Received: 18 May 2022 | Revised: 23 August 2022 | Accepted: 30 August 2022

DOI: 10.1002/ecy.3890

REPORT

ECOLOGY
ECOLOGICAL SOCIETY OF AMERICA

Skewness in bee and flower phenological distributions

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Funding information
Earthwatch Institute; NC State University; National Science Foundation (NSF), Grant/Award Numbers: DEB 0922080, DEB 94-08382, DEB-0238331, DEB-0922080, DEB-1354104, DEB-1912006, IBN-98-14509; NSF Graduate Research Fellowship, Grant/Award Number: 1745048

Handling Editor: Nicholas J. Gotelli

Abstract

Phenological distributions are characterized by their central tendency, breadth, and shape, and all three determine the extent to which interacting species overlap in time. Pollination mutualisms rely on temporal co-occurrence of pollinators and their floral resources, and although much work has been done to characterize the shapes of flower phenological distributions, similar studies that include pollinators are lacking. Here, we provide the first broad assessment of skewness, a component of distribution shape, for a bee community. We compare skewness in bees to that in flowers, relate bee and flower skewness to other properties of their phenology, and quantify the potential consequences of differences in skewness between bees and flowers. Both bee and flower phenologies tend to be right-skewed, with a more exaggerated asymmetry in bees. Early-season species tend to be the most skewed, and this relationship is also stronger in bees than in flowers. Based on a simulation experiment, differences in bee and flower skewness could account for up to 14% of pairwise overlap differences. Given the potential for interaction loss, we argue that difference in skewness of interacting species is an underappreciated property of phenological change.

KEYWORDS
asymmetry, bees, community, mismatch, pollination, skew, temporal overlap, wildflowers

INTRODUCTION

Timings of seasonal life-history events (phenology) are often characterized by single points in time (e.g., first-appearance date), but in reality, these events are typically distributed processes (Carter et al., 2018; Inouye et al., 2019). Species phenological distributions are characterized by their central tendency, their breadth,

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and their shape (e.g., mean, standard deviation, and skewness) (Rathcke & Lacey, 1985). Ecological interactions usually require temporal co-occurrence, where the population performance of any species is dependent on phenological overlap with resource availability. In the case of pollination and other mutualistic interactions, interacting species benefit from maximizing temporal overlap with one another, while dealing with the fitness costs of changing their phenology (Visser et al., 2012). The degree of overlap between interacting species is determined by the mean, breadth, and shape of both species' phenological distributions (Figure 1), with differences in any one of the three properties being enough to reduce overlap. While the shape of phenological distributions has been recognized as an important component of species interactions (Thomson, 1980), studies of phenological match/mismatch in plants and pollinators have focused primarily on how first or mean dates of seasonal activity shift in response to varying cues (Inouye et al., 2019) and how the temporal breadth of their activity stretches or contracts. The importance of skewness differences in determining mismatch in pollination interactions remains unclear. This is in part because there has not been a systematic analysis of skewness in phenological distributions across many species of pollinators and flowering plants together.

Flower phenological distributions are often right-skewed, with a long, trailing tail after the peak of flowering in prairie (Rabinowitz et al., 1981) and montane (Thomson, 1980) ecosystems. Within populations, the degree of skewness can vary among years (Blionis et al., 2001; Forrest & Thomson, 2010). Phenological distribution shape may also be affected by local resource competition that reduces plant size, which is in turn correlated with floral phenology skewness (Schmitt, 1983). It has also been suggested that the right-skewness of flowering phenologies may be a product of selective pressure for early flowering (Forrest & Thomson, 2010) and that recent climate change has affected the shapes of flower phenological distributions (CaraDonna et al., 2014). Although the typical patterns of flower phenological skewness are well understood, we do not know if these patterns are also similar for pollinators. There is reason to suspect that phenological sensitivity differs between plants and pollinators and that the seasonal onset and end of activity in pollinators (such as bees) shift at different rates (Stemkovski et al., 2020). Thus, a community-wide assessment to compare bee and flower phenological skewness is warranted.

