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Asynchronous changes in phenology of migrating Broad-tailed Hummingbirds and their early-season nectar resources

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Abstract. Phenological advancements driven by climate change are especially pronounced at higher latitudes, so that migrants from lower latitudes may increasingly arrive at breeding grounds after the appearance of seasonal resources. To explore this possibility, we compared dates of first arrival of Broad-tailed Hummingbirds (*Selasphorus platycercus*) to dates of flowering of plants they visit for nectar. Near the southern limit of the breeding range, neither hummingbird arrival nor first flowering dates have changed significantly over the past few decades. At a nearby migration stopover site, first flowering of a major food plant has advanced, but peak flowering has not. Near the northern limit of the breeding range, first and peak flowering of early-season food plants have shifted to earlier dates, resulting in a shorter interval between appearance of first hummingbirds and first flowers. If phenological shifts continue at current rates, hummingbirds will eventually arrive at northern breeding grounds after flowering begins, which could reduce their nesting success. These results support the prediction that migratory species may experience the greatest phenological mismatches at the poleward limits of their migration. A novel hypothesis based on these results posits that the poleward limit for some species may contract toward lower latitudes under continued warming.

Key words: Broad-tailed Hummingbird; climate change; ecological interactions; flowering time; latitude; migration; phenological shifts; pollination; reproductive success; Rocky Mountain Biological Laboratory, Colorado (USA); Selasphorus platycercus; *synchrony*.

Introduction

Climate change affects many ecological processes and interactions (Walther et al. 2002), in part, by altering the timing (phenology) of biological events (Sparks and Menzel 2002, Parmesan 2007). Phenological shifts associated with warming temperatures range from advancement, especially in the spring, to retardation or no change, especially in the summer and autumn (Sparks and Menzel 2002). Such shifts can lead to altered synchrony between interacting species (Winder and Schindler 2004).

Interactions involving species that migrate seasonally across latitudes may be especially prone to altered synchrony, particularly at the poleward limits of migratory routes, where phenological advancements in the spring are progressing more rapidly than at lower latitudes (IPCC 2007). Here we address this possibility using long-term data on a migratory pollinator, the Broad-tailed Hummingbird (*Selasphorus platycercus*), and several of the plants whose flowers it visits for nectar. We first explore how the dates of arrival of hummingbirds have changed over the past several decades at sites near the southern limit of the breeding range of the species, and at a site near the northern limit of the range. We compare these dates to those of flowering, expecting that arrival is more delayed relative to flowering at the higher latitude. Finally, we extrapolate from recent changes to predict future asynchrony of hummingbirds and their flowers, and consider likely effects on the hummingbirds.

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Methods

Study species and sites

Broad-tailed Hummingbirds (*Selasphorus platycercus*, Swainson; see Plate 1), hereafter Broad-tails, migrate in the spring from Central America to summer breeding grounds in mountains of the western USA (Bent 1940, Calder and Calder 1992). The best available evidence indicates that floral nectar is an essential part of the diet of temperate flame-throated hummingbirds such as Broad-tails (e.g., Calder and Hiebert 1983, Brice 1992, Martínez del Rio et al. 1992). The negative correlation observed between floral abundance and Broad-tail use of hummingbird feeders also suggests dependence on floral nectar (including the floral abundances of *Erythronium* and *Delphinium* species in this study; Inouye et al. 1991, see also McCaffrey and Wethington 2008). The timing of each segment of northward flight is therefore likely to depend on local nectar availability, and phenology of food plants along the migration route may constrain how quickly individuals are able to reach breeding grounds. Individual Broad-tails exhibit strong fidelity to past breeding sites, with experienced adults arriving first (with males usually, but apparently not always, preceding females), followed by younger individuals (Calder et al. 1983, Calder and Calder 1992). First arrival of males may not represent actual residency, but rather diurnal movement from lower elevations of mountain ranges where nectar-producing flowers bloom before those at higher elevations (Calder and Calder 1992). The promiscuous mating system is likely to place a premium on such anticipatory forays, because males that make them are likely to obtain breeding territories as the first flowers appear and therefore to obtain copulations with females as they begin nesting (e.g., Armstrong 1987).

