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Winter Conditions Influence Biological Responses of Migrating Hummingbirds

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Winter conditions influence biological responses of migrating hummingbirds

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Abstract. Conserving biological diversity given ongoing environmental changes requires the knowledge of how organisms respond biologically to these changes; however, we rarely have this information. This data deficiency can be addressed with coordinated monitoring programs that provide field data across temporal and spatial scales and with process-based models, which provide a method for predicting how species, in particular migrating species that face different conditions across their range, will respond to climate change. We evaluate whether environmental conditions in the wintering grounds of broad-tailed hummingbirds influence physiological and behavioral attributes of their migration. To quantify winter ground conditions, we used operative temperature as a proxy for physiological constraint, and precipitation and the normalized difference vegetation index (NDVI) as surrogates of resource availability. We measured four biological response variables: molt stage, timing of arrival at stopover sites, body mass, and fat. Consistent with our predictions, we found that birds migrating north were in earlier stages of molt and arrived at stopover sites later when NDVI was low. These results indicate that wintering conditions impact the timing and condition of birds as they migrate north. In addition, our results suggest that biologically informed environmental surrogates provide a valuable tool for predicting how climate variability across years influences the animal populations.

Key words: broad-tailed hummingbird (*Selasphorus platycercus*); climate change; coordinated monitoring programs; extreme weather events; operative temperature; physiological model; remote sensing.

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INTRODUCTION

In response to climate change and associated changes in the biotic environment, species are shifting their geographic distributions (Parmesan and Yohe 2003, Lehikoinen et al. 2004, Bellard et al. 2012, Burrows et al. 2014), altering their behavior (e.g., Cotton 2003, Coppack and

Pulido 2004, Dunn and Moller 2014, Ko et al. 2014, Ockendon et al. 2014), and surviving by either adapting to these new conditions or tracking their current climatic niche and resources (Parmesan 2006, Berg et al. 2010, Charmantier and Gienapp 2014, Merila and Hendry 2014). Increased interannual variability in climate, such as the frequency and intensity of extreme weather

events, may alter species distributions and cause population declines that potentially have lasting impacts (Easterling et al. 2000, Boucek and Rehage 2014, Lynch et al. 2014, Vasseur et al. 2014). While predicting how species will respond to interannual weather variability is critical, the vast majority of predictive models use climate data summarized over many years and correlative methods to estimate how species' geographic ranges might shift in response to climate change. Although these approaches can provide valuable insight into how species might respond, they generally do not uncover the mechanisms that influence species responses (Kearney and Porter 2009, Berg et al. 2010, Dormann et al. 2012, Sunday et al. 2014).

Recent attempts to develop process-based models (reviewed by Dormann et al. 2012) are starting to provide alternative ways to deal with the complex problem of predicting how species will respond to the climate change. We advance this research area by developing a general mechanistic approach that combines physiologically informed environmental factors and remote sensing measures of vegetation productivity with information on species behavior and physiological state. Our approach assesses the influence of environmental change, including extreme cold events, on organisms over short timescales. To exemplify our approach, we studied how wintering conditions affected the migratory behavior and condition of the broad-tailed hummingbird (*Selasphorus platycercus*) at migratory stopover sites. Broad-tailed hummingbirds are a latitudinal migratory species that occurs at high elevations on both breeding and wintering grounds and thus may be particularly sensitive to the changes in climate (Warren et al. 2013). In addition, due to their small body size (high surface area-to-volume ratio), hummingbirds have both high thermoregulatory costs and a high basal metabolic rate (Lasiewski 1963) and therefore should be strongly influenced by weather and resource fluctuations.

Physiology-based models aimed at understanding species distributions use information about the biophysical characteristics of an organism (e.g., Porter et al. 2002, Kearney and Porter 2004, Buckley 2008, Huey et al. 2012). For hummingbirds, as with many other organisms, there are two key components to consider

in physiological models: (1) the physiological demand associated with the organism's activities under a given set of weather conditions (e.g., cold temperatures) and (2) the ability to acquire minimally sufficient resources to meet the metabolic demands for survival, including energetically demanding activities such as reproduction and molt (e.g., Weathers and Stiles 1989, Hiebert 1993, Powers and Conley 1994).

Temperature plays a critical role in the physiological demands on an organism. For instance, low temperatures increase thermoregulatory costs and could decrease the energy available for other activities. One well-established measure of temperature associated with thermoregulatory costs is operative temperature (T_e), which measures the thermal environment an individual experiences in its microhabitat (Bakken 1980). Because operative temperature integrates radiant (i.e., energy gained from the sun or bounced off warm surfaces and lost from an organism), conductive (i.e., heat transferred between an organism and the environment), and convective (i.e., heat transferred by a fluid—liquids/gasses) heat transfer, it should be a more accurate measure than ambient temperature, which is the temperature of the air itself, and does not account for how the organism experiences temperature (Bakken 1976, 1992, Dzialowski 2005). When the operative temperature of the environment falls below a bird's thermoneutral zone (a range of temperatures within which an endotherm spends almost no energy on maintaining its body temperature), additional energy resources must be acquired to support the increased heat production required to maintain a constant body temperature (Lasiewski 1963, McWhorter and Martinez del Rio 2000). Thus, during extreme cold events, hummingbirds must increase the energy consumption to fuel their higher thermoregulatory costs and/or move to warmer, less costly conditions to decrease these costs. Even if sufficient energy resources are available to fuel-increased thermoregulation and the corresponding foraging costs, hummingbirds are limited in the rate that they can consume and process nectar, which may create a physiological limit on energy intake (McWhorter and Martinez del Rio 2000) and thus likely limit the extreme weather conditions they can tolerate.

