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Avian upsloping in the tropics: *Myioborus miniatus* and *Myioborus torquatus* abundance in different altitudinal ranges in Boquete, Chiriquí, Panama

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SIT Panama: Tropical Ecology, Marine Ecosystems, and Biodiversity Conservation

Spring 2019

Abstract

Direct and indirect effects of warming global temperatures due to climate change are known to cause upwards shifts of the altitudinal ranges of some avian species. Most susceptible to this trend and at risk of riding the “escalator to extinction” are endemic species in tropical montane cloud forests, such as *Myioborus torquatus*. There are abiotic factors, like temperature, and biotic interactions, such as the presence of its altitudinal neighbor *Myioborus miniatus*, that limit the altitudinal range of this bird species in the Neotropics. This study measured abundance of *M. miniatus* and *M. torquatus* populations at different altitudinal ranges by point count observations. Analysis of the data revealed that there may be changes in preferred altitudinal ranges of both species, as well as a range of altitudinal overlap, implicating competition for resources. There were significant differences in both the population abundances of *M. miniatus* and *M. torquatus* at the lower and higher altitudinal ranges of observation. The results serve as preliminary evidence in the upsloping of the lower altitudinal limit of *M. torquatus* and the upper altitudinal limit of *M. miniatus* in the western highlands of Panama. Existing literature about the factors influencing altitudinal ranges, impacts of climate change on certain animal species, and ensuing interspecific and intraspecific competition were compiled to elaborate on the possible causes and consequences of shifting *M. miniatus* and *M. torquatus* altitudinal ranges.

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Introduction

With the implications of global warming becoming more serious with the exponential advancement of climate change, many organisms and ecosystems are being disrupted. By 2100, it is projected that climate change will have led to extinctions of 10% of all eukaryotic species worldwide (Freeman et al. 2018). In accordance, many avian species are threatened by changing conditions of established habitats. An increase in global temperatures aligns with a shift of altitudinal ranges of many birds in the tropics (Buermann et al. 2011).

While other factors may play a role in the upsloping of avian species, there is ample evidence that suggests distributional shifts of many birds are directly linked to climate change (Sekercioglu et al. 2012). Overall, altitudinal ranges of birds are dictated largely by habitat temperature and biotic interactions (Jankowski et al. 2010; Freeman et al. 2018). Habitat temperature is regarded as one of the most important factors in determining altitudinal range, and many avian species have been observed shifting upwards towards new habitats to pursue their optimal habitat temperature in association with increasing global temperatures (Freeman et al. 2018).

Habitat temperature is not only indicative of what temperature is most ideal for a species' productivity, but also indicates the conditions and resources in the habitat. For example, in many tropical montane cloud forests, the presence of many epiphytes provides birds with ample food and nesting material (Sekercioglu et al. 2012; Auer and Martin 2013). However, epiphytes can have narrow environmental niches, and a climatic change can cause widespread mortality, causing cascading impacts on the intricate resource web of that habitat (Sekercioglu et al. 2012). With fewer food and nesting resources, birds may experience negative effects on reproductive success and become less abundant in the area (Auer and Martin 2013).

In a similar fashion, temperature may affect altitudinal ranges of other animals, such as insects, which could indirectly affect the altitudinal ranges of birds. Temperature is known to strongly impact tropical insect species because limited temperature variation allowed for greater thermal physiological specialization to occur in these insects (Freeman et al. 2018). Because many avian species depend on insect populations for sustenance, it is speculated that altitudinal range shifts of these species are occurring because of indirect interactions with the tropical ectotherms that may be initially upsloping (Freeman et al. 2018).

In general, warming temperatures in the tropics are associated with reduced cloud cover, less water capture, and drier ecosystems in cloud forests (Sekercioglu et al. 2012). When these conditions occur on tropical mountains, avian species are forced upward to follow optimal habitat conditions (Sekercioglu et al. 2012; Freeman et al. 2018). In this way, a change in habitat temperature can prompt direct and indirect changes in avian abundance at a certain altitude.

The influences that temperature has on avian altitudinal ranges are more prominent in tropical avian species than in temperate species (Freeman et al. 2018). Range shifts of temperate zone species show a lag when compared to predictions of shifts, while tropical avian species approximately match those predicted by climate change models (Freeman et al. 2018). This suggests that temperature is the primary influential factor in the altitudinal limits of most tropical avian species (Freeman et al. 2018). Moreover, as most tropical montane birds are restricted by smaller altitudinal ranges, they are very sensitive to changes in their habitat (Jankowski et al. 2010).

Among tropical bird species, mountaintop species are more susceptible to the harmful warming of habitats. In the tropics, there is very little gradient in temperature by changes in latitude (Freeman et al. 2018). As a result, tropical montane species are unlikely to migrate by latitude to follow hospitable habitat conditions, which is a solution available to species in temperate areas where latitudinal temperature gradient is more evident (Freeman et al. 2018). Temperature sensitivity coupled with the sedentary nature of avian species isolated to mountains greatly increases tropical avian vulnerability to extinction (Sekercioglu et al. 2012).

The upwards shifting of altitudinal range, or upsloping, of avian species has been termed "an escalator to extinction" (Freeman et al. 2018). This concept suggests that, if global warming is not significantly slowed or stopped, the upsloping of birds will continue to become increasingly severe. If avian species continue to shift their altitudinal ranges upwards on a mountain, there may be a point in the future at which there is very little or no remaining habitat to upslope into (Buermann et al. 2011).

Avian upsloping and extinction

Emphasizing the "escalator to extinction" concept, existing research and predictions of avian species abundance demonstrate disconcerting facts. Existing research about avian upsloping includes a study done in Sira, Peru, which estimated that 55 species have moved upwards by 12 meters per decade based on historical temperature patterns (Forero-Medina et al. 2011). This is especially alarming because there are no other competing hypotheses besides climate change as to why the upsloping of avian species is occurring in this area (Forero-Medina et al. 2011). In addition to the study done in Sira, Peru, there are studies observing changes in altitudinal ranges of different avian species from various locations. In Southeast Asia, 94 tropical bird species, including *Bradypterus luteoventris* and *Passer rutilans*, were observed to have moved the upper, lower, or both ends of their altitudinal range upwards from 1971 to 1999 as temperatures increased (Sekercioglu et al. 2012).

Using two climate change scenarios, mean temperatures in the Northern Andes were predicted to increase by 1.8-2.6 °C in a conservative projection and 2.6-5.3 °C in an extreme projection by 2080 (Buermann et al. 2011). The extreme projection of increased mean temperature agrees closely with the Intergovernmental Panel on Climate Change, or IPCC, assessment of a likely increase of 3.5 °C of the Earth's surface temperature by 2100 (Buermann et al. 2011; Sekercioglu et al. 2012). The consequent response of montane Neotropical hummingbirds is expected to mirror the trend of avian upsloping. Altitudinal shifts upward are predicted to vary between 300 and 700 meters depending on the scenario and the species (Buermann et al. 2011).