The natural history of isolated mountain ranges ("sky islands") in southeastern Arizona, near the southern limit of the breeding range of Broad-tails, is well known (e.g., Shreve 1915, Bailey 1923, Marshall 1957). The sky islands support populations of several species of hummingbirds and their food plants. For example, Broad-tails breed in the Santa Catalina Mountains near Tucson, southeastern Arizona (32.12° N, 110.93° W), where they feed at a number of brightly colored flowers with concealed nectar (Grant and Grant 1966), and also at the very-early-flowering manzanita, *Arctostaphylos pungens* (Kunth), with small pale-colored flowers that also attract insects (C. D. Bertelsen, *unpublished data*). Individuals breeding farther north pass through desert valleys below sky islands, including the Tucson Basin below the Santa Catalinas, where they frequently feed at flowers of ocotillo, *Fouquieria splendens* (Engelm.; Waser 1979, Calder 2004).

Interactions between Broad-tails and their food plants have been studied extensively in western Colorado, near the northern limit of the breeding range. At the Rocky Mountain Biological Laboratory (RMBL; 38.96° N, 106.99° W, 2900 m above sea level [a.s.l.], >6 degrees of latitude north of Tucson), territorial male and nesting female Broad-tails forage for nectar at a series of herbaceous perennial plant species that flower in sequence through the summer. The earliest of these is glacier lily, *Erythronium grandiflorum* (Pursh), whose flowering begins about one week after snowmelt and ceases about two weeks later (Lambert et al. 2010). In some years, returning males especially forage at the yellow flowers of this species (Inouye and McGuire 1991). Initiation of hummingbird nesting, in turn, appears to be synchronized with the flowering of dwarf larkspur, *Delphinium nuttallianum* (Pritz. ex Walp., = *D. nelsonii* Greene), which begins about two weeks after snowmelt and lasts for about four weeks (Waser 1976). Hummingbirds join long-tongued queen bumble bees (*Bombus* spp.) as primary pollinators of the blue-purple flowers of this species (Waser and Price 1990).

Study sites and data collection

We monitored hummingbirds and flowering of their food plants over several decades at two sites near Tucson. First, from 1984 through 2010, we recorded presence of hummingbirds and flowers approximately once per week in pine–oak woodland at 1940–2213 m a.s.l. in Finger Rock Canyon in the Santa Catalina Mountains (mean = 4.25 censuses/month, median = 4; see Crimmins et al. 2008). Here we focus on first arrival of male Broad-tails and on first flowering of Santa Catalina paintbrush, *Castilleja tenuiflora* (Benth.), an early-flowering nectar source. Across 27 years of records for Finger Rock Canyon, we have 25 years for first arrival of male Broad-tails and 24 years for first flowering of *C. tenuiflora*, defined as the first day a hummingbird or flower, respectively, was observed during a census. Second, from 1974 through 1977, and again from 2005 through 2011, we recorded first and peak flowering in a population of 15 marked *F. splendens* plants approximately weekly at the University of Arizona Desert Laboratory on Tumamoc Hill (820 m a.s.l.), just west of downtown Tucson (Waser 1979). As for Finger Rock Canyon, date of first flowering was taken as that of the first census on which an open flower was observed. Date of peak flowering was defined as the day on which 100% of plants had open flowers. When this occurred in two successive censuses, we took as peak flowering the date halfway in between; when it occurred in only one census, we took as peak the date halfway between that census and the previous one in which <100% of plants carried open flowers.

We monitored spring arrival of male Broad-tails and phenology of their early-season nectar plants in Colorado over a similar span of years. From 1975 through 2011, we listened for male Broad-tails while walking or skiing a ~800-m transect at the RMBL at least every two days. Males make a distinctive trilling noise with their wings that can be heard up to 100 m

away (Miller and Inouye 1983). In 1973 we established a series of 2 × 2 m permanent plots in wet and dry meadows around the RMBL in which phenology of flowering has been monitored approximately every 2 d during each summer through 2011 (Inouye 2008). *Erythronium grandiflorum* occurs in six plots, and *D. nuttallianum* in seven plots; all are <800 m from the hummingbird transect. Flower counts were summed across plots in each year to determine the day of first and peak flowering. First flowering was the first day on which a flower of either species was observed in any of the plots, i.e., the very beginning of the across-plot cumulative flowering curve for each species. Peak flowering was the day on which the maximum number of flowers was counted. Hummingbird records are missing for 1977 and 1987, flowering records are missing for 1978 and 1990, and first-flowering data are missing for five years for *E. grandiflorum* and for three years for *D. nuttallianum*. This leaves 35 years of hummingbird first arrival data and 30 and 32 years of *E. grandiflorum* and *D. nuttallianum* first-flowering data, respectively, spanning 1975–2011. Date of peak flowering is available for both plant species for 35 of 37 years. Finally, we obtained monthly mean air temperature data, calculated from daily mean temperatures, from a NOAA weather station located in Crested Butte, Colorado (2704 m a.s.l.), ~9.5 km south of the RMBL (NOAA; data *available online*).[6]

