

Projected changes in elevational distribution and flight performance of montane Neotropical hummingbirds in response to climate change

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Abstract

The hovering flight of hummingbirds is one of the most energetically demanding forms of animal locomotion and is influenced by both atmospheric oxygen availability and air density. Montane Neotropical hummingbirds are expected to shift altitudinally upwards in response to climate change to track their ancestral climatic regime, which is predicted to influence their flight performance. In this study, we use the climate envelope approach to estimate upward elevational shifts for five Andean hummingbird species under two climate change scenarios. We then use field-based data on hummingbird flight mechanics to estimate the resulting impact of climate change on aerodynamic performance in hovering flight. Our results show that in addition to significant habitat loss and fragmentation, projected upwards elevational shifts vary between 300 and 700 m, depending on climate change scenario and original mean elevation of the target species. Biomechanical analysis indicates that such upwards elevational shifts would yield a $\sim 2\text{--}5^\circ$ increase in wing stroke amplitude with no substantial effect on wingbeat frequency. Overall, the physiological impact of elevational shifts of < 1000 m in response to climate change is likely to be small relative to other factors such as habitat loss, changes in floristic composition, and increased interspecific competition.

Keywords: climate change, elevational shift, hummingbird flight kinematics, wing stroke amplitude, wingbeat frequency

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Introduction

In response to global warming, many species are expected to shift their geographic distributions to track their ancestral climatic regimes rather than remain stationary and evolve to match their new circumstances (Huntley, 1991; Davis & Zabiniski, 1992; Coope, 1994; Parmesan & Yohe, 2003; Wiens & Graham, 2005; Parmesan, 2006). More specifically, species ranges are expected to shift toward higher latitudes and elevations as temperatures rise. Such predictions assume niche conservatism – in which intrinsic physiological constraints, and the associated set of biotic and abiotic conditions in which species are able to persist, are not free to vary (Grinnell, 1917; Hutchinson, 1957). Despite the ongoing debate regarding whether niches are in fact conserved (Wiens & Graham, 2005; Losos, 2008; Wiens, 2008), this hypothesis is congruent with marked elevational stratification of biota specialized for different thermal

regimes, as well as documented shifts in elevational occurrence for some species, which appear linked to the recent warming trend (Moritz *et al.*, 2008).

Although tropical montane systems are expected to be negatively impacted by global climate change, few studies have focused on these regions (Still *et al.*, 1999). The Tropical Andes represents a critically endangered hotspot of biological diversity, and a major region expected to undergo dramatically altered climate due to current global warming (Markham, 1998; Bradley *et al.*, 2004; Williams *et al.*, 2007). This region could face extraordinary changes in biotic composition as species shift their elevational ranges upward, substantially reducing the geographic range sizes of montane species (Pounds *et al.*, 1999; Shoo *et al.*, 2005; Peh, 2007). Most importantly, contraction in range size will increase the extinction risk of many of these species (Erasmus *et al.*, 2002; Gage *et al.*, 2004; Thomas *et al.*, 2004, 2006; Parmesan, 2006; Pimm *et al.*, 2006; Sekercioglu *et al.*, 2008), especially those living at the highest elevations that have little or no remaining habitat to colonize (Benning *et al.*, 2002; Williams *et al.*, 2003; Pimm *et al.*, 2006). In addition, given the negative

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impact that current habitat fragmentation has had on montane Neotropical forests (Sierra *et al.*, 2002; Bubb *et al.*, 2004), elevational shifts could enhance negative effects on species because the impacts of global warming and habitat modification are expected to be additive (Pimm *et al.*, 2006; Jetz *et al.*, 2007).

Although the situation could be dire for tropical Andean species, standard ecological niche models, which largely focus on available land area given a species' climatic tolerances, do not account for other physiological performance variables which may also have important consequences regarding elevational range shifts. For example, locomotor performance in flying animals is influenced by air density and oxygen availability, both of which vary substantially across elevational gradients. Thus, if species' elevational ranges are predicted to shift upwards to follow displaced thermal regimes, the impact of such shifts on locomotor performance might constrain their ability to follow their preferred climatic regime. Here, we explore the impact of predicted climate change on tropical Andean hummingbirds from a climatic perspective, and then extend the model to consider potentially relevant features of flight performance.

Few examples better illustrate the tightly linked relationship between changing climatic and abiotic characteristics and physiological performance than the hovering flight of hummingbirds. Although hovering is one of the most energetically demanding forms of animal locomotion (Suarez, 1998), and should be more difficult at higher elevations due to reduced air density and oxygen availability, hummingbirds have radiated impressively in the Andes (Bleiweiss, 1998; McGuire *et al.*, 2007). Not surprisingly, hummingbirds exhibit corresponding adaptations in flight-related morphology and physiology that enhance their ability to occupy these challenging environments. Detailed studies in the field and laboratory have demonstrated that high-elevation hummingbirds have lower wing loadings relative to low-elevation species (Feinsinger *et al.*, 1979; Altshuler & Dudley, 2002). Furthermore, changes in hummingbird flight kinematics provide an additional means of compensation for altitudinal effects. Wing stroke amplitude during hovering flight increases with the decline in air density across elevations (Chai & Dudley, 1995; Altshuler & Dudley, 2003), concomitantly limiting the excess power available at higher elevations for flight maneuvers beyond that required for hovering flight. Thus, hummingbirds at higher elevations live closer to their upper limits for aerodynamic and biomechanical performance (Altshuler *et al.*, 2004).

