity and quality of food provided by the parents (Skutch 1949; Lack 1968; Ricklefs 1984). In this paper I focus only on the egg stage, because the embryonic development rate depends exclusively on egg temperature, which is regulated by the incubating parent (Turner 2002) and parental behavior or decisions will be affected by external factors such as predation risk and ambient temperature (Lack 1968; Skutch 1985; Conway & Martin 2000b; Ghalambor & Martin 2000). Specifically, I evaluate how life-history traits involving the egg stage vary along an elevation gradient in response to the decrease in nest predation and ambient temperature with elevation (Janzen 1967; Skutch 1985;

Boyle 2008; Jankowski *et al.* 2013). I hypothesized that the observed variation in incubation length among bird species would be associated with differences in egg size and egg temperature (Turner 2002; Gillooly *et al.* 2008), and the remaining variation would be associated with differences in nest predation risk and ambient temperature. Based on allometric models, I predicted that species with larger eggs would have longer incubation periods and eggs maintained at warmer temperatures would have shorter incubation periods. Second, I predicted that birds nesting in elevation bands characterized by high rates of nest predation would have smaller clutches and eggs (Skutch 1985; Martin *et al.* 2006; Zarette *et al.* 2011), longer incubation bouts (Ghalambor & Martin 2000; Ghalambor & Martin 2002; Fontaine & Martin 2006), which would result in higher egg temperatures, and shorter incubation periods (Martin *et al.* 2007) (Table 1). In contrast, birds living in colder elevation bands should have smaller clutches (Badyaev 1997; Badyaev & Ghalambor 2001; Lu *et al.* 2010), cooler egg temperatures as a result of higher egg cooling rates during foraging trips as a result of lower ambient temperatures, and, therefore, longer incubation periods (Lu *et al.* 2010) (Table 3-1). In this study, I used nesting data that I gathered from 84 tropical bird species nesting in contrasting environments (high and low predation and ambient temperature) in a diverse community (Walker *et al.* 2006) located in the eastern slope of the Andes in southeastern Peru between 350 and 3100 m.

Methods

Avian nesting data were collected from 2008 to 2011 from an elevation range of 350 to 3100 m in the southeastern Peruvian Andes. Daily nest searches were conducted by 6-8 people at each of the four field stations distributed along the Manu Road gradient. The Pantiacolla Lodge station located in a lowland rainforest adjacent to

the Alto Madre De Dios river included an elevation range from 350 to 550 m (12° 39' 21.4" S; 71° 13' 54.6" W). The Tono station located in the foothills of the Andes next to the Tono river included an elevation range between 800 and 1000m (12° 57' 58.2" S, 71° 34' 05.3" W). The Cock-of-the-Rock Lodge station was located in cloud forest at the intersection of the San Pedro and Kcosñipata rivers between 1200 and 1500 m (13° 03' 19.4" S; 71° 32' 48.5" W). The fourth station, Wayqecha, was in elfin forest between 2700 and 3000 m (13° 10' 30.1" S; 71° 35' 14.6" W).

When a nest was found with eggs I set up two thermistors, one inside a fresh egg and a second one outside the nest; both were attached to U12 4-channel hobo data logger (Onset Computer Corporation, MA, USA <http://www.onsetcomp.com>) that was programmed to store and record temperatures every minute. I only placed thermistors inside fresh eggs (no embryonic development) to measure egg temperature, by drilling a hole in the wider end of the egg and the hole was sealed with super glue. The thermistor outside the nest that provided nest microclimate information was attached to a branch near the nest (~ 15 cm). Because inserting the thermistor in the egg stopped embryonic development, I did not drill more than 4 eggs per species to reduce population impacts. The overall fitness impact produced by egg drilling was very small because nest predation rates were very high (see below) and the overall number of nests encountered with fresh eggs was small. Therefore, the likelihood that any of the eggs sacrificed for this study would fledge was very small and the proportion of eggs for any one species was also very small. All the animal manipulations were approved by the University of Florida IACUC # 201004590.

Incubation period was measured as the number of days between the dates on which the last egg was laid and the last egg hatched. All of my egg and clutch mass analyses were conducted with fresh eggs (no embryonic development) to avoid biases caused by egg water loss (Rahn & Ar 1974).

Nest monitoring and nest predation estimation: Data loggers allowed us to continuously monitor nest survival and to reduce nest visitation rate to one visit every six days. Nests without data loggers were visited every 3-4 days. To estimate nest predation I used bird nests with known fates in a nest survival model constructed within the program MARK (Dinsmore *et al.* 2002; Rotella 2007). This model allowed us to estimate daily nest predation rate by using the number of exposure days to calculate the probability of predation. I used all nests with known fate (depredated or successful) regardless of monitoring technique ($n = 1134$); on average I had 13.5 nests per species (± 17.2 standard deviation; min-max = 1-86).

Data Analysis: As expected, egg ($r^2 = 0.89$, $p < 0.0001$) and clutch ($r^2 = 0.72$, $p < 0.0001$) mass were highly correlated with body mass; therefore in my analyses I corrected for body mass using $\ln(\text{egg mass/body mass})$ and $\ln(\text{clutch mass/body mass})$. In all linear models I checked for normality using the Shapiro test (Gotelli & Ellison 2004); if the variables were not normal I transformed them. All but nest predation variables were normalized using logarithmic transformation and the nest predation data were Arcsine transformed.

Allometry: To evaluate the effect of metabolic rate combined with egg mass and temperature on incubation period (ontogenetic growth rate), I used the equation proposed by (Gillooly *et al.* 2002) and tested by (Gillooly *et al.* 2008) on a particular

embryonic development stage. I used my data to test the main prediction that the logarithm of the body size-corrected time to egg hatching, $\ln(T_i m_i^{-1/4})$, should be a linear function of the inverse absolute temperature, $1/kT$, with a slope of $E \approx 0.65$ eV, reflecting the exponential effects of temperature on metabolic rate.

Explaining variation in incubation period: To explain what factors affect incubation period among my 84 bird species I conducted an Analysis of Covariance (ANCOVA) with bird species as a random effect, and, bird body mass, egg temperature, egg and clutch mass, nest microclimate, and daily nest predation as response variables.

Community comparison: To evaluate if the nesting (incubation length, egg mass, clutch mass, egg temperature) and selective (nest microclimate and nest predation) variables occurred randomly throughout the gradient or if they were associated with particular bird communities along the gradient, I used two different approaches. My first approach was to search for general associations among all variables and the bird communities of different elevation bands. To do this I conducted a Principal Component Analysis (PCAs) that included the 62 individuals and 56 species for which I had complete nesting information.

In my second approach, I quantified how my different nesting variables and selective factors varied among the four bird communities by conducting an Analysis of Variance (ANOVA). In this analysis I used incubation period, egg temperature, egg mass, clutch mass, nest microclimate, and daily nest predation as response variables, and bird community as a factor. I used Tukey's analysis as post-hoc tests of what?.

Results

Among the 84 bird species with known incubation periods from my study sites, the average incubation period was 18 days (± 4.2 SD), clutch size 2.2 eggs (± 0.63),

egg mass 5.76g (± 8.7) and egg temperature 34.80 °C (± 1.5). Average proportion of nests depredated daily was 0.04 (± 0.03), and average nest microclimate was 18.7 °C (± 3.9).

Incubation length: The observed variation in incubation period was mainly associated with changes in egg temperature ($F_{1,62} = 5.33$, $p = 0.03$) and marginally explained by changes in daily nest predation ($F_{1,62} = 3.21$, $p = 0.09$) and bird body mass ($F_{3,62} = 3.33$, $p = 0.08$) (Table 3-2). In general bird eggs that were incubated at higher temperatures had shorter incubation periods (Figure 3-1a). Thus, my data support the metabolic prediction (Figure 3-1a): a plot of the logarithm of mass-corrected time to egg hatching, $\ln(t_i m_i^{-1/4})$, versus the inverse absolute temperature, $1/kT$, yielded a significant relationship with a fitted slope of 0.62 (eV; CI 95% 0.52-0.71). However, the metabolic prediction only explained 20% of the variation ($r^2 = 0.20$, $p < 0.0001$) observed among my 84 birds species. The remaining variation was weakly associated with nest daily predation rate ($r^2 = 0.08$, $p = 0.02$; Figure 1b), but not with nest microclimate ($r^2 = 0.02$, $p = 0.91$; Figure 3-1c).

Elevation gradient and community comparisons: Daily nest predation varied among bird communities ($F_{3,91} = 6.08$, $p = 0.0008$; Figure 3-2a), in which the highest daily nest predation rates were recorded in the foothill forest community (6.9% \pm 4.2%), followed by lowland (5.3% \pm 2.9), elfin (3.9% \pm 2.0) and cloud (3.3% \pm 2.1%) forest communities. Nest predation rates differed significantly between the cloud forest and the foothill (Tukey: $p = 0.008$) and lowland (Tukey: $p = 0.002$) bird communities, and elfin forest nest predation rates were nearly significantly different from the foothill

community (Tukey: $p = 0.07$; Figure 2a). Nest microclimate decreased linearly with elevation ($r^2 = 0.86$, $p < 0.0001$; Figure 3-2b).

Among the 56 bird species and 62 individuals for which I had complete information, I found different incubation strategies and selective factors among bird communities along the gradient (Figure 3-3; Table 3-3). Most elfin forest species had similar incubation periods, whereas most lowland species shared similarities in egg temperature and nest microclimate (Figure 3-3).

Among communities, egg mass had a strong tendency to increase in high elevation bird communities ($F_{3,91} = 2.64$; $p = 0.05$), in which birds in elfin forest communities laid between 9.0 and 20.5% larger eggs (Tukey: $p = 0.07$; Figure 3-3a). In contrast, clutch mass did not change significantly among bird communities ($F_{3,91} = 1.64$, $p = 0.19$; Figure 3-3b). Average egg temperature varied among bird communities ($F_{3,91} = 3.19$, $p = 0.03$), in which egg temperatures decreased at higher elevations (Figure 3-3c). However, the only communities that differed significantly in egg temperature were the lowland and elfin forest communities, in which birds nesting in the elfin forest communities maintained their eggs on average 1.6 °C cooler (Tukey: $p = 0.02$; Figure 3-3c). Although average incubation period increased with elevation ($F_{3,91} = 2.58$, $p = 0.05$), nearly significant differences only occurred between cloud and lowland forest (Tukey: $p = 0.08$; Figure 3-3d). Overall, however, the observed variation in incubation period among bird communities in my full model was explained mainly by differences in daily nest predation ($F_{3,62} = 4.51$, $p = 0.01$) and clutch mass ($F_{3,92} = 6.91$, $p = 0.001$) (Table 3-2).

Discussion

My results partially supported my predictions. Although in general there was a significant negative correlation between daily nest predation rate and incubation period, incubation period, clutch and egg mass, and egg temperature did not change significantly among elevations with contrasting nest predation risk. In contrast, ambient temperature was not significantly associated with general variation in bird incubation period. Thus, my data suggest that nest predation rates, but not ambient temperature, contribute to the suite of life-history traits characteristic of many tropical bird species. However, the observed variation in clutch size, egg mass, egg temperature and incubation period were concordant with elevation prediction (Table 3-1). Throughout the rest of the discussion I will discuss how my results advance our understanding of how nest predation and ambient temperature could shape incubation strategies in tropical bird communities.

