# Mating Opportunity Increases with Synchrony of Flowering among Years More than Synchrony within Years in a Nonmasting Perennial

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ABSTRACT: The timing and synchrony of mating activity in a population may vary both within and among years. With the exception of masting species, in which reproductive activity fluctuates dramatically among years, mating synchrony is typically studied within years. However, opportunities to mate also vary among years in nonmasting iteroparous species. We demonstrate that studying only within-year flowering synchrony fails to accurately quantify variation in mating opportunity in an experimental population ($n = 286$) of a nonmasting species, *Echinacea angustifolia*. We quantified individuals' synchrony of flowering within and among years and partitioned the contribution of each measure to mean daily mating potential, the number of potential mates per individual per day, averaged over every day that it flowered during the 11-year study period. Individual within- and among-year synchrony displayed wide variation and were weakly correlated. In particular, among-year synchrony explained 39% more variation in mean daily mating potential than did within-year synchrony. Among-year synchrony could have underappreciated significance for mating dynamics in nonmasting species.

*Keywords:* phenology, masting, reproductive fitness, mate limitation, *Echinacea angustifolia*.

## Introduction

The time when individuals are available to mate determines the number and identity of their potential partners (Calabrese and Fagan 2004; Hendry and Day 2005; Elzinga et al. 2007; Gascoigne et al. 2009). Within-year timing, or phenology, of mating is defined by the days that an individual is available to participate in mating activity (Forrest and Miller-Rushing 2010) and has important consequences for reproductive success and selection (Ims 1990; Elzinga et al.

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2007; Munguía-Rosas et al. 2011). Likewise, among-year timing of mating can be defined as the year or years that individuals exert reproductive effort. For many iteroparous species, reproductive years may be interspersed with years of reproductive inactivity (Kelly and Sork 2002). Because plants are immobile and cannot compensate for spatial isolation from potential mates by active searching, timing of mating is especially critical to their mating success. The consequences of synchronizing mating among years have received considerable attention in masting species (i.e., those that reproduce with a high degree of variation among years; Taylor and Inouye 1985; de Steven and Wright 2002; Wesołowski et al. 2015). In contrast, the consequences of synchronizing mating among years are rarely considered in nonmasting species.

Definitions of mating synchrony are specific to a level of organization (i.e., population or individual) and a temporal scale (i.e., within or among years). At the population level, variation in the number of individuals seeking to mate simultaneously, either within or among years, can be quantified as population synchrony (fig. 1; Koenig et al. 1994; Crone et al. 2009; Archibald et al. 2012; Kaiser et al. 2017). Similarly, we measure individual synchrony as how an individual's timing of mating aligns with the mating activity of the population within or among years. While reproductive synchrony could refer to other processes (e.g., sexual maturation, embryo development, or birth), we focus on the synchrony of when individuals are available to outcross or mate with other individuals. Outcrossing is obligatory for successful reproduction in most animals and self-incompatible plants, which comprise 60% of all plant species (de Nettancourt 2013). Opportunities for an individual to interact with prospective mates at either temporal scale can be quantified as mating potential: the number of conspecifics available to mate with the individual. The mag-
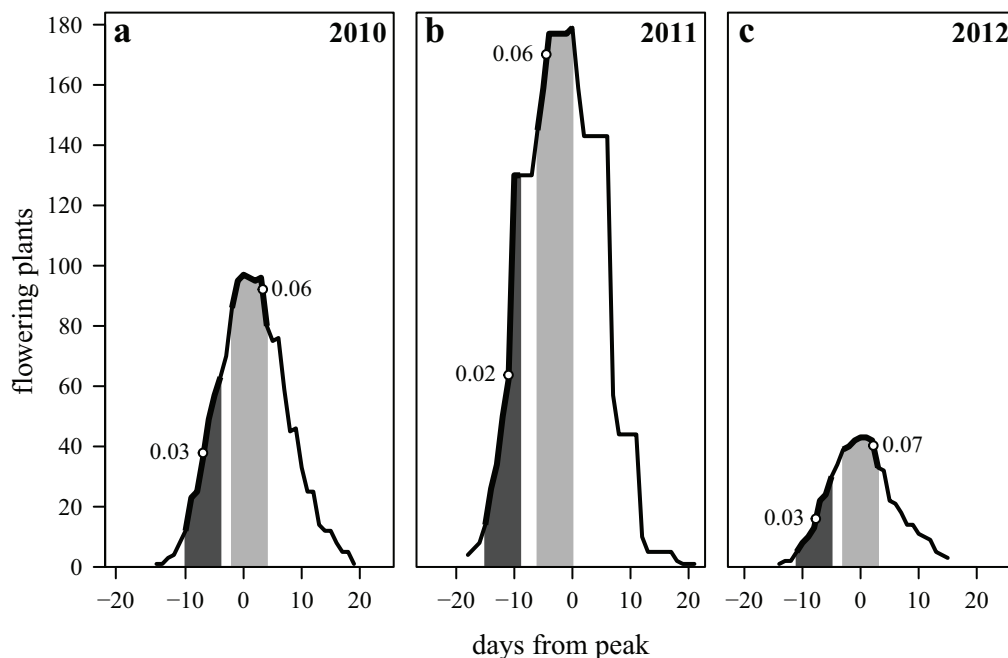
**Figure 1:** Temporal distribution of mating potential in 2010–2012 (*a–c*, respectively), chosen to highlight within- and among-year variation in flowering in our study population. The *X*-axis indicates days after peak (the day with maximum number of individuals flowering) in each year, and the *Y*-axis indicates the number of individuals flowering. Lines indicate mating potential for each day. Dark and light shaded areas illustrate cumulative mating potential of hypothetical early- and peak-flowering individuals with each flowering 7 days. The total sum of potential mating interactions in 2010, 2011, and 2012 was 1,425, 3,062, and 585, respectively. The differences in absolute mating potential per year influence individuals' among-year synchrony. Open circles are positioned at an individual's mean within-year mating potential and are labeled with the individuals' within-year synchrony (e.g., on average, 39 individuals were flowering on the same days as the early-flowering individual in 2010 [*a*], so its mean within-year mating potential in 2010 equals 39 and its within-year synchrony equals 39 divided by 1,425, or 0.03).