In predicting elevational range shifts of hummingbirds under climate change, we hypothesize that hummingbirds will migrate up the Andean flanks to track their ancestral

climatic regime as has been observed in other avian taxa in the Neotropics (Pounds *et al.*, 1999). Given the projected effects of climate change on habitat elevations and the well documented effects of elevation on hummingbird flight performance, we ask: (1) How will the future distributions of hummingbird shift upwards in response to global warming? and, (2) How will this shift affect their aerodynamic performance in hovering flight? To address these questions, we use the climate envelope approach and projections of two climate change scenarios to estimate shifts in the elevational distribution of five Andean hummingbird species. In addition, we utilize an extensive data set on flight mechanics to estimate the implications for flight performance given these elevational shifts.

Materials and methods

Study species and area

To model the impact of future climate change on Andean hummingbird distributions and metabolic performance we obtained locality data for five hummingbirds species that occupy a range of altitudes: *Phaethornis guy* (Green Hermit, 900–2000 m, 57 sites), *Doryfera ludoviciae* (Green-fronted Lancebill, 1400–2700 m, 66 sites), *Agelaiocercus kingi* (Long-tailed Sylph, 1400–3000 m, 55 sites), *Colibri coruscans* (Sparkling Violetear, 1300–3600 m, 143 sites) and *Metallura tyrianthina* (Tyrian Metalltail, 1700–3600 m, 73 sites). All of the five target hummingbird species have strict montane distributions (above 900 m) and are mostly found along the entire Andean range from Venezuela to Bolivia in forested habitats, including humid forests, second growth, cloud forests and moss-clad tree-line shrub (Fjelds  & Krabbe, 1990; Schuchmann, 1999).

We acquired precise GPS locality data for the five target species using mist nets during multiple field surveys throughout Ecuador between 1999 and 2006 and Venezuela in 2007. In addition, we acquired locality data, particularly for Colombia, from other sources (see Appendix S1). The restriction of the study region to the Northern Andes is due to the limited availability of reliable locality data for the five target species in the south. As a consequence, the projected distributional shifts under climate change also apply strictly to the target species that reside in the Northern Andes.

Present and future climate data

Projecting current species-climate envelopes into the future for Andean hummingbirds relies on the availability of observed and simulated limiting climatic factors (e.g. height of orographic cloud formation and potential evapotranspiration) for both present and future climates. Direct observations or modeled outputs of such specific variables are either unavailable or are too coarse to resolve the heterogeneous Andean topography. However, results from a previous climate modeling study suggest that certain temperature and moisture variables can be used as a first proxy to predict cloud forest

locations (Still *et al.*, 1999). Specifically, the *warmth index*, defined as the sum of all monthly mean temperatures that exceed 5 °C (Kira, 1976), has been shown to be a credible predictor of cloud forests, in part due to its linear relationship with potential evapotranspiration (Still *et al.*, 1999).

We utilized contemporary climatic variables from data provided by WorldClim (version 1.4; Hijmans *et al.*, 2005). The monthly temperature and rainfall climatologies were developed using long time series (1960–1990) of a global network of weather stations from various sources such as the Global Historical Climatology Network (GHCN), the United Nations Food and Agricultural Organization (FAO), the World Meteorological Organization (WMO), the International Center for Tropical Agriculture (CIAT), and additional country-based station networks. The station data were interpolated to monthly climate surfaces at 5 km spatial resolution by using a thin-plate spline smoothing algorithm with latitude, longitude, and elevation as independent variables (Hijmans *et al.*, 2005). Of the many monthly and annual climatic metrics available, we selected a smaller subset, based on our assessment that they would likely have relevance for the species being modeled and that credible future climate projections were available. Specifically, we selected the warmth index, maximum temperature of the warmest month, minimum temperature of the coldest month, annual precipitation, precipitation of the wettest quarter, and precipitation of the driest quarter.

Corresponding downscaled future climate variables based on IPCC third assessment projections were also provided by WorldClim. To estimate uncertainty in future distributions of the hummingbird target species resulting from uncertainty in climate change projections, we utilized results based on two general circulation models (GCMs) with differing climate sensitivities (HADCM3 and CCCMA) and two IPCC SRES greenhouse gas emission scenarios (A2 and B2). Specifically, for the target year 2080, upper bounds of projected climate change stem from a GCM with comparably high climate sensitivity (HADCM3) forced with a more 'pessimistic' emission scenario (A2; 720 ppm by year 2080), whereas lower bounds derive from a GCM with lower climate sensitivity (CCCMA) forced with a more 'optimistic' emission scenario (B2; 560 ppm).

