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ORIGINAL RESEARCH

Asynchrony between solitary bee emergence and flower availability reduces flower visitation rate and may affect offspring size

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Abstract

Climate change can disrupt plant-pollinator interactions when shifts in the timing of pollinator activity and flowering occur unequally (i.e., phenological asynchrony). Phenological asynchrony between spring-emerging solitary bees and spring-flowering plants may cause bees to experience food deprivation that can affect their reproductive success. However, the mechanisms underlying the effects of food deprivation on solitary bee reproduction remain unknown. We investigated 1) whether food deprivation caused by phenological asynchrony affects solitary bee reproduction by influencing female lifespan and/or visitation to flowers, and 2) the relationship between the magnitude of asynchrony and bee responses. We simulated phenological asynchrony by depriving emerged female *Osmia cornifrons* (a spring-active solitary bee species) of nectar and pollen for 0 to 16 days. Following asynchrony treatments, we used flight cages to monitor 1) post-treatment female lifespan, 2) flower visitation, and 3) reproduction (i.e., total offspring, offspring weight, sex ratio). We found that post-treatment female lifespan was not affected by phenological asynchrony treatments, but that flower visitation rate and offspring weight decreased as the magnitude of asynchrony increased. Due to low offspring production and a lack of female offspring across treatments, we were unable to assess the effects of phenological asynchrony on total offspring produced or sex ratio. Findings suggest that post-emergence food deprivation caused by phenological asynchrony may affect offspring size by influencing nest-provisioning rates. In solitary bees, body size influences wintering survival, fecundity, and mating success. Thus, phenological asynchrony may have consequences for solitary bee populations that stem from reduced flower visitation rates, and these consequences may increase as the magnitude of asynchrony increases. Because many wild flowering plants and crops rely on pollination services provided by bees for reproductive success, bee responses to phenological asynchrony may also affect wild plant biodiversity and crop yields.

Keywords: Climate change; Phenology; Phenological mismatch; Reproduction; Offspring weight

Introduction

Reduced or complete phenological asynchrony between interacting taxa is one possible result of rapid climate change (Kharouba, Ehrlen, Gelman, Bolmgren, Allen et al. 2018; Parmesan & Yohe 2003; Thackeray, Henrys, Hemming,

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Bell, Botham et al. 2016). For plant-pollinator mutualisms, phenological asynchrony is expected to have negative implications for both partners (Renner & Zohner 2018), and could affect pollination services vital in supporting wild plant reproduction and crop yields (Ollerton, Winfree & Tarrant 2011; Klein, Vaissiere, Cane, Steffan-Dewenter, Cunningham et al. 2007). However, most research investigating phenological asynchrony between plants and pollinators has focused on plant fitness (e.g., Burkle et al. 2013; Gezon, Inouye & Irwin 2016; Kudo & Cooper 2019; Thomson 2010, but see, Farzan & Yang 2018; Schenk, Krauss & Holzschuh 2018), leaving gaps in our understanding of how climate change is affecting pollinators and pollination services (Forrest 2015). In particular, understanding the consequences of phenological asynchrony for bees is timely, given that bees are the most abundant and diverse pollinators, coupled with ongoing and poorly understood global bee population declines (Biesmeijer, Roberts, Reemer, Ohlemuller, Edwards et al. 2006; Potts, Biesmeijer, Kremen, Neumann, Schweiger et al. 2010).

Mixed evidence, thus far, that phenological asynchrony between pollinators and their host plants is occurring (Forrest 2015; Renner et al. 2018) suggests that some pollinators and plants may be at a greater risk of experiencing asynchrony than others. In temperate systems, adult-wintering bees with spring emergence phenologies − such as many solitary bees in the genus *Osmia* − may be at a higher risk of experiencing phenological asynchrony for several reasons. First, shifts in phenology can be particularly large during spring (Fitter & Fitter 2002; Parmesan & Yohe 2003). If so, there is increased opportunity for significant variation in phenological responses between spring-active bees and their host plants. Second, adult emergence from nests in some species of *Osmia* is primarily cued by ambient temperature (Forrest and Thomson 2011), whereas flowering in the same systems can be initated by snowmelt date (Inouye 2008; Inouye, Saavedra & Lee-Yang 2003). The use of different phenological cues such as temperature and snowmelt date could cause asynchronous phenological responses (Forrest 2015), particularly given that long-term changes in temperature and snowmelt date under climate change are not always strongly correlated (Inouye, Barr, Armitage & Inouye 2000; Lambert, Miller-Rushing & Inouye 2010). Third, adult-wintering bees can emerge promptly in response to increased temperature (Slominski & Burkle 2019), and emergence can occur following a wide range of wintering durations (Bosch & Kemp 2003). This suggests that species in the genus *Osmia* may be prone to emerging in response to short periods of warm weather that occur prior to the start of flowering. Such a scenario may be increasingly likely given predictions of increasingly milder winters with fewer cold anomalies under climate change (Tamarin-Brodsky, Hodges, Hoskins & Shepherd 2020; USGCRP 2017).

Solitary bees that emerge as adults prior to the start of flowering would likely face fitness consequences stemming from post-emergence food deprivation (hereafter, 'deprivation'). When examined using flight cages, deprivation reduced activity levels and reproductive success in three species of *Osmia* (Schenk et al. 2018). Importantly, however, it remains unknown whether the effects of deprivation on solitary bee reproduction are associated with bee-plant interactions. The answer would be important for understanding the consequences of climate change for solitary bees, as well as for pollination services provided to plants (Garibaldi, Saez, Aizen, Fijen & Bartomeus 2020). In addition, conducting deprivation treatments inside flight cages (e.g., Schenk et al. 2018) may cause bees to be unusually active while attempting to escape their enclosure. Conducting deprivation treatments prior to placing bees into flight cages may therefore control for unrealistic metabolic expenditure during deprivation, which could influence the effect of deprivation on bee behavior and reproduction. Also, the relationship between the magnitude of phenological asynchrony (i.e., days of food deprivation) and the severity of the consequences for pollinators remains unknown. Addressing this gap in knowledge will help build a more complete understanding of both the current and future consequences of climate change for pollinators and plants.