nitude of fluctuations in population synchrony within and among years determines the importance of individual synchrony for individuals' opportunities to outcross. For example, consider two individuals that each reproduce in two out of five years. One individual seeks to mate in the population's two peak years of mating activity, but late relative to the peak activity within each year. The other individual seeks to mate in two off-peak years but at peak days of mating activity for the population within each year. The difference in mating potential between these two hypothetical individuals depends on the degree of population synchrony both within and among years. Quantifying the relationship between mating potential and synchrony both within and among years would indicate the potential for timing at each temporal scale to affect reproductive success (Inouye 2008; Forrest and Miller-Rushing 2010), mating patterns (Weis and Kossler 2004), and evolution of reproductive timing by natural selection (Devaux and Lande 2010).

In this study, we quantified the relative contributions of individual synchrony in flowering within and among years to the long-term mating potential of individuals for a long-lived herbaceous perennial plant. We applied a novel statistical approach to an 11-year data set of individual flowering phenology in a population of the narrow-leaved purple coneflower (*Echinacea angustifolia*, Asteraceae; hereafter "*Echinacea*"). Populations of this species vary in flowering rates among years (Ison et al. 2014), but it is not considered to be masting. We (1) measured the degree of within- and among-year synchrony of the population and tested for departures from expected flowering patterns using randomization techniques, (2) developed measures of individual synchrony that enabled us to partition the relative contribution of within- and among-year synchrony to individuals' long-term mating potential using regression analysis, and (3) quantified how variation in the duration of mating activity among individuals influences mating potential.

## Methods

### Study System and Field Monitoring

Our study focuses on a cohort of *Echinacea* plants in an experimental plot located in Solem Township, Minnesota.

These plants were collected as seeds from seven nearby natural populations and then planted in 1996. We included all plants that survived through 2015 and flowered at least once during 2005–2015, $n = 286$ individuals. A full description of experiments in the plot can be found elsewhere (Geyer et al. 2007). *Echinacea* is a long-lived (>25 year) perennial. Adult individuals may or may not flower in a given year. In flowering years, individuals produce one or more flowering heads, each comprising many florets (typically 80–250). Multiple-headed individuals may flower longer to the extent that their heads do not flower concurrently. In nonflowering years, individuals produce one to several rosettes of basal leaves. *Echinacea* is self-incompatible and bee-pollinated: reproduction in natural populations in our study site is mate-limited (Wagenius 2006; Wagenius and Lyon 2010). The plot was burned regularly (in spring of 2006, 2008, 2011, 2013, and 2015). Spring fires stimulate flowering and increase within- and among-year synchrony of flowering in a nearby natural population of *Echinacea* (S. Wagenius, J. Beck, and G. Kiefer, unpublished manuscript).