In this study, we quantified phenological skewness for multiple bee and flower species within a montane community. We determined the relative prevalence of right-skewed, left-skewed, and symmetrical distributions and examined the differences between bees and flowers in how skewness relates to other properties of their phenological distributions. A priori, we predicted that the skewness of bee phenologies would be similar to that of

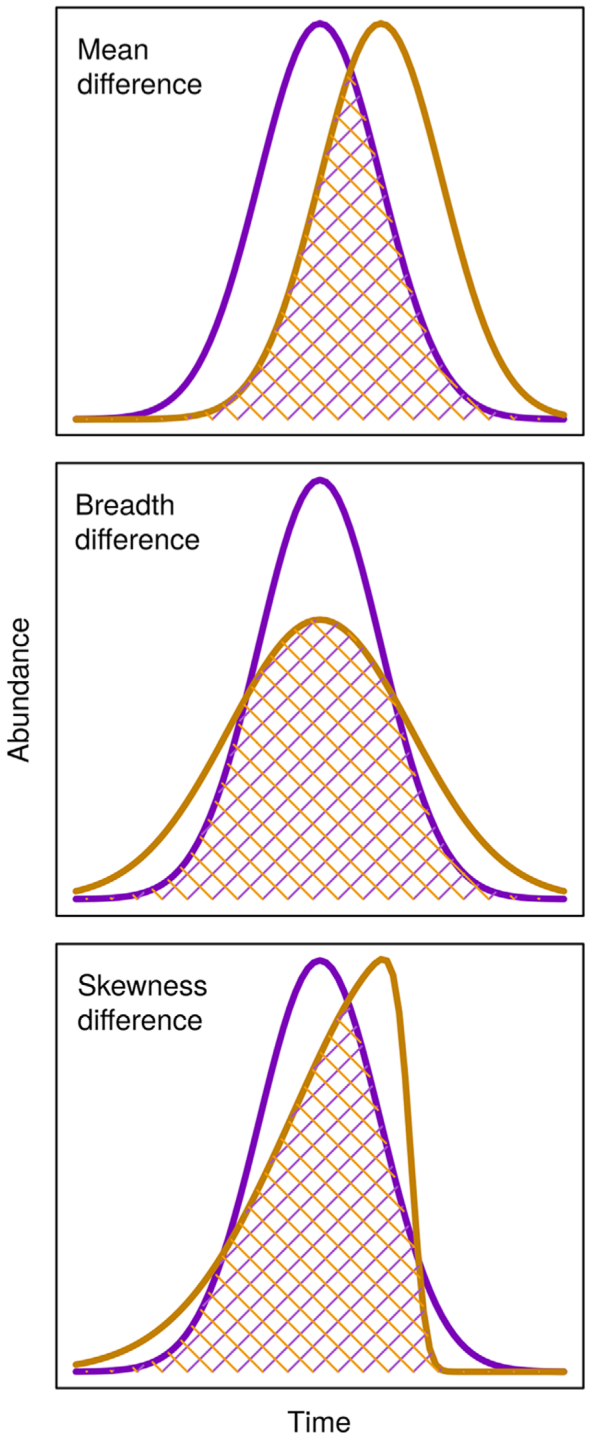

FIGURE 1 Conceptual diagram of causes of phenological mismatch. Differences in the phenological mean timing (top panel), breadth (center panel), and skewness (bottom panel) of species determine the extent to which interacting species overlap in time. The purple and gold curves represent phenological distributions of two species, and the hatched areas are times of phenological overlap.

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flowers but that bees active in the early season would have phenologies more strongly right-skewed than those in the late season due to a hard limit on activity before snowmelt in the study system. Lastly, we performed a simulation study to gain perspective on the potential consequences that variation in skewness in this community may have on phenological overlap between bees and flowers.