Species distribution modeling

Potential geographic distributions of five hummingbird species for present and future climates were modeled with the Maxent algorithm (Phillips *et al.*, 2006). Maxent has several characteristics that make it very suitable for the task of modeling species distributions (Phillips *et al.*, 2006), including a deterministic framework, the ability to run with presence-only point occurrences, high performance with few point localities (Hernandez *et al.*, 2006), better computing efficiency enabling the use of large-scale high-resolution data layers, continuous output from least to most suitable conditions, and ability to model complex responses through a number of different feature classes (e.g., functions of environmental variables). As a consequence, in a recent large model-intercomparison project with 15 other algorithms, Maxent's performance was generally rated among the highest (Elith *et al.*, 2006).

The output of the Maxent model consists of a continuous probability distribution (0–1) indicating least suitable to most suitable conditions for the taxa under consideration (Phillips *et al.*, 2006). To quantify predicted area of the target species for present climates and under future climate change, we converted the continuous Maxent output into a presence/absence map by using an optimized threshold that balanced under and over predictions.

Hovering flight kinematics

We filmed hovering hummingbirds as part of a larger study investigating interspecific differences in maximum flight performance (Altshuler *et al.*, 2004; Altshuler, 2006). The complete data set for the larger study includes over 70 taxa from field sites in the Colorado Rocky Mountains, the Costa Rican central Cordillera, and the Andes of southeastern Peru. However, only some of these taxa were studied at multiple elevations (see 'Results'). We used a combination of barometers and regional topographic maps to either determine or confirm the elevations of all sites. Depending upon the site, we used mist nets, drop-door traps, or Hall traps to capture hummingbirds. All birds were immediately transported from the site of capture to a nearby field laboratory to conduct flight trials. All hummingbirds were tested within 50 m elevation from their site of capture, and at an elevation where the species had been observed flying freely. The testing chamber was located outside in most but not all cases. At the few sites where animals were tested inside, the building were not insulated so temperature and humidity matched outside values. All flight tests were always performed in still air. We scored individuals as either molting or nonmolting, and included only the latter category in the present analysis.

At the beginning of each flight trial, we released individual hummingbirds into a rectangular flight chamber (0.45 m × 0.45 m × 0.9 m height) constructed from walls of either opaque acrylic or dark nylon mesh; the roof of the chamber was clear acrylic. We filmed continuously until birds attained stable hovering, defined as the animal moving less than one body length in several seconds in either the horizontal or vertical dimension, while maintaining a position minimally 2 1/2 wing lengths from any boundary of the chamber.

A single analog (Sony Video 8 CCD-TR44 operated at 60 fields s⁻¹) or digital (Redlake MotionMeter operated at 500 frames s⁻¹) camera recorded the horizontal projection of wingbeat kinematics from a large mirror positioned at 45° above the chamber. Frame-by-frame analysis of the video images yielded wingbeat kinematic parameters. For recordings made with analog video, we determined wingbeat frequency using the interaction frequency between the wingbeat frequency and the filming rate of the video film (see Chai & Dudley, 1995, 1996). The much higher temporal resolution of the Redlake digital camera permitted direct frame-by-frame counting to assign wingbeat frequency. We determined stroke amplitude from wing positions at the maximum and minimum positional angles within the nominally horizontal stroke plane.

The intraspecific difference in kinematic variables was defined as the species average of either wing stroke amplitude or wingbeat frequency at the highest elevation site minus the

average for that same species at the lowest elevation site. The concomitant difference in elevation was defined as the elevation of the highest site minus the elevation at the lowest site. We analyzed these relationships using linear regression on both raw species data and phylogenetically controlled independent contrasts. The phylogenetic hypothesis that served as the historical framework for independent contrasts analyses was based on an analysis of two nuclear and two mitochondrial markers for 151 hummingbird and 12 outgroup taxa (McGuire *et al.*, 2007). Independent contrasts were calculated using the PDAP module (Midford *et al.*, 2007) of the program Mesquite (Maddison & Maddison, 2010); all intercepts were constrained to pass through the origin (see Garland *et al.*, 1992).

Results

Elevational shifts of hummingbird distributions under climate change

In a first step, using a set of point localities, observed climate data and the Maxent algorithm, we predicted

the present potential geographic distribution of the five target hummingbird species in the northern Andes from the southern border of Ecuador to the coastal regions of Venezuela. Figure 1 shows the potential present-day geographic distributions for the two hummingbird species that reside at lowest (*P. guy*) and highest (*M. tyrianthina*) mean elevations. Quantitative performance measures suggested robust model performance for present-day conditions in the case of all five hummingbirds (see Appendix S2), and the corresponding predictions also agree well with known published distributions (Hilty & Brown, 1986; Fjeldså & Krabbe, 1990; Schuchmann, 1999). In respect to variable importance, the *warmth index* and to some extent *precipitation of the driest quarter* were generally the most important climate factors in the predictions for the contemporary climate (see Appendix S3). Suitable environments for the target hummingbirds were characterized by warmth indices between 200–280 °C-months for *P. guy* and 80–250 °C for *M. tyrianthina*, respectively, as well as precipitation of the driest quarter of typically larger than 100 mm.