We used a longitudinal data set of individual flowering phenology of *Echinacea* from 2005 to 2015 that was collected initially for a study of spatiotemporal reproductive isolation (Ison and Wagenius 2014). We defined an individual as flowering on any day or year that it produced pollen, depending on the temporal scale being considered. Each year, we determined start and end dates of flowering of all individuals that developed a flowering head by visiting each plant at least once every 3 days until pollen production ended. The regular pattern of *Echinacea* floral development allowed us to determine the exact start date of flowering for over 60% of plants and within 2 days for the rest (Wagenius 2004). When we had two possible start dates, we used the earlier one for analysis. We obtained a range of less than or equal to three possible end flowering dates for each individual; for analysis we use the latest date in this range. Flowering phenology data and analyses are deposited in the Dryad Digital Repository: https://doi.org/10.5061/dryad.487db24 (Waananen et al. 2018).

## Data Analysis

Our goal was to assess variation in synchrony at each temporal scale and their consequences for mating potential. Focusing on a single cohort within the experimental plot allowed us to compare synchrony among individuals and minimize noise from environmental conditions and potential age-specific variation in likelihood or timing of flowering. However, our cohort represents a fraction of all individuals in the experimental plot, where pollen moves among all flowering individuals, including other cohorts and individuals that died before the end of the study period (Ison et al. 2014). Thus, within-cohort measures of syn-chrony may not necessarily predict reproductive success (seed set). For this reason, we limited analysis to measures of mating potential rather than reproductive success. Similarly, we did not analyze potential contributions of spatial isolation for predicting mating potential because the study cohort is centrally located within the plot and appropriate measures of spatial isolation would require considering proximity to neighbors outside of the cohort. We completed all data analysis using R, version 3.2.4 (R Development Core Team 2016).

## Population Synchrony

To quantify within-year population synchrony, we calculated mean overlap in flowering of all pairs of individuals. We defined overlap for a pair as the number of days that both individuals flowered divided by the days that either flowered, which can range from 0 (no overlap) to 1 (total overlap; Augspurger 1983). This measure is equivalent to a breeding synchrony index commonly used in avian studies (Kempenaers 1993). To test whether the degree of synchrony that we observed in each year might result from random processes, we compared observed synchrony to mid-domain effect (MDE) null models, which randomly simulate population flowering schedules based on observed constraints imposed by the growing season (Morales et al. 2005). To create these null models, we randomly selected flowering individuals with replacement from the flowering individuals in each year. We maintained the duration of individuals' flowering. We weighted our sampling by the absolute value of individuals' $z$-score of midpoint date of flowering (i.e., the number of SDs of individuals' midpoint date of flowering from the population mean midpoint date of flowering; hereafter, "midpoint date"), such that choosing individuals with flowering midpoint dates at any time during the season was equally likely. Because midpoint date and annual flowering duration are weakly correlated in our population (Pearson's $r = 0.23$, $p < .0001$), we resampled individuals rather than reassigning midpoint dates (sensu Morales et al. 2005). This maintained the relationship between flowering midpoint date and annual flowering duration in our null models. For each year, we calculated synchrony of the null population 10,000 times to generate a distribution of expected synchrony values under the MDE null model. We calculated the proportion of simulations in which synchrony was equal to or greater than observed synchrony to quantify the unlikeliness that the degree of synchrony in the observed data in each year could have occurred due to random processes.

To measure among-year synchrony, we first characterized individuals' flowering for each year from 2005 to 2015 by assigning 1 if flowering in a year and 0 if not. We calculated the overlap of all pairs of individuals' among-

year flowering schedules—the number of years that both individuals were flowering together divided by the number of years that either was flowering—and calculated population synchrony as the mean pairwise overlap. This measure is analogous to Augspurger's (1983) synchrony index applied at an annual temporal scale and likewise ranges from 0 to 1. We assessed the extent to which observed population among-year synchrony differed from expectations of an asynchronous population by generating flowering schedules in which we randomly reassigned flowering years while maintaining the number of years that each individual flowered. Repeating this process for the entire population 10,000 times, we generated a distribution of expected among-year synchrony values and calculated the proportion of simulations in which population synchrony was equal to or greater than observed. Deviation of observed synchrony from random expectations quantified the extent to which population among-year synchrony differed from what could be expected by chance. As a measure of overall population variation in flowering among years, we calculated the population coefficient of variation ($CV_p$) of flowering in all years, the SD of the annual number of flowering individuals divided by the mean annual number of flowering individuals (Koenig et al. 2003).

### Individual Synchrony

Individual synchrony depends on the temporal scope of the study and its scale of resolution (Levin 1992). We considered mating potential at two temporal scales of resolution, daily and annual, and over two scopes, 1 year or the entire 11-year study period (fig. 2). In this way, we measured individual synchrony within and among seasons and their respective contributions to variance in long-term mating opportunity. We calculated all measures of synchrony using R package mateable (Wagenius et al. 2016).