METHODS

Data sources

We used flower phenology data from a long-term monitoring program spanning from 1974 to 2019 at the Rocky Mountain Biological Laboratory (RMBL) in Gothic, Colorado, USA, a mountainous location with a short summer growing season set ~2890 m above sea level (CaraDonna et al., 2014; Inouye, 2008). The total number of flowers was counted approximately three times per week for the extent of the growing season for all flowering species in 4-m^2 fixed plots. This data set included mainly long-lived perennial forb species. Further details on this program are reported by CaraDonna et al. (2014) and Inouye (2008), and source data are available through Open Science Framework (Inouye et al., 2022). For our analysis, we included 35 flower plots aggregated into eight sites by proximity to agree with the spatial scale of the bee phenology sites. We obtained bee phenology data from a companion study of the flower phenology project that tracked bee abundance from 2009 to 2020 at the RMBL (Ogilvie et al., 2017; Stemkovski et al., 2020). Bee abundance was measured using pan traps approximately every 2 weeks across the growing season at 18 sites spaced across an elevation gradient (Gezon et al., 2015). Because pan traps are biased toward collecting smaller-bodied bees, hand netting was used for bumblebees (*Bombus* spp.). Additional details on bee data collection and all data are available through Open Science Framework (Irwin et al., 2018). All data and processing steps and analyses for this study can be viewed and reproduced using data and code available online (https://doi.org/10.5281/zenodo.6561297; Stemkovski, 2022).

Data processing

We formatted and standardized flower and bee data to make them directly comparable. For all data, we excluded records with uncertain identifications and those that were identified only to genus. We excluded all grass and sedge species but included shrubs. The bee abundance data were derived from multiple pan traps or netters, so we aggregated flower and bee counts across plots/traps/netters per site. For the bee data, we included only female bees because female specimen identifications were more fully resolved and because combining females and males could lead to inaccurate estimates of skewness because males often emerge later than females in social species. We distinguished queen and worker castes of bumblebees (*Bombus* spp.) to avoid biasing skewness estimation by confounding an early-season queen peak in abundance and a later peak in worker abundance. Because bumblebees were sampled explicitly by netting and due to difficulties of combining sampling effort between netting and pan traps, we excluded pan-trapped *Bombus* and net-trapped non-*Bombus* bees. To ensure that we only included sampling periods that consistently captured representative samples of abundance, we excluded sampling days when traps were deployed for less than 3 h and excluded netting days with less than 1 h of effort (excluding 17 of 778 trap sampling days and 21 of 809 net sampling days). Lastly, to ensure adequate sample size and robust skewness estimation, we only considered time series with at least 10 individual bee records and at least 100 flower records. Thus, we excluded 1932 of 18,710 bee records (10.3%) and 126,659 of 3,943,796 flower records (3.2%).

Skewness calculation and predictors

We calculated skewness as the Fisher–Pearson standardized third-moment coefficient of skewness (g_1), as implemented in the moments R package (Komsta & Novomestky, 2015) for each site/year/species phenological abundance distribution (i.e., frequencies of bee and flower abundance by date). This approach uses only the data and avoids making assumptions about functional form necessary for more complex model fitting. We tested whether skewness in individual time series was different from zero (corresponding to a symmetrical distribution) using D'Agostino's K^2 test (D'Agostino, 1970). We used a one-sample *t*-test to assess whether skewness across flower time series was significantly different from zero and a two-sample *t*-test to test whether bee skewness was significantly different from flower skewness.

To examine whether and how skewness in bees and flowers was related to other properties of their phenological abundance distributions, we calculated the means and SDs of each distribution. To test whether the phenological position of species (how early or late they are active in a season) predicted their skewness, we modeled skewness as a mixed-effects model with phenological mean interacting with guild (flowers vs. bees) as fixed

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effects and accounted for repeated measures with species, site, and year as variable-slope random effects. Note that, statistically, means are shifted by skewness, so the two are necessarily linked to a certain extent. To test whether species with longer active seasons tended to be more skewed, we modeled skewness as a mixed-effects model with distributions' SD interacting with guild as fixed effects and the same random effects structure as in the previous model.