Here, our objective was to investigate two mechanisms − both involving bee-plant interactions − by which deprivation caused by phenological asynchrony might indirectly affect reproduction in solitary bees. First, depleted lipid reserves caused by deprivation could reduce a female's lifespan. A shorter lifespan would likely result in a truncated nesting period (Fig. 1A, mechanism 1), which could reduce reproductive success by reducing the number of eggs a female can lay, and the number of brood cells that a female can provision (Fig. 1B pathway 1). Second, depleted lipid reserves following deprivation might reduce female activity levels (Schenk et al. 2018), which could cause females to visit flowers at a reduced rate. Reduced visitation rates could reduce the total quantity of nectar and pollen a female could provision to offspring during her nesting period (Fig. 1A, mechanism 2). Females that provision less nectar and pollen to nests could produce fewer offspring (Sgolastra, Arnan, Pitts-Singer, Maini, Kemp et al. 2016), smaller offspring (Bosch 2008; Bosch & Vicens 2002, 2006; Roulston & Cane 2000), or a greater proportion of male offspring (i.e., males are the smaller of the sexes and require smaller provisions compared to females; Bosch & Vicens 2005) (Fig 1B, pathway 2). Reduced offspring production, and the production of smaller offspring, which are more likely to die while overwintering (Bosch 2008), could both reduce solitary bee population sizes. In addition, smaller individuals may have reduced reproductive potential (O'Neill, Delphia & O'Neill 2014), and increased male bias in sex ratios could jeopardize the future total reproductive output of a population (Torchio & Tepedino 1980). The potential negative effects of phenological asynchrony on female bee lifespan and flower visitation rates could therefore exacerbate declines in pollinator population densities (Potts et al. 2010) and pollination services (Garibaldi et al. 2020). Alternatively, spring-active

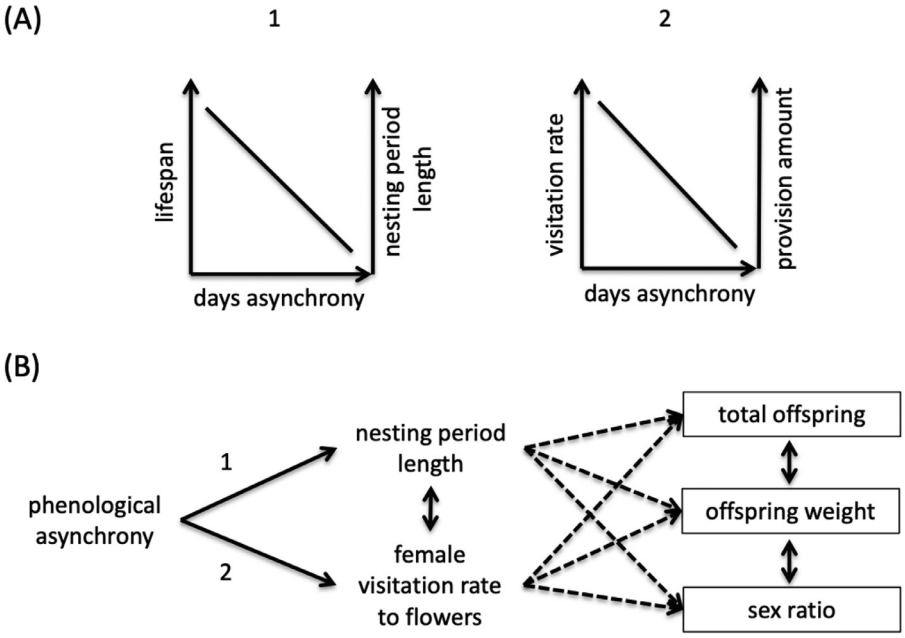

Fig. 1. Conceptual diagram illustrating (A) the hypothesized mechanisms underlying the indirect effects of phenological asynchrony on reproductive success in solitary bees, and (B) the hypothesized indirect pathways by which we expect phenological asynchrony to influence solitary bee reproductive success (shown in boxes). Mechanisms 1 and 2 in panel A correspond with pathways 1 and 2 in panel B. Panel A depicts the hypothesized relationships between the magnitude of phenological asynchrony and 1) a female's lifespan and nesting period length, and 2) a female's visitation rate to flowers and provision amount. Panel B depicts the hypothesized indirect effects of phenological asynchrony on reproductive success (dashed directional arrows) caused by the direct effects (solid directional arrows) of phenological asynchrony on nesting period length and visitation rate to flowers. Double arrows represent anticipated correlations among variables.

solitary bees may have strategies to help them tolerate deprivation (Schenk et al. 2018), such as the ability to replenish their depleted lipid reserves by consuming nectar and pollen once plants begin blooming. Such strategies could mitigate any negative effects of deprivation on lifespan and flower visitation.

To accomplish our objective, we conducted a flight cage experiment using *Osmia cornifrons*. *Osmia cornifrons* is a spring-active, generalist foraging, cavity-nesting solitary bee species willing to nest in artificial trap-nests (White, Son & Park 2009). *Osmia cornifrons* is native to Asia and was introduced to North America for agricultural pollination (Bosch & Kemp 2002). *Osmia cornifrons* overwinters in the adult life-stage and emerges during the first weeks of spring in response to warming temperatures (White et al. 2009). Spring emergence, and earlier emergence phenology in response to increasing temperatures associated with climate change (Lee, He & Park 2018), as well as the economic importance of *O. cornifrons* as a managed crop pollinator, make *O. cornifrons* a relevant model species with which to investigate the consequences of phenological asynchrony for solitary bees.

We manipulated phenological asynchrony by creating treatments that deprived emerged females of access to nectar and pollen for between 0 and 16 days prior to releasing them into flight cages that contained flowering plants and artificial nesting habitat (Fig. 2). We investigated how the duration of deprivation influenced 1) post-treatment female lifespan (i.e., the number of days females survived after being placed in cages with flowering plants; hereafter 'lifespan'), 2) visitation rates by females to flowers, and 3) metrics of reproductive success (i.e., the number of brood cells produced, the number of emerged offspring, offspring sex ratio, and emerged offspring weight). We hypothesized that female lifespan and visitation rates by females to flowers, as well as the number of offspring produced, offspring size, and female offspring production, would all be reduced as the duration of phenological asynchrony increased.