*Mating Potential.* We define mating potential at a daily scale of resolution as the count of flowering individuals on a given day ($P_{daily}$). The total mating potential of a season may be described as the sum of $P_{daily}$ over all days of the season. Likewise, we define mating potential at an annual scale of resolution as the count of flowering individuals in a given year ($P_{annual}$), and the total mating potential of a multiyear period is the sum of $P_{annual}$ over all years.

To isolate the consequences of synchrony within and among years for individuals' long-term mating potential, we calculated measures of mating potential at three combinations of temporal scale and scope (equations provided in app. A; apps. A and B are available online). First, we determined individuals' mating potential at a daily temporal scale over 1 year to quantify within-year synchrony (fig. 2b). To do this, we measured the proportion of the season's total mating potential occurring on the days that the individual was flowering. Specifically, we divided the sum of the difference $P_{daily} - 1$ on each day that the individual flowered by the sum of $P_{daily}$ for all days of the season. We subtracted 1 from $P_{daily}$ each day because the indi-
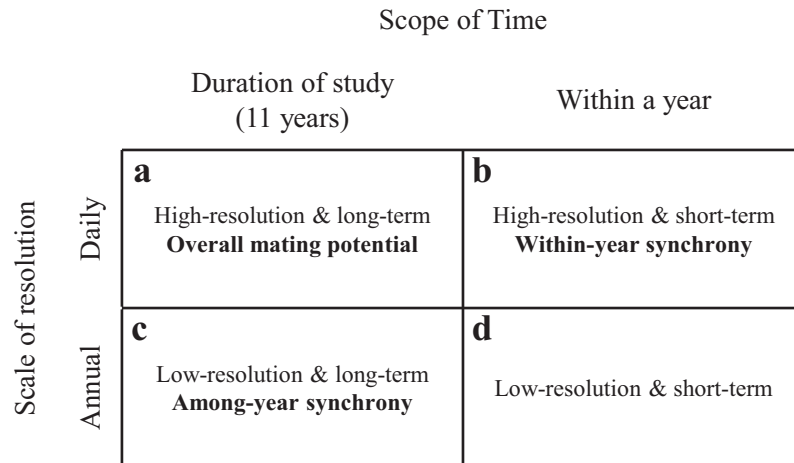
Scope of Time



**Figure 2:** Summary of the scope and scale of resolution of measures of individual and population mating potential used in the analysis. The terms in boldface are defined here: *a*, An individual's overall mating potential is the mean number of other individuals flowering on concurrent days as the individual averaged over all days that the individual flowered during the study period. *b*, Within-year synchrony at the population level is the mean pairwise overlap in days flowering between all individuals. At the individual level, within-year synchrony is the mean proportion of a single season's daily mating opportunities that occurred on days that the individual flowered. *c*, Among-year synchrony at the population level is the mean pairwise overlap in years flowering between all individuals. At the individual level, among-year synchrony is the proportion of the study period's annual mating opportunities that occurred in years that the individual flowered. *d*, The annual overlap in flowering years of individuals within a single year, which is trivial: 1 for flowering individuals and 0 for nonflowering individuals.

vidual is not a potential mate with itself. Because it is a proportion, this measure of within-year synchrony is independent of the number of flowering individuals in a year; it quantifies variation in mating potential resulting only from variation in timing of flowering within each year. We used individuals' average within-year synchrony from all years for analysis. Second, to isolate the effect of among-year synchrony, we quantified mating potential for each individual at an annual temporal scale over all years (fig. 2c). In this case, we divided the sum of the difference $P_{\text{annual}} - 1$ in each year that the individual flowered by the sum of $P_{\text{annual}}$ over all years of the study. Individuals flowering in concurrent years are synchronous regardless of timing within years, and thus this measure quantifies variation in mating potential resulting only from variation in timing of flowering among years. Third, we measured mating potential at a daily scale of resolution over all years (mean daily mating potential) as the mean number of individuals flowering concurrently with the individual per day in all years of the study period. This measure (in units of potential mates) quantifies total synchrony both within and among years (fig. 2a).

*Regression Analysis.* We used a multiple linear regression approach to determine the relative importance of within- and among-year timing for mean daily mating potential. Standardized regression coefficients, $\beta$, of multiple linear regressions measure the unique effect of standard predictors. Thus, we standardized within- and among-year synchrony (e.g., subtracted the mean and divided by the SD) and modeled mean daily mating potential as a function of the standardized synchrony values. We obtained coefficients $\beta_w$ and $\beta_a$ for both within- and among-year synchrony, respectively, to measure the relative contribution of synchrony at each scale to variation in mean daily mating potential. Additionally, to test the hypothesis that synchrony at one scale counteracts asynchrony at the other, we quantified the interaction term between them, $\beta_i$.