Even though egg and clutch mass were not associated with variation in incubation period, I observed significant interactions between communities and clutch and egg mass that were significantly associated with incubation periods. Bird species inhabiting higher elevations had longer incubation periods and invested more per egg despite the lack of a linear decrease in daily nest predation rate, which is puzzling as nest predation has been linked to the decrease in nesting investment observed in tropical areas (Skutch 1985; Martin *et al.* 2006). More confusing, yet, is the observed trend of clutch size reduction with elevation, which could be the reason why I did not observe an increase in clutch mass with elevation despite the incremental gain in egg mass. Because egg mass, clutch mass, and clutch size did not change significantly between high (lowland and foothill) and low predation areas (Cloud forest), my data

suggest that daily nest predation rate is a poor predictor of clutch mass and egg mass in the Neotropics, as suggested by Martin *et al.* (2006). Instead, egg mass increases, a pattern reported previously (Berven 1982a, b; Howard & Wallace 1985; Blanckenhorn 1997; Rohr 1997; Hancock *et al.* 1998; Lu *et al.* 2010), and clutch size decreases, another pattern that has been shown in other areas (Zang 1980; Krementz & Handford 1984; Badyaev 1997; Badyaev & Ghalambor 2001; Lu *et al.* 2010). In addition to these changes, nest predation at high elevations was just as high as in the lowlands, but ambient temperature and productivity (Salinas *et al.* 2011) are lower. Because incubating large clutches (Visser & Lessells 2001; Nord & Nilsson 2012) at colder temperature (Haftorn & Reinertsen 1985) is costly, I propose that increasing egg mass and decreasing clutch size is a nesting strategy that increases nesting success in harsh environments such as the high Andes. Providing extra resources for the embryo may reduce embryonic mortality at high elevations. Embryos at high elevations encounter pronounced cooling periods (lower ambient temperatures) during incubation recess, which increases embryonic stress reflected in smaller embryonic mass and lower yolk reserves (Olson *et al.* 2006). Under these conditions, extra resources within eggs could increase embryonic survival probabilities by providing the energy necessary for increased metabolic rates. In contrast, clutch size reduction may be advantageous because it reduces the high energetic cost of egg formation and incubation in this harsh environment (Biebach 1981; Haftorn & Reinertsen 1985; Tinberger & Dietz 1994; Williams 1996; Bryant & Bryant 1999). Similarly, and not mutually exclusively, low primary productivity at high elevations (Salinas *et al.* 2011) could reduce the amount of food resources available during the nesting period, which would increase the cost of

egg production and potentially increase the amount of foraging time required during incubation recesses. Hence, clutch size reductions at high elevations could reduce incubation and egg production costs, allowing birds to increase investment in the remaining eggs and decrease intervals between nesting attempts as a result of reduced stress on the adults (Roper *et al.* 2010).

Because of the high energetic costs encountered by birds nesting at high elevations, it is unlikely that birds can simply increase their time on the nest incubating their eggs to reduce egg heat loss. However, birds can modify their incubation behavior when incubating at colder temperatures (Conway & Martin 2000a) by increasing the number of foraging trips, which could allow them to frequently refuel their energetic demands and simultaneously reduce egg-cooling time (short trips). But, increasing the number of foraging trips could increase nest predation probability (Fontaine & Martin 2006; Ibáñez-Álamo & Soler 2012; Smith *et al.* 2012), especially at this elevation in which all-diurnal nest predation is conducted by birds that use visual cues (Chapter 1). This possible change in the frequency and duration of off-bouts could be the reason why I observed an increase in daily nest predation rate between the cloud and elfin forest. Thus, the high cost of nesting in colder ambient temperatures at higher elevations could limit the options available to reduce negative fitness effects such as nest predation. At high elevation birds are investing more per egg but reducing their clutch size, which is the opposite strategy to that used by lowland birds under similar nest predation but warmer climate and higher primary productivity (Salinas *et al.* 2011). The harsh conditions encountered by nesting birds at high elevations may limit their ability to employ behaviors that could reduce nest predation (e. g., a reduced number of

trips to and from the nest), which forces them to use other strategies (e. g., decrease clutch size). However, until I have quantified how and if bird incubation behaviors change with elevation, however, I cannot draw strong conclusions.

Daily nest predation rates were negatively associated with overall incubation period (Bosque & Bosque 1995; Martin *et al.* 2007), which was supported by the nearly significant differences in incubation period between lowland (high nest predation and short incubation period) and cloud forest (low nest predation and long incubation period) bird communities. Overall, however, daily nest predation explained only a small percentage of the variation observed in the incubation period throughout the gradient. Birds incubating at elevations with high nest predation rates but colder temperatures (foothill and elfin forest communities) did not reduce their incubation periods; instead average incubation period increased at these elevations. Thus, lower ambient temperatures could constrain birds from adopting life-history strategies such as reducing trips to and from the nest that might reduce nest predation rates. Additionally I did not find differences in egg and clutch mass among communities with contrasting daily nest predation rates (foothill-lowland and cloud forest; Figure 3-3a,b), suggesting that at least in my tropical gradient, egg and clutch mass investment are not associated with differences in nest predation. Instead, it appears that these variables were more strongly associated with ambient temperature.

Another surprising result was that nest microclimate did not contribute to the overall incubation period variation, in spite of the strong association observed between low temperature nest microclimate and low egg temperature. Although frequent egg cooling periods slowed embryonic development (Olson *et al.* 2006; Nord & Nilsson

2012), I know little about how the length and frequency of these cooling periods affect embryonic development and, thus, the length of the incubation period.

The relationship between egg mass (m) and incubation period (t), $\ln(t; m_i^{-1/4})$, and nest microclimate ($1/kT$), had a slope (0.62) close to the predicted value based on allometric models of metabolism (0.65) (Gillooly *et al.* 2008). Nevertheless, this relationship was relatively weak and only accounted for 20% of the variation, suggesting that other factors may determine investment in clutches and incubation. The residual variation was negatively correlated with nest predation rates, but not ambient temperature. When I compared if clutch and incubation investment were associated with different bird communities along the gradient, I found that communities had distinctive nesting traits associated with their unique combination of abiotic (temperature) and biotic (nest predation) conditions. Although allometric hypotheses are intended for comparisons among organisms that differ in mass by several order of magnitude (Brown *et al.* 2004), it is interesting that I found that bird incubation period is fundamentally related to metabolic properties, despite the limited range of body masses represented in my sample (Gillooly *et al.* 2002; Gillooly *et al.* 2008). In general bird species that maintained their eggs at warmer temperatures had shorter incubation periods; however, incubation period corrected for egg mass varied greatly among species that had similar average egg temperatures (Martin 2004; Tieleman *et al.* 2004; Martin *et al.* 2007). This variation could result from differences in egg investment among bird species, in which those with proportionally larger eggs and higher nutrient content within eggs have longer incubation periods (Martin 2008)(Figure 1a). Variation in the length of incubation bouts, which tend to be shorter in small species that lay large eggs,

could also account for differences in the length of the incubation period because of differences in the length of time when eggs are warm enough to allow embryonic development.

In general, my results only partially supported my hypothesis that nest predation is a primary driver of the suite of life-history traits observed in tropical birds. The different incubation strategies and investment decisions documented in the Manu Andean elevation gradient reflect the complexity and diversity of life history strategies concealed in this hyper-diverse tropical area. Overall bird species that encounter higher daily nest predation rates and maintained their egg at warmer temperatures had shorter incubation periods (Martin *et al.* 2007). These characteristics were mainly associated with lowland bird communities. But, generally, daily nest predation and egg temperature alone explained only a small percentage of the variation observed on this tropical elevation gradient (Martin 2004; Tieleman *et al.* 2004; Robinson *et al.* 2010). The large variation in incubation strategies observed along the elevation gradient and within bird communities suggest that previously documented contradictory results may be resolved by studying two different tropical forest bird communities, lowlands (Tieleman *et al.* 2004) and cloud forest (Martin *et al.* 2007), which have contrasting incubation strategies. Therefore I need to explore additional factors that could explain the observed variation within tropical communities (Martin 2004), for example, by comparing nesting strategies among tropical bird species within a community (Ricklefs & Brawn 2012).

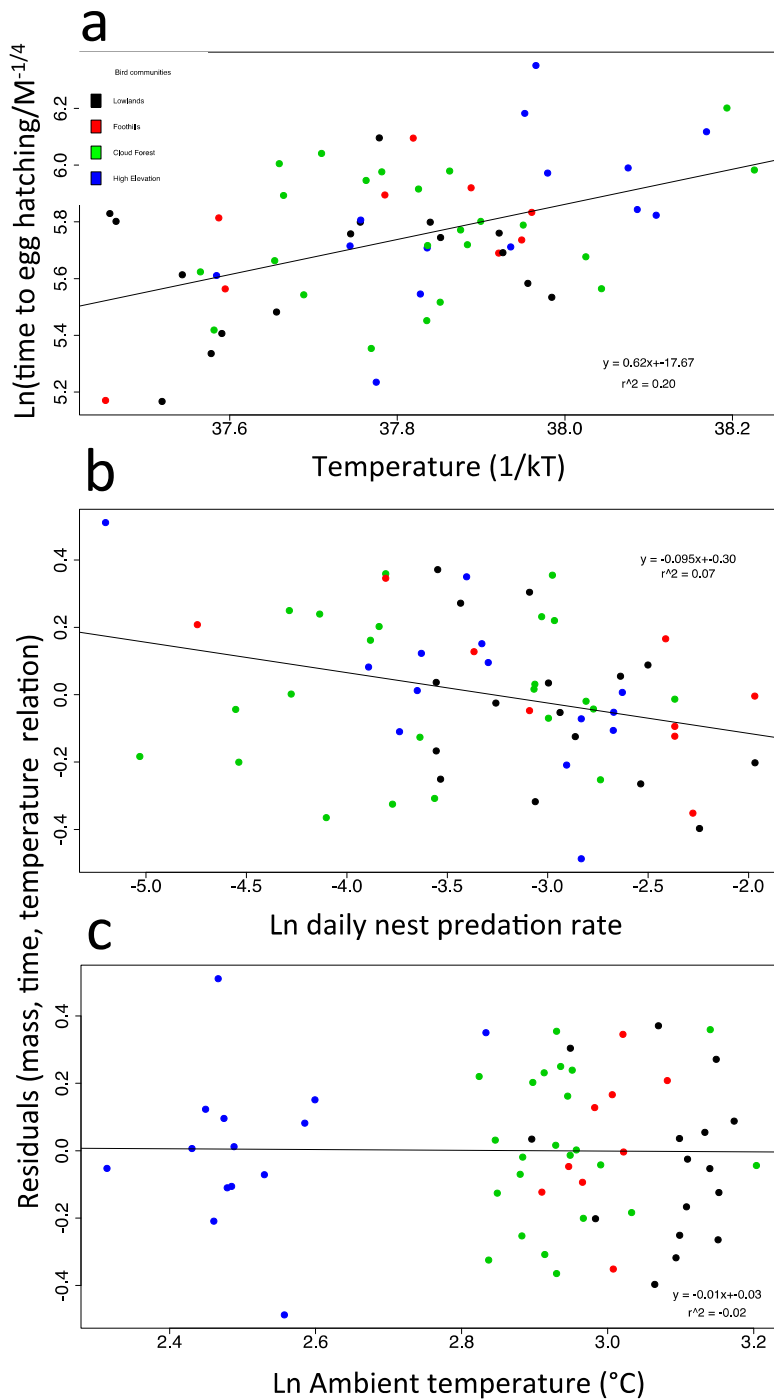


Figure 3-1. Associations between the main factors that affect bird embryonic development (egg mass and egg temperature). A) Graphical test of the metabolic prediction (Gillooly et al. 2008), in which the fitted slope of 0.62 is very close to the predicted slope 0.65. Association of the residual variation observed in the metabolic prediction with the B) daily nest predation rate and C) nest microclimate.