Analysis

We controlled for the timing of the vernal equinox to avoid overestimates of phenological advancements, by subtracting the date of the equinox from each phenological date (Sagarin 2001; see Appendix A for vernal equinox data). We then used simple linear regression with year as the explanatory variable to describe change through time in hummingbird arrival and flowering phenology at both breeding sites. Because residuals from our phenology time series at Tumamoc Hill were autocorrelated, we used *t* tests to compare the mean timing of onset and peak flowering between the 1970s and 2000s. A lower sampling frequency at the Arizona sites compared to the Colorado site should not compromise estimates of phenological change through time (Miller-Rushing et al. 2008). We also calculated the number of days between hummingbird arrival and first flowering for each species at breeding grounds. The day of Broad-tail appearance was subtracted from the day of first flowering of each species, so that negative values represent years when Broad-tails arrive after first flowering. To assess whether phenological changes through time are consistent with variation in temperature, we repeated analyses for the RMBL using temperature as a continuous explanatory variable. We removed four years of extremely late first flowering relative to other years for the analysis of *C. tenuiflora* phenology (Appendix B). These late-flowering years occur in dry years, particularly in the spring; because later flowering at Finger Rock Canyon is at least partly associated with low precipitation (Crimmins et al. 2010), low rainfall may explain these extreme deviations. Removing these four years normalizes residuals, which various transformations failed to do, does not alter the direction or significance of results (Appendix B); because results based on normally distributed residuals should be more accurate, we present results without the outliers. All analyses were conducted in R v. 2.11.1 (R Development Core Team 2008).

[6] http://www.ncdc.noaa.gov



PLATE 1. A nesting Broad-tailed Hummingbird (*Selasphorus platycercus*) female at the Rocky Mountain Biological Laboratory (RMBL, Colorado, USA). Photo credit: N. M. Waser.

RESULTS

Although arrival of male Broad-tails over 27 years at a southern breeding site, Finger Rock Canyon, has trended toward later (rather than earlier) dates in the spring by an average of 6.5 ± 6.8 d per decade (mean ± SE), the trend is very weak and far from significant ($R^2 = 0.04$, $F_{1,23} = 0.92$, $P = 0.35$; Fig. 1a). Likewise, the timing of first *C. tenuiflora* flowers is also quite variable and trends insignificantly toward later flowering by 2.3 ± 4.1 days per decade ($R^2 = 0.02$, $F_{1,18} = 0.30$, $P = 0.59$; Fig. 1a). At Tumamoc Hill, neither first nor peak flowering of *F. splendens* has significantly changed since the early 1970s ($t = 1.83$, $P = 0.13$; $t = 0.76$, $P = 0.48$, respectively; Fig. 2).

First arrival of male Broad-tails at our northern site, the RMBL, has advanced by 1.5 ± 0.93 days per decade over the last 37 years ($R^2 = 0.07$, $F_{1,33} = 2.45$, $P = 0.13$; Fig. 1b, c). First and peak flowering of *E. grandiflorum* have advanced by 4.6 ± 1.6 days and 2.7 ± 1.4 d per decade, respectively ($R^2 = 0.22$, $F_{1,28} = 7.93$, $P = 0.0088$; $R^2 = 0.10$, $F_{1,33} = 3.82$, $P = 0.059$, respectively; Fig. 1b), whereas first and peak flowering of *D. nuttallianum* have advanced by 4.3 ± 1.5 d and 2.8 ± 1.4 d, respectively ($R^2 = 0.21$, $F_{1,30} = 7.97$, $P = 0.0084$; $R^2 = 0.12$, $F_{1,33} =$