Increased surface temperatures are associated with upwards altitudinal shifts of avian species, and are expected to coincide with massive avian extinctions. Combining the temperature projection models provided by the IPCC and habitat loss scenarios from the Millennium Ecosystem Assessment indicates that, in the scenario with the highest projected surface warming of 6.4 °C, over 2500 land bird extinctions could occur by 2100 (Sekercioglu et al. 2012). Another analysis derived from emissions pledges in December 2011 at the international climate change negotiations in Durban, concludes that there will likely be an increase of 3.5 °C of the Earth's surface temperature by 2100, causing the extinctions of up to 900 avian species (Sekercioglu et al. 2012). Of the species predicted to become extinct, 89% are species that originate in the tropics (Sekercioglu et al. 2012). In 80% of climate change simulations used for the tropical and biodiverse region of Central America, it was found that 25-38% of the endemic species currently present would be lost (Sekercioglu et al. 2012).

Another altitudinal model was used to predict that twelve avian species will become extinct on the Pacific slope of the Tilarán Mountains of Costa Rica as the average temperature increases by 3 °C within the next century (Gasner et al. 2010). The extinctions stem from a predicted decline in almost half of the avian species present in the area (Gasner et al. 2010). Among those bird species is the *Myioborus miniatus*, or the Slate-throated Redstart, and the regionally endemic *Myioborus torquatus*, or the Collared Redstart (Gasner et al. 2010).

Myioborus miniatus and Myioborus torquatus

The genus *Myioborus* consists of small, sexually monomorphic New World warblers of the family *Parulidae* (Mumme 2015). They are found in montane forests of the American subtropics and tropics (Mumme 2015). The parulids have tails that are contrasting white and black colors; the tails are fanned and fluttered to startle and flush insect prey from vegetation (Mumme 2015).

Adult individuals of *Myioborus miniatus* have slate-gray heads, yellow breasts and bellies, and rufous crowns (Angehr and Dean 2010). They are the most widely distributed species of the *Myioborus* genus and inhabit mountainous habitats from northern Mexico to southern Bolivia (Mumme 2015). *M. miniatus* individuals do not migrate and frequently build nests along roads and trails (Mumme 2015). They were recorded to have an altitudinal range of 600-2100m in 2010 (Angehr and Dean 2010).

The *Myioborus torquatus* is a parulid found in humid, highland forests, and is endemic to the areas of Costa Rica and western Panama (Skutch 1945). It has bright, distinctive yellow coloring on its forehead, face, and throat and a rufous crown (Skutch 1945). Although similar in appearance to *M. miniatus*, *M. torquatus* can be differentiated by its yellow face (Angehr and Dean 2010). Known amiably by locals as the “amigo del hombre,” the birds enjoy woodland edges and open areas of mountain forests without much fear of people (Skutch 1945). In 1910, *M. torquatus* had an altitudinal range of 1500-2400m (Skutch 1945). A rise in the upper limit of the altitudinal range of *M. torquatus* has been observed. Today, *M. torquatus* birds are seen anywhere from 1400m to 3500m (Ocampo-Peñuela 2016).

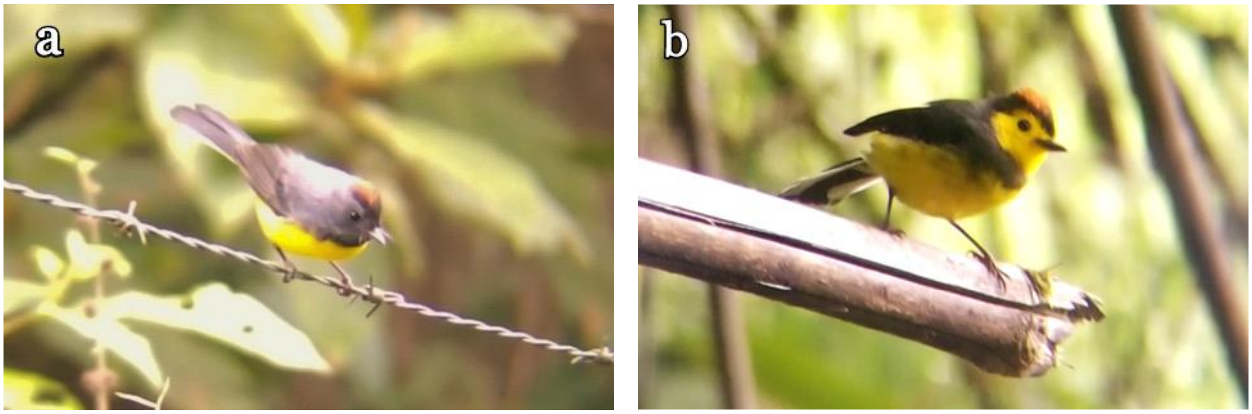

Figure 1. Images of (a) *Myioborus miniatus* and (b) *Myioborus torquatus*. Although inhabiting similar areas and appearing like in size, the two bird species are easily distinguished by the color of their face. Photos by Julie Yoon.

Typically, *M. miniatus* is observed at lower altitudes and *M. torquatus* is observed at higher altitudes. Given their altitudinal ranges and the similarities in habitat characteristics, both *M. miniatus* and *M. torquatus* are present in the montane cloud forests of the highlands in Panama (Angehr and Dean 2010). Because there is considerable overlap from 1400m to 2100m between the altitudinal ranges of each species, there may be a sharing of habitats (Angehr and

Dean 2010; Ocampo-Peñuela 2016; Gabrielsson 2006). Although they are both present in cloud forests, it is unclear how the altitudinal overlap of 700 meters is affecting the viability of these two bird species, if at all. It is possible that, because the insects both species prey on are similar, any overlap between the altitudinal ranges inhabited by each species implies competition for the same resources (Gabrielsson 2006). This competition may be exacerbated by the possible upsloping of *M. miniatus* and *M. torquatus* on mountaintops because of an increase in the altitudinal overlap between the two species.

Effects of avian upsloping

On a community level, the narrowing of a species' altitudinal range translates into a smaller area of possible occupation (Sekercioglu et al. 2012). For example, if both the lower end and upper ends of an altitudinal range shift upward along the slope of a mountain in equal increments, there will be a smaller surface area of the mountain for the species to inhabit. Likewise, an upsloping of just the lower altitudinal boundary would also shrink the altitudinal range and the amount of possible area for occupation. This has occurred in a mountainous region of southeastern Peru, where a study revealed that the lower altitudinal limit of some avian species rose (Freeman et al. 2018). As a result, the altitudinal range of these species decreased by an average of 110 meters (Freeman et al. 2018). This implies that members of the same species will have fewer resources to sustain the population, possibly resulting in a decline in abundance of the species population in that area (Jankowski et al. 2010). Such resources can include insect prey and nest building materials.