Changing climate conditions influence the identity, quantity, and quality of food resources at any given time, which can make it challenging for organisms to obtain sufficient resources (Carroll et al. 2001, Memmott et al. 2007). Hummingbirds obtain much of their energy from nectar and most of their protein from insects. With their high metabolic rates, hummingbirds are particularly susceptible to fluctuations in the availability of these resources. For example, when the amount or concentration of sucrose in nectar available to birds is experimentally decreased, hummingbirds lose weight and exhibit negative energy balance (Brice 1992, Powers and McKee 1994, López-Calleja et al. 1997, McWhorter et al. 2003). Further, numerous studies documenting hummingbird movement patterns show that hummingbird diversity and abundance correspond to flower and nectar abundance (Stiles 1980, Araujo and Sazima 2003, Cotton 2007, Abrahamczyk and Kessler 2010), which can be impacted by frost and low temperatures (Inouye 2000, 2008, Inouye et al. 2002). While evaluating the availability of resources (nectar and insects) across broad geographic regions is challenging, bird distribution, abundance, and migratory condition are often correlated with remote sensing measures of productivity, such as vegetation indices (normalized difference vegetation index, NDVI; enhanced vegetation index, EVI), indicating that these variables might provide a rough measure of resource abundance (Zimmerman 1988, Stervander et al. 2005, Goetz et al. 2014, McBride et al. 2014, Paxton et al. 2014). Further, recently remotely sensed productivity (EVI) has been linked to nectar abundance using groundtruthed data from flowers, thereby suggesting that it may be an approximate surrogate (Feldman and McGill 2014).

For broad-tailed hummingbirds, we developed hypotheses that relate thermoregulatory costs (measured by operative temperature) and resource availability (using NDVI as a proxy) on their wintering grounds to both physiological and behavioral attributes detected at spring migration stopover sites as birds returned to their high-elevation breeding sites in the mountains of United States and Canada (Fig. 1). Specifically, we expect that high thermoregulatory costs (e.g., due to lower-than-average temperatures) and low resource availability

constrain the investment in high energy activities on the wintering grounds, such as molt (Lindstrom et al. 1993, Klaassen 1995), and generate the changes in migratory behavior to adjust to these constraints. Therefore, we predict that in cold, low-resource winters, broad-tailed hummingbirds delay their annual winter molt, arrive later at spring migratory stopover sites, and have lower body mass and fat scores than in years where the wintering grounds experience average or above-average temperatures and resources. We used an 11-yr time series of broad-tailed hummingbird capture data taken at 18 migratory stopover sites located early in their migratory route to assess the role of winter thermal demand and resources in body condition and migratory behavior. Taken together, our model allowed us to use thermal ecology (operative temperature) and a proxy for resource availability (NDVI) to explore how wintering ground conditions influence hummingbird condition and behavior as they move northward to their breeding grounds and, more generally, to test a new framework for understanding how migrating animals will respond to climate change.

METHODS

Winter range

We defined the wintering period as 15 November to 15 March (Calder and Calder 2013). To determine the winter range during this period, we queried observation locations from the Global Biodiversity Information Facility (GBIF; www.gbif.org) for broad-tailed hummingbirds from 1936 to 2011 (www.gbif.org/resource/80761). We used wintering ground observations above an elevation of 1500 m because this reflects the known distributional limits of broad-tailed hummingbirds in their wintering area in Mexico (Calder and Calder 2013). We lumped GBIF data across years instead of considering each year independently because we did not have sufficient observations in the wintering range on a yearly basis. While we realize that GBIF observations may have some limitations and error, our data filtering should provide an estimate of the geographic locations of overwintering birds because they fall within and span the known range of the species. In total, we had 201 locations for defining winter conditions (Fig. 2).

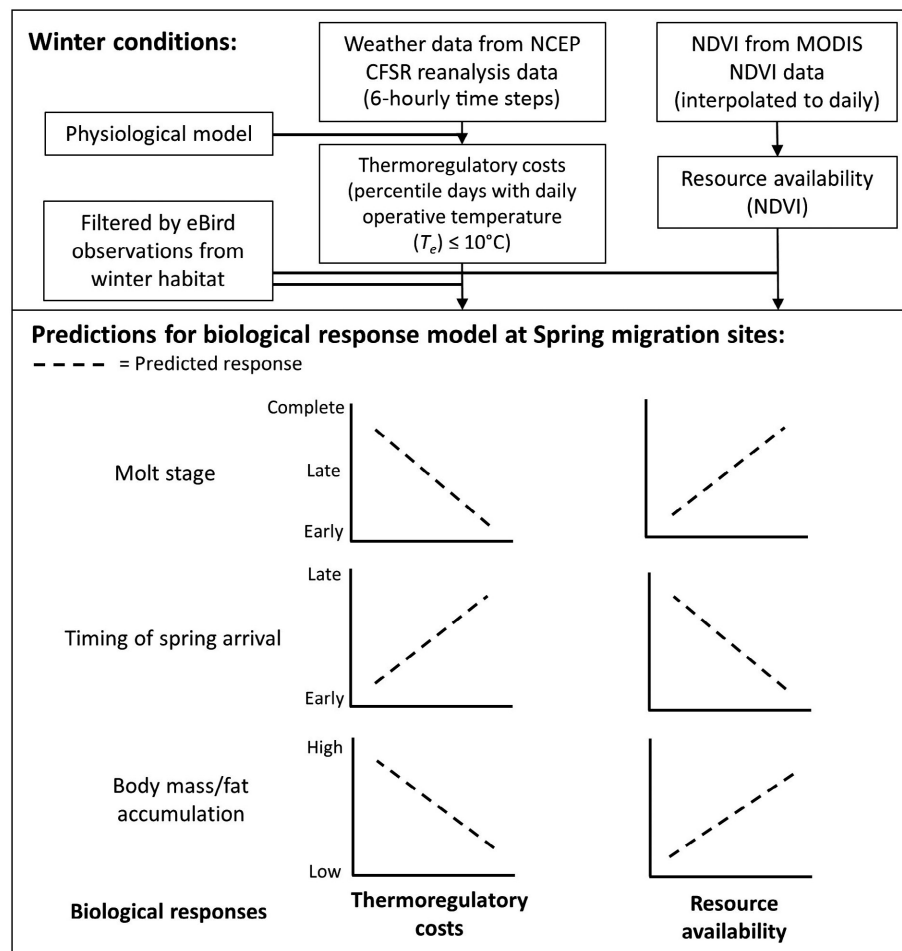


Fig. 1. Conceptual figure developing our physiological modeling approach. The top box shows the data that went into our models, while the lower box shows the predicted biological responses at the spring migration sites to each of the winter predictor variables.