Parametric analysis of contributions of individual synchrony within and among years to long-term mating potential, as we present in this study, is most appropriate in systems where residuals of timing within and among years are normally distributed. We also developed nonparametric methods of quantifying the relative importance of individual synchrony, which yielded the same conclusions and may be useful in systems that do not satisfy parametric requirements (app. B).

### Total Duration of Mating

We calculated cumulative measures of absolute mating potential to evaluate the role of total duration of mating for individuals' long-term mating potential. We quantified

individuals' cumulative daily mating potential as the sum of all individuals flowering on the same days as the individual in all 11 years. We measured individuals' total duration of mating as the number of days that they flowered over the duration of the study period. We related total duration of mating to cumulative daily mating potential using a linear regression. Analysis of cumulative and mean daily mating potential with lifetime mating duration measured at an annual scale of resolution, by number of years flowering, indicated the same results (app. B). We applied a Fligner-Killeen test of homogeneity of variances, a non-parametric method that tests the hypothesis that variances are the same among groups (Conover et al. 1981; Sambatti et al. 2006), to test the null hypothesis that variability in mean daily mating potential was unrelated to mating duration. For this test, we grouped individuals by the number of years that they flowered.

### Results

#### Temporal Variation in Mating Potential

The number of flowering individuals on a day with at least one flowering individual fluctuated substantially from one to 179 ($n = 448$ days, mean $= 50.6$, SD $= 48.5$). The number of individuals that flowered per year also exhibited substantial variation, ranging from 47 to 188 (out of 286 total plants; $n = 11$ years, mean $= 126$, SD $= 40.9$). Consequently, the mean number of individuals flowering per day varied among years, from 19.5 in 2012 ($n = 29$ days, SD $= 14.1$) to 76.6 in 2011 ($n = 40$ days, SD $= 68.7$). The number of days that at least one individual was flowering in each year ranged from 29 days in 2012 to 49 days in 2008 ($n = 11$ years, mean $= 39.7$, SD $= 6.1$). We used these summaries of daily and annual mating potential to calculate population and individual synchrony.

#### Population Synchrony

The population flowered synchronously within each year compared to the null model. The yearly mean pairwise overlap in days flowering for all individuals ranged from 0.63 to 0.76, significantly exceeding mean MDE null model predictions in each year, which ranged from 0.51 to 0.66 ($n = 10,000$ iterations; 2005–2011, 2013–2015: $p < .0001$; 2012: $p = .03$; figs. B2, B3; figs. B1–B4 are available online). The MDE null models consistently overestimated the number of flowering plants early and late in the season and underestimated flowering near midseason peak flowering dates.

Population flowering among years also exhibited synchronization. Observed mean overlap in flowering years was 0.21, indicating that on average pairs of individuals

flowered concurrently approximately once in every 5 years. This exceeded null expectations of among-year flowering overlap, which were distributed around a mean of 0.19 and did not exceed 0.20 ($n = 10{,}000$ iterations, $p < .0001$). In contrast, the coefficient of variation in population ($CV_P$) annual flowering of 0.32 indicates low overall variation in flowering among years relative to reported $CV_P$ values of mast-reproducing species (reviewed in Kelly and Sork 2002).

### Individual Synchrony

Within-year synchrony measures the mean proportion of a year's mating opportunities that concurred with each day that an individual flowered, with mating opportunities measured at a daily scale of resolution. Individuals with the lowest within-year synchrony flowered on days coinciding with an average of 1% of that year's mating opportunities. Six times more individuals were flowering on the days when the most synchronous individuals within-years flowered, as quantified by the range of individual within-year synchrony from 0.01 to 0.06. Thus, if an individual with within-year synchrony of 0.06 flowered for 10 days, the individual's flowering would have coincided with approximately 60% of the year's daily mating opportunities.

Among-year measures of synchrony calculate the mean proportion of all mating opportunities in the study period, measured at an annual scale of resolution, coinciding with years that an individual flowered. Individuals with the lowest among-year synchrony flowered in years when an average of 5% of all mating opportunities in the study period occurred, while individuals with the highest among-year synchrony flowered in years when an average of 13% of all mating opportunities occurred. Individuals with average among-year synchrony flowered concurrently with a mean of 10% of all mating opportunities in the study period per year. Within- and among-year synchrony were weakly correlated (Spearman's rank $\rho = 0.13$, $p = .019$), which indicates a slight tendency for individuals to flower with a similar degree of synchrony at both scales of resolution, but this explains little of the variation.