Similarly, upsloping of a bird species may also induce stronger interspecific competition. The upsloping entails major encroachments on already established relationships between resource availability and use. With the induced introduction of more birds of varying species into occupied habitats, it is possible that a detrimental imbalance of abiotic and biotic factors of an environment will follow (Gabrielsson 2006). Depending on the ecosystem and the different abiotic and biotic factors present, the effects of introducing a new species to the local resource web could create an imbalance of varying degrees. For example, a study of competition for food between the introduced *Psittacula krameri* and native birds like *Sturnus vulgaris* in Paris, France found that the *P. krameri* was the most aggressive of species at bird feeders and may outcompete native birds (Louarn et al. 2016). In this case, the introduction of a foreign bird species indirectly caused a decrease in the fitness of native avian species (Louarn et al. 2016). Therefore, such an introduction of a species into a habitat could possibly lead to decreases in abundance, causing extinctions of other species present.

Interspecific competition for resources is especially more impactful on an ecosystem when species of similar niches, lifestyles, and foraging behaviors overlap. A study done in Costa Rica observing the differences in foraging behaviors of *M. miniatus* and *M. torquatus* at different altitudes suggests a sharing of habitats by the two species may implicate interspecific competition and have negative impacts on the population abundances of both bird species (Gabrielsson 2006). The study asserts that, in the Monteverde Cloud Forest Reserve, *M. miniatus* individuals were never observed above 1600m before 2006 (Gabrielsson 2006). The observations of *M. miniatus* individuals above 1600m in this particular habitat during and after 2006 is attributed to upsloping because this species is not an altitudinal migrant (Gabrielsson 2006). This increase in the upper limit of *M. miniatus* altitudinal range is suggested to cause greater interspecific competition between *M. miniatus* and *M. torquatus*, as both species have the same class of prey (Gabrielsson 2006).

Interspecific competition between *M. miniatus* and *M. torquatus* affects each species at different magnitudes. The competition was found to be more of a threat to *M. torquatus* because the two species were observed to forage with different levels of urgency and activity (Gabrielsson 2006). For example, *M. miniatus* was noted to have more active foraging behavior, frequently flashing its tail to flush out insects and pursue them (Gabrielsson 2006). It was also noted that *M. miniatus* was generally more active and prepared to forage by exhibiting animated behavior like flying and hopping around (Gabrielsson 2006). In contrast, *M. torquatus* seemed to exhibit calmer behavior, sitting and responding to playback recordings for longer periods of time (Gabrielsson 2006).

A suggestion for the difference in behavior is that, at higher altitudes, *M. torquatus* evolved with lower levels of competition, whereas *M. miniatus* evolved with higher pressures of interspecific competition because of migrant species and higher species diversity at lower altitudes (Gabrielsson 2006). As a result, it was concluded that *M. miniatus* may feel more pressure to forage urgently, and may consume an insect more quickly than *M. torquatus* if all three organisms are present in the same habitat. Therefore, upsloping of *M. miniatus* into historically *M. torquatus* habitats can pose a threat on an established relationship between prey availability and consumption, leading to decreased fitness in *M. torquatus* individuals (Gabrielsson 2006).

Asymmetric aggression in foraging behavior could cause avian species at higher altitudes to be forced even more upwards. As stated previously, altitudinal ranges of birds are often influenced by biotic, interspecific interactions as well as increasing habitat temperatures. One historically popular hypothesis asserts that closely related avian species do not have overlapping altitudinal distributions, instead replacing each other along an altitudinal gradient (Jankowski et al. 2010). Therefore, it is possible that a rise in the upper altitudinal limit of a one species can lead to the rise in the lower altitudinal limit of another species (Jankowski et al. 2010).

One study of two tropical songbirds in Costa Rica demonstrated that the lower-altitude *Catharus mexicanus* was more aggressive than the upper-altitude *Catharus fuscater* in terms of responding to playback recordings of other birds (Jankowski et al. 2010). The *C. mexicanus* population was determined to be interspecifically dominant, and the influences of asymmetric dominance on upsloping and interactions between similar species were emphasized in the study (Jankowski et al. 2010). By incorporating the results of this study with the hypothesis that *M. miniatus* is a more dominant competitor, it is possible that *M. torquatus* populations will be even more jeopardized if there is an upsloping of *M. miniatus* populations, which could lead to a larger overlap of altitudinal ranges between the two species or the consequent upsloping of *M. torquatus* populations. In this way, climatic changes and biotic interactions can have compounded impacts on altitudinal shifting in avian species, threatening the viability of high-altitude species populations.

Location

The upsloping of bird species is seen in many locations outside of the Monteverde Cloud Forest Reserve in Costa Rica, such as in the western highlands of Panama (Gasner et al. 2010). Avifauna near Boquete, a town in the Panamanian highlands, exemplifies the upsloping phenomenon. Located in the northern part of the Chiriquí province, the terrain of Boquete is defined by the multitude of mountains formed by the Talamanca mountain range, which extends past the western border of Panama into Costa Rica (Tierney et al. 2008). As a result, the western highlands exhibit a wide altitudinal range (Tierney et al. 2008). Near the town center of Boquete is Volcan Barú National Park, which is a publicly owned park consisting of mostly secondary-growth cloud forests (Crino et al. 2010). The national park houses Barú Volcano, Panama's highest peak, and is a tropical landscape that accommodates many highland species (Tierney et al. 2008). Although there is a dry season, there is precipitation every month, and total annual precipitation is about 4000-5000mm (Tierney et al. 2008). As a result of the mountainous terrain and consistent presence of precipitation, tropical montane cloud forests are common and provide for much of Panama's avifauna (Benson 2015).

Boquete boasts great abundance and diversity of avifauna (Benson 2015). In addition to being a biodiverse hotspot, the tropical montane cloud forests of Boquete are home to many regionally endemic species (Sekercioglu et al. 2012). This quality may actually be more cause for concern in regards to threats of extinction. Areas around the bases of mountains usually have higher average temperatures, and avian species that are used to cooler temperatures at higher altitudes on mountains may be accordingly isolated to those mountains (Sekercioglu et al. 2012). As a result, endemic species in tropical mountain cloud forests are especially at high risk of extinction as global warming occurs (Sekercioglu et al. 2012).

Research significance

As awareness about climate change increases, so does the understanding of its effects. Historically, tropical mountain habitats were less fragmented by human populations and anthropogenic impacts (Sekercioglu et al. 2012). As a result, tropical mountain avian species were mostly deemed as low conservation concern (Sekercioglu et al. 2012). However, there is an increased recognition of the effects of climate change on bird populations and the importance of incorporating related data in considering extinction risk of species currently (Sekercioglu et al. 2012).

Similarly, information about climate change impacts on avian species can be used to assess the effectiveness of current conservation practices and suggest changes to better prevent avian extinctions (Sekercioglu et al. 2012; Freeman et al. 2018). Different avian species will have different abilities in adapting to changes in availability of resources such as food and vegetation due to warming temperatures (Sekercioglu et al. 2012). There is an increased effort to understand the rate at which these ecosystems are changing and the consequent effects on avian species. With heightened understanding comes a more robust and comprehensive plan for the conservation of migratory environments and the prevention of population extinctions (Freeman et al. 2018).