Materials and methods

Phenological asynchrony treatments

Cocoons of wintering *Osmia cornifrons* Radoszkowski (Hymenoptera: Megachilidae) were purchased from Crown bees (Woodinville, WA, USA) in January of 2016 and held at 4°C. Wintering females (inside cocoons) were placed into gelatin capsules and randomly assigned to one of seven phenological asynchrony treatments (i.e., 0, 2, 4, 6, 12, 14, or 16 days; Fig. 2). This range of phenological asynchrony treatments was chosen to reflect the magnitudes of phenological asynchrony currently reported in the literature for bee species (e.g., Burkle et al. 2013; Gordo & Sanz, 2005; Hegland et al.

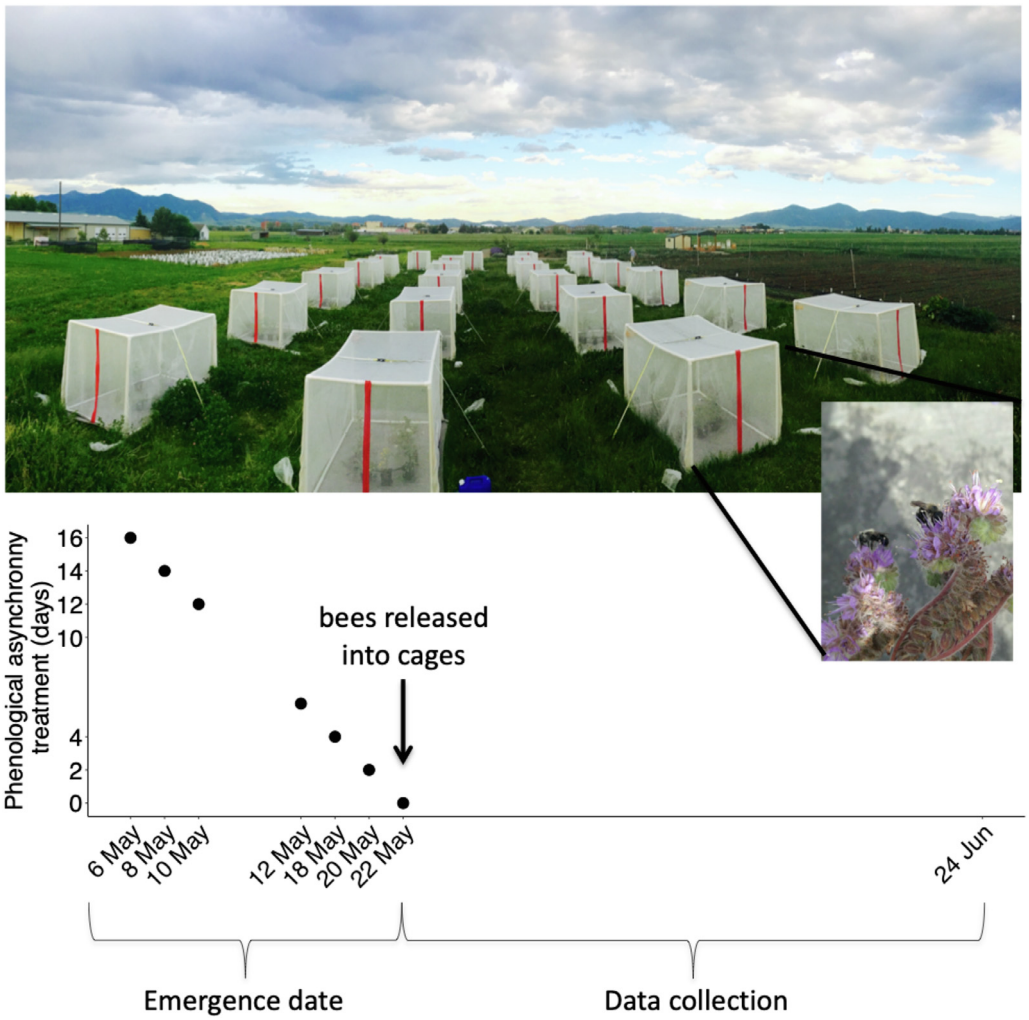

Fig. 2. Field site (top panel) showing flight cages located at the Montana State University Agricultural Research Station and Horticulture Farm. Diagram (bottom panel) showing the timeframe during which phenological asynchrony treatments and data collection were conducted.

2009; Kudo 2014). Beginning in early May, females were incubated at 28°C using a 4.5 × 4.5 m Conviron temperature-controlled chamber. Incubation occurred under 24 hours of darkness and humidity was not controlled or recorded. After emerging, sex was confirmed, and individual females were held in a single refrigerated room at 4°C inside a gelatin capsule without access to nectar, pollen, or water for the duration of their assigned treatment (Fig. 2). We conducted asynchrony treatments at 4°C to mimic a return to cooler temperatures following a short warm spell that might cause *O. cornifrons* (and other spring-active solitary bees) to emerge prior to the start of flowering. Bees that emerge in response to warm spring weather that persists after they emerge may be less likely to experience deprivation, as prolonged warm weather would also initiate earlier flowering of food plants, either by melting the snow (Inouye 2008; Inouye et al. 2003), or via degree day accumulation (Forrest & Thomson 2011). Thus, treatments controlled for metabolic expenditures during deprivation that may be unrealistic under phenological asynchrony experienced by bees in the field.

Following the completion of their assigned treatment, four females and six males, a typical sex ratio for *O. cornifrons* (Lee, Yoon, Lee & Jin 2016), were released into a randomly assigned flight cage. Females placed together in each cage had all received the same phenological asynchrony treatment and were randomly selected from the group of females that survived their respective treatment. Male bees did not receive phenological asynchrony treatments. Males were incubated at 28°C to promote emergence and were placed into cages with females within one day of emerging.

Flight cage design and resources for adult bees

We monitored female survival, flower visitation, and reproductive success inside 24 1.5 × 1.5 × 2.5 m mesh-sided flight cages that provided food plants and nesting materials (Fig. 2). Flight cages were located outdoors at the Montana State University Agricultural Research Station and Horticulture Farm (Bozeman, MT, USA). Mesh net with

Table 1. ANOVA tables showing *F*, *Z*, and *P* values for models fitted to female lifespan, visitation rate, visit duration, brood cells produced, emerged offspring, and offspring weight. Bolded *p*-values represent significance at $\alpha \leq 0.05$.