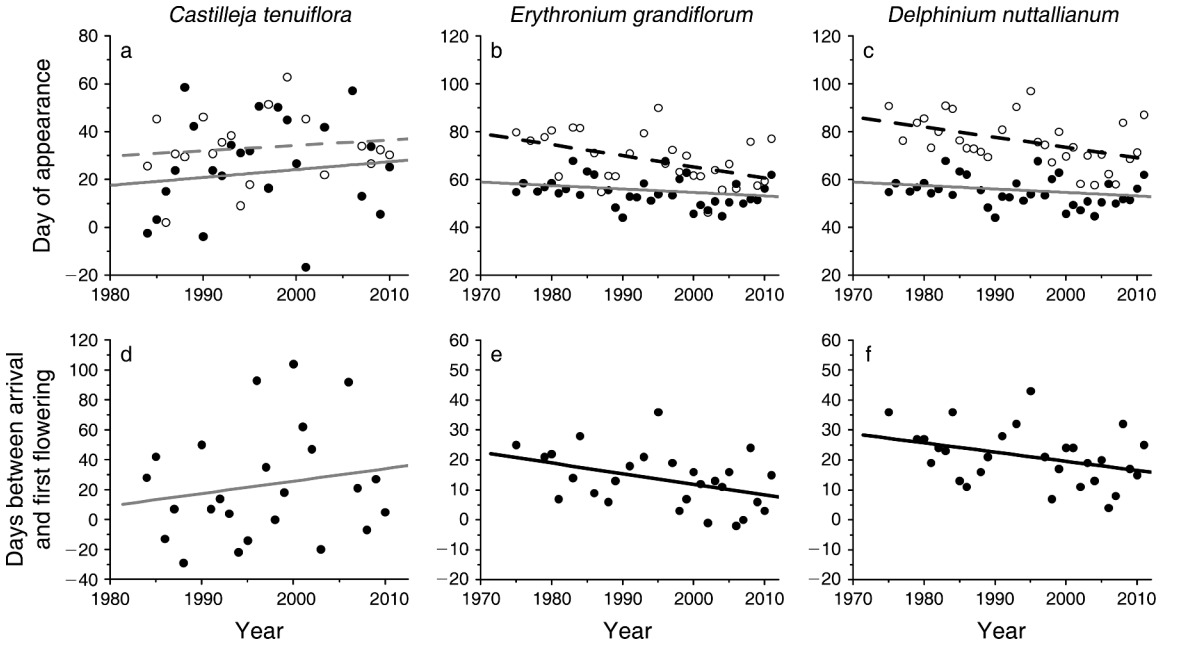

FIG. 1. Timing of first arrival of the Broad-tailed Hummingbird, *Selasphorus platycercus* (solid circles, solid lines), and first flowering of its early-season nectar resources (open circles, dashed lines): (a, d) *Castilleja tenuiflora* at a southern breeding site (Finger Rock Canyon, Arizona, USA) and (b, e) *Erythronium grandiflorum* and (c, f) *Delphinium nuttallianum*, both species at a northern breeding site (Rocky Mountain Biological Laboratory, Colorado, USA). Timing of appearance is expressed as the number of days after the vernal equinox, and the actual number of days is shown between arrival and first flowering. Gray lines represent nonsignificant fits, and black lines show significant fits ($P < 0.059$). Note that the range of the *y*-axis is constant, but dates are later in panels (b) and (c) compared to panel (a); the range of the *y*-axis in panel (d) is double that of panels (e) and (f). Broad-tail arrival in 2006 was 114 days after the vernal equinox and is not visible in panel (a).

4.31, $P = 0.046$, respectively; Fig. 1c). Hummingbird arrival and flowering phenology at the RMBL exhibit similar, even stronger trends in relationship to mean April–May air temperature (Appendix C), suggesting that temperature increases largely drive these phenological shifts at the RMBL.

Arrival of the first male Broad-tails has typically preceded the appearance of first *C. tenuiflora* flowers in Finger Rock Canyon through the decades of this study. There is no indication of a directional trend in the relationship between hummingbird arrival and onset of *C. tenuiflora* flowering over a 27-year period ($R^2 = 0.03$, $F_{1,22} = 0.72$, $P = 0.40$; Fig. 1d). Likewise, arrival of the first male Broad-tails has historically preceded the appearance of first *E. grandiflorum* and *D. nuttallianum* flowers at the RMBL. In this case, however, the dates have been converging, with shorter intervals between arrival and onset of flowering (arrival converging with *E. grandiflorum* by 3.5 ± 1.6 days per decade, $R^2 = 0.17$, $F_{1,25} = 4.96$, $P = 0.035$, and with *D. nuttallianum* by 3.1 ± 1.5 days per decade, $R^2 = 0.13$, $F_{1,27} = 3.91$, $P = 0.058$; Fig. 1e, f). This trend also holds true for the relationship between arrival and peak flowering, though not as strongly (arrival converging with *E. grandiflorum* by 2.3 ± 1.3 days per decade, $R^2 = 0.10$, $F_{1,30} = 3.42$, $P = 0.074$, and with *D. nuttallianum* by 1.9 ± 1.2 days per decade, $R^2 = 0.08$, $F_{1,30} = 2.56$, $P = 0.12$). If these phenological shifts continue into the future at the same rate, hummingbirds will arrive, on average, after first flowering in *E. grandiflorum* by 2033 and after first flowering in *D. nuttallianum* by 2069 (Fig. 3).