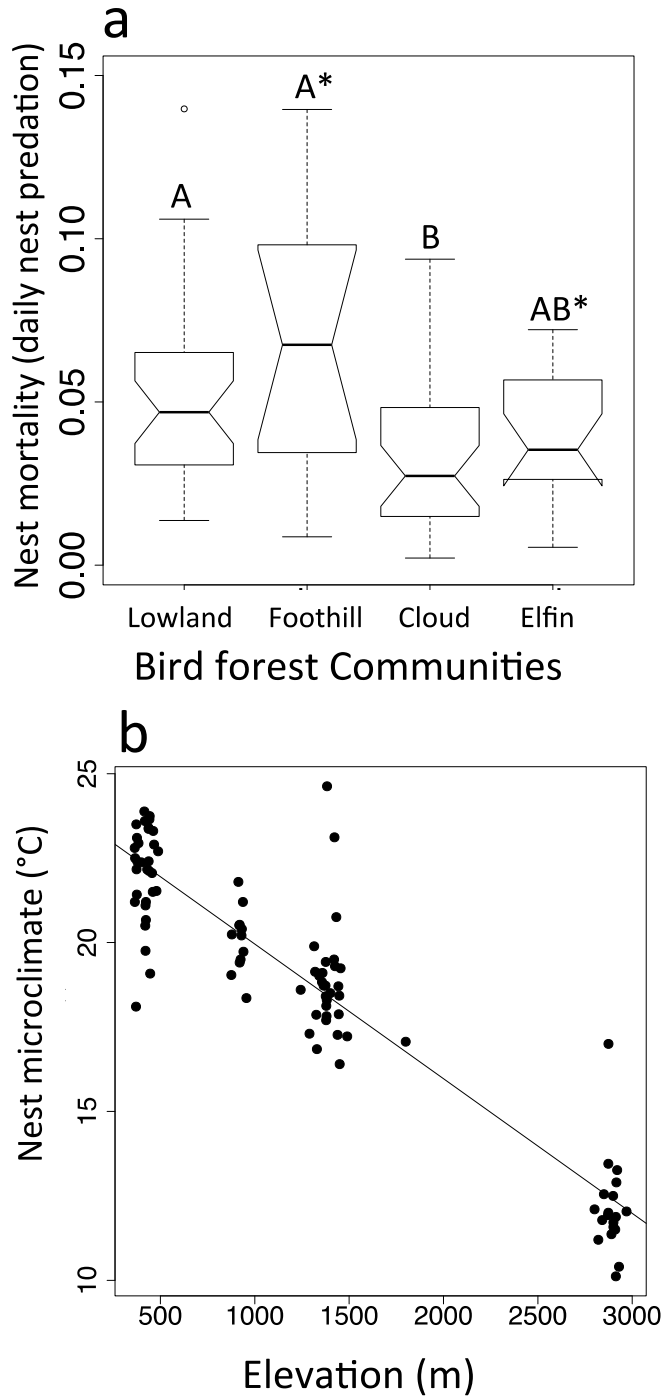


Figure 3-2. Variation in selective factors among bird communities on the elevation gradient, A) daily nest predation rate (Proportion of nests depredated daily) and B) Nest microclimate.

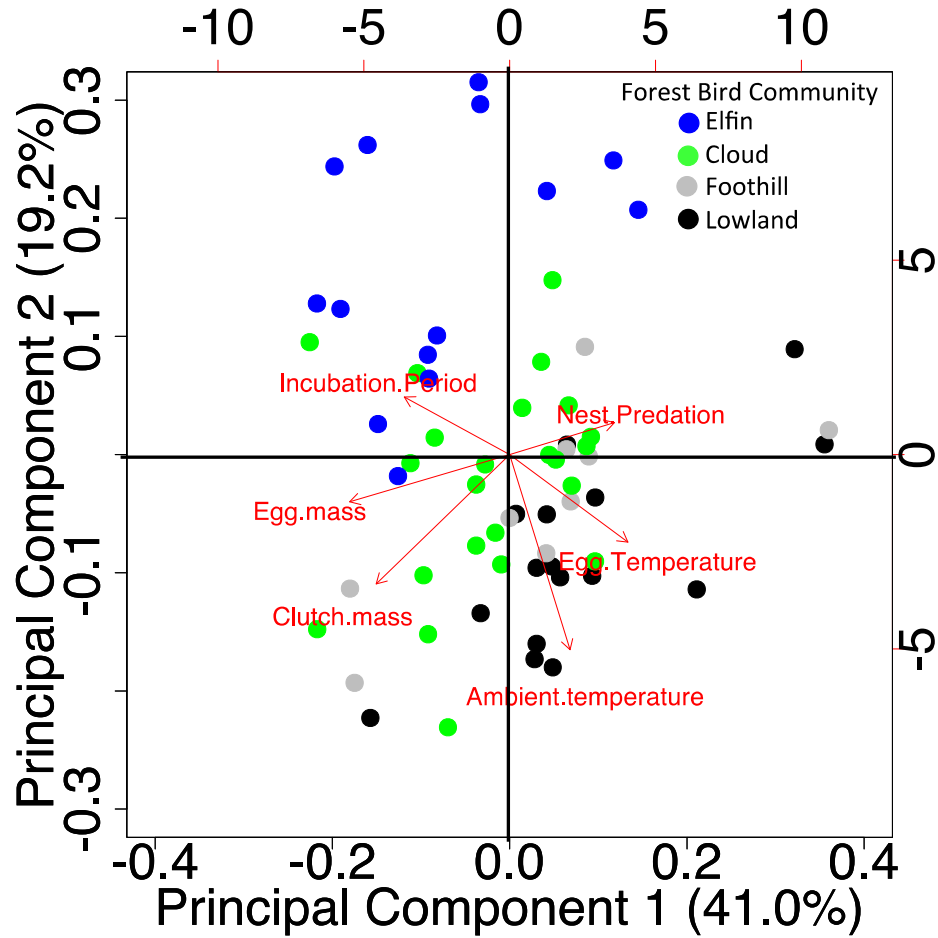


Figure 3-3. Principal Component Analysis among nesting variables (egg and clutch mass, incubation period, egg temperature) and selective factors (nest microclimate and daily nest predation rate) in four bird communities along an Andean elevation gradient, Cusco, Peru. Data are from 54 species and 62 individuals.

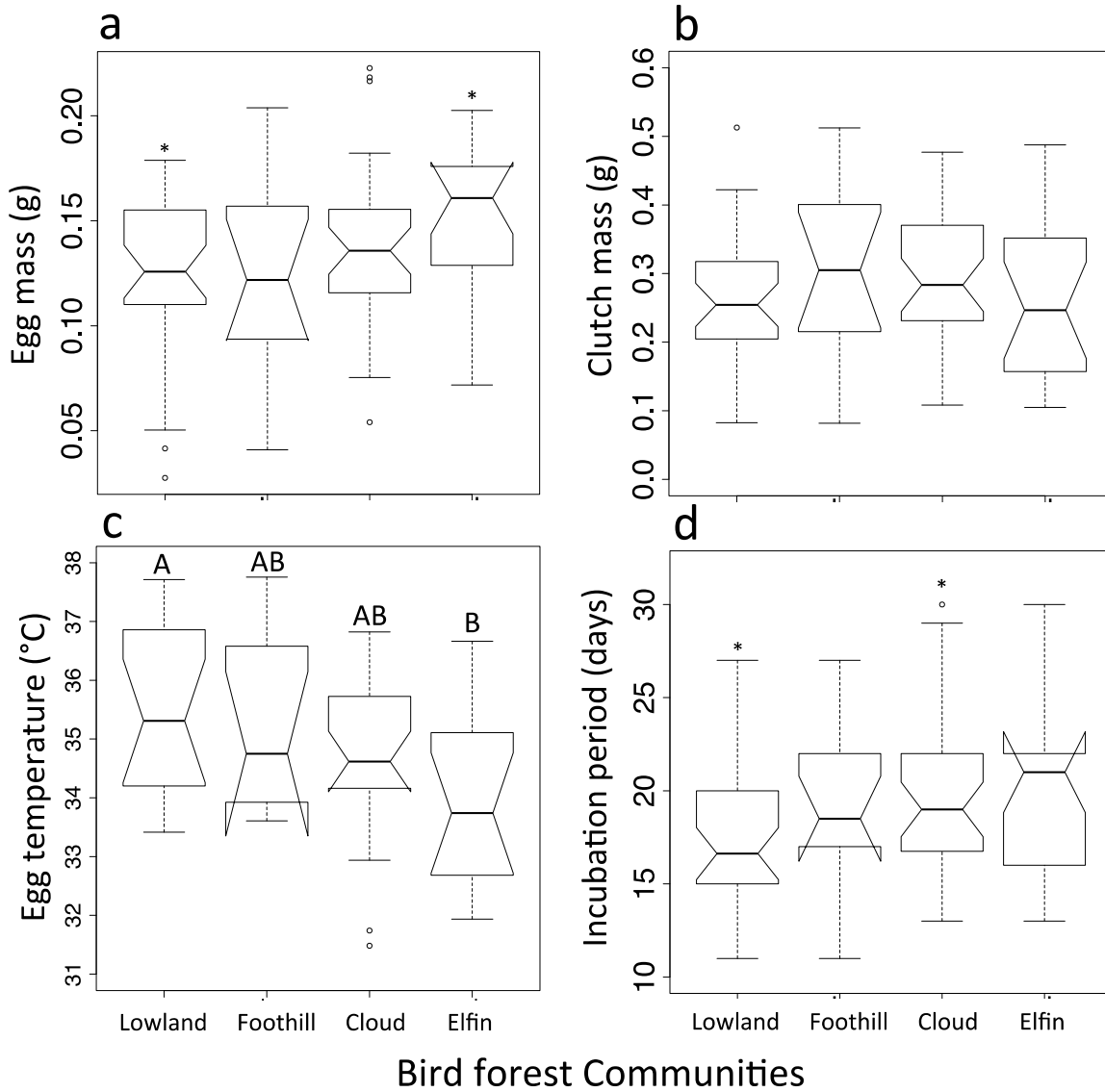


Figure 3-4. Changes in nesting variables (A: egg mass; B: clutch mass; C: Egg temperature; and D: incubation period) among bird communities of different elevation bands along the Manu gradient. * Communities where nesting variables are close to be significant.