	Female lifespan		*Visitation rate*		*Visit duration*		*Brood cells*		*Emerged offspring*		*Offspring weight*	
	F	*P*	*F*	*P*	*F*	*P*	*Z*	*P*	*Z*	*P*	*F*	*P*
Treatment	0.76	0.395	5.94	**0.023**	0.13	0.722	3.23	**0.001**	-0.80	0.424	18.79	**0.012**
Start time	-	-	2.50	0.116	0.81	0.369	-	-	-	-	-	-
Females	-	-	0.16	0.688	0.14	0.710	-0.98	0.326	1.54	0.123	2.86	0.166
P. hastata	0.21	0.652	0.13	0.718	0.83	0.365	0.21	0.837	-0.88	0.379	-	-
A. urticifolia	0.12	0.738	1.03	0.312	0.28	0.599	-0.30	0.765	0.81	0.417	-	-
C. rotundifolia	1.06	0.317	0.61	0.438	0.02	0.902	0.86	0.392	-1.43	0.153	-	-
M. tancetifolia	0.04	0.846	0.21	0.649	0.21	0.649	-0.44	0.662	1.43	0.152	-	-
Total flowers	-	-	-	-	-	-	-	-	-	-	5.32	0.082

hole sizes of 0.72 × 0.97 mm used to construct the cages was purchased from Green-Tek Inc. Wooden blocks containing 24 seven mm inside-diameter cardboard tubes with paper inserts (i.e., trap-nests) were used as nesting habitat inside each cage (Lee et al. 2016). A moist mixture of sandy-loam soil was provided as a substrate for nest construction (McKinney & Park 2012). The 0-, 4-, and 6-day asynchrony treatments were replicated in four cages each, whereas 2-, 12-, 14-, and 16-day asynchrony treatments were replicated in three cages each (i.e., 24 total cages). The number of replicates per treatment resulted from variation in successful emergence and emergence timing by females during incubation. All 24 cages were established with bees and flowering plants between 22 May and 27 May (Fig. 2). Bee activity was monitored for 25 days, an observed nesting period length for *O. cornifrons* (Lee et al. 2016).

We provided five flowering individuals each of *Phacelia hastata* Douglas (Boraginaceae), *Agastache urticifolia* (Benth.) Kuntze (Lamiaceae), *Machaeranthera tanacetifolia* (Kunth) Nees (Asteraceae), and *Campanula rotundifolia* L. (Campanulaceae) as food resources for bees inside each cage (i.e., 20 total individual plants per cage). Individual plants were grown from seed in a greenhouse using 2.6 L (156 cu. in.) pots. *Phacelia hastata* is both a pollen and nectar source for bees (Sgolastra et al. 2016) and has been used to successfully rear species in the genus *Osmia* (Sgolastra et al. 2016). *Agastache urticifolia* is visited by bees primarily for nectar (Pleasants 1977), and the zygomorphic flower shape in *A. urticifolia* is accessible to long-tongued bees in the family Megachilidae (Ostler & Harper 1978). Species from the family Asteraceae are visited by *O. cornifrons* as a pollen source (Vaudo, Biddinger, Sickel, Keller & Lopez-Uribe 2020), and thus it is likely that *M. tanacetifolia* was used as a pollen source in this study. *Campanula rotundifolia* is predominantly pollinated by solitary bees in the family Megachilidae (Blionis & Vokou 2001) and can serve as both a pollen and nectar source for bees during the male and female flower phases, respectively (Cresswell & Robertson 1994). Each species has a spring or early-summer flowering phenology (USDA, NRCS 2020) that would overlap with the phenology of *O. cornifrons* in a natural setting.

Open flowers were counted on the date each individual plant was placed into a cage, and these initial flower counts were used to distribute flower availability as equally as possible across cages. Flower abundances for each species were counted weekly thereafter in each cage and individual plants were replaced as needed to ensure consistent and fresh flower availability across the duration of the study (see **Results** and Appendix A: Table 1 for a summary of flower abundances by treatment). No additional effort (e.g., clipping flowers) was made to control flower availability across cages.

Lifespan of adult bees

To document post-treatment female lifespan inside cages (up to 25 days), all females placed together in a cage were marked with a different color of paint on their thorax using a paint pen. Living females were then visually located 3 times each week. Days alive were counted up to the last confirmed live sighting, and thus bee lifespans could have been underestimated by a maximum of 2 days (i.e., bees that died shortly after being confirmed alive on Friday would not have been counted as dead until the following Monday).

Flower visitation

We recorded visitation by females to flowers a maximum of 10 times per cage over the course of the study (i.e., 3 times per week), and a maximum of 20 minutes per observation session. A visit was recorded each time a female bee contacted the reproductive tissues of a flower for more than one second. The duration of time a bee remained in contact with a flower during each visit (hereafter 'visit duration') was also recorded, as visit duration may influence overall visitation rate (Neff 2008). We did not conduct observation sessions when weather conditions were not conducive to female flight (McKinney et al. 2012), and some sessions were stopped before 20 minutes if weather conditions changed. This resulted in variation in the number of observation sessions and the total observation time each cage

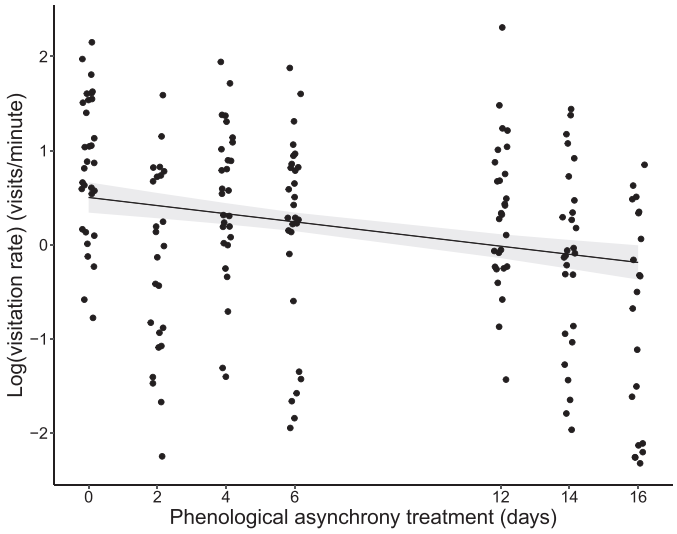

Fig. 3. Regression showing the relationship between phenological asynchrony treatment and log(visitation rate). The shaded area represents the standard error and points are log(visits per minute of observation time) during an observation session. Points are jittered to improve visualization.