Thermoregulatory cost estimate

We used operative temperature (T_e) to estimate thermoregulatory costs. T_e integrates the effects of radiant heat exchange, conduction, and to a lesser degree, convection. In other words, it accounts for the effects of direct solar radiation and wind and is therefore a better predictor of an organism's thermoregulatory demands than ambient temperature (Bakken 1976). Because T_e does not fully account for the effects of convection (Bakken 1980), which can substantially increase the thermoregulatory costs in cold temperatures, modeling hummingbird response to extreme cold using T_e represents a conservative best-case scenario (i.e., the effects of wind chill could make winters even colder, increasing

thermoregulatory costs). T_e is also likely to be conservative because the small body size of hummingbirds will likely heighten the sensitivity to temperature extremes.

Estimates of T_e were made using a linearized solution of the energy budget equation from Greek et al. (1989):

$$T_e = T_a + (R_{\text{abs}} - \epsilon \sigma T_a^4) / (\rho C_p / r_a + 4 \epsilon \sigma T_a^3), \quad (1)$$

where T_a is ambient temperature, R_{abs} is the absorbed longwave and shortwave radiation flux density (W/m^2 ; Eq. 2), ϵ is the emissivity of the bird's surface (0.95; Walsberg 1992), σ is the Stefan-Boltzmann constant ($5.67 \times 10^{-8} \text{ W} \cdot \text{m}^{-2} \cdot \text{K}^{-4}$), ρC_p is the product of density

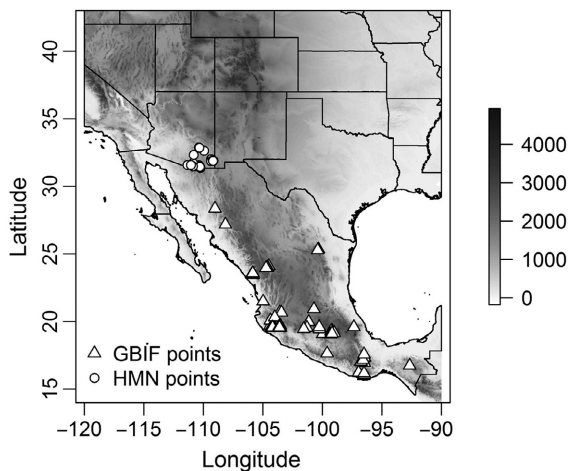


Fig. 2. Map showing broad-tailed hummingbird localities (triangles are Global Biodiversity Information Facility locality data, and circles are Hummingbird Monitoring Network locality data). Elevation (in meters) is shown in the gray shading on the map.

and specific heat capacity of air ($1200 \text{ J} \cdot \text{m}^{-3} \cdot \text{K}^{-1}$), and r_a is the aerodynamic resistance to convective heat transfer (s/m). We assumed $r_a = 37.76 u^{-0.495}$ (Greek et al. 1989), where u is wind speed (m/s).

R_{abs} was estimated as follows:

$$R_{\text{abs}} = (S_p(A_p/A) + S_d)a_s + a_L L_i, \quad (2)$$

where S_p is direct shortwave radiation (W/m^2); A_p/A is ratio of projected shadow area on a surface perpendicular to the solar beam to the total surface area (estimated to be 0.25; Greek et al. 1989) and is used to estimate the proportion of the total surface area directly exposed to S_p ; S_d is diffuse shortwave radiation (W/m^2); a_s is mean shortwave absorptivity (0.89; Greek et al. 1989); a_L is mean longwave absorptivity (0.97; Walsberg 1992); and L_i is incoming longwave radiation.

Thermal surface properties (ϵ , a_s , and a_L) have not yet been measured for hummingbirds; therefore, we used the values from other avian species as detailed above in our description of the equations above (Greek et al. 1989, Walsberg and Wolf 1995). This is appropriate because the ϵ and a_L of feathers show little variation across multiple bird species (Walsberg 1992), and a_s varies by <10% in birds with darker dorsal surfaces (Campbell 1977). Further, error in our assumed value of a_s has reduced impact on the calculated operative

temperature in small species (Greek et al. 1989). For meteorological data (T_a , S_p , S_d , and L_i), we used the National Centers for Environmental Prediction (NCEP) Climate Forecast System version 2 (CFSv2; Saha et al. 2014). The CFSv2 is a global high-resolution circulation model that couples atmosphere, ocean, land surface, and sea ice to estimate weather conditions of these coupled domains on six-hourly time steps at 0.2° spatial resolution (Saha et al. 2014).

To generate the thermoregulatory cost variable, we determined the percentile of days that had a six-hour period (i.e., the lowest resolution of our weather data) where the operative temperatures $\leq 10^\circ\text{C}$ (referred to as “percentile days with $T_e \leq 10^\circ\text{C}$ ”). We chose the threshold value of 10°C because in laboratory studies broad-tailed hummingbirds were unable to maintain body mass when kept at 10°C regardless of diet quality, suggesting a physiological bottleneck with regard to energy intake (McWhorter and Martinez del Rio 2000). Thus, when wintering grounds have many cold days and when percentile days with $T_e \leq 10^\circ\text{C}$ is high, the birds are expected to have high thermoregulatory cost and as a result high physiological demand. When percentile days with $T_e \leq 10^\circ\text{C}$ is low, the thermoregulatory cost on the wintering ground is low.

Our estimate of thermoregulatory cost is based on meteorological data that describe general atmospheric conditions, but do not reflect small-scale microclimate variability. Hummingbirds characteristically perch on trees and shrubs that might offer microclimate refuge from wind, but not from extreme cold temperature. Therefore, even though our physiological model is parameterized with broad-scale data, it should be a good predictor of the general impact of environmental temperature on animals that use large-scale landscapes, such as hummingbirds (e.g., Weathers and Sullivan 1993, Kearney et al. 2009).