Table 3-1. Avian incubation investment predictions in environments with different nest predation risk and ambient temperatures.

Life History Trait	Nest Predation		Ambient Temperature	
	High	Low	High	Low
Egg mass	Low	High	Low	High
Clutch size	Low	High	High	Low
Egg Temperature	High	Low	High	Low
Incubation period	Short	Long	Short	Long

Table 3-2. Full model for general and community analysis of covariance (ANCOVA).

Variables	df	F value	Probability
I) Variables that explain incubation period (error df = 62)			
Egg mass	1	1.5	0.23
Clutch mass	1	1.83	0.18
Body mass	1	3.33	0.08
Daily nest predation rate	1	3.21	0.09
Egg temperature	1	5.33	0.03
Nest microclimate	1	1.24	0.27
II) Incubation period and bird communities (error df = 62)			
Community	3	0.16	0.93
Egg mass	1	1.14	0.71
Clutch mass	1	0.87	0.36
Daily nest predation rate	1	6.45	0.02
Egg temperature	1	0.85	0.36
Nest microclimate	1	0.8	0.38
Body mass	1	0.09	0.76
Community*Egg mass	3	1.37	0.27
Community*Clutch mass	3	6.91	0.001
Community*Daily nest predation rate	3	4.51	0.01
Community*Egg temperature	3	1.26	0.31
Community*Nest microclimate	3	0.26	0.86
Community*Body mass	3	0.33	0.81

Table 3-3. Output from the Principal Component Analysis (PCA) realized in the 56 species and 62 individuals from the four bird communities (lowland, foothill, cloud and elfin forest) distributed along the Manu elevation gradient, Cusco, Peru.

Variables	Component1	Component2	Component3
Egg mass	-0.55	-0.81	0.3
Clutch mass	-0.46	-0.49	0.21
Incubation period	-0.36	0.22	-0.57
Daily nest predation	0.36	0.12	0.63
Ambient temperature	0.21	-0.74	-0.11
Egg temperature	0.41	-0.33	-0.37
standard deviation	1.57	1.07	1.05
Proportion of variance	0.41	0.19	0.18

CHAPTER 4 TANAGERS OF THE HIGH ANDES HAVE AN ULTRA-SLOW PACE OF LIFE

Introduction

Life-history traits related to reproductive effort have been used to characterize differences in the “pace of life” among organisms (Stearns 1992; Roff 2002). Many lines of evidence suggest, for example, that tropical birds have a suite of life-history traits that can be characterized as a “slow” pace of life (Ricklefs & Wikelski 2002). This suite of traits includes small clutches, long incubation and nestling periods, low nest attentiveness, and low feeding rates of young (Moreau 1944; Lack 1947; Skutch 1949; Martin 2004; Jetz *et al.* 2008; Robinson *et al.* 2010; Martin *et al.* 2011; Gill & Haggerty 2012). More recently, studies of metabolic rates have shown that tropical birds also have lower basal metabolic rates than their temperate counterparts (Wikelski *et al.* 2003; Wiersma *et al.* 2007), further supporting the hypothesis that tropical birds have a slow pace of life. Typically, traits associated with a slow pace are considered adaptations to a climatically benign, but biotically challenging environment in which adult survival is favored at the expense of each nesting attempt (Martin 2004; Robinson *et al.* 2010).

Not all tropical environments, however, are climatically benign. High elevations of tropical mountains, for example, are much colder and less productive year-round than nearby lowlands (Janzen 1967; Ghalambor *et al.* 2006; Salinas *et al.* 2011). Given this contrast, one might expect tropical birds to vary in their nesting strategies along elevation gradients in ways that reflect the greater abiotic constraints to nesting at higher elevations. Specifically, I predicted that species nesting at higher elevations will have lower fecundity (e. g., reduced clutch size)(Badyaev 1997; Badyaev & Ghalambor

2001; Lu *et al.* 2010) compared with lowland counterparts. I tested this prediction by examining how egg and clutch mass, nest attentiveness, egg temperature, nest predation risk, nestling growth, and development times of eggs and nestlings vary among neotropical tanagers (Sedano & Burns 2010; Jetz *et al.* 2012) inhabiting different elevations. Additionally I conducted a literature review and contrasted my results with other species in the tanager clade to evaluate if my findings for high elevation tanagers were present in other species of tanagers and if they were randomly distributed in the clade. Specifically I compared variation in elevation distribution, clutch size, and incubation and nestling development times in the tanager clade.

I focused on tanagers because they occur at all elevations at densities sufficient to obtain data necessary to quantify life-history traits, and they do not show the pattern of decreasing nest predation rates with elevation documented for the community as a whole (Skutch 1985; Boyle 2008), see chapter 1. Therefore, tanagers provide an opportunity to study how life histories of tropical birds respond to increasing abiotic constraints without the additional complication of associated changes in nest predation rates, which are well known to be strong determinants of life histories (Martin 1995, 2004). I show that tanagers nesting at high elevations have an especially slow-paced life-history strategy, which reflects an environment with harsh abiotic factors.

Methods

Study site: This study has two components, one based on original data and one based on published data. Original data came from a field study conducted between 350 and 3100 m elevation in the Manu National Park, in the adjacent departments of Cusco and Madre de Dios, which are in the Andes of southeastern Peru. The goal of this study was to provide highly detailed information on nesting behavior and nest predation for as

many tanager species as possible along the elevational gradient. Annually from 2008 to 2011, I worked at four stations distributed along the gradient: Pantiacolla (350-900 m; 12° 39' 21.4" S; 71° 13' 54.6" W), Tono (800-1100 m; 12° 57' 58.2" S, 71° 34' 05.3" W), San Pedro (1100-1600 m; 13° 03' 19.4" S; 71° 32' 48.5" W) and Wayqecha (2300-3100 m; 13° 10' 30.1" S; 71° 35' 14.6" W).

Nest searching: was conducted between August and December, six days per week, ten hours per day between 6:00 and 18:00. Seventy-two field assistants found and monitored 206 nests from 13 tanager species (Thraupidae; Appendix 1). All eggs and nestlings were weighed to the nearest 0.05g. Eggs and nestlings were weighed the day they were found, and nestlings were weighed daily until they fledged or died. Data loggers and motion cameras allowed continuous monitoring of nests; those without these monitoring systems were checked every 2-4 days. The incubation period was calculated as the number of days between clutch completion and when the last egg hatched. Similarly, the nestling period was estimated from the day the last nestling hatched to the day the last nestling left the nest. When eggs or young nestlings disappeared between nest checks, I assumed they had been depredated. If nestlings with primary (flight) feathers that were more than half grown disappeared between nest checks, I assumed they had fledged.

Incubation behavior: I was able to monitor incubation behavior in 81 nests of nine species. To determine incubation behavior and nest survival, I placed one thermocouple (2x3 mm) inside the nest under the eggs and a second thermocouple outside the nest; both were attached to data loggers (Onset Computer Corporation, <http://www.onsetcomp.com>) that recorded and stored temperature every minute. The

thermocouple inside the nest allowed us to quantify length of incubation bouts (time on the nest incubating the egg) and foraging bouts (when the bird was absent from the nest). Bouts were obviously demarcated by rapid changes in temperature of at least 1°C. The thermocouple outside the nest provided data on ambient microclimate. I placed a third thermocouple inside the fresh egg (undeveloped embryo) on a subset of 17 nests (5 species), to monitor egg temperature, which can be used to understand differences in incubation period among bird species (Martin *et al.* 2007). To reduce nesting mortality occasioned by inserting the thermocouple inside the fresh egg, particularly in species with one-egg clutches, I did not drill more than three fresh eggs per species. In analyses I included only days in which I collected incubation data for 24 continuous hours (from 00:00 to 23:59), a sample consisting of 520 incubation days and 94 temperature days. All the animal manipulations were approved by the university of Florida IACUC # 201004590.

Data from Literature: To augment the data from my field study, I obtained data from published studies on clutch size, incubation and nestling period, and elevation range for additional species of tanagers. I used these data to evaluate if the similar associations that I found among clutch size, elevation, and incubation and nestling periods on the Manu elevation gradient applied to the tanager clade. The literature review mainly came from two review books (Isler & Isler 1999; Hilty 2011); additionally I reviewed large databases (ISI Web of Science 1864-2013), SORA (<http://sora.unm.edu/node>), and google scholar for small publications not indexed in the Web of Science.

Data Analysis: For species along my elevation gradient, I used PCA to evaluate the relationships among the following variables: body mass, number of foraging trips from the nest, nest attentiveness, nest microclimate, incubation period, egg temperature, daily nest predation rate, nestling growth rate, nestling period, and clutch size. I only included in my analyses eggs for which I had initial mass ($n = 187$) to avoid mass variation produced by water loss after the onset of incubation (Rahn & Ar 1974). Nestling growth rate was calculated using a logistic equation transformation K (Ricklefs 1967). Egg and clutch mass comparison were made using logarithmic transformed data to correct for body mass.

Nest predation was estimated using a nest survival model constructed within the program MARK (Dinsmore *et al.* 2002; Rotella 2007). This model allowed us to estimate daily nest predation rate by using the number of exposure days to calculate the probability of predation. I used all nests with known fate (depredated or successful), regardless of monitoring technique ($n = 198$). Variables included in the model were: 1) the first day that an active nest was encountered, 2) the last day the nest was checked and eggs or nestlings were present, 3) the last day the nest was checked, 4) the fate of the nest (0 = successful, 1 = depredated). To estimate nesting success, I raised the probability of nesting success to the length of the average nesting period observed in the Manu gradient, which was 0.935^{39} and 0.946^{31} for species with one and two-egg clutches, respectively.

For the general literature review, I calculated averages for each species (including those from the Manu elevation gradient), and conducted PCA to explore associations among clutch size, elevation distribution, incubation and nestling period.

To evaluate if clutch size was randomly distributed in the tanager clade, I used a recently published bird phylogeny (Jetz *et al.* 2012) that included all the Manu gradient tanagers for the analysis. I used two methods to estimate phylogenetic signal: Blomberg's *K* statistic (Blomberg *et al.* 2003) and Pagel's lambda and I compared the two measures between the observed tanager tree and a tanager tree without phylogenetic structure, using a Chi-square test (Pagel 1999).

Results

I found that six of the 13 tanager species distributed along the Manu elevation gradient for which I obtained reliable nesting information had one-egg clutches (n= 101 nests). In the elevation gradient clutches from tanagers with single eggs weighed on average 56% less than those from species with two-egg clutches; incubation periods in tanagers with one-egg clutches were 22 % (5 days) longer than those with two-egg clutches and nestling periods averaged 22% longer (4 days) in tanagers with one-egg clutches.