received. To account for the influence that the time of day has on female foraging behavior (McKinney et al. 2012), observation start times were equally distributed across treatments (see **Results** and Appendix A: Table 2 for a summary of observation start times and durations by treatment). To account for differences in observation times at each cage, we used 'visitation rate' (i.e., visits/minute) during each observation session to compare flower visitation among treatments.

Nesting success, offspring size, and sex ratios

At the end of the 25-day nesting period, trap-nests were stored at ambient temperature (Appendix A: Figure 1) in a garage in Bozeman, MT until bees emerged during spring 2017. Each individual trap-nest was enclosed in a plastic container allowing emerged bees to be counted. Emergence was monitored daily, and emerged bees were immediately frozen. Emerged bees were then dried in a drying oven at 38°C for 48 hours and weighed to the nearest 0.1 mg using a Mettler Toledo NewClassic MF electronic balance. Bee mass was used to compare bee size among treatments. No female offspring were produced in this study, and thus sex ratio was not calculated. After all bees had emerged, nests were dissected, and total brood cells and non-emerged bees were counted.

Statistical analyses

All analyses were conducted using R statistical software version 3.6.2 (R core team 2019). The effect of phenological asynchrony treatments on female lifespan, visitation rate to flowers, and metrics of reproductive success were analyzed separately. Because our replicated regression study design (Cottingham, Lennon & Brown 2005) lacked the replication to perform a path analysis (Grace 2006), we instead report the correlations among response variables as a tool to gauge the potential indirect effects of female lifespan and visitation rate on reproduction.

Individual female lifespans, and visitation rate in each cage were analyzed using linear mixed effects models fit using the 'lmer' function in the 'lme4' package (Bates, Maechler, Bolker & Walker 2015). The female lifespan model included asynchrony treatment as a numerical predictor variable, as well as mean flower abundances of *P. hastata, A. urticifolia, M. tanacetifolia,* and *C. rotundifolia* in each cage as separate numerical covariates. 'Cage' was included as a random intercept.

The visitation rate model and the visit duration model included asynchrony treatment as a numerical predictor variable, as well as weekly flower abundances of *P. hastata, A. urticifolia, M. tanacetifolia,* and *C. rotundifolia* as separate numerical covariates. In addition, the number of females alive in a cage during each observation session, and the time of day that each observation session began were included as covariates. 'Cage' was included as a random intercept. Visitation rate was log-transformed to improve normality. Degrees of freedom and p-values associated with each mixed effects model were produced by the 'lmerTest' package using Satterthwaite's method (Kuznetsova, Brockhoff & Christensen 2017). Including a random slope for asynchrony treatment within each cage (i.e., a 'crossed' random effect) was not warranted based on AIC model comparisons (Zuur, Ieno, Walker, Saveliev & Smith 2009).

Total brood cells produced in each cage and total emerged offspring in each cage were both analyzed using 'poisson' generalized linear models fit using the 'glm' function (R core team 2019). Cages that did not produce

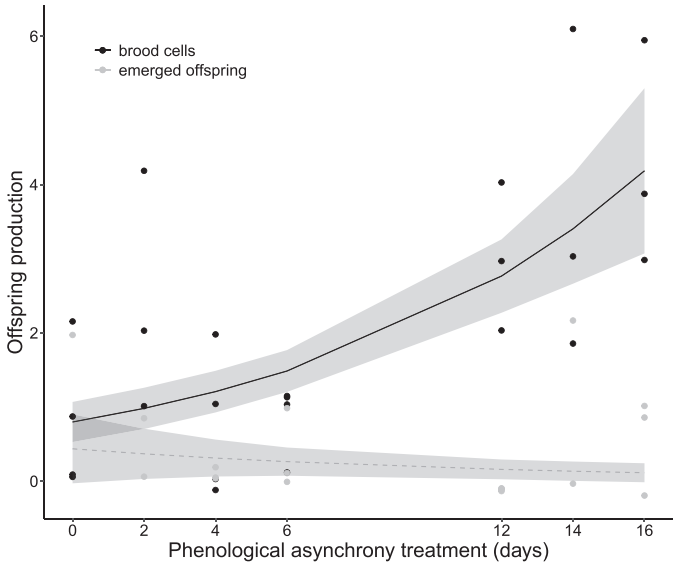

Fig. 4. Generalized linear regression showing the relationship between phenological asynchrony treatment and brood cells produced (black solid line), and emerged offspring (gray dashed line). The shaded areas represent the standard errors. Model estimates and standard errors are back-transformed to the response scale. Black points represent brood cells produced per cage, and gray points represent emerged offspring per cage. Points are jittered to improve visualization.

any brood cells were excluded from the models fitted to total emerged offspring. Overdispersion (i.e., variance larger than the mean) was assessed and determined not to be present in either generalized linear model (Zuur et al. 2009). Models fitted to both total brood cells and total emerged offspring included asynchrony treatment as a numerical predictor variable, as well as the mean number of females present, and mean flower abundances of *P. hastata, A. urticifolia, M. tanacetifolia,* and *C. rotundifolia* in each cage as separate numerical covariates. A random intercept for 'cage' could not be included in these models due to small sample sizes. No females were produced in this study, and thus sex ratio was not analyzed. Offspring weight was analyzed using a linear regression model that was fit using the 'lm' function (R Core Team 2019). The offspring weight model included asynchrony treatment as a numerical predictor variable, as well as the mean number of females present, and mean total flower abundance in each cage as separate numerical covariates. We could not include mean flower abundance for each plant species nor a random intercept for 'cage' in the offspring weight model due to small sample sizes.