The minimum adequate model of mean daily mating potential included individuals' within- and among-year synchrony and an interaction term between synchrony at both scales. This model explained a large proportion of variation in mean daily mating potential ($R^2 = 0.93$, $F_{3, 282} = 1{,}189$, $p < .0001$; fig. 3). Individuals' among-year synchrony had the larger effect on mean daily mating potential ($\beta_a = 14.50$, 95% confidence interval [CI]: 13.78–15.22, $p < .0001$); within-year synchrony predicted mean
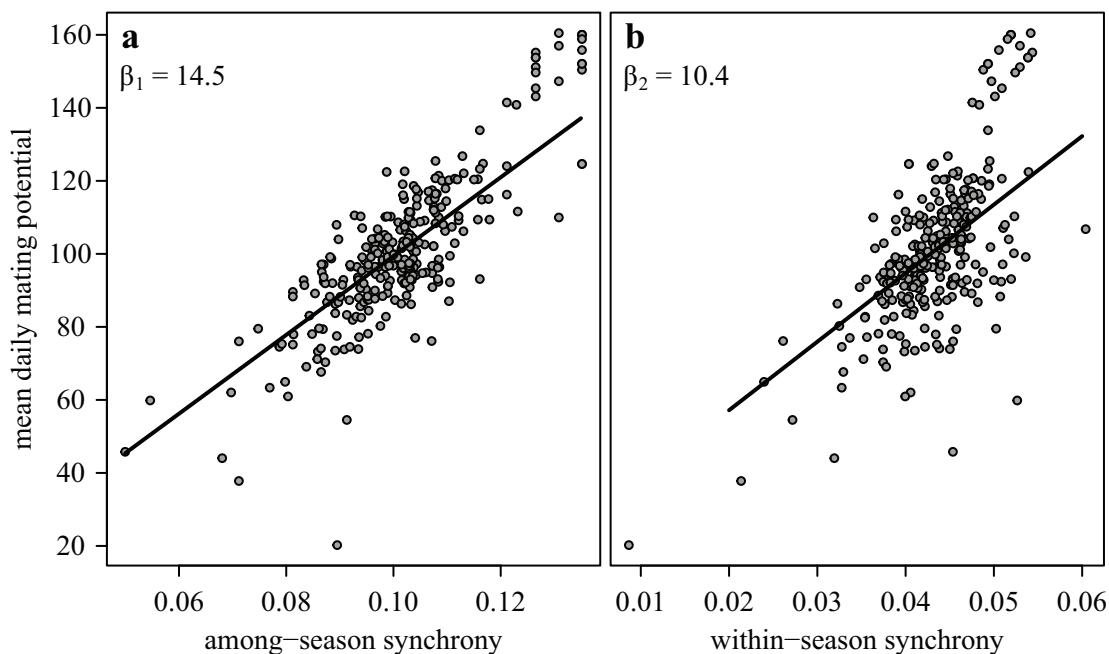


**Figure 3:** Measures of synchrony at two temporal scales predict mating potential for all individuals in the study ($n = 286$). The relationship between long-term mating potential, quantified as the mean number of conspecifics flowering on each day that an individual flowered over the duration of the study period, and mating potential, quantified by an individual's among-year (*a*) or within-year (*b*) synchrony. Lines in each panel represent the linear regression for each scale of synchrony calculated using the mean value of synchrony at the other scale. The values $\beta_a$ and $\beta_w$ represent the standardized regression coefficient for among- and within-year synchrony, respectively: $\beta_a$ is 39% greater than $\beta_w$.

daily mating potential to a strong but lesser extent ($\beta_w$ = 10.42, 95% CI: 9.72–11.12, $p < .0001$). Among-year synchrony had a 39% greater statistical effect than within-year synchrony ($\beta_a/\beta_w \times 100$). A positive interaction existed between within- and among-year synchrony ($\beta_i$ = 1.45, 95% CI: 0.92–1.99, $p < .0001$), indicating that for a given increase in synchrony at one temporal scale, the effect on mean daily mating potential is amplified by a change in synchrony at the other. Thus, the difference in long-term mating potential between two individuals with equivalent among-year synchrony is predicted in large part by the difference in their within-year synchrony.

### Total Duration of Mating

The total time that individuals flowered varied widely at both scales, from 6 to 36 days per year and from 1 to 10 years over the 11-year study period. Shorter duration of mating, measured in either days or years flowering, was associated with greater variation in individual synchrony. For instance, individuals that flowered in only 1 year had both the highest and lowest among-year synchrony—the most synchronous individuals flowered only in 2011 (the highest-flowering year) and the least synchronous in 2012 (the lowest-flowering year). Total duration of mating closely predicted cumulative daily mating potential, whether measured in days ($R^2$ = 0.94) or years ($R^2$ = 0.89; fig. 4a). Variability in mean daily mating potential among individuals was inversely related to total duration of mating (Fligner-Killeen: median $\chi^2$ = 151.64, df = 9, $p < .0001$), while population mean daily mating potential was consistent across variation in total duration of mating (fig. 4b).