When I explored nesting characteristics associated with the one egg-clutch in the tanagers along the Manu elevation gradient, I found that the first three PCA axes explained 77.4% of the variation (Table 3-1). The one egg-clutch species were associated with longer incubation and nestling periods, lower nestling growth and colder climates (PC1 44.4%; Figure 3-1). The second PC2-axis explained 20.7% and the main variables were body mass, nest attentiveness and egg temperature, but they varied largely among species with the same clutch sizes (PC2 20.7%; Figure 3-1).

The one-egg clutch size tanager species in the Manu gradient were not randomly distributed in the "Tanager" clade ($K= 0.96$), ($\lambda = -89.98$, $P<0.0001$; Figure 3-2). I found that the three PCA axes associated with nesting and elevation characteristics explained

82.9% variance among tanager species with different clutch sizes (Table 3-1). In general species with smaller clutches had longer incubation and nestling periods and inhabited higher elevations (PC1 48.7%; Figure 3-3). The second axis (PC2) explained 20.7% of the variation and was largely influenced by adult body mass, but body mass varied largely among species with the same clutch size (Figure 3-3).

Discussion

Several life-history traits of the tanager clade changed with elevation in ways that generally conformed to the expectation that increased abiotic stressors select for a slower pace of life. Clutch size decreased from two or three eggs in most species at low elevations to one egg in the majority of higher-elevation tanagers. Although one-egg species partially compensated for clutch reduction by increasing egg mass on average by 15.7%, their clutch mass was still much (44.9%) less than those with two eggs. Species with one-egg clutches also had longer incubation and nestling periods, and lower nestling growth rates than species with two-egg clutches. Therefore, even though tanagers nesting at high elevations substantially reduced their investment in each clutch, development rate and parental care did not decrease. In the rest of the discussion, I develop the argument that one-egg clutches and long incubation and nestling periods, which reflect an ultra-slow pace of life for a Neotropical passerine bird (Deeming 2002a; Martin *et al.* 2006; Auer *et al.* 2007; Jetz *et al.* 2008), result from the addition of harsh abiotic factors at high elevations to the already-documented harsh biotic constraints of the tropics.

The one-egg clutch in six species of high elevation tanagers illustrates a new extreme in life history trade-offs of tropical passerines. This dramatic reduction in reproductive investment — by nearly 50% compared to most other tropical passerines

that have two-egg clutches (Jetz *et al.* 2008) — is very rare in passerines. Although bird clutch size reduction has been documented previously along elevation gradients (Badyaev & Ghalambor 2001; Lu *et al.* 2010), these studies reported a small clutch reduction, between 10.9 and 15.6% (from 5.5 to 4.9, and 3.2 to 2.7 eggs), from low to high elevations, compared to the 50% (from two to one egg) reduction observed in tanagers in my gradient. Although tanagers significantly reduced their clutch size and mass with elevation, species with one-egg clutches at least partially compensated by laying larger eggs. Proportionally larger eggs in tropical passerine species are associated with lower nest attentiveness, in which species compensate for their reduced parental care by laying larger eggs (Martin 2008). Although, average nest attentiveness was lower in one-egg (60.2 ± 12.8) compared to two-egg (66.1 ± 10.6) clutches, it varied greatly among species. Thus, other selective pressures may influence egg mass increases and clutch reduction in high elevation tanagers (see below).

Nest predation is commonly hypothesized to be an important selective pressure affecting bird nesting investment decisions (Lima 2009); high nest predation rates have been associated with smaller clutches and eggs (Skutch 1985; Martin *et al.* 2006). Nest predation rates in my study, however, did not vary with elevation in the tanager clade and did not vary with clutch size, suggesting that predation is unlikely to be a causal mechanism for the observed reduction in clutch size with elevation in my study system. Overall nesting success, however, did decrease because of the observed longer incubation and nestling periods at higher elevations. Another important selective factor that is commonly proposed to affect bird nesting strategies and investment decisions is ambient temperature (Conway & Martin 2000b). The costs of producing eggs,

incubating clutches, and feeding nestlings are all higher in colder climates (Biebach 1981; Haftorn & Reinertsen 1985; Tinberger & Dietz 1994; Williams 1996; Bryant & Bryant 1999), all of which would select for clutch reduction in high elevation Andean tanagers. Because nest predation rate did not vary with elevation among tanagers, the ~12°C reduction in ambient temperature observed could well be the dominant selective factor favoring clutch reduction in my system.

Lower temperatures may also be responsible for the longer incubation and nestling periods of high-elevation tanagers. Previous studies on elevation gradients also found that species inhabiting higher elevations had longer incubation and nestling periods (Badyaev & Ghalambor 2001; Lu *et al.* 2010). The lower nestling growth rates observed in tanagers with one-egg clutches suggest that the quantity and/or quality of food delivered to nestlings may be reduced at high elevations. Because daily nest predation was similar between one- and two-egg clutch tanagers, it is unlikely that differences in tanager nestling growth are promoted by changes in nest predation. Alternatively, colder nest microclimates may impose higher thermoregulatory costs on developing nestlings, which might make it necessary for nestlings from one egg-clutches to invest less in growth and more in maintenance (Mertens 1977). Similarly, lower egg temperatures may be responsible for longer incubation periods. In support of this possibility tanagers with one-egg clutches have lower egg temperatures (32.0 ± 1.4) compared to species with two-egg clutches (34.2 ± 0.4) clutches, although there is a great deal of variation and my sample size is small (5 species). Because nest attentiveness did not vary among species, lower egg temperatures may result from the rapid cooling of eggs during foraging trips at higher elevations, which would slow

embryonic development and increase stress and metabolic rates (Olson *et al.* 2006).

Thus, the incremental increase in egg mass documented in tanager species inhabiting high elevations could reflect selection to provide extra resources for the embryo to survive during frequent cooling periods.

In conclusion, my results suggest that the extreme clutch size reduction and associated slow pace of life in high-elevation tropical tanagers is a strategy of “making the best of a bad situation” in a perpetually cold environment characterized by low productivity (Salinas *et al.* 2011) and low nesting success (Robinson *et al.* 2000; Martin *et al.* 2006; Robinson *et al.* 2010). Tanagers with single-egg clutches had longer incubation and nestling periods than those at lower elevations with two-egg clutches. Given the constant high nest predation rates along the entire elevation gradient in tanagers, there should be intense selection for rapid incubation and development; therefore, the long nesting period at high elevations suggests that shorter periods are not an option. Indeed, correcting for length of nesting cycle, tanagers of high elevation actually have lower nesting success than those with two-egg clutches nesting at lower elevations. Thus, maintaining viable populations at high elevations might only be possible with frequent re-nesting (Roper *et al.* 2010) and high survival of adults (Gill & Haggerty 2012) and fledglings (Tarwater *et al.* 2011; Gill & Haggerty 2012). Given that most high-elevation tanagers are relatively large, 51% larger than those in the lowlands, they may live longer (Peterson & Wroblewski 1984; Brown *et al.* 2004). Until I have data on these additional life-history variables, however, I will not be able to assess the whole suite of life-history traits that characterize tanagers living at these high elevations.

Table 4-1. Association between environmental and nesting variables in the tanager clade species. Principal Component Analysis output.

Variables	PC1	PC2	PC3	PC4
Body mass (g)	0.31	-0.47	-0.03	-0.20
Number of foraging trips	0.27	-0.39	0.50	-0.11
Incubation Atentiveness (%)	-0.17	-0.43	0.32	0.45
Nest microclimate (°C)	-0.35	0.01	0.32	0.41
Incubation period	0.42	-0.11	0.22	-0.17
Egg temperature	-0.13	-0.45	-0.28	0.30
Nest mortality (daily nest predation)	0.26	-0.14	-0.54	0.41
Nestling growth (k)	-0.36	-0.31	-0.12	-0.27
Nestling period	0.30	0.34	0.28	0.41
Clutch size	-0.44	0.01	0.16	-0.22
Standard deviation	2.11	1.44	1.11	0.95
Proportion of Variance (%)	44.44	20.65	12.31	9.12

Table 4-2. Association between environmental and nesting variables in the tanager clade species. Principal Component Analysis output.

Variables	PC1	PC2	PC3	PC4
Incubation period	-0.49	-0.14	0.43	0.75
Nestling period	-0.43	-0.47	0.43	-0.62
Elevation	-0.48	-0.02	-0.65	0.06
Body mass (g)	-0.25	0.86	0.33	-0.19
Clutch size	0.53	-0.13	0.32	0.15
Standard deviation	1.5611	0.9937	0.85	0.68799
Proportion of Variance (%)	48.74	19.75	14.45	9.467

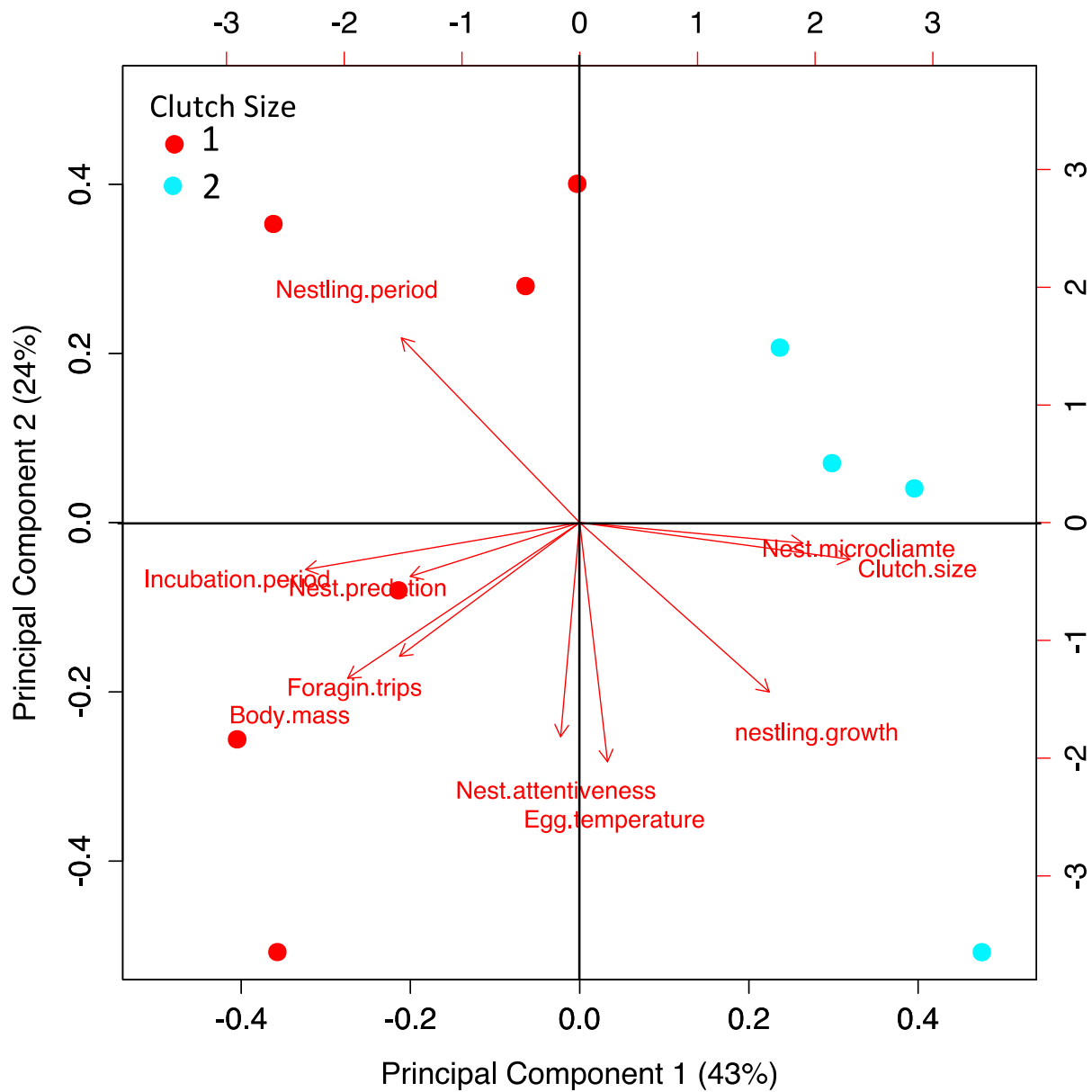


Figure 4-1. Principal component axes that explain 65% of the variation for nesting variables associated with tanagers nesting in the Manu elevation gradient. The first axis explain 44% of the variation, ambient temperature, nestling growth (K), incubation period and clutch size are the main variables associated with this axis variation. The second axis explained 21% of the variation and the main variables associated with this variation are egg temperature, nest attentiveness and body mass.