As many biogeographical and physiological characteristics are shared between avian species and other non-avian organisms, such information about the effects of global warming on avifauna may also be extended to help conservation of species in other groups that are also vulnerable to climate change effects (Sekercioglu et al. 2012). For these reasons, it is imperative to conduct more population studies and analyze differences in abundance so that accurate information may be acquired. Regular research and analysis of how populations change over time is a strong indicator of patterns that can be used to better conservation efforts in the future (Freeman et al. 2018). Measuring abundance of upsloping avian species at different altitudes is an insightful method of tracing climate change, monitoring its effects on shifting species, and observing the implications of the introduction of a new species in an established ecosystem (Pauchard et al. 2016).

This study examined the abundance of *Myioborus torquatus* and *Myioborus miniatus* along the lower altitude Pipeline Trail and the upper altitude Quetzal Trail in Boquete, Chiriquí.

The abundance of each warbler along the two different trails was analyzed to determine if there is a significant upsloping of either species in the western highlands of Panama and what possible causes and implications of upsloping may exist.

Research Question

What is the abundance of *Myioborus torquatus* and *Myioborus miniatus* along two hiking trails of different altitudinal ranges in Boquete, Chiriquí?

Research Objectives

- Measure abundance of *Myioborus torquatus* and *Myioborus miniatus* at different altitudinal ranges
- Suggest reasons and implications for any altitudinal shifts

Methods

Study sites

The abundance of *Myioborus torquatus* and *Myioborus miniatus* was measured along two trails in Boquete, Panama. Sites were chosen based on their altitudinal ranges. Both trailheads of each trail were reachable by taxi. The two selected trails were the Pipeline Trail and the Quetzal Trail.

The Pipeline Trail was the low altitude trail, and includes point counts at 1450-1650m. It is approximately 11 kilometers from the Boquete town center. The trailhead is within the altitudinal range of study, but is in close proximity to a couple of homes with chickens, dogs, and small pets. Farther along the trail are forested areas besides small rivers with occasional open areas. The altitudinal rise of the Pipeline Trail is gradual.

The Quetzal Trail was the high altitude trail, and point counts were taken at altitudes between 2100 and 2300 meters. It is approximately 14 kilometers from the Boquete town center. The trailhead begins at about 1800 meters, and there is a visitor center and ranger station called Alto Chiquero. The first portion of the trail is through an open area with scattered houses and livestock. Later, the trail goes through lush montane cloud forests with open areas, and has steep inclines and declines. Much of the trail follows or crosses extensions of the Caldera River. The entire trail is about 8.5 kilometers long and connects Boquete to Cerro Punta, another city in the Chiriquí province. Altitudinal gain throughout the trail is about 700 meters, and the maximum altitude is 2500 meters.

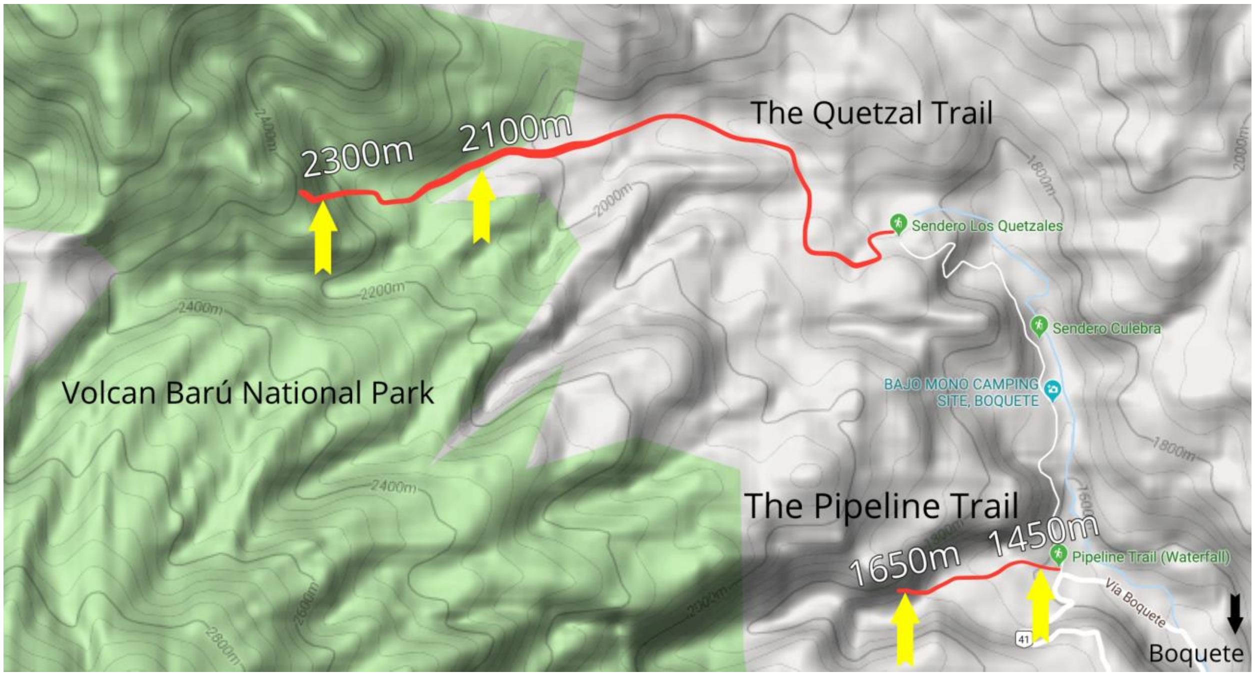

Figure 2. The Pipeline Trail and the Quetzal Trail are two hiking trails northwest of Boquete. The yellow arrows mark the lower and upper altitudinal limits of interest for each trail. Photo retrieved from Google Maps.

Data collection

Myioborus torquatus and *Myioborus miniatus* abundance was measured at different altitudes using point count surveys along the Pipeline Trail and the Quetzal Trail. Point counts are a widely used method to estimate relative or absolute abundance of birds (Matsuoka et al. 2014). In order to complete a point count, an observer will stand at a count station and record birds detected during the count period within the count radius (Matsuoka et al. 2014).

For this study, there were ten count stations on each of the two trails in Boquete. The count period was ten minutes and the count radius was unlimited. Temperature, humidity and weather conditions were recorded at the first point count station. At least 500 meters were placed between the trailheads and the first point count station. For the Pipeline Trail, the first point count station was approximately 550 meters from the trailhead. This was to decrease the factor of anthropogenic influence on avian abundance. For the Quetzal Trail, the first point count station was located where the trail hit 2100 meters above sea level, about four kilometers in. Every station after the first was approximately 100 meters from the previous station. The predetermination of 100m distances between count stations ensured that the sites at which abundance were measured were randomly selected.