DISCUSSION

A combination of serendipity and foresight allowed us to assemble overlapping phenological records spanning roughly the last three decades and representing two latitudes along the northward spring migration route and within the summer breeding range of Broad-tailed Hummingbirds. Whereas records from additional sites would be welcome, the data in hand suggest that the earliest nectar-producing plants exhibit larger advancements in flowering at the northerly Colorado site than the southerly Arizona site, consistent with a larger mean temperature increase over the same period at higher latitudes (IPCC 2007). The consequence is a shrinking interval between arrival of the first Broad-tails to the Colorado site, experienced adult males who wait to establish territories and overnight residence until appearance of first flowers, and both first and peak flowering of two important early-season nectar plants. This shrinking time interval between arrival and first flowering is consistent with the expectation that arrival is constrained by slower shifts in flowering phenology farther south along the migration route.

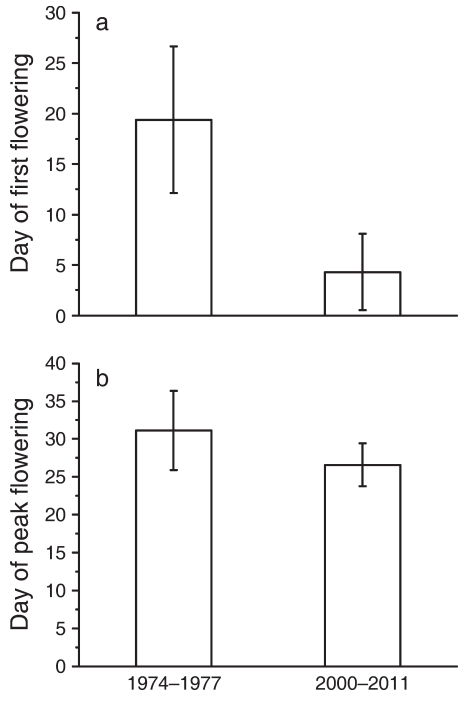

FIG. 2. Timing of (a) first and (b) peak flowering of a nectar resource, *Fouquieria splendens*, along the migration route of Broad-tail Hummingbirds at Tumamoc Hill, near Tucson, Arizona, USA. Flowering is shown as number of days after the vernal equinox and was compared between censuses carried out in the 1970s ($N = 4$ years) and 2000s ($N = 7$ years) using t tests. Error bars show ±SE. Timing of flowering did not differ significantly between these two time periods, although both first and peak flowering appear to have advanced from the 1970s to the 2000s.

Directional climate trends of the last few decades are forecast to continue into the foreseeable future, and phenological shifts are likely to continue as well. An increase in mean temperature of 2.0–4.5°C is forecast over the next century (Kerr 2004, IPCC 2007), and a linear extrapolation from the phenological shifts we observed over the past 37 years shows that the first Broad-tails will begin to arrive in Colorado after flowering of their first food plants well within this same century, rather than arriving in anticipation of flowering, as now occurs. Linear extrapolation may overestimate actual phenological convergence, insofar as sprouting and flowering of long-lived herbaceous root perennials such as *E. grandiflorum* and *D. nuttallianum* will not track temperature increase indefinitely, and insofar as temperature is not the only cue for phenology that is changing with anthropogenic climate change. On the other hand, some additional cues also are changing in ways that will advance flowering; snowmelt, for example, which correlates strongly with flowering of both plant species, has advanced by four days per decade from 1975 to 2008 at the RMBL (Miller-Rushing and Inouye 2009, Lambert et al. 2010). Furthermore, linear extrapolation may underestimate at least the short-term phenological convergence insofar as temperature increase and other aspects of climate change now appear to be accelerating (IPCC 2007). We conclude in any case that phenological convergence of hummingbirds and flowers is likely to continue for some time.