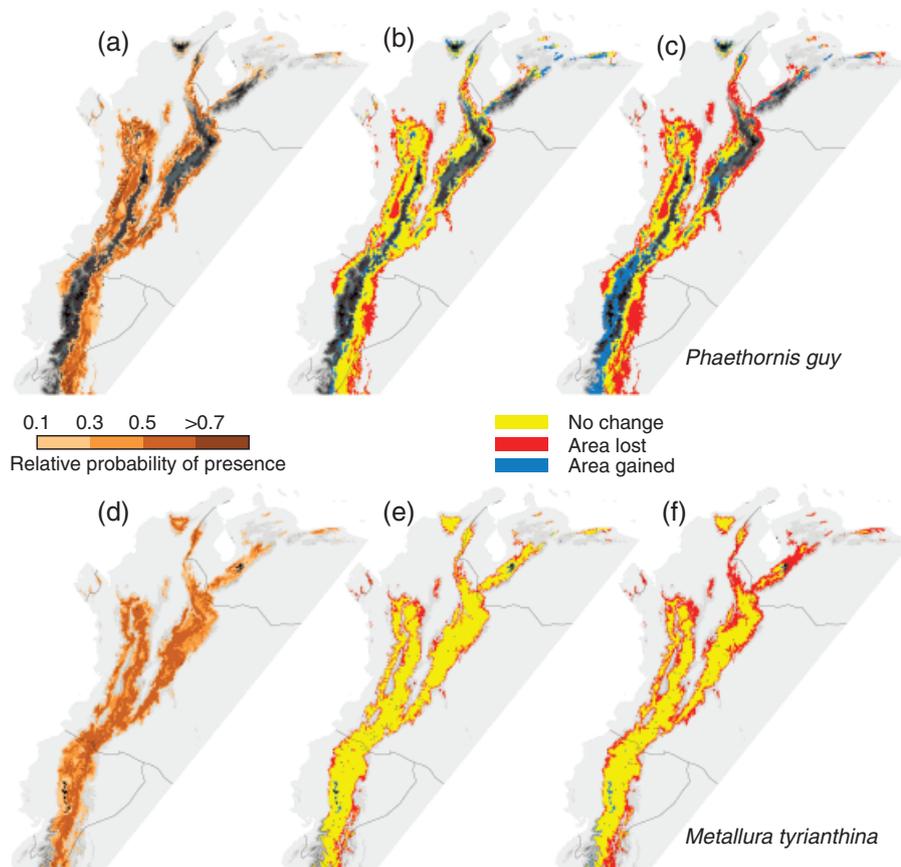


Fig. 1 Present potential geographic distribution and distributional shifts under future climate change for two target hummingbird species and two climate change scenarios. The two left panels show the present-day potential geographic distributions for *Phaethornis guy* (a) and *Metallura tyrianthina* (c), respectively. The four middle and right panels depict the corresponding distributional shifts based on lower (b, e) and upper (c, f) bounds of future climate change scenarios for the year 2080.

As a second step, we projected the contemporary species-climate relationships on simulated future climate data assuming unlimited dispersal to estimate distributional shifts for the five target species. Depending on the mean elevation of the target species and on whether more moderate or more extreme climate projections are considered, upward shifts and net area reduction of suitable habitats along the Andean flanks vary between 260–730 m and 13–40%, respectively (Table 1). More specifically, for hummingbirds that reside at lower elevations (e.g. *P. guy*), projected distributional shifts across altitudes are more extreme with significant changes in both losses of suitable habitat at lower elevations and corresponding gains at higher elevations (Fig. 1a–c). For high-elevation hummingbird species (e.g. *M. tyrianthina*) the projected distributional shifts across elevation are more moderate and largely due to losses of suitable habitat at lower elevations (Fig. 1d–f). It should be noted that these projections are based on mean elevational shifts, and that in cases where expansion at the upper range boundary is not constrained the shifts between low and high elevation species will be more comparable.

The most important climate factor that drove the projections of elevational shifts and corresponding losses and gains in suitable habitats for the five hummingbird species was generally the *warmth index* due to its importance in the present-day predictions and its consistent projected increase in the future climate of 20–30 °C-months (CCCMA_B2) and 30–65 °C-months (HADCM3_A2) in the vicinity of the northern Andes. Projected trends in precipitation had generally only

marginal influences on future distributions with one notable exception. In the case for *P. guy* that resides at lowest elevations, and for the climate change scenario based on the Hadley climate model (HADCM3_A2), a projected trend towards wetter conditions during the driest quarter in the vicinity of the western Andes of Ecuador led to considerable gains in suitable environments (Fig. 1c). It is noteworthy that the majority of the 21 climate models in the more recent IPCC fourth assessment (Christensen *et al.*, 2007) project a similar trend towards wetter conditions in the vicinity of the northern Andes, providing more credibility to these predictions.