Because *M. torquatus* or *M. miniatus* have similar calls and songs, individuals were only recorded if they were observed by sight. When a *M. torquatus* or *M. miniatus* bird was observed, the time interval of discovery was recorded as 0-3, 3-5, and 5-10 minutes, as this is a standard of point count surveys (Matsuoka et al. 2014). The distance range from the point station to the first sighting of the bird was also recorded; it was estimated to be in the interval 0-50m or >50m as is recommended by standards for the sake of consistency in point count survey data across studies (Matsuoka et al. 2014). Both the time interval of detection and distance interval were recorded for each individual detected at the count station.

Data Analysis

Point count surveys are greatly beneficial in that they can be used to monitor species and assess population trends over time (Matsuoka et al. 2014). Data collected over five days for each altitude was summed by altitude. Comparing the number of individuals found at each altitude revealed the altitudinal range at which *M. torquatus* and *M. miniatus* populations were most and least abundant, in addition to which altitudes the two populations overlapped in resource use. The upsloping of the lower or upper altitudinal limits *M. torquatus* and *M. miniatus* populations was analyzed with t-test to determine the significance in the differences in population abundance between the two altitudinal ranges.

The time intervals during which *M. miniatus* and *M. torquatus* were detected at the low and high altitudinal ranges were included after summing data over five days of study in each range, in addition to the point count radius interval. The ranges and averages of temperature and humidity for each altitudinal range were calculated.

Ethical Statement

An application for approval was sent to the local review board and the SIT Institutional Review Board after assessing the possible risks that may affect the subjects. The methods of this independent study project were put into action after it was approved. For this project, the subjects of research are *Myioborus torquatus* and *Myioborus miniatus* in the forests of Boquete, Chiriquí. In conducting point count surveys, there is little risk of harm to birds because there is no physical handling. Birds were not physically touched, and all observations were made from a distance by sight or hearing. Possible harms to the ecosystem included stepping on plants on other organisms while hiking. To minimize these risks, all point count stations were on hiking trails of study and a conscious effort was made to ensure negligible harm was done to the areas of study.

Results

Site observations

Data from the Pipeline Trail was collected over five days between April 14 and April 26, 2019. All point counts on this trail were conducted between 6:30 A.M. and 9:20 A.M. Temperatures ranged from 16.2 °C to 17.1 °C, with an average of 16.7 °C. Humidity ranged from 85.7% to 97.8%, with an average of 91.5%. During data collection on the Pipeline Trail, the weather was mostly clear, but there were infrequent times of partially cloudy skies and misting rain. In most areas, the trail was approximately a meter wide with an abundance of open areas.

For the Quetzal trail, data was collected over five days between April 15 and April 27, 2019. As the first point count was approximately four kilometers from the trailhead, the time range for point counts was a bit later in the day. Point counts on this trail occurred between 8:25 A.M. and 11:20 A.M. Temperatures on the Quetzal Trail at this time of day ranged from 17.5 °C to 19.7 °C, with an average of 18.7 °C. Humidity ranged from 74.8% to 87.5%, with an average of 82.1%. During data collection on this trail, the weather was usually overcast with interspersed moments of clear skies and misting rain. The trail was generally about 0.5 meters wide with some open areas.

M. miniatus and M. torquatus at different altitudes

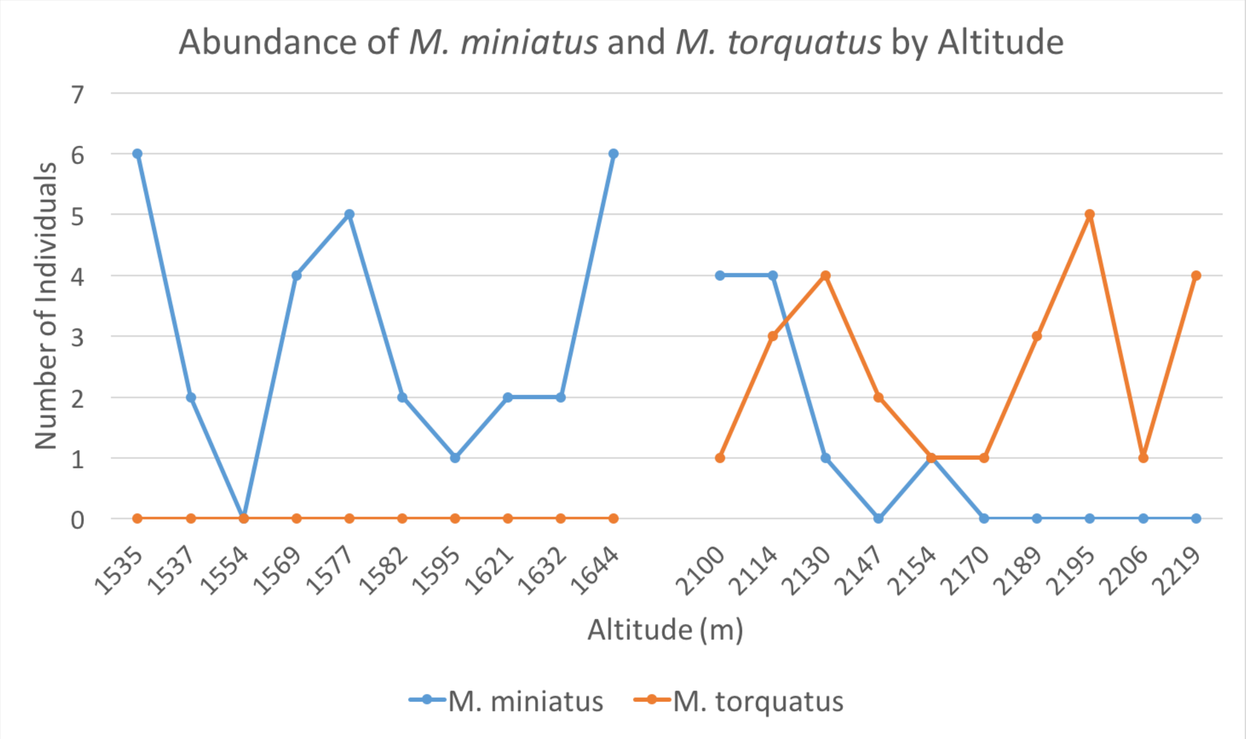

Figure 3. Number of individuals of *M. miniatus* and *M. torquatus* observed at different altitudes.

	Expected Presence		Observed Individuals	
	1450-1650m	2100-2300m	1450-1650m	2100-2300m
M. miniatus	X		30	10
M. torquatus	X	X	0	23

Table 1. The expected presence and number of observed individuals of *M. miniatus* and *M. torquatus* at the low and high altitudinal ranges. The marked boxes represent where presence was expected (Angehr and Dean 2010; Ocampo-Peñuela 2016). The highlighted boxes represent findings that are inconsistent with literature (Angehr and Dean 2010; Ocampo-Peñuela 2016).