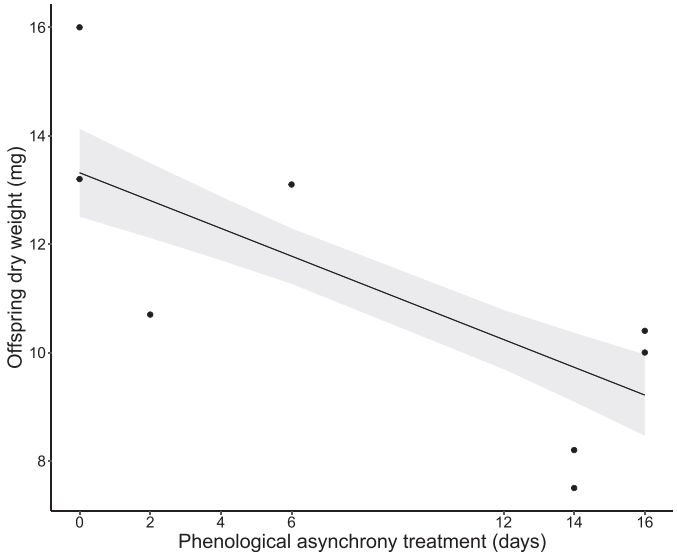

Fig. 5. Regression showing the relationship between phenological asynchrony treatment and offspring weight. The shaded area represents the standard error. Points are individual offspring weights.

For all models, the assumptions of equal variance and normality were assessed by plotting the residuals against the fitted values, and with normal QQ plots of the residuals. Model estimates and standard errors were produced using the 'emmeans' package (Lenth 2020). All figures were produced using the 'ggplot2' package (Wickham 2016).

Results

Flower abundance in cages

Across all cages and weekly flower counts, total flower abundance averaged 409.2 ± 14.2 (mean ± SE) flowers, and total flower abundance did not differ statistically ($\alpha \leq 0.05$) by treatment ($F_{6,77} = 0.70$, $p = 0.653$), or by cage ($F_{23,60} = 1.07$, $p = 0.408$). Across weeks, flower abundance (Appendix A: Table 1) did not differ statistically for *P. hastata* (by treatment: $F_{6,77} = 0.21$, $p = 0.973$; by cage: $F_{23,60} = 0.53$, $p = 0.951$), *A. urticifolia* (by treatment: $F_{6,77} = 1.57$, $p = 0.168$; by cage: $F_{23,60} = 1.15$, $p = 0.325$), or *M. tanacetifolia* (by treatment: $F_{6,77} = 1.68$, $p = 0.137$; by cage: $F_{23,60} = 0.1.34$, $p = 0.182$), but did differ for *C. rotundifolia* (by treatment: $F_{6,77} = 3.49$, $p = 0.004$; by cage: $F_{23,60} = 2.37$, $p = 0.004$).

Female lifespan

Across all cages, female bee lifespan inside cages averaged 21.5 ± 0.7 days and did not differ statistically by treatment (Table 1). In each treatment, at least 50% of females survived the full 25 days inside cages (0 days asynchrony = 81.3%, 2 days asynchrony = 66.7%, 4 days asynchrony = 100%, 6 days asynchrony = 87.5%, 12 days asynchrony = 50.0%, 14 days asynchrony = 58.3%, 16 days asynchrony = 75.0%).

Visitation rate

Total observation time per treatment ranged from 259 to 405 minutes, with an average of 12.7 ± 0.3 minutes per observation session (Appendix A: Table 2). Observation start time averaged 13:21 ± 0:09 (24 hr) and did not differ statistically by treatment ($F_{1,171} = 0.00$, $p = 0.961$; Appendix A: Table 2). We observed 4,224 total visits, of which 68.8% were observed on *P. hastata,* 27.0% were observed on *A. urticifolia*, 2.5% were observed on *C. rotundifolia*, and 1.7% were observed on *M. tanacetifolia*. On average, female bees experiencing zero days asynchrony visited 1.6 ± 0.3 flowers/minute of observation time (Fig. 3). Visitation rate decreased by an estimated 4.3 ± 1.8% per each 1-day increase in asynchrony (Table 1, Fig. 3). Visit duration averaged 7.7 ± 0.3 seconds/visit and did not differ statistically by treatment (Table 1).

Reproduction

Brood cells were produced in 19 of 24 cages (brood cells by treatment: $N_0 = 3$, $N_2 = 7$, $N_4 = 3$, $N_6 = 3$, $N_{12} = 9$, $N_{14} = 11$, $N_{16} = 13$; Appendix A: Table 3). There was a statistically significant increase in total brood cells produced as phenological asynchrony increased (Table 1; Fig. 4). Of the 19 cages that produced brood cells, seven cages produced emerged offspring (eight total offspring), and all emerged offspring were male (emerged offspring by treatment: $N_0 = 2$, $N_2 = 1$, $N_4 = 0$, $N_6 = 1$, $N_{12} = 0$, $N_{14} = 2$, $N_{16} = 2$; Appendix A: Table 3). In cages that produced emerged offspring, 1.3 ± 0.2 offspring were produced on average, and the number of emerged offspring did not differ statistically by treatment (Table 1; Fig. 4). Offspring dry weight averaged 14.6 ± 1.4 mg in cages where females experienced zero days of asynchrony, and there was a statistically significant decrease in emerged offspring dry weight as phenological asynchrony increased (Table 1; Fig. 5).

Correlations Among female lifespan, visitation rate, and reproduction

There were no statistically significant correlations ($\alpha \leq 0.05$) among female lifespan inside cages and female visitation rate to flowers ($r = 0.22$, $p = 0.298$), total brood cells produced ($r = 0.34$, $p = 0.103$), emerged offspring ($r = 0.03$, $p = 0.896$), or emerged offspring dry weight ($r = 0.27$, $p = 0.557$). Visitation rate was not significantly correlated with total brood cells produced ($r = 0.33$, $p = 0.113$), or emerged offspring ($r = 0.12$, $p = 0.592$). Visitation rate was positively significantly correlated with offspring weight ($r = 0.76$, $p = 0.046$).