Flight kinematics

We obtained hovering kinematic data from different individuals at multiple elevations for 29 hummingbird taxa, whereby three of these were included in the climate change projections (Table 2). The maximum difference in elevation between the highest and lowest site evaluated per taxon ranged from 100 to 3158 m. All of the hummingbirds, except for *Amazilia edward*, were represented in the utilized phylogenetic hypothesis (McGuire *et al.*, 2007), and were therefore included in the independent contrasts analysis.

Hummingbirds employed larger wing stroke amplitudes at higher elevations (Fig. 2a and b). These intraspecific field-based measurements therefore lend broader support to a relationship previously documented for within-individual responses to hypodense laboratory manipulations (Chai & Dudley, 1995) and for

Table 1 Predicted mean elevation for the five target hummingbird species based on present climate and corresponding distributional shifts under two climate projections for the year 2080

Species	Present		Future	
	Mean Elevation* (m)	Scenario	Elevational Shift (m)	Areal Change† (%)
<i>Phaethornis guy</i>	1408	HADCM3_A2‡	706	–28 (–52, + 24)
		CCCMA_B2‡	365	–18 (–31, + 13)
<i>Doryfera ludoviciae</i>	1637	HADCM3_A2	730	–35 (–47, + 12)
		CCCMA_B2	383	–26 (–30, + 4)
<i>Agelaiocercus kingi</i>	1906	HADCM3_A2	613	–37 (–42, + 5)
		CCCMA_B2	323	–21 (–24, + 3)
<i>Colibri coruscans</i>	2107	HADCM3_A2	493	–40 (–48, + 8)
		CCCMA_B2	260	–13 (–21, + 8)
<i>Metallura tyrianthina</i>	2187	HADCM3_A2	548	–37 (–38, + 1)
		CCCMA_B2	266	–20 (–21, 1)

*Based on predicted distribution for present climate and optimized threshold (equate entropy of thresholded and non-thresholded distribution).

†Area lost (negative) and gained (positive) are provided in brackets.

‡Two scenarios representing upper (HADCM3_A2) and lower (CCCMA_B2) bounds of projected future climate change (see 'Materials and methods').

Table 2 The kinematic data for hummingbird taxa included in the elevational analysis

Taxon	<i>n</i>	<i>d</i> _{elev} (m)	<i>d</i> _{<i>n</i>} (Hz)	<i>d</i> _{<i>φ</i>} (°)
<i>Acestrura mulsant</i>	3	1170	-1.51	19.31
<i>Aglaeactis castelnaudii</i>	4	1000	5.01	15.93
<i>Aglaeactis cupripennis</i>	14	1003	1.28	-1.52
<i>Amazilia edward*</i>	8	1500	-0.42	12.90
<i>Amazilia tzacatl</i>	19	1060	-0.70	5.18
<i>Campylopterus hemileucurus</i>	7	100	-0.01	1.25
<i>Campylopterus largipennis</i>	30	100	0.87	-4.40
<i>Chlorostilbon mellisugus</i>	2	100	-2.61	-10.87
<i>Chrysuronia oenone</i>	6	100	4.11	-9.69
<i>Coeligena violifer</i>	4	1000	0.29	10.16
<i>Colibri coruscans†</i>	18	3158	1.32	16.21
<i>Colibri thalassinus</i>	5	400	1.10	4.16
<i>Doryfera ludovicicae†</i>	6	1336	0.25	4.34
<i>Eutoxeres condamini</i>	6	980	-6.49	23.88
<i>Glaucis aenea</i>	4	1160	-0.36	9.41
<i>Glaucis hirsuta</i>	7	100	-0.16	-8.07
<i>Heliangelus amethysticollis</i>	8	1170	1.76	2.16
<i>Lesbia nuna</i>	11	423	-2.09	2.48
<i>Metallura tyrianthina†</i>	19	1000	1.88	8.78
<i>Patagona gigas</i>	2	770	0.32	8.80
<i>Phaethornis hispidus</i>	12	100	1.46	5.61
<i>Phaethornis koepckeae</i>	16	100	0.63	-6.10
<i>Phaethornis longuemareus</i>	9	1135	0.45	2.80
<i>Phaethornis malaris</i>	12	100	0.16	7.41
<i>Selasphorus platycercus</i>	22	1025	2.15	3.98
<i>Selasphorus rufus</i>	20	1025	2.19	9.88
<i>Thalurania columbica</i>	12	1160	0.23	2.97
<i>Thalurania furcata</i>	21	100	-0.07	6.15
<i>Threnetes niger</i>	17	100	1.11	-5.54

The total sample size for individuals at the highest and lowest elevation sites is denoted by *n*. The differences in elevation (*d*_{elev}), wingbeat frequency (*d*_{*n*}), and stroke amplitude (*d*_{*φ*}) are calculated as the value at the highest elevation site minus the value at the lowest elevation site.