Resource availability estimate

To estimate the resource availability for the winter period, we used vegetation productivity from the NDVI as a proxy of gross photosynthesis (Sellers 1987, Goetz and Prince 1999) and total precipitation. While a direct measure of resource availability (such as flower counts) would be preferable, these data are not yet available at the broad scale. NDVI images from MODIS are

compiled into 16-d composite images for each 1-km pixel globally since January 2000 (Tucker 1979, Huete et al. 2002). These images are annotated with quality flags (MOD13A1 and MYD13A1 data products, representing Terra-MODIS and Aqua-MODIS NDVI products, respectively; <https://lpdaac.usgs.gov>; Huete et al. 2002). Given that MODIS is a passive sensor (basically a picture, see Graham and Goetz 2009 for review) and therefore is influenced by atmospheric conditions such as cloud cover, we used the quality flags to retain the three highest quality values. Because optimal conditions for obtaining NDVI values vary temporally, readings that met our retention criteria were between 1 and 30 d apart (mean: 15 d). Obtaining an estimate of NDVI over the entire winter season required a summary of these high-quality observations. Given that these observations were not evenly spread across a given wintering season, simply taking an average might bias our estimate of NDVI. Therefore, we interpolated the daily NDVI values for each day and 1-km cell using univariate Akima interpolation (Akima 1991). Resource availability was then estimated as the average observed daily NDVI value across all grid cells with broad-tailed hummingbird observations during the winter season. Total precipitation across the season was derived from the Climate Forest System version 2 (CFSv2; Saha et al. 2014).

Biological response data

We gathered biological response data during the spring migration from the Hummingbird Monitoring Network (HMN; partially processed data in Data S1). For this study, we used 11 yr of data (2002–2012) from sampling periods in March through early June at low- and mid-elevation sites in Arizona (18 total sites, 5–11 sampled each year for molt, arrival, mass, and fat; Appendix S1: Tables S1 and S2; Fig. 2).

We chose these sites because broad-tailed hummingbirds were captured during north-bound migration, but not in habitats where they nest (Calder and Calder 2013). At each site, hummingbirds were baited with a 4:1 sugar solution in hummingbird feeders within two modified Hall traps (Russell and Russell 2001). Monitoring occurred once every two weeks from early March to late October, and each session lasted

5 h. All captured hummingbirds were banded with United States Geological Survey (USGS)—Biological Resources Division-numbered aluminum leg bands if not already so marked. No bird was held longer than 30 min because hummingbirds have high metabolic rates and need to feed frequently throughout the day.

Biological responses derived from banding data included molt stage, date of spring arrival, body mass, and fat (Pyle 1997). The molt stage of hummingbirds was measured at 14 levels (pre-molt through postmolt) and was determined by the sequence of flight feather replacement, which occurs in ascending order (innermost to outermost) from primary feather 1 (P1) to primary feather 8 (P8), but the sequence is inverted for the outermost two feathers, where primary feather 10 (P0 in the data) is replaced before primary feather 9 (P9), an inversion unique to hummingbirds. Premolt stages were ranked as moderately worn (M) or ragged (R) feathers, and postmolt as fresh (F) or lightly worn (L). To simplify analyses, we grouped molt into three categories: (1) premolt and early molt (M, R, and P1–P8), (2) late molt (P0 or P9), and (3) completed molt (F or L) (Appendix S1: Fig. S1). For a given site and year, we used the molt stage of the 50th quantile bird (i.e., at a site-year where $2n + 1$ birds were caught, the molt category of the $n + 1$ th bird was used). Bird arrival date is the date by which 50% of the total number of birds for each year and site were caught (for distribution of the arrival data, see Appendix S1: Figs. S1 and S2). Body mass is how much a bird weighed in grams when it was captured, before feeding and release (Appendix S1: Fig. S4). Fat was scored at five levels, based on the visual inspection of the bird's throat and abdominal region in an ordinal sequence: 0 = no fat; *T* = trace of fat on the throat; 1 = up to half-furculum; 2 = half- to full furculum; and 3 = bulging throat and on side (Appendix S1: Fig. S5).

Biological response models

We designed a set of regression models to test each of our predictions, using molt stage, arrival date, body mass, and fat as response variables and using thermoregulatory cost (percentile days with $T_e \leq 10^\circ\text{C}$), resource availability (average winter NDVI), and an interactive term of operative temperature and NDVI as predictor variables. The percentile days with $T_e \leq 10^\circ\text{C}$ was

log-transformed to improve normality. Predictor variables were rescaled by centering at the grand mean with a standard deviation of 1.

In the regression analysis, response variables that represented quantiles (molt stage and arrival date) were weighted by the total number of birds caught at each site in each year. The ordinal response variable fat score was treated as continuous in the regression models because distance among the values was constant. However, given that the timing between each of the three molt categories is not constant, we treated molt as a binomial factor. The progress through the three molt categories was represented as a number of successes relative to the total number of possible categories it could have completed at the time the birds at a given site were captured. For example, a bird captured in early molt would be considered to have begun early molt, but failed to enter the other molt categories. Because all response data were gathered at the fixed capture stations of the HMN, “capture station” was included as a random effect to account for between-site differences or any site fidelity exhibited by the migrant bird populations as well as unmeasured variables such as elevation and resources that may likely cause stations to be different. Models were run at an annual time step from the 2000–2001 winter to the 2011–2012 winter. We used linear mixed-effects models in R (R Core Team 2013; package lme4, Bates et al. 2014; package bbmle, Bolker and R Development Core Team 2014). For binomial response variables (molt category), we used a generalized linear mixed model (glmer, package lme4, Bates et al. 2014), and for numeric response variables (arrival date, body mass, and fat), we used a linear mixed-effects model (lmer, package lme4).

For each of our four response variables, we first evaluated whether including the predictor variables, or their interaction, was justified (Bauer and Curran 2005, Afshartous and Preston 2011). To this effect, the full model, including both predictor variables and their interaction, was compared with all its submodels and with a null model without fixed effects (but including random effects for capture station) using Akaike’s information criterion, corrected for small sample sizes (AICc; Burnham and Anderson 2002, Hurvich and Tsai 1989). Furthermore, Akaike weights (w_i ; Hobbs and Hilborn 2006) were

calculated to compare the models that differed little in AIC. Akaike weights quantify the probability that the model emerges as the best supported by the data for each model among a given set. We compared the models using both a conservative and a liberal AICc. The conservative AICc uses the number of sites as the number of groups ($n_{\text{sites}} = 18$) and is likely to overestimate as the number of true classes, while the liberal AICc uses the number of data rows as the number of groups and is likely to underestimate the number of true classes. We report the liberal value here, but the results from both AICc’s were qualitatively similar, indicating that they are robust to how we consider groups. To evaluate the model fit, we calculated pseudo- R^2 because traditional R^2 are problematic for mixed-effects models (Bolker et al. 2009). The pseudo- R^2 was calculated as the residual variance of the model against the residual variance of a fixed intercept-only null model ($1 - [\text{model deviance}/\text{null deviance}]$). Analyses were conducted in R 3.0, and the code and partially processed data to replicate the analyses can be found in Data S1.