Eventual arrival of Broad-tails after their first nectar sources begin flowering, in turn, may have consequences for hummingbird nesting success and population dynamics, especially given that declining population trends are more prominent among migratory bird species that do not advance their spring migration compared to species that advance their migration, and among Nearctic species that experience discrepancies between warming at breeding grounds compared to overwintering grounds (Møller et al. 2008, Jones and Cresswell 2010). As is true of other hummingbirds, female Broad-tails lay a clutch of only two eggs, and a short summer flowering season currently limits them to a single clutch per year in montane sites such as the RMBL. The consequence of this low fecundity and of an expected female life span of less than two years (Calder 1990) is an estimated finite rate of increase, λ, near unity (Calder et al. 1983). Any disruption of the current match between flowering and the nesting cycle might reduce the value of λ (see Waser 1976), so that populations at the northern boundary of the breeding range are below replacement. Counterintuitively, then, further climate warming might actually contract the northern limit of the Broad-tail breeding range toward lower latitudes.

How likely are the continuing phenological shifts that we extrapolate to have such drastic effects on hummingbirds? On the one hand, the entire summer flowering season of important hummingbird food plants

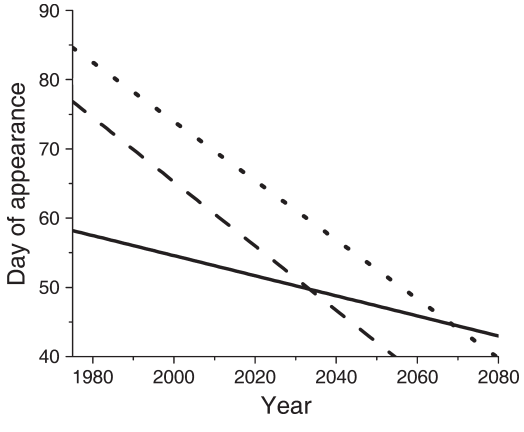

FIG. 3. Linear regression fits of change through time extrapolated until the first flowering of two plant species at the Rocky Mountain Biological Laboratory (broken lines) intersects with first arrival of Broad-tail Hummingbirds (solid line). Day of appearance is the number of days after the vernal equinox. Linear equations are based on data from 1975 to 2011. The dashed line is the first flowering date of *Erythronium grandiflorum*; the dotted line is first flowering date of *Delphinium nuttallianum*.

might shift to earlier dates. In this case, arrival of hummingbirds after the earliest species appear could increasingly squeeze the nesting cycle (about six weeks from egg laying to fledging of young, not including time for nest building; Waser 1976, Calder and Calder 1992) into a shrinking temporal window of resource availability, eventually reducing the chance of successful completion. The alternative possibility is that the entire flowering season is expanding; indeed, the last days of flowering of two of the latest-flowering nectar resources for Broad-tails at the RMBL, *Delphinium barbeyi* and *Castilleja linariifolia*, are not changing significantly, though both are trending toward earlier dates (by 2.3 $\pm$ 2.0 and 11.2 $\pm$ 8.2 days per decade respectively; D. W. Inouye, *unpublished data*). However, an extended flowering season does not guarantee $\lambda \geq 1$. If flower densities decline correspondingly throughout the summer or during a critical period, a longer growing season would not be beneficial. Indeed, long-term data suggest an increasingly strong mid-summer decline in community-level floral densities in montane meadows around the RMBL (Aldridge et al. 2011). Finally, the assumption that Broad-tails can adjust the phenology of their nesting cycle indefinitely to match shifts in flowering onset may be incorrect, as a study by Schaper et al. (2012) suggests.

Understanding disparate shifts among interacting species is critical for improving our prediction of biological responses to climate change (Parmesan 2007). Our study supports the hypothesis that such a disparate shift can occur in latitudinal migrants and their local resources because climate change and phenological change are more pronounced at higher latitudes. By extension, this implication extends to other Neotropical hummingbird migrants, migratory bats that follow nectar corridors, and migratory insectivorous birds whose prey are tied to the phenology of their host plants at breeding grounds (e.g., Both et al. 2009). In the case of the Broad-tailed Hummingbird, extrapolation into the future suggests the novel prediction that more northern breeding sites may become unsuitable; combined with increased warming at lower latitudes, this implies the future possibility of an overall shrinkage of the breeding range.

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Supplemental Material

Appendix A

Long-term phenology data from three study sites used for analyses (*Ecological Archives* E093-188-A1).

Appendix B

Flowering onset of *Castilleja tenuiflora* (with outliers included), an early-season nectar source for breeding Broad-tailed Hummingbirds (*Selasphorus platycercus*) at Finger Rock Canyon, Arizona, USA (*Ecological Archives* E093-188-A2).

Appendix C

Relationships between temperature and arrival of Broad-tailed Hummingbirds and flowering onset in its early-season nectar resources at the Rocky Mountain Biological Laboratory in Colorado, USA (*Ecological Archives* E093-188-A3).