*Not included in the phylogenetic hypothesis.

†Included in the climate change projections.

evolutionary responses among multiple taxa using field measurements (Altshuler & Dudley, 2003). Although the analysis was highly significant for both raw species data ($y = 7.66 \times 10^{-3}x - 1.189$, $R^2 = 0.364$, $P < 0.001$) and independent contrasts ($y = 6.73 \times 10^{-3}x$, $R^2 = 0.257$, $P < 0.01$) analyses, the slopes correspond to only modest increases in increased stroke amplitude. If we extrapolate assuming a mean elevation increase of either 260 m on the low end or 730 m on the high end, this increase would yield a ~ 2 – 5° change in wing stroke amplitude. Hummingbirds did not modulate wingbeat frequency across elevations (Fig. 2c and d), as analyzed using either raw species values ($y = 1.02 \times 10^{-4}x + 0.341$,

$R^2 = 0.001$, $P = 0.87$) or independent contrasts ($y = 4.36 \times 10^{-5}x$, $R^2 = 2.39 \times 10^{-4}$, $P = 0.94$).

One species, *Colbiri coruscans*, is unusual in that it is a high elevation hummingbird that migrates to low elevations to undergo molt. Its difference value in elevation was the most extreme for our data set whereas its difference value in stroke amplitude was relatively modest. Although the analysis was restricted to non-molting birds, it is still possible that this unusual migratory behavior could have a disproportionate influence on the regression coefficients and related extrapolation. We therefore repeated the analyses without *C. coruscans*, which yielded slightly higher slopes, but still relatively modest predicted increases in stroke amplitude ranging from 2.6 to 7.4° depending on the overall predicted change in elevation. However, it is important to emphasize that these extrapolation are based on multiple species and that some taxa, e.g., *Eutoxeres condamini*, appear to be more sensitive to changes in elevation than others.

Discussion

Using the climate envelope approach, we estimated the possible extent of upward displacement of five Andean hummingbird species under two climate change scenarios. These scenarios are based on two GCMs (HADCM3 and CCCMA) and two greenhouse gas emission scenarios (B2 and A2) to bracket upper and lower bounds of anticipated climate change. For the 2080 projections, mean annual temperatures in the vicinity of the Northern Andes increase between 1.8–2.6 °C (conservative) and 2.5–5.3 °C (extreme). These ranges of predicted warming correspond closely to those reported in the more recent IPCC fourth assessment (Christensen *et al.*, 2007), suggesting that the employed scenarios provide credible uncertainty estimates.

The range in projected upward shifts of hummingbirds of approximately 300–700 m in response to climate change appears to be realistic in the context of paleoclimatic and GCM studies. For example, paleo-pollen records indicate that northern Andean montane forests were displaced by as much as 500–700 m towards lower elevations during the Last Glacial Maximum when the mean climate was about 5 °C cooler relative to the present climate (Hooghiemstra & Van der Hammen, 2004). GCM based estimates indicate upward translation of climate regimes suitable for tropical montane cloud forests of approximately 200–400 m under a doubling of CO₂ relative to preindustrial levels (Still *et al.*, 1999). The marked climate sensitivity of tropical cloud forest ecosystems is further evidenced by the tight positive relationship between temperature and the