### Discussion

Traditionally, studies of reproductive timing in nonmasting species have focused on synchrony within years rather than among years (Augspurger 1983). Using an 11-year data set with daily resolution, we showed that among-year synchrony had a 39% greater effect on mating potential than within-year synchrony. The strong influence of among-year synchrony is striking because mating opportunity among years did not fluctuate dramatically. We observed substantially lower population variability in flowering ($CV_p$ = 0.32) compared to masting ($CV_p \cong 1$; Silvertown 1980; Kelly 1994; Herrera et al. 1998; Crone et al. 2011) species. Our findings in a nonmasting species suggest that the consequences of among-year synchrony for mating opportunity have been overlooked in other nonmasting species. In moderately synchronous populations, individual synchrony varies widely and thus timing of mating may have consequences for reproduction in a large portion of the popula-
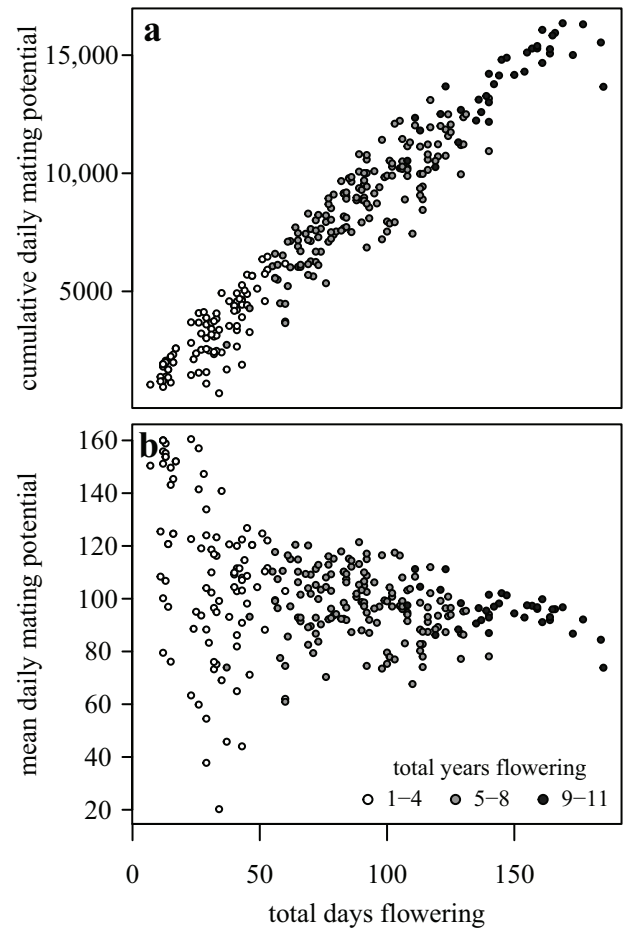


**Figure 4:** Relationship between the total number of days that an individual flowered over all years and mating potential, quantified at a daily scale of resolution over all years as the number of other individuals flowering concurrently with each individual. Mating potential is presented here as cumulative over all years (*a*) and by its mean value over all days that the individual flowered (*b*). Shading of points indicates total time flowering at an annual scale of resolution (total years flowering), grouped into three categories.

tion. In contrast, in highly synchronous populations, timing may have a minor effect on most of the population because few individuals are asynchronous. Investigating synchrony in less extreme cases generates broader understanding of its consequences. We posit, in general, that if variation in population mating activity is greater among years than within years, then among-year synchrony will have a greater influence on individuals' mating potential than within-year synchrony.

Synchronous phenology and flowering for longer periods of time both increase potential for individuals to find mates. While certain aspects of population phenology, such as the

onset and length of flowering seasons, varied among years, population synchrony of mating activity was relatively consistent in *Echinacea* (fig. B2). Within-year population synchrony varied independently of the number of individuals flowering in each year—for example, the degree of synchrony was equivalent in 2008 and 2012, despite a threefold difference in number of individuals flowering. The within-year synchrony of our population ranged from 0.63 to 0.76, similar to populations of six tropical shrubs observed by Augspurger (1983; 0.48–0.95) and spiny madwort populations (*Hormathophylla spinosa*; 0.76–0.86; Gomez 1993). Our observations are also similar to analogous measures in animals; for example, breeding synchrony in blue tits (*Parus caeruleus*), a Eurasian bird, ranged from 0.54 to 0.61 over 3 years (Kempenaers 1993). It is important to note that mating potential depends on not only variation in timing of mating activity but also its duration. Individuals flowering for the longest time had the greatest cumulative mating potential (fig. 4a), increasing on average by 89 potential mating interactions for each additional day flowering and exhibiting lower variation in potential gained per unit time. Plants flowering for less time had lower cumulative mean mating potential but higher variability in potential gained per unit time flowering (fig. 4b).