Overlap calculation

To demonstrate the potential phenological match/mismatch consequences of skewness differences between bees and flowers, we simulated the maximum possible overlap of distributions with different skews. To do this, we repeatedly generated pairs of skew-normal density distributions (Azzalini, 2020) with two different skewness parameters, representing the phenological distributions of one flower species and one bee species. To find the maximum possible overlap, we perturbed the mean and standard deviation of one distribution in 2000 total parameter combinations. This was a somewhat coarse discretization, so slightly distorted results are expected at a fine scale of comparison. For each pair of perturbed distributions, we then calculated the overlap coefficient (Inman & Bradley, 1989) by integrating to find the area encompassed by both probability density curves (as illustrated in Figure 1) and recorded the largest of the resulting overlap coefficients. We repeated this procedure for every pairwise combination of 50 skewness values sequenced evenly between −5 and 5, resulting in 2500 (i.e., 50^2) total comparisons. In other words, we calculated the largest possible overlap of paired distributions by keeping skewness constant and allowing mean and SD to vary freely. A visual representation of this simulation process is provided in Appendix S1: Section S4. To provide perspective, we calculated the bounds of the middle 95% of skewness values from the empirical data sets and overlaid these onto the simulated overlap estimates.

RESULTS

We estimated skewness for 2754 flower time series and 480 bee time series. The time series represented 92 plant species across 71 genera and 49 bee species/castes across 14 genera. In time series with sufficient data to calculate skewness, the average flowering period (across all years, sites, and species) was centered on 10 July and bee foraging on 2 July. The typical phenological breadth, measured as one SD on either side of center, was 14 days in flowers and 39 days in bees. Flower time series were significantly right-skewed ($g_1 = 0.33$, $t_{3232} = 20.05$, $p < 0.01$), and bee time-series were also right skewed ($g_1 = 0.89$), significantly more so than flowers ($t_{3232} = 13.84$, $p < 0.01$). Viewed individually, 48.7% of flower time series were significantly right-skewed, only 13.6% were significantly left-skewed, and 37.7% were not significantly different from symmetrical. Of bee time series, 48.5% were right-skewed, 9.4% were left-skewed, and 42.1% were not significantly different from symmetrical (Figure 2). Skewness was somewhat affected by data truncation, though both bees and flower curves were still right-skewed regardless of truncation type (Appendix S1: Section S1).

Skewness in plants was significantly predicted by how early or late in the season a species flowered, with early season species being more strongly right-skewed (mean-to-skew slope significantly different from zero; $t = -8.32$, $p < 0.01$). This relationship was more pronounced in bees (mean-to-skew slope significantly steeper in bees than in flowers; $t = -13.01$, $p < 0.01$), with early-season bees being right-skewed and later-season bees being left-skewed (Figure 3, top panel). Plants with longer flowering periods tended to be more right-skewed ($t = 7.03$, $p < 0.01$), whereas bees with longer active periods tended to be more symmetrical ($t = -10.06$, $p < 0.01$) (Figure 3, bottom panel).

Simulated overlap losses between interacting species ranged from 0% at perfectly matched skewness values to 25% for distributions where one has $g_1 = 5$ and the other $g_1 = -5$ (Figure 4). The maximum overlap loss for the central 95% of bee and flower skewness values found in our data sets was 14%. We do not directly compare bee and flower distribution breadth because the frequency of bee data collection inherently discounted species with short active periods. Comprehensive species lists and summary statistics are provided in Appendix S1: Section S3.

DISCUSSION

We found that both bee and flower phenological distributions tended to be right-skewed (Figure 2), suggesting that similar processes were acting on bees and plants to determine the shape of their phenological distributions. Multiple explanations have been offered for skewness in flowering time, including selection for skewed flowering driven by pollinators and resources (Forrest & Thomson, 2010; Thomson, 1980), byproducts of intraspecific competition (Schmitt, 1983), and simple geometrical necessity because daily survival probabilities are cumulative and inherently skewed (Blionis et al., 2001). Multiple distinct scenarios that may lead to skewed phenological