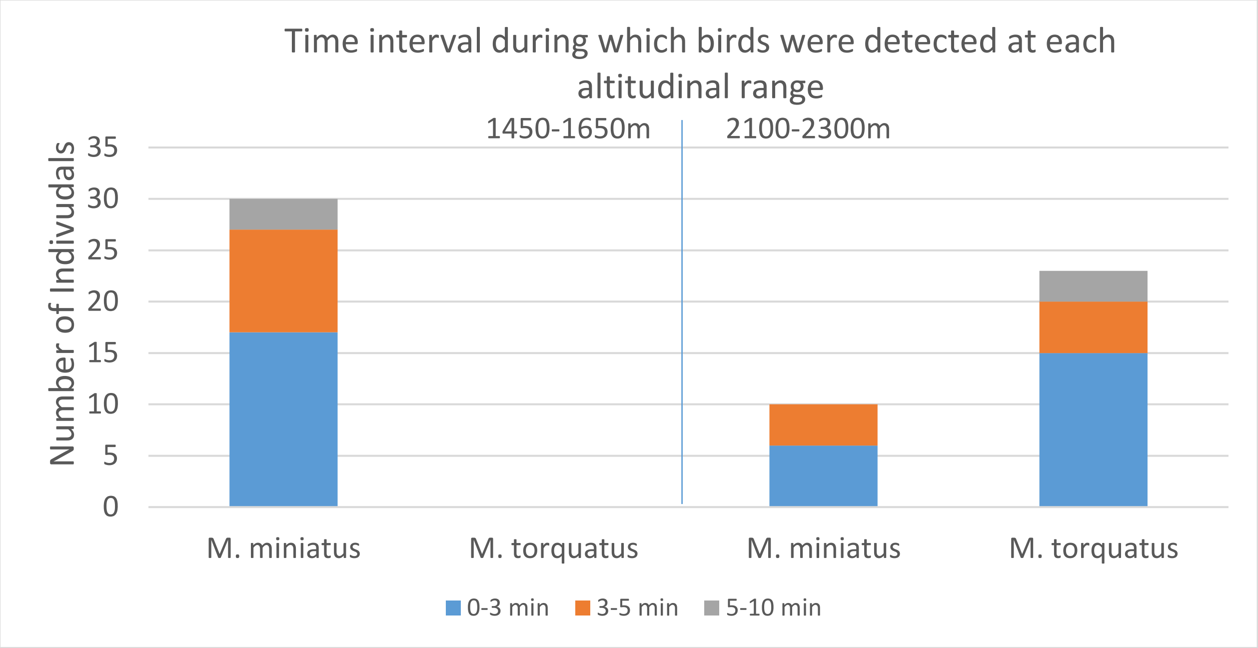

Figure 4. The time intervals during which *M. miniatus* and *M. torquatus* were detected at the low and high altitudinal ranges. All birds were observed to be in the radius interval of 0-50m.

Statistical tests on observations

A total of 63 *M. miniatus* and *M. torquatus* individuals were observed over the course of the study. Along the low-altitude Pipeline Trail, 30 *M. miniatus* and 0 *M. torquatus* individuals were observed (Table 1). Along the high-altitude Quetzal Trail, 10 *M. miniatus* and 23 *M. torquatus* individuals were observed (Table 1). Statistical t-tests were conducted comparing the population abundance of each bird at the two altitudinal ranges. There is a significant difference in population abundances of *M. miniatus* at the low and high altitudinal ranges (*p*-value=0.03). There is also a significant difference in population abundances of *M. torquatus* at the low and high altitudinal ranges (*p*-value=0.0005).

Discussion

Observed altitudinal shifts

From collected data, there were two instances where unexpected observations were made based on previous literature (Angehr and Dean 2010; Ocampo-Peñuela 2016). This suggests possible changes in the preferred altitudinal ranges of *M. miniatus* and *M. torquatus* populations (Table 1). The presence of *M. miniatus* in the 2100-2300m altitudinal range, which is typically dominated by *M. torquatus* populations, can possibly be interpreted as an upwards shift of the upper altitudinal limit of the species in this area. Similarly, the absence of *M. torquatus* from the 1450-1650m altitude range indicates a possible upwards shift of its lower altitudinal limit in this area. The significance of the performed t-tests for both species populations at both altitudinal ranges demonstrates that the difference in population abundance found in this study is relevant. The results of this study may serve as notable preliminary evidence of shifting altitudinal ranges for both *M. miniatus* and *M. torquatus* populations in Boquete.

The results of this study suggest that there is a shift in the upper altitudinal limit of *M. miniatus* populations in the area. Previously, *M. miniatus* was noted to be common in the

Panamanian highlands from 600 meters to 2100 meters in altitude (Angehr and Dean 2010). As such, the detection of the species at the lower altitudinal range, which covered 1450-1650m in altitude, was expected. In contrast, the detection of *M. miniatus* individuals in the upper altitudinal range, which encompassed 2100-2300m in altitude, was unexpected. The data indicates that the observations of *M. miniatus* individuals in the upper altitudinal range in this study are not an anomaly, meaning *M. miniatus* individuals are naturally observed above 2100m in Boquete at the time of this study. This contradicts the previously noted *M. miniatus* altitudinal range of 600 meters to 2100 meters (Angehr and Dean 2010). Because *M. miniatus* individuals were not usually observed above 2100m previously, the results of this study provide preliminary evidence for the upsloping of *M. miniatus* populations.

Similarly, the observed upwards shifting of the lower altitudinal limit of *M. torquatus* in Boquete provides preliminary evidence for possible *M. torquatus* upsloping. In 1910, *M. torquatus* was observed to have an altitudinal range of 1500-2400m (Skutch 1945). Ocampo-Peñuela (2016) documented *M. torquatus* to have an altitudinal range of 1400-3500m in the highlands of Costa Rica. In Panama, *M. torquatus* is typically observed above 1800m, but has been seen at altitudes as low as 1050m (Angehr and Dean 2010). Therefore, the observation of *M. torquatus* individuals was expected for both the lower and upper altitudinal ranges of this study. Consequently, the absence of *M. torquatus* from the lower altitudinal range was not anticipated. Considering the results of data analysis between the two altitudinal ranges, it can be suggested that an upsloping of the lower altitudinal limit of *M. torquatus* may be occurring.

Possible reasons for altitudinal upsloping

Habitat temperature is representative of the ideal temperature range a species is best able to feed and reproduce, as bird populations living in their thermal optimum are the most likely to exhibit high productivity (Meller et al. 2018). Because warming temperatures brought on by climate change are altering the landscapes of tropical montane cloud forests, previously hospitable habitats are becoming less able to support existing populations (Freeman et al. 2018). It is known that birds may follow their niche into newer territories to pursue habitats with their thermal optimum; for tropical montane avian species, this usually means altitudinal upsloping (Meller et al. 2018).