RESULTS

Resource availability estimate

Normalized difference vegetation index and precipitation varied substantially in the wintering ground across the 12 yr we evaluated (Fig. 3). These two variables were correlated such that NDVI declined quickly in years of low cumulative rainfall ($\text{cor} = 0.85$; $P < 0.001$, $\text{df} = 10$; Appendix S1: Fig. S6). Given the strong correlation between NDVI and cumulative precipitation, we only retained NDVI for further analyses as an integrative variable. During winter season, 2006–2007, 2009–2010, and 2011–2012 had high NDVI values and thus resource availability. In contrast, 2005–2006, 2008–2009, and 2010–2011 had low NDVI values that dropped quickly during the winter season. In general, years with a positive Oceanic Niño Index (La Niña years) had lower NDVI values and cumulative precipitation and also tended to be colder (Fig. 3; Appendix S1: Fig. S1).

Thermoregulatory cost estimate

The percentile days with $T_e \leq 10^\circ\text{C}$, our estimate of thermoregulatory cost, also varied across years. The winter of 2010–2011 was particularly

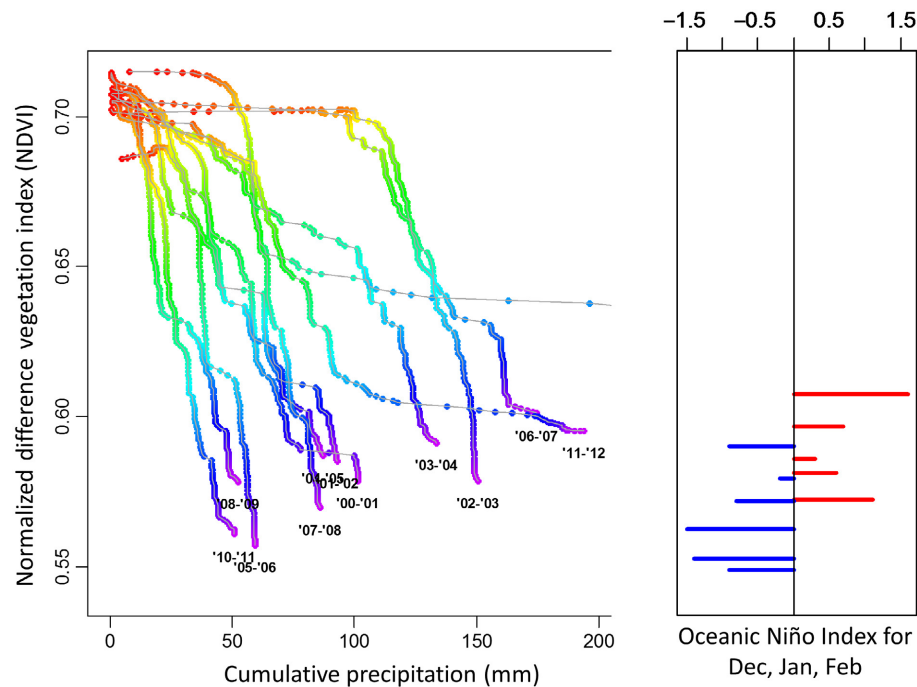


Fig. 3. Daily estimated normalized difference vegetation index and cumulative precipitation at the wintering grounds for broad-tailed hummingbirds for 11 yr. The mean Oceanic Niño Index (www.cpc.noaa.gov/products/analysis_monitoring/ensostuff/ensoyears.shtml) is shown for the same period.

costly in terms of thermoregulation with over 150 d with 6-h periods where operative temperature (T_e) was below 10°C in mountain regions (i.e., areas above 1500 m, which generally defines the distribution of broad-tailed hummingbirds; Calder and Calder 2013) in Mexico (Fig. 4). Finally, the percentile days with $T_e \leq 10^{\circ}\text{C}$ and NDVI were not significantly correlated ($\text{cor} = -0.23$; $P = 0.29$, $\text{df} = 10$; Fig. 4), although there were some years, notably 2010–2011, when thermoregulatory cost was particularly high and NDVI was particularly low. Hence, we used both the percentile days with $T_e \leq 10^{\circ}\text{C}$ and NDVI in our analyses.

Biological response models

The 50th quantile broad-tailed hummingbirds were most commonly in the completed molt (F-L; 48.44%) or late molt (10-9; 42.19%) categories as compared to the pre- and early molt category (M-8; 9.38%). However, in spring 2010, all migratory birds had completed molt, while in spring 2011 only 16.89% had completed molt, only 36.43% had entered late molt, and 46.68%

were still in the pre- to early molt category. In spring 2006 and 2009, birds were also captured in pre- to early molt (12.45% and 9.09%, respectively) and late molt (73.09–52.27%, respectively) with relatively fewer birds having completed molt (for the distribution of data, see Appendix S1: Fig. S2). The best model for molt stage included the individual effects of NDVI and percentile days with $T_e \leq 10^{\circ}\text{C}$, but no interaction term ($\text{AICc weight} = 0.99$; $\text{pseudo-}R^2 = 0.20$; Table 1, Fig. 5). The effect of NDVI is positive ($\beta = 0.88$), indicating that birds arrive in later molt stages when resources on the wintering ground are high. Percentile days with $T_e \leq 10^{\circ}\text{C}$ and molt stage are negatively related ($\beta = -0.60$), indicating that when the winter is colder, migrating birds have higher thermoregulatory costs and arrive in earlier molt stages. Molt category was calculated for a given site and year as the molt stage of the 50% quantile bird, but the results for the 25% and 75% quantile birds yielded similar patterns of significance (see Appendix S2). The date by which 50% of the birds had arrived was 26 April on average across the sites and years (range = 22

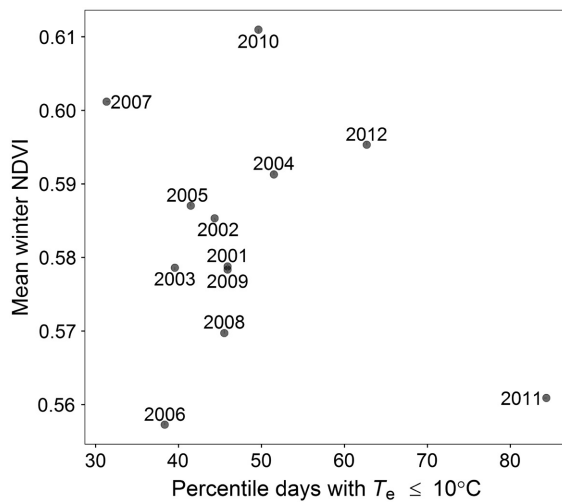


Fig. 4. Mean winter normalized difference vegetation index (NDVI; resource availability) and the percentile of days with operative temperature $\leq 10^{\circ}\text{C}$ (thermoregulatory cost) across winter periods.