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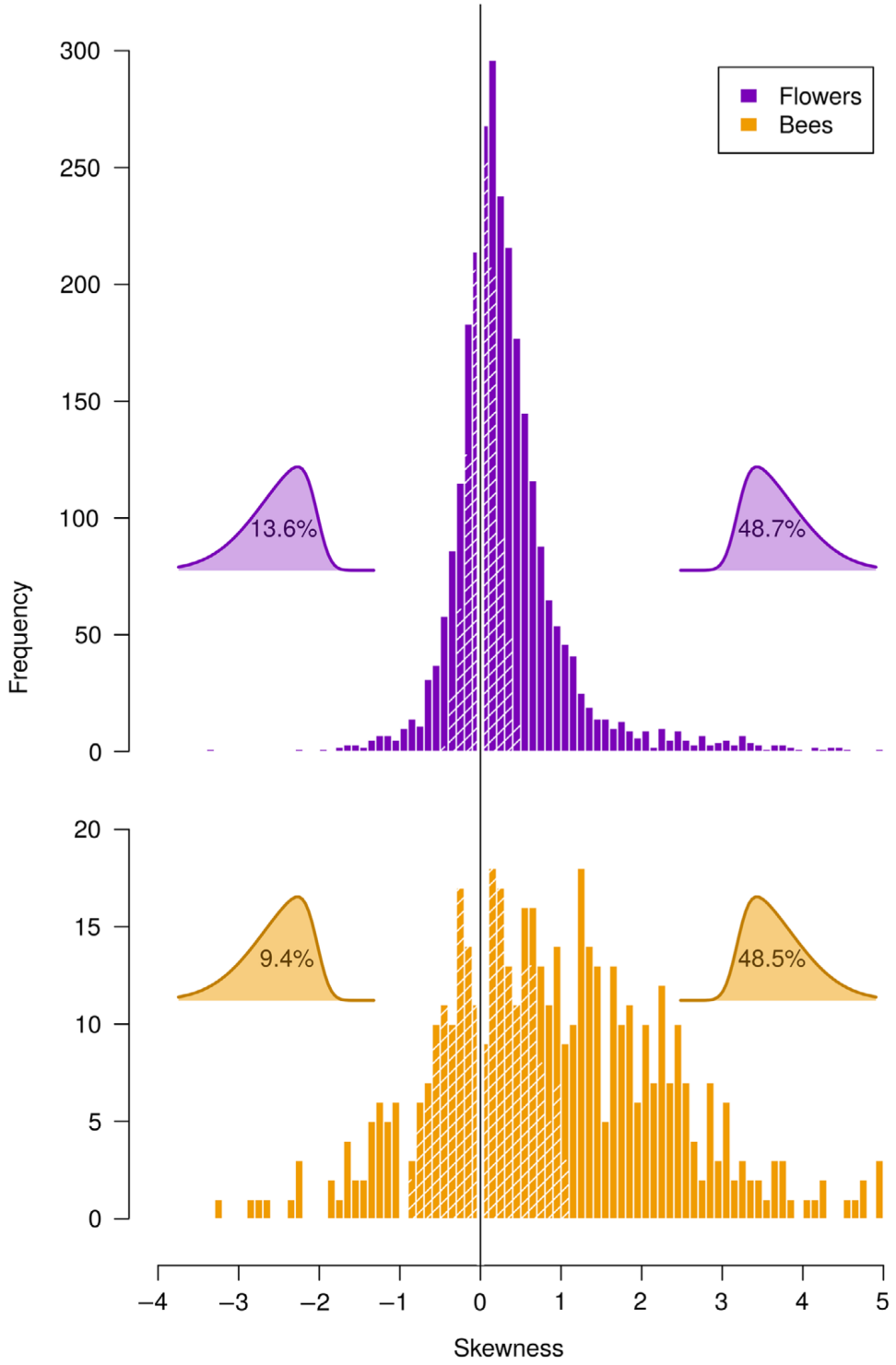

FIGURE 2 Flower (top panel) and bee (bottom panel) phenological skewness. Both flower and bee species tend to have right-skewed phenological distributions, though there is substantial variation in shape, and many distributions in both groups are not significantly different from symmetrical (white shaded bars). Skewed distribution icons give the percentage of individual time-series that are significantly left- and right-skewed.

distributions can be examined by focusing on onset rates (e.g., flower opening, bee emergence) and cessation rates (e.g., floral senescence, bee mortality). First, differences in the intra-annual dispersion of onset and cessation rates may produce phenological skewness. Second, variable phenology among individuals with unequal representation (e.g., different numbers of flowers per individual plant) may produce skewed aggregate