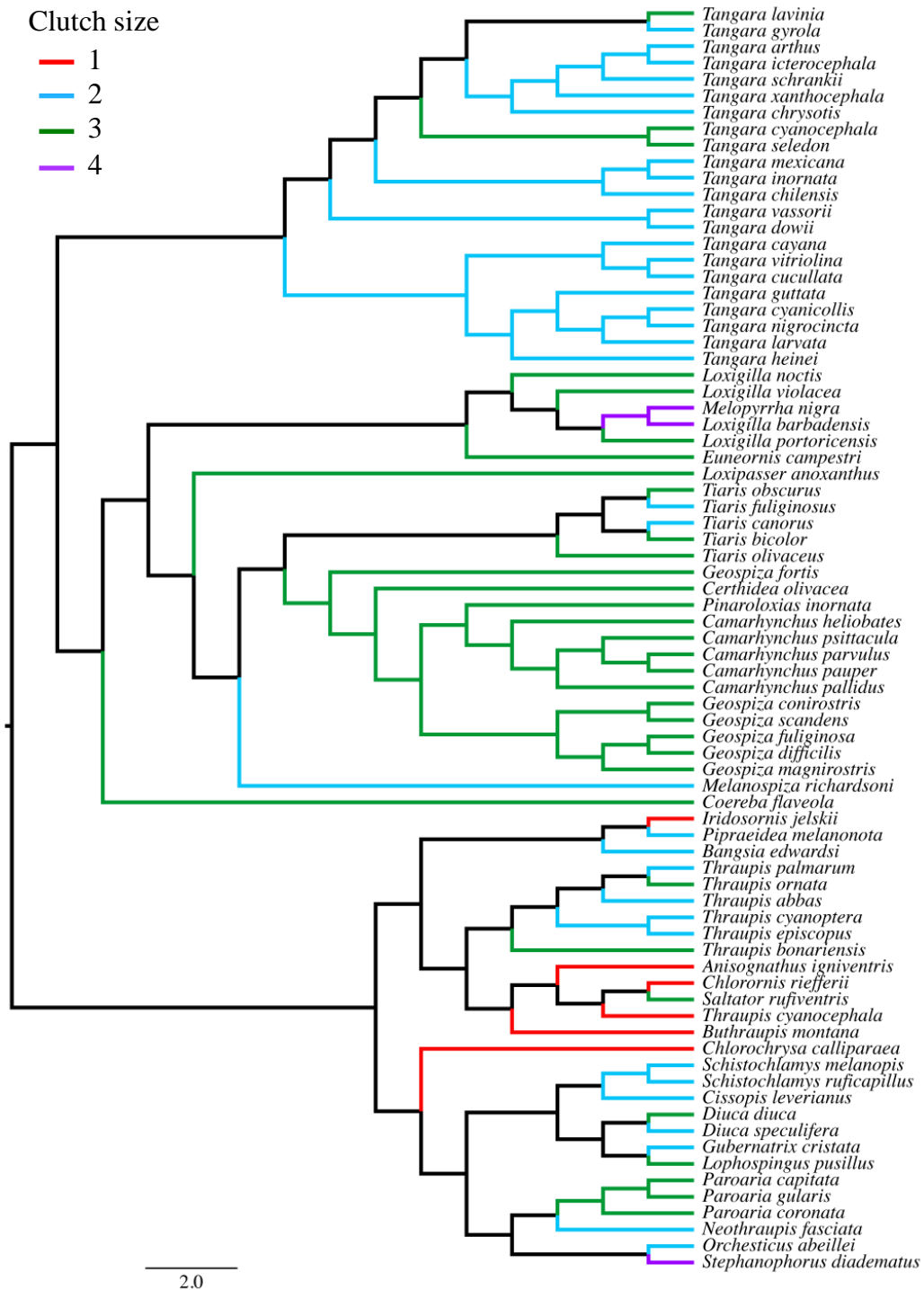


Figure 4-2. Clutch size phylogenetic signal in the tanager clade ($\lambda = -89.98$, $P < 0.0001$). This tree is based on published information by Jetz et al. 2012, and clutch information was obtained from literature (see appendix B).

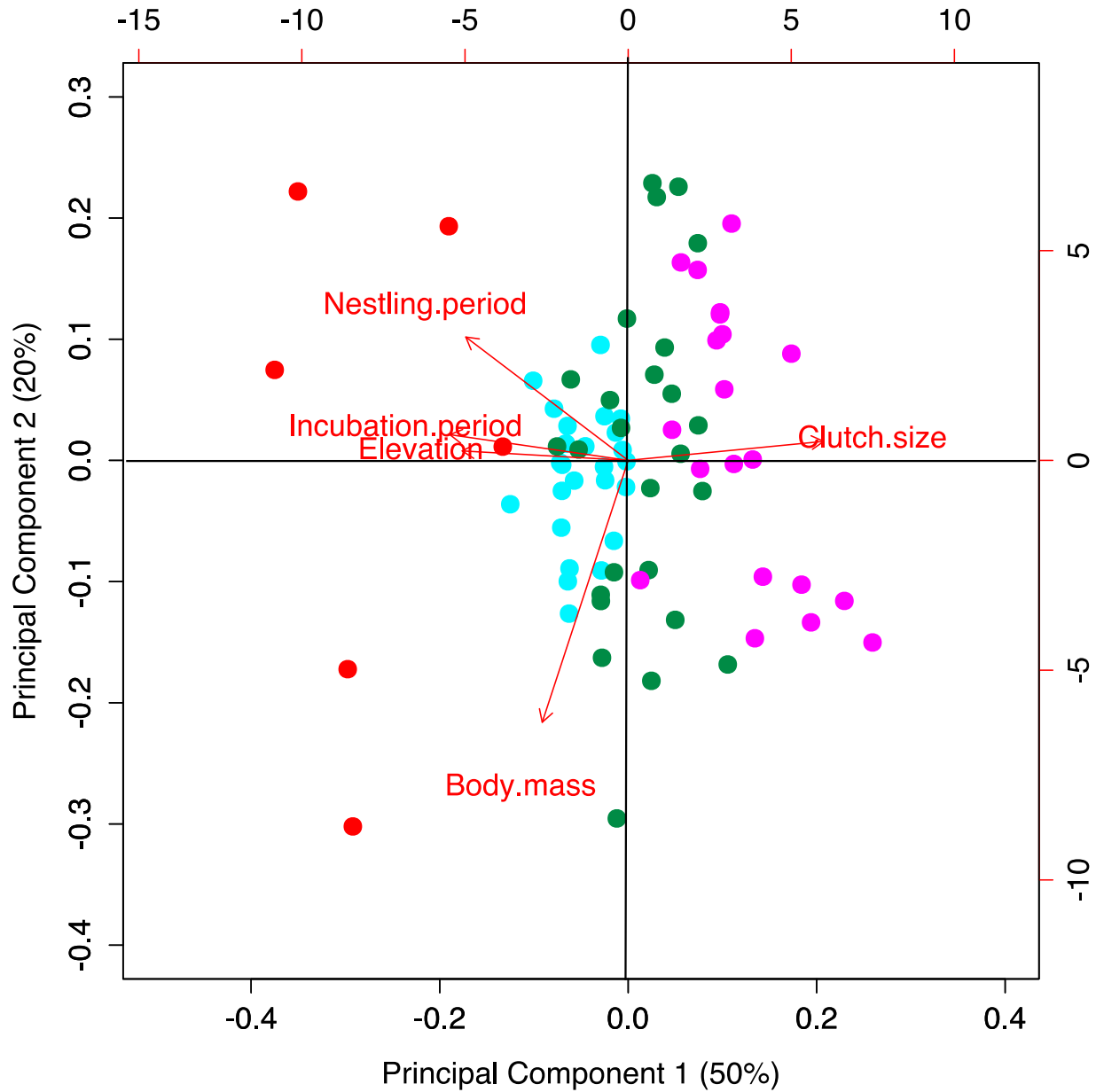


Figure 4-3. Principal component axes that explain 68% of the variation associated with the nesting variables in the tanager clade. The first axis explains 49% of the variation and incubation, nestling period, elevation and clutch size are the main variables associated with this variation. The second axis explains 20% of the variation and body mass and nestling period are the main variables associated with this variation.

CHAPTER 5 CONCLUSION

Tropical mountains offer an exceptional opportunity to explore the mechanism that may be responsible for the slow pace of life observed in neotropical bird species (Ricklefs and Wikelski 2002). Not only do important selective factors such as nest predation and temperature change in a predictable way along the gradient, but there is also enough variation in nesting strategies that I can link variation in investment decisions with contrasting selective pressures. Overall the harsh environment (e. g., colder temperatures) encountered by nesting bird at high elevation seems to have a stronger impact on investment decision made by nesting tropical birds than variation in nest predation. However, both nest predation and ambient temperature seem to shape the slow pace of life observed in tropical nesting birds, in areas where both abiotic and biotic conditions are harsh such as in elfin forest, there is an even slower pace of life available to birds.