March–9 June, $\text{SD} = 16.82$ d). During years of low NDVI (2005–2006, 2008–2009, and 2010–2011), the average bird arrival date was 16 May, 25 April, and 23 April, respectively; during high resource years (2006–2007, 2009–2010, and 2011–2012), the average bird arrival date was 21 April,

26 April, and 23 April, respectively (for the distribution of data, see Appendix S1: Fig. S3). The full model for arrival data fit best, indicating that the individual effects of NDVI and percentile days with $T_e \leq 10^{\circ}\text{C}$ as well as their interaction are important ($\text{AICc weight} = 1$; $\text{pseudo-}R^2 = 0.16$; Table 1, Fig. 5). There was a negative relationship between arrival timing and NDVI ($\beta = -3.84$), indicating that in years where NDVI was high and resources were potentially plentiful, birds arrived earlier. The relationship between percentile days with $T_e \leq 10^{\circ}\text{C}$ and arrival time was weaker than NDVI and in the opposite direction as predicted ($\beta = 0.87$); when thermoregulatory cost is high, birds arrived earlier. The interaction was positive ($\beta = 4.01$), indicating that when there were many percentile days with $T_e \leq 10^{\circ}\text{C}$ (i.e., high thermoregulatory cost), NDVI had a greater negative effect on arrival time (i.e., birds arrived even earlier; Fig. 6). The same qualitative result was obtained when the 25% quantile of standardized cumulative captures was used (see Appendix S2).

There was a considerable variation in both body mass (mean = 3.39 g, $\text{SD} = 0.30$, range = 2.5–5.0 g; for the distribution of data, see Appendix S1: Fig. S4) and fat accumulation (68% of birds had no fat and 23% had a fat score of

Table 1. Summary of the results for the best model where the percentile days with $T_e \leq 10^{\circ}\text{C}$ (T_e) was used to measure the physiological demand and NDVI was used as a surrogate of resources for each biological response variable.

Biological response	Best model	No. obs	No. groups	Liberal AICc weight	Liberal dAICc	df	Pseudo- R^2	Percentile days $T_e \leq 10^{\circ}\text{C}$ estimate	NDVI estimate	$T_e \times \text{NDVI}$ estimate
								(95% CI)	(95% CI)	(95% CI)
Molt	$T_e + \text{NDVI}$	128	17	0.99	0	4	0.2	–0.6	0.88	NA
								(–0.70, –0.49)	(0.71, 1.05)	
Arrival	$T_e \times \text{NDVI}$	68	18	1	0	6	0.16	0.12	0.08	
								0.87	–3.84	4.01
Body mass	NDVI	1318	18	1	0	4	0.03	(–3.48, 5.21)	(–7.56, –0.11)	(0.33, 7.7)
								2.22	1.9	1.88
Fat	Null	1318	18	1	0	3	0.09	NA	0.03	NA
									(0.02, 0.05)	

Notes: AIC, Akaike's information criterion; NDVI, normalized difference vegetation index.

dAICc is reported as the difference between each model from the top model. 95% confidence intervals (CI) are in parentheses, and standard error (SE) is in italics. Model fit is reported as pseudo- R^2 . The number of observations is the number of rows entering the model and the number of groups is the number of sites (random effects).

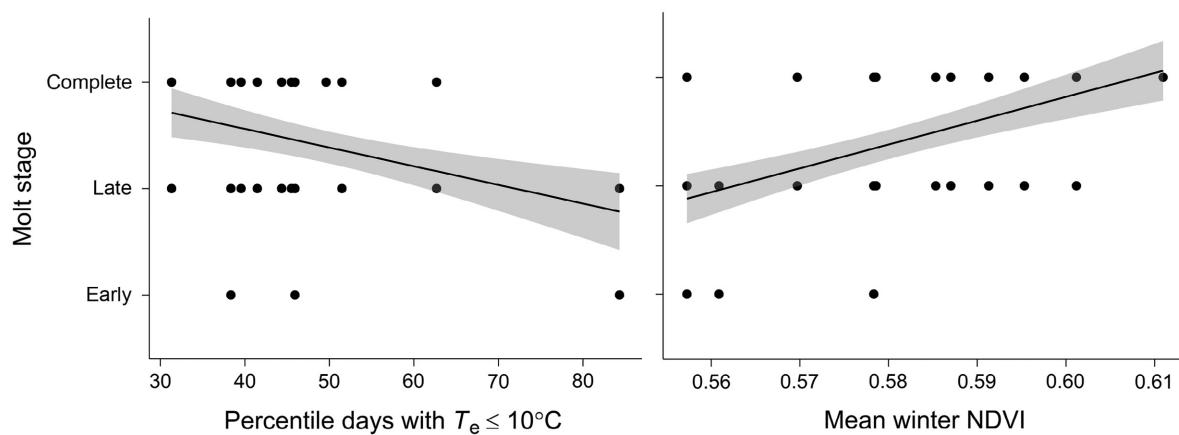


Fig. 5. Individual response curves derived from our model for the molt stage of the 50th quantile bird (see *Methods*) for percentile of days with operative temperature $\leq 10^\circ\text{C}$ (thermoregulatory cost) and mean winter normalized difference vegetation index (NDVI; resource availability). Each point represents the response of a site in a given year.

1; for the distribution of data, see Appendix S1: Fig. S5). The best model for body mass indicated only a very weak positive relationship between body mass and NDVI (AICc weight = 1; pseudo- $R^2 = 0.03$; $\beta = 0.03$), suggesting that birds have slightly lower mass in years when resources are low (Table 1, Fig. 5). For body fat, AICc did not indicate a model better than the null, suggesting no significant response of fat to NDVI or percentile days with $T_e \leq 10^\circ\text{C}$ (Table 1, Fig. 5).