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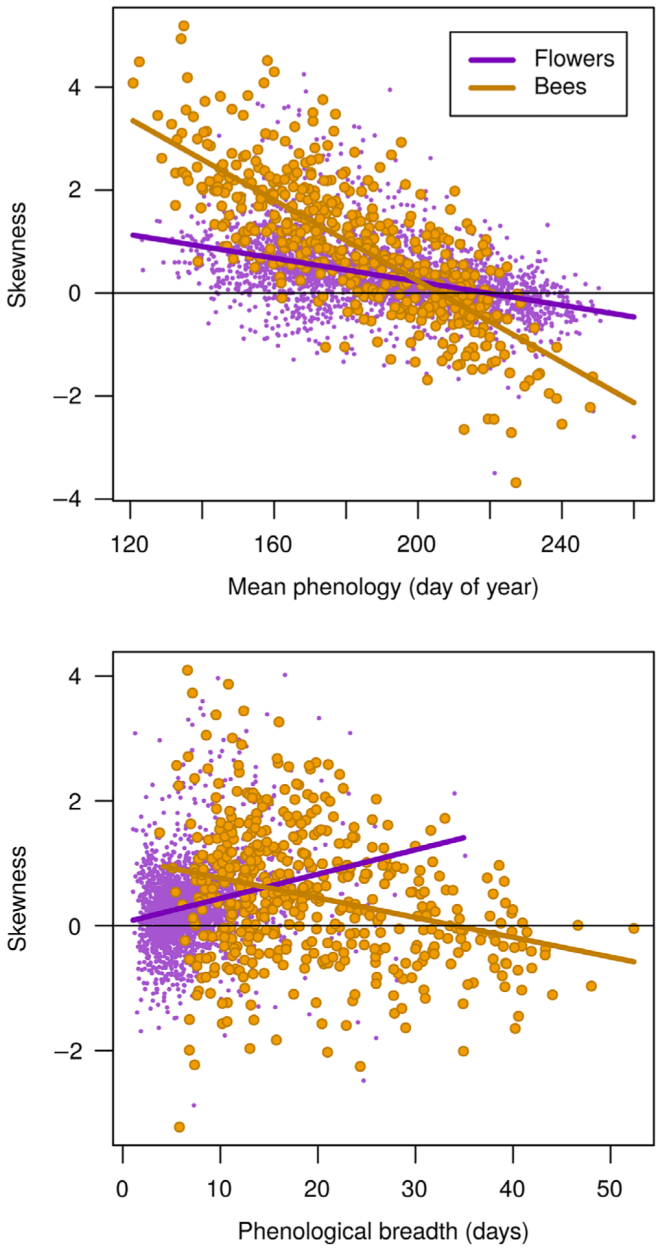

FIGURE 3 Skewness is predicted by mean and breadth. Early-season bees and flowers tended to be more heavily right-skewed (top panel), though the effect was more pronounced in bees than in flowers. Flowers with broader phenological distributions tended to be more skewed, whereas bees with broader phenology tended to be less skewed in either direction (bottom panel).

distributions even when the component onset and end rates are equally dispersed. Third, onset or cessation distributions themselves may be skewed. Further, combinations of these processes may influence the shapes of phenological distributions in complex ways. In the context of our findings, the prevalence of right skewness in bee phenological distributions suggests that, on average, bees emerge with more synchrony than with which they cease foraging. Drawing conclusions about the processes behind the observed skewness in flower phenology is more difficult because flower counts were aggregated across individual plants in our data.