My study revealed that changes in the relative importance of different nest predators and their activity patterns likely contribute to variation in nesting success along an elevational gradient. Furthermore, my work suggests that this variation may limit the elevational distributions of some tropical bird species, with community-wide implications. Nest predation seems especially likely to contribute to changes in bird species composition in the foothills of tropical mountains, and possibly within upper cloud forest. I view this study as a first step towards evaluating the hypothesis that nest predation contributes to species turnover and life history evolution along Neotropical montane gradients, and propose that nest predation is a critical factor both promoting and maintaining the high beta diversity and extraordinary regional diversity found in the

Andes (Rahbek & Graves 2001). The next steps for testing this hypothesis will require data on life-history traits as potential adaptations to nest predation, such as egg and clutch mass, incubation and nestling periods and behaviors during nesting, consideration of abiotic factors that change along the gradient (i.e., temperature, rainfall and productivity) and biotic factors such as interspecific competition. Understanding the interactions and relative importance of these factors will provide a more complete picture of the ecological mechanisms that promote species turnover along tropical elevational gradients.

In general, my results partially supported the hypothesis that nest predation is a primary driver of the suite of life-history traits observed in tropical birds. The different incubation strategies and investment decisions documented in the Manu Andean elevation gradient reflect the complexity and diversity of life history strategies concealed in this hyper-diverse tropical area. Overall bird species that encounter higher daily nest predation rates and maintained their egg at warmer temperatures had shorter incubation periods (Martin *et al.* 2007). These characteristics were mainly associated with lowland bird communities. But, generally, daily nest predation and egg temperature alone explained only a small percentage of the variation observed on this tropical elevation gradient (Martin 2004; Tieleman *et al.* 2004; Robinson *et al.* 2010). The large variation in incubation strategies observed along the elevation gradient and within bird communities suggest that previously documented contradictory results may be resolved by studying two different tropical forest bird communities, lowlands (Tieleman *et al.* 2004) and cloud forest (Martin *et al.* 2007), which have contrasting incubation strategies. Therefore I need to explore additional factors that could explain

the observed variation within tropical communities (Martin 2004), for example, by comparing nesting strategies among tropical bird species within a community (Ricklefs & Brawn 2012).

Finally, the extreme clutch size reduction and associated slow pace of life in high-elevation tropical tanagers is a strategy of “making the best of a bad situation” in a perpetually cold environment characterized by low productivity (Salinas *et al.* 2011) and low nesting success (Robinson *et al.* 2000; Martin *et al.* 2006; Robinson *et al.* 2010). Tanagers with single-egg clutches had longer incubation and nestling periods than those at lower elevations with two-egg clutches. Given the constant high nest predation rates along the entire elevation gradient in tanagers, there should be intense selection for rapid incubation and development; therefore, the long nesting period at high elevations suggests that shorter periods are not an option. Indeed, correcting for length of nesting cycle, tanagers of high elevation actually have lower nesting success than those with two-egg clutches nesting at lower elevations. Thus, maintaining viable populations at high elevations might only be possible with frequent re-nesting (Roper *et al.* 2010) and high survival of adults (Gill & Haggerty 2012) and fledglings (Tarwater *et al.* 2011; Gill & Haggerty 2012). Given that most high-elevation tanagers are relatively large, 51% larger than those in the lowlands, they may live longer (Peterson & Wroblewski 1984; Brown *et al.* 2004). Until I have data on these additional life-history variables, however, I will not be able to assess the whole suite of life-history traits that characterize tanagers living at these high elevations.

APPENDIX A
NUMBER OF NESTS DEPREDATED BY INDICATED SPECIES OF TAXONOMIC
GROUPS.

Table A-1. Number of nests depredated by indicated species of taxonomic groups.

Predator Taxonomic Group	Species	Number of Nest Predated
Birds	Emerald Toucanet (<i>Aulacorhynchus prasinus</i>)	25
	Chestnut-tipped Toucanet (<i>Aulacorhynchus derbianus</i>)	4
	Curl-crested Aracari (<i>Pteroglossus beauharnaesii</i>)	1
	White-throated Toucan (<i>Ramphastos tucanus</i>)	1
	Golden-collared Toucanet (<i>Selenidera reinwardtii</i>)	1
	Barred Forest Falcon (<i>Micrastur ruficollis</i>)	3
	White-Collared Jay (<i>Cyanolyca viridicyanus</i>)	2
	Andean Pygmy Owl (<i>Glaucidium jardinii</i>)	1
	Barn Owl (<i>Tyto alba</i>)	1
	Great Thrush(<i>Turdus fuscater</i>)	8
	House Wren (<i>Troglodytes aedon</i>)	1
	Mammals	
White-lipped Peccary (<i>Tayassu pecari</i>)		1
Ocelot (<i>Leopardus pardalis</i>)		1
Common Opossum (<i>Dedelphis marsupialis</i>)		2
White-fronted capuchin (<i>Cebus albifrons</i>)		3
Tufted capuchin (<i>Sapajus apella</i>)		6
Saddle-back Tamarin (<i>Saguinus fuscicollis</i>)		9
Tayra (<i>Eira barbara</i>)		1
Andean Skunk (<i>Conepatus sp</i>)		1
Marmosa (<i>Marmosa lepida</i>)		4
Marmosa (<i>Marmosa spp.</i>)		11
Unknown Marsupial		3
<i>Oryzomys spp.</i>		5
Unknown Rodents	9	
Reptiles		46
	Gold Tegu (<i>Tupinambis teguixin</i>)	2
	Puffing Snake (<i>Pseustes poecilonotus</i>)	36
	Amazon Tree Boa (<i>Corallus hortulanus</i>)	1
	Rainbow Boa (<i>Epichrates cenchria</i>)	2
	Forest Flame Snake (<i>Oxyrhopus petola</i>)	4
	Mussurana (<i>Clelia clelia</i>)	1
Invertebrates		9
	Bullet Ant (<i>Paraponera clavata</i>)	1
	Unknown Ants	5
	Bees	2
	Snail	1
Total		136

Table A-2. Tanager species list. Environmental and nesting variables associated with the tanager clade

Species	Clutch size	Incubation period (days)	Nestling Period (days)	Elevation (m)	References
<i>Anisognathus igniventris</i>	1	21	21	3050	This study
<i>Bangsia edwardsi</i>	2			1050	Isler and Isler 1999, Hilty 2011
<i>Buthraupis montana</i>	1	20		2700	This study
<i>Camarhynchus heliobates</i>	3.5	12	10	500	Isler and Isler 1999, Hilty 2011
<i>Camarhynchus pallidus</i>	3.5			500	Isler and Isler 1999, Hilty 2011
<i>Camarhynchus parvulus</i>	3.5			500	Isler and Isler 1999, Hilty 2011
<i>Camarhynchus pauper</i>	3.5		14.5	500	Isler and Isler 1999, Hilty 2011
<i>Camarhynchus psittacula</i>	3.5	12	11	500	Isler and Isler 1999, Hilty 2011
<i>Certhidae olivacea</i>	3.5			500	Isler and Isler 1999, Hilty 2011
<i>Chlorochrysa calliparea</i>	1		21	1450	This study
<i>Chlorornis riefferii</i>	1	22		2500	This study
<i>Cissopis leverianus</i>	2.5	12.5	15	1150	Isler and Isler 1999, Hilty 2011
<i>Coereba flaveola</i>	3	12.5	17	1200	Isler and Isler 1999, Hilty 2011
<i>Diuca diuca</i>	3			1250	Isler and Isler 1999, Hilty 2011
<i>Diuca speculifera</i>	2.5			4750	Isler and Isler 1999, Hilty 2011
<i>Euneornis campestri</i>	3			750	Isler and Isler 1999, Hilty 2011
<i>Geospiza conirostris</i>	3.5	12	14	500	Isler and Isler 1999, Hilty 2011
<i>Geospiza difficilis</i>	3.5	12	14	500	Isler and Isler 1999, Hilty 2011
<i>Geospiza fortis</i>	3.5	12	12	500	Isler and Isler 1999, Hilty 2011
<i>Geospiza fuliginosa</i>	3.5			500	Isler and Isler 1999, Hilty 2011
<i>Geospiza magnirostris</i>	3.5	12	14	500	Isler and Isler 1999, Hilty 2011
<i>Geospiza scandens</i>	3.5	12	12.5	500	Isler and Isler 1999, Hilty 2011
<i>Gubernatrix cristata</i>	2.5			350	Isler and Isler 1999, Hilty 2011
<i>Iridosornis jelskii</i>	1			2950	Isler and Isler 1999, Hilty 2011
<i>Lophospingus pusillus</i>	3			650	Isler and Isler 1999, Hilty 2011
<i>Loxigilla barbadensis</i>	4			170	Isler and Isler 1999, Hilty 2011

Table A-2. Continued

Species	Clutch size	Incubation period (days)	Nestling Period (days)	Elevation (m)	References
<i>Loxigilla noctis</i>	3			495	Isler and Isler 1999, Hilty 2011
<i>Loxigilla portoricensis</i>	3			500	Isler and Isler 1999, Hilty 2011
<i>Loxigilla violacea</i>	3.5			1000	Isler and Isler 1999, Hilty 2011
<i>Loxipasser anoxanthus</i>	3.5			900	Isler and Isler 1999, Hilty 2011
<i>Melanospiza richardsoni</i>	2			475	Isler and Isler 1999, Hilty 2011
<i>Melopyrrha nigra</i>	4			450	Isler and Isler 1999, Hilty 2011
<i>Neothraupis fasciata</i>	2.5	13	11.7	825	Duca and Marini 2011, Isler and Isler 1999
<i>Orchesticus abeillei</i>	2			1175	Isler and Isler 1999, Hilty 2011
<i>Paroaria capitata</i>	3.5			250	Isler and Isler 1999, Hilty 2011
<i>Paroaria coronata</i>	3			250	Isler and Isler 1999, Hilty 2011
<i>Paroaria gularis</i>	3			200	Isler and Isler 1999, Hilty 2011
<i>Pinaroloxias inornata</i>	3.5			500	Isler and Isler 1999, Hilty 2011
<i>Pipraeidea melanonota</i>	2.5	14	17	1900	Alquezar et al. 2010, This study
<i>Saltator rufiventris</i>	3			3000	Isler and Isler 1999, Hilty 2011
<i>Schistochlamys melanopis</i>	2			1175	Isler and Isler 1999, Hilty 2011
<i>Schistochlamys ruficapillus</i>	2			600	Isler and Isler 1999, Hilty 2011
<i>Stephanophorus diadematus</i>	4			1300	Isler and Isler 1999, Hilty 2011
<i>Tanager cyanocephala</i>	3	12.5	15	600	Isler and Isler 1999, Hilty 2011
<i>Tangara arthus</i>	2	14.5		1550	Isler and Isler 1999, Hilty 2011
<i>Tangara cayana</i>	2			850	Isler and Isler 1999, Hilty 2011
<i>Tangara chilensis</i>	2.5		16	850	Isler and Isler 1999, Hilty 2011
<i>Tangara cucullata</i>	2			500	Isler and Isler 1999, Hilty 2011
<i>Tangara cyanicollis</i>	2	17	15	1350	Isler and Isler 1999, Hilty 2011
<i>Tangara dowii</i>	2			1900	Isler and Isler 1999, Hilty 2011
<i>Tangara guttata</i>	2	13	15	1150	Skutch 1989
<i>Tangara gyrola</i>	2	13.5	15.5	1300	Skutch 1989