DISCUSSION

Given ongoing climate change, and in particular increases in weather variability across years, determining how animals cope with change and whether they are able to adjust to particularly cold or low productivity conditions is key for mitigating the effects of these changes, particularly if this increased variability results in carry-over effects where the conditions in one time period influence the success of individuals in the following period (Saino et al. 2004, Gordo and Sanz 2008, Balbontin et al. 2009, Harrison et al. 2011, Conklin and Battley 2012, Catry et al. 2013, Senner et al. 2014, Cooper et al. 2015). Here, we show that broad-tailed hummingbirds moving northward during migration demonstrate plasticity in their behavior and physiology and that these responses can be explored using biologically informed models with relatively simple

environmental surrogates for thermoregulatory costs and resource availability on their wintering grounds. We find that in years when our remote sensing proxy for resources (NDVI) indicates that low productivity and our thermoregulatory cost estimate (based on the number of days that had six-hour periods below a bird's operative temperature) are high, birds migrating north are in earlier stages of molt. In addition, when resources are high on the wintering ground, birds migrate earlier, presumably to obtain high-quality breeding sites and to initiate earlier breeding. While remote sensing variables have been shown to correlate with migration timing and bird condition (Saino et al. 2004, Gordo and Sanz 2008, Balbontin et al. 2009), broad-scale measures of operative temperature have rarely been attempted. Our estimate of operative temperature was not correlated with NDVI, indicating that both these biologically informed environmental surrogates for both resources and thermoregulatory cost can provide a valuable tool for predicting how climate variability might influence the animal populations. Our approach provides new avenues for integrating different types of data including remote sensing observations, physiological measurements, and field monitoring to address the impacts of ongoing climate change. In addition, our results emphasize the importance of monitoring networks and citizen science data, which gather broad-scale

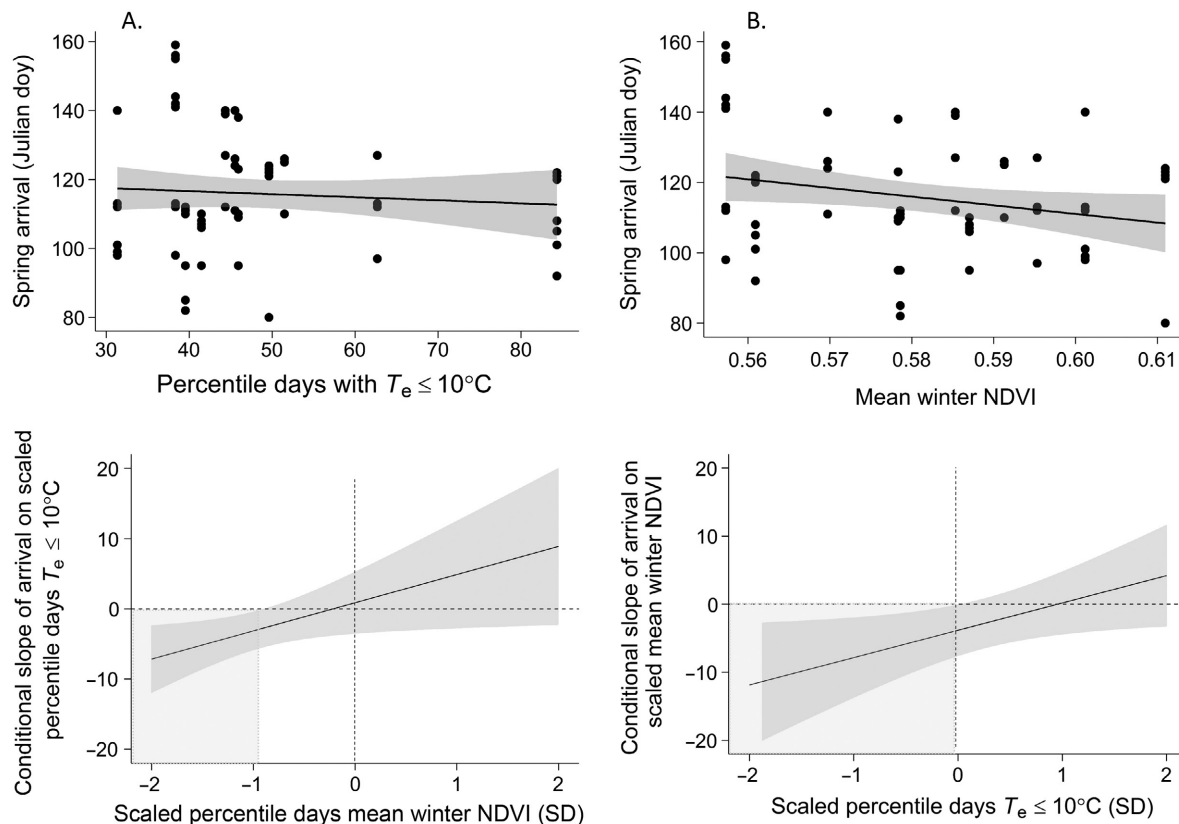


Fig. 6. The top row shows individual response curves derived from our model for the arrival date (Julian day of year) of the 50th quantile bird (see *Methods*) for percentile of days with operative temperature $\leq 10^{\circ}\text{C}$ (thermoregulatory cost) and mean winter normalized difference vegetation index (NDVI; resource availability) (both variables are scaled and plotted in standard deviation units). The best supported model for arrival date suggested an interactive effect between predictor variables, as shown in the bottom row (shaded boxes indicate the region of statistical significance). (A) In the top plot, spring arrival time is shown as predicted by thermoregulatory costs to the birds and the slope is conditional on resource availability, as shown in the lower plot. As resource availability decreases, the slope for arrival time and thermoregulatory cost switches from positive to negative. (B) The top plot shows spring arrival time as predicted by resource availability and the slope is conditional on thermoregulatory cost. As thermoregulatory cost decreases, the slope for arrival time and resource availability becomes more negative.

observations through time (Wethington and Russell 2003, Telleria et al. 2013, Sullivan et al. 2014, Supp et al. 2015), for evaluating how weather variability will affect the animal populations.