Although demographic data (i.e., tracking individual plants and insects) beyond what we present here are needed to determine the mechanistic causes of the differences in onset/end variance that produce skewed phenology, some information can be gleaned by comparing skewness with other phenological properties. We found that bees that were active closer to the beginning of the growing season tended to be more right-skewed (Figure 3). For example, the early-season sweat bee *Lasioglossum sedi*, with an average capture date of June 16 across all sites and years, was strongly right-skewed ($g_1 = 1.94$), whereas the later-season masked bee *Hylaeus annulatus*, with a capture date of 5 August on average, tended to be left-skewed ($g_1 = -0.27$). A similar but weaker pattern was seen in flowers, though flowers did not tend to flip to left skewness at the end of the season. In the snowy subalpine environment of the present study, the onset of activity is strongly limited for flowers (Inouye, 2008) and bees (Stemkovski et al., 2020) by the timing of snowmelt. Because species closer in time to this unambiguous onset cue tended to be more strongly right-skewed, we can reasonably infer that this cue, or at least the phenological response of species to this cue, is less intra-annually variable than the processes that lead to flower senescence and the end of bee foraging (e.g., frost events, precipitation, inherent lifespan/persistence). By extension, these findings suggest that later-season onset cues, or species' phenological responses to them, are more variable than the early snowmelt cue.

Our finding of right skewness in flowering phenology was broadly similar to previously published results, though we found that average flowering skewness in this study ($g_1 = 0.33$) was less positively skewed than in a previous study in the same area ($g_1 = 0.46$; Thomson, 1980) and a prairie community ($g_1 = 0.41$; Rabinowitz et al., 1981). Although this comparison is useful, we caution against overinterpretation owing to differences between the studies such as frequency and duration of monitoring and size of sampling plots. Turning to insects, we lack other studies focused specifically on phenological skewness in other insect groups, but individual abundance time series indicate that right skewness may also be found in univoltine butterflies (Dennis et al., 2017; Zonneveld, 1991), flies (Haab et al., 2019; Judd et al., 1991), and hemipterans (Gamarra et al., 2020; Ma & Bechinski, 2008). Comparisons with multivoltine species in areas with longer growing seasons are difficult, and further research is needed to compare uni- and multimodal phenological distributions, especially as climate change creates

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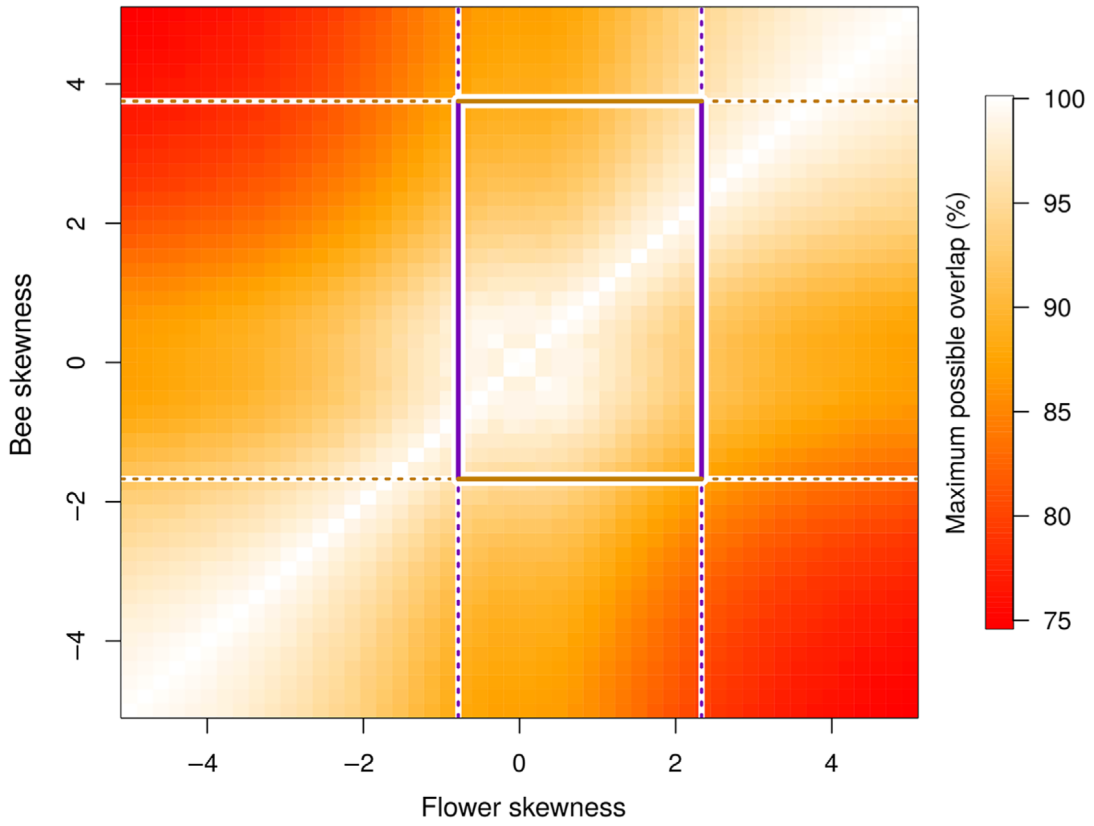