Discussion

We investigated whether post-emergence food deprivation caused by phenological asynchrony may impact reproductive success in solitary bees by affecting female bee lifespan and visitation rates to flowers. We found that the post-treatment lifespan of female *O. cornifrons* was unaffected by deprivation lasting up to 16 days, but that visitation rates to flowers and offspring size decreased as a function of the deprivation period (days). Findings suggests that deprivation may indirectly affect offspring size in solitary bees by reducing nest-provisioning rates, and that the severity of this effect may increase with the duration of deprivation. Although we focused on bee responses in this study, the effect of phenological asynchrony on visitation rates could also have implications for plant reproduction by impacting pollination services (Garibaldi et al. 2020). Due to small sample sizes of emerged offspring across treatments, and the production of only male offspring, we were

unable to assess the effects of deprivation on reproductive output and progeny sex ratio. We discuss the implications of these findings, as well as the potential causes of the observed low reproductive output in the context of phenological asynchrony.

Species of *Osmia* overwinter on a fixed energy budget, relying completely on reserves derived from the nectar and pollen provision they consume as larvae to sustain them through their wintering period (Torchio 1989). Because of this, lipid reserves are depleted at emergence (Sgolastra, Kemp, Buckner, Pitts-Singer & Maini 2011), and bees must consume nectar and pollen after they emerge to meet the energetic requirements for survival and reproduction (O'Neill et al. 2015; Strohm, Daniels, Warmers & Stoll 2002). That we found no effect of deprivation on the lifespan of female *O. cornifrons* suggests either that deprivation did not cause lipid depletion to a degree that affected mortality during the nesting period, or that females were able to replenish enough of their lipid reserves when they began foraging to avoid mortality.

It is possible that some species of spring-emerging solitary bees have adaptations that help them tolerate periods of food deprivation. Such adaptations would be consistent with the inherent risks of phenological asynchrony associated with an early-spring phenology. For instance, Schenk et al. (2018) reported lower mortality caused by deprivation in *Osmia cornuta* (an early-spring species) compared to *Osmia bicornis* and *Osmia brevicornis* (mid- and late-spring species, respectively). *Osmia cornuta* is larger on average compared to *O. bicornis* and *O. brevicornis*, suggesting that larger body sizes may correlate with greater lipid reserves (O'Neill, Delphia & O'Neill 2014) that could help early-spring bee species tolerate deprivation (Schenk et al. 2018). However, *O. cornifrons* (studied here) is smaller on average compared to *O. cornuta* (Bosch & Vicens 2002; Greenleaf, Williams, Winfree & Kremen 2007), and emerges several weeks later in the spring on average. Thus, we do not necessarily expect *O. cornifrons* to be as resilient to deprivation compared to *O. cornuta*. Here, it is likely that the cool temperature *O. cornifrons* experienced during phenological asynchrony treatments minimized the effects of deprivation on lipid depletion (Bosch & Kemp 2004; O'Neill, O'Neill, Kemp & Delphia 2011). This conclusion is consistent with Schenk et al. (2018) who observed lower mortality in female *Osmia bicornis* (a mid-spring species) when post-emergence food deprivation occurred under cooler ambient temperatures. In addition, Straka et al. (2014) found that lifespans in the solitary bee species *Andrena vaga* and *Anthophora plumipes* increased when individuals experienced cold weather after emergence compared to warmer conditions. Taken together, it appears that post-emergence lifespan in solitary bees may be influenced by the temperature they experience after emergence, with periods of low metabolic activity due to cold having little impact on their lifespan. Therefore, the temperature that bees experience during periods of deprivation, as well as their life history, will likely be important in determining the consequences of phenological asynchrony.

Although we did not observe an effect of deprivation on female lifespan, it is possible that reduced visitation rates associated with phenological asynchrony in this study were caused by reduced female vigor stemming from lipid depletion. Over the duration of a female solitary bee's nesting period, declining lipid levels can be associated with declining nest-provisioning rates (Seidelmann 2006). Therefore, it is possible that solitary bees rely on surplus lipid reserves to achieve higher nest-provisioning rates during their nesting period. In this study, deprivation may have caused moderate levels of lipid depletion in *O. cornifrons*, which may not have been significant enough to affect lifespan, but that could have influenced visitation rates to flowers. This interpretation is consistent with Schenk et al. (2018) who found that activity levels in female *O. cornuta, O. brevis*, and *O. brevicornis* were reduced in bees that survived deprivation and were then allowed to forage and provision nests. In addition, visitation rates decreased in this study as the duration of deprivation increased, suggesting that the amount of time bees experience deprivation may influence how significantly their activity levels are reduced.

Because provision size strongly influences body size in solitary bees from the genus *Osmia* (Bosch et al. 2002, 2006; Klostermeyer, Mech & Rasmussen 1973; Radmacher & Strohm 2010), it is possible that phenological asynchrony indirectly affected offspring size in this study via the effect of visitation rate decline on nest-provision size (Bosch et al. 2002). While provisioning nests, female solitary bees will seal off brood cells after a limited amount of provisioning time, presumably to mitigate the risk of parasite infestation (Seidelmann 2006). Because of this, provision quanities can decrease as nest-provisioning rates slow, resulting in the production of smaller offspring and a greater proportion of male offspring (Seidelmann 2006; Tepedino and Torchio 1982). Here it is possible that reduced visitation rates also reduced nest-provisioning rates, resulting in smaller provisions per brood cell and smaller mature offspring. In solitary bees, offspring size influences winter survival (Bosch 2008; Bosch & Kemp 2004; Tepedino et al. 1982), and female fecundity (O'Neill et al. 2014; Sugiura & Maeta 1989). Therefore, any effect of phenological asynchrony on offspring size could have fitness consequences for solitary bees.