A conservative temperature trend demonstrating an increase of 3 °C nationwide in Panama from 1988 to 2013 could be cause for *M. miniatus* and *M. torquatus* upsloping (Hurtado et al. 2014). The upsloping of these populations in Boquete may be an attempt to adapt to the warming of historic habitats past the thermal optimum in order to continue levels of productivity and lifestyles. For example, it is possible that these bird populations shifted upwards in altitudinal range in order to combat an increase in habitat temperature that could detrimentally affect productivity and lead to a decrease in population abundance over time (Meller et al. 2018). A study on *M. miniatus* breeding biology and nesting success found that, when ambient temperatures were cool and ideal in a montane cloud forest of Costa Rica, there was high egg hatching success (Mumme 2010). This is consistent with the hypothesis that high ambient temperatures during the laying season of *M. miniatus* is a primary reason for decreased egg viability and increased hatching failure (Mumme 2010). Consequently, the upsloping of *M. miniatus* and *M. torquatus* populations may act to counter adverse habitat conditions that could lead to decreased productivity in warmer habitats.

In addition to breeding and nesting success, changing climate is known to be an influencing factor on foraging behaviors of birds (Tayleur et al. 2015). For a habitat to be deemed hospitable for an avian species, there must be adequate resources for sustaining life, such as an abundant prey population. Birds of the *Myioborus* genus usually prey on insects by using the contrasting colors of their tails to startle the insects out of forest vegetation, pursuing them, and capturing them in flight (Jaboski et al. 2006). Tropical insects are strongly influenced by ambient temperature because of their evolution in areas of limited temperature variation (Freeman et al. 2018). Research suggests that some insect species may have adapted to warming ambient temperatures and have better viability success at higher altitudes than recorded previously (Pureswaran et al. 2018). These insect populations are expanding into higher altitudinal ranges, and it can be speculated that avian species may follow (Pureswaran et al. 2018; Freeman et al. 2018). Therefore, it is possible that the upsloping of *M. miniatus* and *M. torquatus* populations may be a result of indirect biotic interactions (Freeman et al. 2018).

Implications of M. miniatus and M. torquatus upsloping

It is common for tropical bird species to be limited in their altitudinal range due to their biotic interactions with other, nearby species (Jankowski et al. 2010). These biotic interactions dictate that the altitudinal ranges of similar, competing species in the tropics are distributed in a way that minimizes overlapping ranges (Jankowski et al. 2010). Strong evidence exists to support the concept that closely related species of birds replace one another as altitude increases on tropical mountains (Jankowski et al. 2010). Observations of *M. miniatus* in the mid-altitude montane forests of Central America, with a different *Myioborus* species replacing it at higher altitudes exist (Mumme 2010). Given this, it may be deduced that, although both *M. miniatus* and *M. torquatus* are present in montane cloud forests, their populations may be distributed accordingly so there is minimal altitudinal overlap (Angehr and Dean 2010). According to Angehr and Dean (2010), there is at least 300 meters of altitudinal overlap between *M. miniatus* and *M. torquatus* populations in Panama: 1800-2100m. It is unclear how the altitudinal overlap of 300 meters affects the viability of the two bird species, if at all. Although there is altitudinal overlap in theory, there may or may not be significant sharing of resources between the two species populations that affects the viability of either species. For example, viability may not be affected if a *M. miniatus* nest is at the same altitude as a *M. torquatus* nest, but 200 meters apart horizontally in the same cloud forest.

The results of this study demonstrate altitudinal overlap in the ranges of *M. miniatus* and *M. torquatus* populations, suggesting it is possible that the viability of *M. miniatus* and *M. torquatus* individuals could be detrimentally affected. A study of three warblers of the family Parulidae in Arizona, United States demonstrated how overlap in nest sites could negatively affect reproductive success among closely related avian species (Auer and Martin 2013). Over two decades, it was found that the nest site overlap between *Oreothlypis celata*, *Oreothlypis virginiae*, and *Cardellina rubrifrons* increased from around 0.6 to almost 1.0, indicating a nearly complete overlap (Auer and Martin 2013). The increase in nest site overlap was correlated with decreased densities of breeding pairs of all three species and tripled nest predation, signifying a negative impact on avian viability and abundance (Auer and Martin 2013).

As such, the overlap between the altitudinal ranges of *M. miniatus* and *M. torquatus* populations may negatively impact reproductive success and population abundance. The overlap of habitat and locations of resource use between *M. miniatus* and *M. torquatus* populations occurred at four different point count stations over the course of ten days (Figure 3). Observed altitudinal overlap occurred from 2100 meters to 2154 meters in altitude (Figure 3). This does not necessarily mean that individuals of the two different species were observed at the same altitude on the same day, but does suggest considerable sharing of habitat and resource use is possible.

Perhaps one of the most important factors in determining avian altitudinal range is the availability of prey in a habitat (Jankowski et al. 2010). An increased overlap in the altitudinal ranges of *M. miniatus* and *M. torquatus* populations can lead to greater interspecific competition for the same resources. As noted previously, this interspecific competition may detrimentally affect *M. miniatus* and *M. torquatus* population abundance, as there is increased predator quantity while the prey quantity remains static. The study in the Monteverde Cloud Forest Reserve of Costa Rica demonstrated that interspecific competition between *M. miniatus* and *M. torquatus* populations is more likely to negatively impact *M. torquatus* abundance than *M. miniatus* abundance due to differences in their foraging behavior (Gabrielsson 2006). *M. miniatus* individuals were observed to be more likely to exhibit higher urgency in foraging, and increased foraging activity precipitated greater success in flushing out insects and capturing them (Gabrielsson 2006). In contrast, *M. torquatus* individuals were observed to be calmer and prioritize foraging less frequently (Gabrielsson 2006). This study concluded that *M. miniatus* individuals were more likely to be the dominant foragers in areas where *M. miniatus* and *M. torquatus* populations overlapped (Gabrielsson 2006). Therefore, possible decreases in *M. miniatus* and *M. torquatus* populations, but especially in *M. torquatus* populations, are major implications of increased altitudinal overlap caused by upsloping.

As such, an increase in the number of predators in an area increases interspecific competition, and a decrease in prey abundance exacerbates the effects of interspecific competition exponentially. It is important to note that upsloping and extinctions due to climate change do not solely affect avian species, but many organisms of different classes (Pureswaran et al. 2018). A comprehensive literature review and analysis of peer-reviewed scientific papers by Pureswaran et al. (2018) revealed that the upper altitudinal limit of certain species of insects have been observed to shift upwards at different locations around the world. These insects are inhabiting areas higher in altitude than usual and are associated with disrupted ecosystems (Pureswaran et al. 2018). For example, the high-altitude pine trees of Yellowstone National Park in the Unites States have seen high levels of mortality caused by the upsloping of *Dendroctonus ponderosae*, an insect that previously did not affect the pines because of inhospitable climatic conditions at the higher altitude (Pureswaran et al. 2018). Another study of insect communities along an altitudinal gradient on Changbai Mountain in China suggested that changing temperatures will facilitate the upsloping of some insects of the family Geometridae and the family Carabidae, causing concern for the species at the top of the mountain (Pureswaran et al. 2018).