Studying the 286 longest-lived individuals of their original cohort ($n = 637$) allowed us to compare synchrony and mating potential precisely by minimizing variation due to plant age and local environments. However, natural populations comprise individuals of differing age and capacity for reproductive effort (Clutton-Brock 1984; Hanzawa and Kalisz 1993; Franco and Silvertown 1996; Hendry et al. 1999; Langvatn et al. 2004). Compared to our cohort, shorter-lived and younger individuals may flower fewer times, leading to lower accumulation of and higher variation in mean daily mating potential. In other words, these short-lived or younger individuals would be similar to individuals on the left side of panels in figure 4. To the extent that age and age-specific lifetime experiences influence variation in individuals' reproductive timing, natural populations may exhibit less among-year synchrony than a single cohort. Decreasing among-year synchrony at the population level would reduce the importance of individuals' among-year synchrony for their overall mating potential. Similarly, variation in individuals' reproductive capacity, which we excluded from our model, likely influences the consequences of synchrony for mating potential. For example, individuals with two or more flowering heads typically present more pollen and styles than individuals with single heads. Therefore, flowering synchronously with multiple-headed individuals likely increases reproductive opportunities more than flowering synchronously with single-headed individuals. Furthermore, such variation in reproductive potential may be influenced by microclimatic conditions and resource availability, which might be more heterogeneous in natural populations than in our experimental plot. Investigations of age and fitness effects on timing of mating will offer insight into how much synchrony and mating potential differ between natural populations and our study population.

Seeking a mate at the wrong time—too early in a season, too late, or in an off-peak year—may inhibit finding suitable mates and lower individual or progeny fitness (Gascoigne et al. 2009), especially in populations where reproduction is mate limited. Synchrony may confer particular advantages in fragmented habitats, where mate limitation is pervasive. For example, in our system, reproduction is strongly mate limited; reproductive success, measured as set seed, depends on individuals' within-year timing and synchrony of flowering, and furthermore, variation in flowering time within years leads to phenological assortative mating (Ison and Wagenius 2014; Ison et al. 2014). In this study, we found that among-year synchrony predicted long-term mating potential better than within-year synchrony, indicating that among-year synchrony may contribute to reproductive success more than within-year synchrony to the extent that mating potential correlates with seed set. Had we quantified timing at only one temporal scale or for a short duration, we would have underestimated the total amount of variation in mating potential within the population. Furthermore, the abundant variation we found in mating potential, which is likely related to variance in reproductive success and therefore fitness, indicates ample opportunity for selection on the timing of mating at each temporal scale.

Considering among-year synchrony enhances our understanding of mating patterns. Wagenius (2006) found that mating success of *Echinacea* individuals in natural populations decreased with isolation from potential mates and interpreted this relationship as a spatial pattern. However, spatial isolation within a year depends on the number of individuals flowering in that year. Quantifying the extent to which reproductive failure results from temporal asynchrony would change our perspective on the nature of mate limitation. Patterns of spatial density dependence that vary among years could be conceptualized as one phenomenon, synchrony, at different temporal scales, instead of two distinct phenomena—spatial and temporal isolation. In contrast to an individual's location, an individual's flowering synchrony can readily be considered a trait subject to selection (Weis et al. 2015). This perspective has illuminated processes driving phenotypic variation in timing of flowering within years (Weis and Kossler 2004; Elzinga et al. 2007; Munguía-Rosas et al. 2011; Ison and Weis 2017). However, the selective forces acting on among-year timing of flowering remain poorly understood, especially in nonmasting species. Investigating the genetic basis for among-year flowering synchrony could provide insight into evolutionary drivers of this important trait.

## Conclusions

Iteroparous species are often categorized by a dichotomy of masting and nonmasting, despite arguments that synchrony varies along a continuum (Herrera et al. 1998; Crone et al. 2011). This binary paradigm may influence researchers' perception of their systems and be responsible for the paucity of studies investigating annual variation in mating opportunity in nonmasting species. Our study supports viewing synchrony of mating as a continuum by demonstrating the relevance of annual variation in mating activity for a species that would not be considered masting by the dichotomous standard (Kelly 1994). Given this insight, we suggest that among-year timing of reproduction may be consequential in any system where mating opportunity depends on how an individual's timing among years aligns with its population, including short-lived plants, annual plants with seed banks, animals, and nontemperate species. When reproduction hinges on the timing of mating opportunities, it may be critical to consider among-year synchrony to understand mating patterns and their consequences for reproductive fitness.

## Acknowledgments

## Literature Cited

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