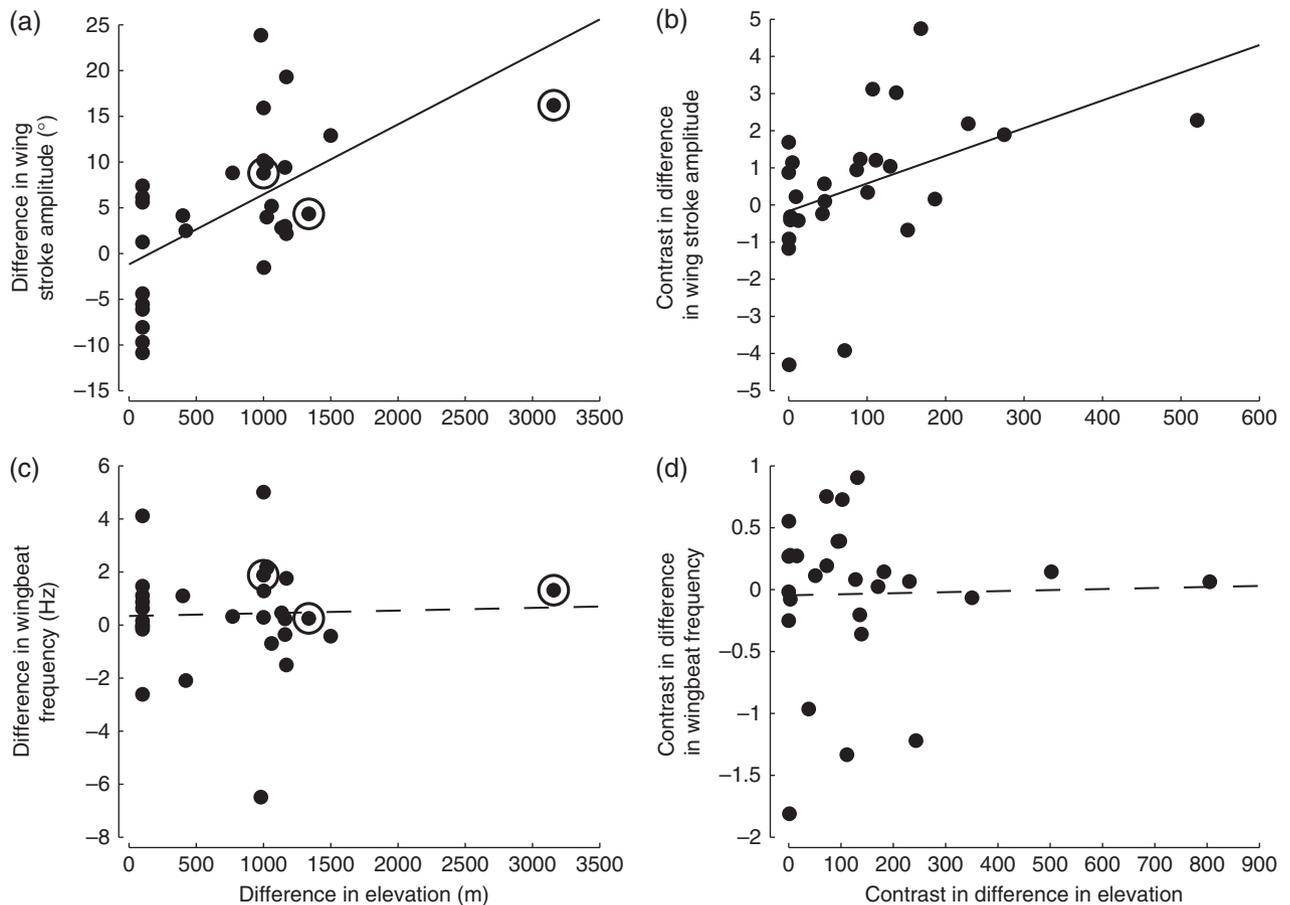


Fig. 2 Intraspecific changes in wing stroke amplitude and wingbeat frequency across elevations. The left panels (a, c) contain plots of raw species data, with each point on the y -axis representing the difference in the kinematic variable calculated by subtracting the value at the lowest elevation site from the value at the highest elevation site. The x -axis value is the difference in elevations between the highest and lowest sites. The points enclosed in circles are the data for the three taxa for which we also provide detailed analysis of elevational shifts (see Fig. 1). The right panels (b, d) contain plots of the standardized independent contrasts. Solid lines indicate significant trends and hatched lines indicate nonsignificant trends. The x -axis in panel d is notably different because this analysis required a branch length transformation (to the $3/4$ power) to correct for a significant correlation between absolute contrasts and their standard deviations before transformation.

height of orographic cloud banks (known as the ‘lifting-cloud-base-hypothesis’) through which the tropical montane cloud forests obtain a significant fraction of their moisture supply (Pounds *et al.*, 1999). Additional uncertainties with respect to the projected upward range shifts of the five target hummingbirds remain because horizontal moisture supply is not modeled explicitly (Still *et al.*, 1999), effects of lowland deforestation on moisture budgets are not considered (Ray *et al.*, 2006), and no analog paleo-pollen record exists for a Northern Andean mean climate that is several degrees warmer than the present one.

In addition, given the significant impact of land use change on the distribution of Northern Andean forests (Sierra *et al.*, 2002), it is clear that many of the predicted suitable habitats based on the climate

envelope approach are not accessible for both present and future climates. Further loss of habitats due to ongoing land use change will thus add to the dramatic habitat losses predicted by our climate envelope approach, exacerbating extinction risks as the probability of extinction increases with the reduction of range size and connectivity, and an increase in fragmentation (Jablonski, 1991; Saunders *et al.*, 1991; Kattan *et al.*, 1994).