In this way, it is possible that the prey of *M. miniatus* and *M. torquatus* has already shifted or will shift upwards in altitude. A common kind of prey that birds of the genus *Myioborus* often consume are insects of the order Diptera (Jaboski et al. 2006). In a study of a section of dipteran insects in Australia, it was found that the species living at high altitudes are especially susceptible to warming global temperatures (Wilson et al. 2007). Using climate envelope models to predict species ranges after incorporating climatic factors, the study found that the insects in the Australian highlands may be at risk of their own escalator to extinction (Wilson et al. 2007). It was predicted that the highest assemblage of the dipterans studied were likely to become locally extinct with a 2-3 °C increase in temperature, which is a temperature change that is projected to happen by 2080 (Wilson et al. 2007; Buermann et al. 2011).

If the rate at which prey exhibits upsloping and extinction is greater than the rate of upsloping in *M. miniatus* and *M. torquatus* populations, decreased prey abundance would occur. Even when there is little or no overlap between the populations of the two species, decreased prey abundance is problematic. Decreased prey abundance in the respective habitats of *M. miniatus* and *M. torquatus* populations could bring about increased intraspecific competition. Increased intraspecific competition can reduce population abundance in that not all individuals among the same species have equal abilities in foraging. With the overlap between the *M. miniatus* and *M. torquatus* populations in Panama, the same decrease in prey abundance may intensify the problematic effects of climate change-induced interspecific competition. Considering the impacts of increased quantities of predators and decreased quantities of prey on population abundance reveals that, while both *M. miniatus* and *M. torquatus* populations may be susceptible, *M. torquatus* populations may be at especially greater risk of extinction.

Potential sources of error and limitations

While this study provided significant results, they should only be regarded as preliminary evidence and not conclusive evidence, as the small sample size derived from a short time period of study is a serious limitation. Extending the days dedicated to data collection would increase the statistical power of the results and conclusions of the study. Because neither species is an altitudinal migrant, conducting a study for a year or several years could minimize the influences of other uncontrolled factors affecting population abundance (Gabrielsson 2006). For example, if this study were conducted over a year, the impacts that the dry or wet season may have on abundance, if any, can be minimized. As this study had ten days of data collection all in one dry season, any influences made by the Panamanian wet season on *M. miniatus* and *M. torquatus* population abundance could not be noted.

Another restriction of this study was the confined time schedule. Point counts occurred between 6:30 A.M. and 9:20 A.M. on the Pipeline Trail and between 8:25 A.M. and 11:20 A.M. on the Quetzal Trail. Ideally, it is suggested that point counts be conducted before 10:00 A.M. local time as to avoid the warmer temperatures of the afternoon where most avian species are less active (Hamel et al. 1996). It is possible that the two-hour disparity in data collection on the two trails affected the results acquired. Because the point counts on the Quetzal Trail were done later in the day, fewer birds may have been active. Therefore, the abundances of *M. miniatus* and *M. torquatus* may actually be higher than recorded if the activity of these species fluctuates throughout the day according to day temperature. If the two species do not demonstrate equal inactivity due to daytime temperature, then the data for the high altitude trail may be skewed.

There were differences not only in data collection times, but also in the physical characteristics of the two trails used for this study. For example, it was noted that majority of the Pipeline Trail was about 1m wide, while most of the Quetzal Trail was less than that. Similar to trail width, it is possible that differences in the amount of open area existed. As both *M. miniatus* and *M. torquatus* birds favor habitats with open areas for nesting, the trail with more open areas and forest gaps may be associated with higher species abundance (Mumme 2015; Skutch 1945). For example, if the Quetzal Trail had more open area than the Pipeline Trail and the *M. torquatus* birds had an intense preference for open area, then it could be possible that the absence of *M. torquatus* individuals on the Pipeline Trail could be correlated with the lack of open area on the same trail rather than altitude. While it is possible that these factors have little or no influence on abundance, the differences in abundance between altitudinal ranges may be affected by other uncontrolled factors, such as the amount of open area, proximity to bodies of water, and flora species present.

Another consideration for this study is the sole use of sight for detection of *M. miniatus* and *M. torquatus* individuals. Had this study incorporated aural observations in addition to those made by sight, similar vocalizations coupled with inexperience and limited knowledge on avian species identification may have increased the likelihood of misidentification of a bird. Ultimately, birds were only counted if they were seen. As a result of solely using sight to identify birds and collect data, there may have been a significant amount of data lost. There were multiple occasions where the familiar warbler vocalization was heard, but the bird producing the sound could not be seen through forest vegetation. Because each species may be different in their inclination to vocalize, and because vocalization frequency may also differ by altitudinal range, the exclusion of aural observations in *M. miniatus* and *M. torquatus* bird detection could have influenced the results, and subsequent analyses of data, of this study.

Conclusion

Data on the abundance of *M. miniatus* and *M. torquatus* populations along the lower altitude and the higher altitude trails was successfully collected by use of point counts. An upwards shift of the upper altitudinal limit of *M. miniatus* and an upwards shift of the lower altitudinal limit of *M. torquatus* populations in Boquete were observed. This study provides preliminary evidence of the possible upsloping of *M. miniatus* and *M. torquatus* populations in the western highlands of Panama.

The possible upsloping of these two species is believed to be a direct or indirect result of climate change and warming global temperatures. Each avian species has its own thermal optimum, where its lifestyle is most efficient and there is ideal productivity. As temperature increases worldwide, *M. miniatus* and *M. torquatus* birds may follow their climatic niche upwards a montane slope. Established habitats may experience changes in vegetation, levels of intraspecific and interspecific competitions, and abundance of resources due to climate change. As a result, previously uninhabited altitudinal ranges may become the preferred domain.

The results of this study accentuate an ongoing ecological shift that is expected to continue. With little to no efforts to slow the impacts of climate change on avifauna, there may be many extinctions that occur worldwide in as little as 60 years, with endemic species in tropical montane cloud forests, like *M. torquatus*, being the first to disappear.

Suggestions for further research

Further research about the upsloping of *M. miniatus* and *M. torquatus* populations could elaborate on the effects of an introduction of these populations into already established habitats. A study on the intraspecific and interspecific interactions a species has with its surroundings can reveal how the same interactions will change with upsloping (Møller et al. 2004). Similarly, it can also help identify factors that precipitate upsloping and distinguish them from the effects of upsloping. For example, a study could determine if the upsloping of *M. miniatus* occurs with a decrease in prey abundance in historic habitats or with an increase in prey abundance in new habitats. These studies could be conducted over a much longer period of time as to understand the ecological interactions a species has with its habitat and what specifically about the habitat changes with warming temperatures. The results of these studies could be used to further aid in conservation of avian species in the future (Freeman et al. 2018).

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