In addition to provision size, temperature (Radmacher et al. 2010), nest-cavity size (O'Neill, Pearce, O'Neill & Miller 2010), and the nutitional properties in nectar and pollen provisions (Burkle & Irwin 2009; Bukovinszky, Rikken, Evers, Wäckers, Biesmeijer et al. 2017; Filipiak & Filipiak 2020) can also influence adult size in solitary bees. Rearing temperature and cavity size were consistent across treatments in this study, and thus it is unlikely that these factors influenced offspring size. While it remains possible that the nutritional properties of the floral resources provided had an effect on reproduction, a variety of plant species were made available, and nearly 96% of visits were observed at *P. hastata* and *A. urticifolia*, two species for which flower abundances did not differ by treatment. These factors make it unlikely that the

relationship between phenological asynchrony and offspring size was influenced by the nutritional quality of provisions. *Campanula rotundifolia*, for which flower abundance differed across treatments, could have provided specific nutritional components to offspring that affected their adult size. However, visits to *C. rotundifolia* did not differ by treatment (F=0.11, p=0.750), and visits to *C. rotundifolia* represented a relatively small proportion of visits overall (2.5% of total visits), making it unlikely that differences in the abundance of *C. rotundifolia* pollen influenced offspring size.

Reproductive output was low across treatments compared to other cage studies using *O. cornifrons* (Lee et al. 2016) and other species of *Osmia* (Bukovinszky et al. 2017; Schenk et al. 2018), and only male offspring were produced. Low reproductive output, and only male offspring indicate that the abundances (Goodell 2003; Pitts-Singer & Bosch 2010) or nutritional composition (Bukovinszky et al. 2017; Filipiak, Woyciechowski & Czarnoleski 2021; Filipiak et al. 2020) of the floral resources in each cage, or environmental conditions such as temperature (McKinney et al. 2012) or nest-cavity size (O'Neill et al. 2010), were not adequate to support maximum reproductive output. It is unlikely that the 7 mm inner-diameter nest-cavities used as nesting habitat influenced reproductive output or sex (Lee et al. 2016). However, it is possible that reproduction was suppressed by flower abundance, which was less than that provided in a similar cage study that reported higher reproductive output (Bukovinszky et al. 2017). It is also possible that a nutritional imbalance due to the food resources provided, or the temperature inside cages affected reproductive outoput. Thus, we cannot reliably assess the effect of phenological asynchrony on reproductive output or sex ratio in this study.

The possibility that flower abundances and/or a nutritional imbalance affected reproductive success in *O. cornifrons* is particularly notable, and highlights two potential mechanisms whereby phenological asynchrony could affect pollinators. First, pollinators that survive periods of deprivation caused by phenological asynchrony might encounter low densities of flowers for a period of time as plants begin flowering, which could limit their ability to recover from deprivation. The results of this study may be representative of this scenario. Second, phenological asynchrony could decouple bees from the bloom periods of host plants on which they rely for specific nutritional requirements in their diet. Such asynchrony could affect pollinators during any point in the growing season, not just during early spring. Specialist pollinators may be at a higher risk of experiencing negative consequences associated with either of these scenarios, because specialists would be less capable of supplementing their diet with pollen from an alternative host when faced with inadequate densities of their preferred host (Praz, Mueller & Dorn 2008).

An increase in the number of brood cells produced per cage as phenological asynchrony increased may have been related to flower visitation and nest-provisioning rates. Given that female solitary bees will shift toward male-biased offspring production when their nest-provisioning rates slow (Seidelmann et al., 2010), it is possible that reduced nest-provisioning rates caused females to attempt to produce fewer female offspring, whereas females that were provisioning nests at a greater rate may have attempted to produce more females. Attempting to produce only male offspring may have reduced the time a female invested in provisioning each brood cell (Bosch et al. 2005), which may have resulting in more total brood cells produced compard to females that attempted to produce females. That no viable females were produced in this study means that if some females did attempt to produce female offffspring, they failed due to other constraints, such as low floral resoure abundance or nutritional imbalance. In addition, total viable offspring did not differ by treatment, meaning that potential attempts by food-deprived females to maximize their reproductive output by producing only male offspring also failed.

Because manipulating emergence phenologies and quantifying reproductive success in the field is particularly challenging for solitary bees, flight cage experiments are useful for investigating solitary bee responses to climate change. However, we acknowledge that solitary bee responses to phenological asynchrony within the artificial conditions used in this study may not be representative of solitary bee responses in the field. For example, spatial and temporal variability in flowering phenologies and flower abundances may provide opportunities for bees that experience phenological asynchrony to locate more abundant and diverse food resources by flying. Flying to find food could potentially reduce the duration during which solitary bees would be without food, while also increasing the diversity in their diet. However, long foraging flights could increase metabolic expenditure compared to what may have occurred in this study, and thus it is possible that responses to deprivation in the field could be equal to or more severe than observed here.

Given the profound importance of pollination services provided to plants by bees, it is urgent that we understand the extent of the anthropogenic threats facing bee populations. Here, we demonstrate a potential mechanism underlying the fitness consequences of anthropogenic climate change for solitary bees. We found that depriving female bees of nectar and pollen after they emerge reduced their flower visitation rate, which may have caused females to produce smaller offspring by reducing their nest-provisioning rate. Results also indicate that the consequences of phenological asynchrony for solitary bees may increase in severity as the duration of asynchrony increases. Responses by *O. cornifrons* to phenological asynchrony in this study may have stemmed from energy depletion. Given this, factors that influence metabolic expenditure in solitary bees, such as body size and temperature, will likely mediate their responses to phenological asynchrony. In addition, flower abundances and/or the nutritional properties of the floral resources provided to *O. cornifrons* in this study may have suppressed reproductive output. This suggests that low flower densities during early spring could have negative

consequences for pollinator reproduction. In addition, bee species with late-spring or summer phenologies may also be negatively affected by phenological asynchrony if they become decoupled from host plants that provide essential nutritional components in their diet. The reduced ability of specialist pollinators to shift host plants may make them more vulnerable to low resource availability and nutritional imbalance compared to generalist foraging pollinators. We urge future researchers to further investigate the role of temperature, resource availability, and nutritional quality in the context of pollinator life histories in order to better understand pollinator responses to climate change.

Declaration of competing interest

All authors declare no conflict of interest.

Declarations

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The first and second author conceived the project, the first author designed and executed the experiment, analyzed the data, and wrote the first draft of the manuscript. The first and second author contributed to revised drafts.

Data availability statement

The raw data supporting the conclusions of the manuscript will be made available by the authors, without undue reservation, to any qualified researcher.

Supplementary materials

Supplementary material associated with this article can be found in the online version at doi:10.1016/j.baae.2021.08.003.

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