Table A-2. Continued

Species	Clutch size	Incubation period (days)	Nestling Period (days)	Elevation (m)	References
<i>Tangara heinei</i>	2	14		1900	Freeman and Greeney 2009
<i>Tangara icterocephala</i>	2	13.2	15	1150	Skutch 1989
<i>Tangara inornata</i>	2			600	Isler and Isler 1999, Hilty 2011
<i>Tangara larvata</i>	2	14.5	15	475	Skutch 1989
<i>Tangara lavinia</i>	3			600	Isler and Isler 1999, Hilty 2011
<i>Tangara mexicana</i>	2.5	13		600	Isler and Isler 1999, Hilty 2011
<i>Tangara nigrocincta</i>	2	13	17	800	Isler and Isler 1999, Hilty 2011
<i>Tangara schrankii</i>	2	15	13.5	700	Isler and Isler 1999, Hilty 2011
<i>Tangara seledon</i>	3	17		550	Isler and Isler 1999, Hilty 2011
<i>Tangara vassorii</i>	2			2500	Isler and Isler 1999, Hilty 2011
<i>Tangara vitriolina</i>	2			1350	Isler and Isler 1999, Hilty 2011
<i>Tangara xanthocephala</i>	2			1800	This study
<i>Thraupis abbas</i>	2.5			1050	Isler and Isler 1999, Hilty 2011
<i>Thraupis bonariensis</i>	3			1275	Isler and Isler 1999, Hilty 2011
<i>Thraupis cyanocephala</i>	1	22	21	2250	Isler and Isler 1999, Hilty 2011
<i>Thraupis cyanoptera</i>	2			750	Isler and Isler 1999, Hilty 2011
<i>Thraupis episcopus</i>	2	13	17.5	900	Isler and Isler 1999, Hilty 2011
<i>Thraupis ornata</i>	3			1025	Isler and Isler 1999, Hilty 2011
<i>Thraupis palmarum</i>	2	14	19	950	Isler and Isler 1999, Hilty 2011
<i>Tiaris bicolor</i>	3			430	Isler and Isler 1999, Hilty 2011
<i>Tiaris canorus</i>	2.5			750	Isler and Isler 1999, Hilty 2011
<i>Tiaris fuliginosus</i>	2.5			1550	Isler and Isler 1999, Hilty 2011
<i>Tiaris obscurus</i>	3.5			1300	Isler and Isler 1999, Hilty 2011
<i>Tiaris olivaceus</i>	3			1150	Isler and Isler 1999, Hilty 2011
<i>Tangara chrysotis</i>	2			1700	Isler and Isler 1999, Hilty 2011

APPENDIX B
NUMBER OF NESTS ENCOUNTERED FOR THE 84 BIRD SPECIES IN THE MANU
GRADIENT AND THE SPECIES ASSOCIATED WITH EACH COMMUNITY. FROM
THE 84 SPECIES, TEN WERE SHARED AMONG COMMUNITIES.

Table B-1. Number of nests encountered for the 84 bird species in the manu gradient and the species associated with each community. From the 84 species, ten were shared among communities.

Species	Number of nest	Forest community
<i>Anisognathus igniventris</i>	23	Elfin
<i>Arremon torquatus</i>	2	Elfin
<i>Atlapetes melanolaemus</i>	25	Cloud/Elfin
<i>Automolus infuscatus</i>	3	Lowland
<i>Basileuterus chrysogaster</i>	4	Foothill
<i>Buthraupis montana</i>	6	Elfin
<i>Catharus dryas</i>	28	Cloud
<i>Chlorornis riefferii</i>	3	Elfin
<i>Chlorospingus flavigularis</i>	20	Cloud
<i>Chlorothraupis carmioli</i>	23	Lowland/Foothill
<i>Conopophaga ardesiaca</i>	26	Cloud
<i>Doryfera johannae</i>	1	Lowland
<i>Doryfera ludovicicae</i>	16	Cloud
<i>Dysithamnus mentalis</i>	13	Cloud
<i>Elaenia albiceps</i>	3	Cloud
<i>Elaenia pallatangae</i>	20	Elfin
<i>Euphonia mesochrysa</i>	1	Cloud
<i>Euphonia xantogaster</i>	51	Foothill/Cloud
<i>Formicarius analis</i>	7	Lowland/Foothill
<i>Geotrygon montana</i>	72	Lowland/Foothill
<i>Glaucis hirsutus</i>	3	Lowland
<i>Glyphorhynchus spirurus</i>	8	Lowland
<i>Grallaria guatimalensis</i>	4	Cloud
<i>Heliodoxa leadbeateri</i>	5	Cloud
<i>Hemitriccus granadensis</i>	2	Elfin
<i>Hydropsalis climacocerca</i>	12	Cloud
<i>Hylophylax naevius</i>	70	Lowland/Foothill
<i>Lanio versicolor</i>	7	Lowland
<i>Leptopogon amaurocephalus</i>	8	Lowland
<i>Leptotila rufaxilla</i>	7	Lowland
<i>Lochmias nematura</i>	2	Cloud

Table B-1. Continued

Species	Number of nest	Forest community
<i>Manacus manacus</i>	2	Lowland
<i>Micromonacha lanceolata</i>	6	Foothill
<i>Mionectes macconnelli</i>	9	Lowland/Foothill/Cloud
<i>Mionectes olivaceus</i>	4	Foothill/Cloud
<i>Myiadestes ralloides</i>	15	Cloud
<i>Myioborus miniatus</i>	28	Cloud
<i>Myiodinastes chrysocephalus</i>	16	Cloud
<i>Myiotheretes fuscorufus</i>	7	Cloud
<i>Myrmeciza fortis</i>	1	Elfin
<i>Nyctiphrynus ocellatus</i>	2	Lowland
<i>Ochthoeca rufipectoralis</i>	9	Lowland
<i>Octhornis litoralis</i>	54	Elfin
<i>Odontophorus stellatus</i>	2	Lowland
<i>Onycorehynchus coronatus</i>	2	Foothill
<i>Ortalis guttata</i>	2	Lowland
<i>Peryglina leuconota</i>	4	Lowland/Cloud
<i>Phaeothlypis fulvicauda</i>	2	Lowland
<i>Phaethornis guy</i>	5	Lowland
<i>Phlegopsis nigromaculata</i>	4	Foothill
<i>Pipra chloromeros</i>	3	Lowland
<i>Pipraeidea melanonota</i>	11	Lowland
<i>Platyrinchus mystaceus</i>	2	Elfin
<i>Premnoplex brunnescens</i>	1	Cloud
<i>Psarocolius atrovirens</i>	24	Cloud
<i>Pyrrhomyias cinnamomea</i>	18	Cloud
<i>Ramphocelus carbo</i>	86	Elfin
<i>Rhynchocyclus fulvipectus</i>	44	Lowland/Cloud
<i>Rupicola peruviana</i>	6	Cloud
<i>Saltator maximus</i>	8	Cloud
<i>Sayornis nigricans</i>	4	Cloud
<i>Schistocicla leucostigma</i>	20	Cloud
<i>Schizoeaca helleri</i>	26	Lowland
<i>Sepophaga cinerea</i>	5	Elfin
<i>Streptoprocne rutila</i>	19	Cloud
<i>Tangara cyanicollis</i>	11	Elfin
<i>Tangara schrankii</i>	3	Cloud
<i>Terenotricus erythrurus</i>	59	Lowland

Table B-1. Continued

Species	Number of nest	Forest community
<i>Tersina viridis</i>	2	Lowland
<i>Thraupis cyanocephala</i>	2	Lowland
<i>Tinamus guttatus</i>	21	Elfin
<i>Tinamus major</i>	4	Foothill
<i>Troglodytes aedon</i>	2	Lowland
<i>Trogon melanurus</i>	3	Elfin
<i>Turdus albicollis</i>	2	Lowland
<i>Turdus fuscater</i>	13	Lowland
<i>Turdus haxwelling</i>	33	Elfin
<i>Turdus leucops</i>	8	Cloud
<i>Uropsalis segmentata</i>	3	Cloud
<i>Willisornis poecilonotus</i>	3	Elfin
<i>Xiphorhynchus guttatus</i>	5	Lowland
<i>Zonotricha capensis</i>	11	Lowland
Total	1134	

APPENDIX C
VOLUNTEERS THAT WORKED DURING LONG HOURS AND MONTHS SEARCHING
AND MONITORING BIRD NESTS BETWEEN AUGUST AND DECEMBER TO MAKE
THIS DISSERTATION POSSIBLE.



Figure C-1. Volunteers that worked during long hours and months searching and monitoring bird nests between August and December to make this dissertation possible.

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BIOGRAPHICAL SKETCH

Gustavo Adolfo Londoño was born in July of 1976 and grew up in Cali, Colombia. During his childhood he wanted to be a soccer player, but also spent most of his summer vacation in a family farm, swimming in rivers, hiking and riding horses in the mountains and valley next to the Cauca river. After finishing high school at Gimnasio la Colina in 1993 he spent one year as an exchange student learning English in Morton, Illinois USA (the Pumpkin capital of the world). After a year, when he returned to the country, he moved to Bogota to start his undergraduate studies in Biology at Los Andes University, in August of 1994. He became interested in birds after participating in field techniques course at the Tinigua National Park, Meta, Colombia, in December of 1997. The following summer he participated in a three months study exploring dietary preferences of the Salvin's Curassows (*Mitu salvini*). In January of 1999 he and four other friends returned to the same place to collect data for their undergraduate thesis on the habitat used and diet of Salvin's Curassows (*Mitu salvini*) and Black Curassows (*Crax alector*) during seven months. After finishing his undergraduate in March of 2000, he spent one month on Costa Rica counting Great Curassows (*Crax rubra*) and three months in a Marbled Murrelet (*Brachyramphus marmoratus*) project in the Queen Charlotte Islands and Desolation Sound in British Columbia, Canada. In February of 2011 he spent one year at Cosha Cashu biological station where he not only studied the Razor-billed Curassows (*Mitu tuberosum*), but he became interested in the nesting biology of tropical birds that year Gustavo monitored more than 130 nests from 57 bird species and published the first nesting records for three neotropical species. When he returned to Colombia he was planning to go back to Peru but due to the lack of funding the study was canceled and Gustavo started work at a local NGO EcoAndian in June of

2002. During two years at EcoAndina Gustavo studied the biology of three Andean Guans at Santuario de Fauna y Flora Otún-Quimbaya, Risaralda, Colombia. In the fall of 2004 Gustavo began his graduate studies at the University of Florida, under the supervision of Scott Robinson and Douglas Levey, where he studied nesting strategies of the Northern Mockingbird (*Mimus polyglottus*) under different temperature regimes and levels of food availability. After obtaining his Master's degree in the spring of 2007 he traveled to the Manu National park during the fall to explore and collect preliminary data for his doctoral study. This dissertation is the result of 23 months of fieldwork in an elevation gradient in Southeastern Peru between 350 and 3100 m. Outside his field season Gustavo continue working with Mockingbirds on UF's campus and travel regularly to Washing DC, to visit Rosario Castañeda his fiancée and now current wife.