Like many birds, North American migrant hummingbirds, including broad-tailed hummingbirds, generally conduct the energetically demanding activities of reproduction and molt at different times of the year (e.g., Baltosser 1995, Barta et al. 2008). As predicted, we found that molt completion during the nonbreeding season

on the wintering grounds was lower in years when the resources were low and the thermoregulatory cost was high. This result is corroborated by several studies on both migrant and resident birds where birds fail to molt when the resources are low (Freed and Cann 2012, Barshep et al. 2013a, b, but see Boone et al. 2010). In years where hummingbirds fail to complete molt before migration, they must conduct multiple energetically expensive activities simultaneously, either completing molt while migrating or when they start breeding. In addition, migration cost may

be higher for hummingbirds that have not completed molt, especially of flight feathers, because greater energy expenditure is required for hovering and forward flight in these birds (Chai 1997, Chai and Dudley 1999).

The role of wintering ground weather in first arrival dates on the breeding grounds has increasingly been documented across different types of migratory birds; birds tend to arrive later to their breeding grounds in years with dry weather often caused by large oscillations such as the North Atlantic Oscillation and El Niño–Southern Oscillation (Cotton 2003, Gordo et al. 2005, Stervander et al. 2005, Rainio et al. 2006, Gordo 2007, Holmes 2011, Robson and Barriocanal 2011, Tottrup et al. 2012). As predicted, broad-tailed hummingbirds tended to arrive earlier at the migration stopover sites across southern Arizona in years when winter NDVI was high, suggesting that hummingbirds reach their breeding grounds early in these more productive years. This result was conditional on thermoregulatory costs; when costs were low, birds were able to further advance their arrival. This result suggests that even if NDVI is somewhat low, low thermoregulatory costs could still permit relatively early arrival of birds to their spring stopover sites.

Early arrival at breeding sites often increases the individual reproductive success, by early establishment and defense of high-quality territories, acquisition of high-quality mates, and increased offspring survival (Perrins 1970, Moller 1994, Newton 2008). The fitness effects of early arrival have been more commonly shown in socially monogamous bird species, but promiscuous species such as broad-tailed hummingbirds may also gain a fitness advantage of early arrival by acquiring a high-quality display location in a lek, a high-quality nest site, or high-quality territories containing early nectar resources (Pitelka 1951, Stiles 1971, 1973, Stiles and Wolf 1979). The potential advantage of early arrival on northern latitude breeding grounds for broad-tailed hummingbirds and other animals may increase if early spring nectar resources become available earlier as a result of ongoing climate change. However, there may be a disadvantage of early arrival if the changes in movement patterns result in asynchrony between animals and their food plants along their migration route (McKinney et al. 2012).

The lack of a relationship between body mass or fat and our environmental predictors likely reflects hummingbird-specific physiology and behavior as well as biological processes that respond quickly to changing conditions experienced along the migration route. Because hummingbirds are adapted to use torpor (rather than fat stores) to compensate for energy shortages, it is perhaps not surprising that we see no relationship between body mass or fat and wintering ground temperatures (Powers et al. 2003). Further, high metabolic costs associated with carrying extra weight may not be advantageous for hummingbirds. For instance, hummingbirds have been observed increasing their weight by >25% before roosting, but such weight gain is not observed during the day, when they tend to maintain a constant mass presumably to maintain flight efficiency (Calder et al. 1990). In general, while weight and fat may be useful predictors for physiological condition during migration in many species, they tend to be poor predictors in very small bird species, perhaps because most individuals are lean and have relatively little fat (Barnett et al. 2015). In addition, fat stores in small birds change rapidly so point measurements of fat content can be difficult to interpret (Carpenter et al. 1993, Powers et al. 2003) and likely reflect the conditions a bird encountered along its migratory path rather than its wintering grounds.

Generating predictor variables that reflect the physiological demand of a given species can be particularly useful for modeling the effects of weather variability on organisms with high metabolic rates, such as hummingbirds (Kearney and Porter 2004, Buckley 2008, Huey et al. 2012). In particular, the short (hourly) temporal scales over which hummingbirds respond (Beuchat et al. 1979, Powers and Conley 1994) are not normally considered when predicting the effects of weather or climate on species behavior and distribution. Newly available weather data such as the remote sensing data we employed (i.e., Saha et al. 2014) can be used to parameterize fine temporal resolution physiological models and more realistically capture organism responses to the environment (Dormann et al. 2012).

Similarly, satellite vegetation indices have become commonly used for many ecological and climate change research questions and have

successfully been used to evaluate the spatial variation in abundance across many animal populations from browsers and grazers (e.g., Bartlam-Brooks et al. 2011, Ryan et al. 2012, Borowik et al. 2013) to migrating birds (e.g., Tottrup et al. 2008, Dodge et al. 2014, La Sorte et al. 2014). These studies suggest that vegetation indices, such as NDVI, may be a viable proxy for resource availability. In particular, flower nectar, on which hummingbirds rely, is affected by environmental variables such as precipitation and soil moisture, which in turn are typically highly correlated with NDVI (Crimmins et al. 2014). However, linking nectar production to hummingbird occurrence and behavior at the local scales over which hummingbirds forage remains an important research challenge (Feldman and McGill 2014).

Periods with a large number of climate anomalies as compared to other periods may be particularly problematic for animal populations, especially those with strong, identifiable, physiological constraints. As such, hummingbirds provide an ideal system for evaluating the effects of environmental changes on biological diversity. We identified one winter in particular, 2010–2011, that was the most extreme example in our time series, with both reduced resources and greater thermoregulatory costs. This reduction was observed between visits just before and just after the cold events at an overwintering area used by hummingbirds in Mexico (C. Rodriguez, G. Stiles, and S. Wethington, *personal observation*). When hummingbirds reach the physiological limits due to the repeated cold weather conditions, they can respond quickly and dramatically. Thus, finding environmental limits on the physiological constraints is critical for mitigating the predicted environmental changes and would be a valuable focus of future research (Sáenz-Romero et al. 2010).

Here, we have shown that proxies for resource availability, such as remote sensing vegetation indices and thermoregulatory cost parameterized using high temporal resolution weather data, are useful for understanding how populations respond to ongoing climate change and weather variability. The continued refinement of mechanistic distribution models and environmental data to drive the models provides new insights into the influences of environmental change on species.

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