Our flight kinematics analysis shows that intraspecific variation in elevational occurrence of hummingbirds was significantly correlated with the wingbeat parameter of stroke amplitude (Fig. 2a and b), but not with wingbeat frequency (Fig. 2c and d). A similar kinematic response was shown interspecifically for multiple hummingbird taxa across a natural 4000 m elevational gra-

dient using the larger data set for the present analysis (Altshuler & Dudley, 2003). This natural pattern among individuals and taxa also mirrors intraspecific biomechanical responses of hovering hummingbirds to reduction in air density alone (i.e., hypodense normoxic challenge), which has been tested with Ruby-throated Hummingbirds (*Archilochus colubris*; Chai & Dudley, 1995), Anna's hummingbirds (*Calypte anna*; Altshuler *et al.*, 2010), and Broad-tailed (*Selasphorus platycercus*) and Rufous (*S. rufus*) hummingbirds (Altshuler & Dudley, 2003). The same patterns have also been observed for other individuals of *A. colubris* challenged with simultaneously imposed reductions in oxygen partial pressure and air density (hypodense hypoxia; Chai & Dudley, 1996), and to hyperoxic but hypodense challenge (Chai *et al.*, 1996). These experimental gas manipulations tested hummingbirds to the point of aerodynamic failure, which occurred in the hypodense normoxic challenge at equivalent air densities of ~ 6000 m, and in the hypodense hypoxic challenge at an equivalent air density of 4000 m and an equivalent oxygen tension of 4500 m. Thus, these laboratory experiments span a much greater range of equivalent altitude (from sea level to between 4000 and 6000 m depending upon study and treatment) than the predicted shifts due to climate change.

For all hummingbird taxa studied in gas mixture experiments, stroke amplitude increased monotonically in response to decreasing air density and was the primary means of modulating lift and power output. However, the response was nonlinear, with smaller changes in stroke amplitude required for air densities changes close to the ambient conditions, as compared air density changes well above ambient condition. Because stroke amplitude and wingbeat frequency are major determinants of the energetic costs of hovering (Ellington, 1984), altitudinal shifts by hummingbirds in response to climate change will mandate similar responses.

A key question then concerns the magnitude of associated metabolic expenditure, given that hummingbirds obligately hover at flowers to obtain the energetic substrate (i.e., floral nectar) necessary for flight. To estimate this effect, note that altitudinal ascent is most closely mimicked by the hypodense hypoxic manipulation imposed by Chai & Dudley (1996) on *A. colubris*. For this species, an experimentally induced increase in stroke amplitude of 5° (the likely upper bound deriving from climate-associated elevational shift and concomitant reduction in air density) correspondingly increases mechanical power output of the flight muscle by about 5% (see Chai & Dudley, 1996). The increase in metabolic rate over the same density reduction, however, was much smaller (on the order of 1–2%), although it not

known if this relative decline resulted from increased flight muscle efficiency associated with the increased stroke amplitude (and thus strain rate of the muscle) or with lower drag on the wings. For *A. colubris* hovering in hypodense but normoxic gas mixtures, metabolic rates also increased in parallel with stroke amplitude, but the magnitude of such increase for an effective elevational change of ~ 750 m was still $<5\%$ (Chai & Dudley, 1995). It is not known if high-elevation hummingbird taxa are more sensitive to the effects of density and oxygen reduction than is *A. colubris*, which ranges in elevation from sea level up to 1900 m (Schuchmann, 1999). Studies of hover-feeding *A. colubris* also indicate that metabolic rates vary relatively little with respect to air temperature; a reduction of 5°C yields an increase of only about 2% in metabolic rate (see Chai *et al.*, 1998).

Overall, the physiological impact of elevational shifts of <1000 m on flight performance and, hence, survivorship, is likely to be small. For example, 2–5% differences in oxygen consumption and aerodynamic power requirements fall within the range of values among individuals of the same species at a given elevation (Chai & Dudley, 1995). It is likely that other factors such as interspecific competition and changes in floristic composition will present greater challenges. In particular, habitat losses due to climate change, on the order of 13–40% relative to current Andean hummingbird range sizes as suggested by our study, and ongoing land use change may represent the most severe factor towards enhanced extinction risk.

Paleoecological studies have suggested that plant taxa respond differentially to changing climate, migrating individually and reassembling into different vegetation types following a major climate change (Graham & Grimm, 1990). The intrinsic relationship between hummingbirds and plants in a complex co-evolutionary mutualism, and its ecological interdependence (Feinsinger, 1976; Wolf *et al.*, 1976; Stiles & Wolf, 1979; Bleiweiss, 1998; Altshuler & Clark, 2003; Temeles & Kress, 2003) poses important uncertainties for these future scenarios. It is very unlikely that species ranges and intact vegetation 'zones' will move up and down the slopes as a cohesive and intact unit in response to changing climate (Graham & Grimm, 1990; Erasmus *et al.*, 2002), but rather idiosyncratic random species associations are likely to form with unknown effects on the pollination community structure and functionality.

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Supporting Information

Additional Supporting Information may be found in the online version of this article:

Appendix S1. Source information on occurrence data for the five focal hummingbird species.

Appendix S2. Summary of model performance in the climate envelope predictions for the 5 focal hummingbirds.

Appendix S3. Importance of climatic variables in the climate envelope predictions for the 5 focal hummingbirds.

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