FIGURE 4 Skewness constrains the degree to which phenological distributions can overlap. The maximum possible overlap of pairwise interacting species with different hypothetical skewness values is shown as colors, with red depicting the lowest overlap, and white depicting perfect overlap. Bounds for 95% of the actual observed skewness values are shown with purple lines for flowers and gold lines for bees. The resulting box in the middle of the figure therefore depicts the potential loss of phenological overlap in pairwise interactions between bees and flowers due to differences in skewness alone, isolated from the effects of mean and breadth changes.

opportunities for additional generations in some insects (Hodgson et al., 2011; Van Dyck et al., 2015). Given the apparent prevalence of skewness in phenological distributions, we encourage researchers to use modeling methods that are designed to capture asymmetry (Belitz et al., 2020). We advise caution when closely comparing skewness values between bees and flowers because there is inherently more uncertainty in the bee data set due to the methodological challenges of tracking wild insects.

The consequences of variable skewness in flower and pollinator distributions for phenological match/mismatch in natural populations are not well understood and require further study. When considering simulated pairwise interactions, the skewness of phenological distributions alone has the potential to cause up to 14% loss in overlap in the species that we studied (Figure 4). We note that this analysis encompassed only phenological differences, and in reality there are other barriers to pollination such as specialization or morphological limitations. It is also important to consider that loss of overlap does not necessarily translate into fitness losses since pollen limitation is not ubiquitous (Knight et al., 2005) and many bees and flowering plants are generalists (Waser et al., 1996). Beyond pollination interactions, differences in skewness have the potential to affect other mutualistic interactions and predator–prey and host–parasite interactions and to alter patterns of inter- and intraspecific competition within guilds. Because both flowers and bees tend to be right-skewed, individuals may compete most strongly with their conspecifics in the early part of their activity. Future studies should examine how phenological skewness translates into fitness consequences through changes in inter- and intraspecific interactions throughout species' active periods.

ACKNOWLEDGMENTS

Michael Stemkovski was funded by the National Science Foundation (NSF) Graduate Research Fellowship under Grant 1745048. Field work for this research was supported by NSF Grants DEB 94-08382, IBN-98-14509, DEB-0238331, DEB 0922080, and DEB-1912006 to DWI, DEB-0922080 and DEB-1354104 to David W. Inouye, Brian D. Inouye, Nora Underwood, and Rebecca E. Irwin, DEB-1912006 to Nora Underwood, A. Classen,

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Brian D. Inouye, and Rebecca E. Irwin, EarthWatch and its Research Corps, and funds from NC State University to Rebecca E. Irwin We thank the many research assistants who aided in the collection of the long-term bee and flower data and the RMBL and private land owners for access to field sites. This research was conducted on the ancestral land of the Tabeguache band of the Ute people. Any opinions, findings, conclusions, or recommendations expressed in this material are those of the authors and do not necessarily reflect the views of the funding agencies.

CONFLICT OF INTEREST

The authors declare no conflict of interest.

DATA AVAILABILITY STATEMENT

The data and reproducible analysis scripts (Stemkovski, 2022) are archived and publicly available through Zenodo at https://doi.org/10.5281/zenodo.6561297.

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How to cite this article: Stemkovski, Michael, Rachel G. Dickson, Sean R. Griffin, Brian D. Inouye, David W. Inouye, Gabriella L. Pardee, Nora Underwood, and Rebecca E. Irwin. 2023. "Skewness in Bee and Flower Phenological Distributions." *Ecology* 104(1): e3890. https://doi.org/10.1002/ecy.3890

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