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HIGHLIGHTED STUDENT RESEARCH

# Voltinism of a solitary bee was influenced by temperature but not provision size

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## Abstract

Changes in the timing and duration of life cycles are distinctive fingerprints of environmental change. Yet, the biotic and abiotic cues underpinning phenology and voltinism, i.e., number of generations per year, are poorly understood. Here, I experimentally test how temperature and provision size influence voltinism and survival to emergence in a solitary bee *Colletes validus*, and how temperature influences voltinism in the brood parasite *Tricrania sanguinipennis*. Within the same population, univoltine individuals emerge after 1 year (1-year form), whereas semivoltine individuals enter prolonged dormancy and emerge after 2 years (2-year form). I reared field-collected bees under 2 × 2 factorial experiments with cool (18.5 °C ± 0.5 °C) vs. warm (24 °C ± 0.5 °C) temperature treatments (bees and beetles) and no supplement vs. supplemental food treatments (+ 20% ± 5% pollen provision by mass); beetles were reared under temperature treatments only. Cool temperatures consistently increased the proportion of 2-year bees regardless of provision size, a finding that was consistent with three years of field observations. There was a demographic cost to prolonged dormancy in that both 1- and 2-year bees survived to emergence as adults, but survival of 2-year bees was approximately 50% lower than 1-year bees. Two-year beetles were produced under cooler temperatures, but unlike bees, beetles had nearly perfect survival to emergence in all treatments. This experiment advances our mechanistic understanding of the environmental drivers of voltinism in diverse insect taxa and underscores the importance of considering cryptic life stages when interpreting responses to environmental change.

**Keywords** Diapause · Dormancy · Parsivoltinism · Phenology · Pollinator

## Introduction

Shifts in life-cycle timing are a distinctive fingerprint of environmental change (Parmesan and Yohe 2003). For example, in the northern hemisphere, there have been consistent advances in the phenology of spring flowering, leaf-out, insect activity, and songbird migration over the past half century (Miller-Rushing and Primack 2008; Dorian et al. 2020). In addition to changes in phenology, many taxa are also exhibiting increases in the number of generations produced per year, i.e., voltinism (Altermatt 2010; Michielini et al. 2021). Despite a strong understanding of where and when shifts in phenology and voltinism are occurring, the biotic and abiotic factors cueing life-cycle timing, and the demographic consequences of variation in timing within a population, are often less clear (Forrest 2016). In particular, clarifying environmental drivers of phenology and voltinism can contextualize widely documented patterns of insect occurrence across space and time and improve our ability to forecast population dynamics under future environmental change (Tang et al. 2016; Chmura et al. 2019).

Within a population, variation in voltinism among individuals can be influenced by environmental cues experienced during development. Biotic and abiotic factors known to influence voltinism include soil moisture (Danforth 1999), temperature (Hairston and Kearns 1995; Forrest et al. 2019),

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This study builds our mechanistic understanding of the biotic and abiotic drivers behind shifts in insect voltinism, and demonstrates the potential of cryptic life stages to mediate responses to environmental change.

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and photoperiod (Norling 1984), as well as certain aspects of food resources such as quality (Hunter and McNeil 1997) and availability (Shintani et al. 2017). For example, many butterfly species are adding one or two extra generations per year because warmer, longer summers cue a switch from overwintering as an immature to directly developing into an adults within the same growing season (Macgregor et al. 2019; Michielini et al. 2021). In insects that have an obligate diapause, and therefore can produce at most one generation per year, environmental cues can still lead to variation between short and long life cycles. Chestnut weevils prolong life-cycle length from a 1-year life cycle to a 2- or 3-year life cycle in response to high food availability in early life (Menu and Desouhant 2002) and remarkably, yucca moths can remain in dormancy for decades in response to temperature (Powell 1989). In all of these cases, variation in life-cycle length is generated by how individuals time entry into dormancy—a critical, and often cryptic, life stage that allows survival during periods unsuitable for growth and reproduction, and typically occupies a large part of the annual time budget (Wilsterman et al. 2021). Despite the importance of dormancy timing for shaping voltinism within a population, for many taxa, the biotic and abiotic factors cueing different developmental trajectories remain unclear.

In this study, I evaluate the drivers of voltinism in a ground-nesting solitary bee (Colletidae: *Colletes validus*) and its blister beetle brood parasite (Meloidae: *Tricrania sanguinipennis*). Like many solitary bees, *C. validus* typically produces a single generation per year. However, intriguingly, nest excavations in 2018 and 2019 revealed that both univoltine and semivoltine individuals occur within the same population, a phenomenon known as cohort-splitting or parsivoltinism (after Torchio and Tepedino 1982). In parsivoltine taxa, univoltine individuals overwinter once as adults and emerge one year after being laid, whereas semivoltine individuals overwinter twice—once as a mature larva, and a second time as adult—and emerge two years after being laid (hereafter 1-year forms and 2-year forms, respectively). Crucially, all individuals undergo at least one diapause period, and variation in voltinism arises from some individuals prolonging dormancy for an extra year.

Temperature and food availability are two factors that might influence voltinism within solitary bees. Each solitary bees develops within a discrete brood cell independent of nest mates, and feeds on a discrete pollen provision provided by the mother, therefore developmental temperatures and provision size are likely to vary across offspring within a population. Although dormancy responds strongly to photoperiod in many temperate insects (Tauber et al. 1986; Danks 1992), it is unlikely to play a large role for ground-nesting solitary bees since development takes place in complete darkness within the nest. For ectotherms like bees, life-cycle length and developmental rate is expected to respond strongly to temperature. For parsivoltine solitary bees, cooler temperatures tend to decrease the number of generations per year, i.e., increase the fraction of semivoltine individuals. In the mason bee *Osmia iridis*, longer, semivoltine life cycles were more common under cooler experimental temperatures (Forrest et al. 2019), and in another study with several species of mason bees *Osmia* spp., higher rates of semivoltinism occurred at higher elevations than at lower elevations (Tepedino et al. 2022). Provision size has also been shown to influence voltinism in bees, consistent with expectations that a greater amount of food delays development and leads to longer life cycles in species that feed on discrete provisions (Danks 1992; Teder et al. 2014). For example, heavier *Macrotera portalis* bees were more likely to delay emergence for an extra year (Danforth 1999) and larger provision sizes are associated with longer life cycles in *Megachile rotundata* (Fischman et al. 2017). Together, these studies inform our understanding of how temperature and food availability independently shape bee voltinism. However, bees within the nest experience multiple environmental cues simultaneously, and multiple environmental cues might interact in non-additive ways to shape life-cycle responses (Tauber et al. 1986; Hairston and Kearns 1995).

To address this knowledge gap, I evaluate how temperature and provision size jointly influence voltinism in a solitary bee (*Colletes validus*). I also ask how temperature influences voltinism of their brood parasitic blister beetle *T. sanguinipennis*, which was included in experiments given the high proportion of beetle-parasitized brood cells recovered during nest excavations. Using crossed factorial experiments between temperature and food availability, I test the predictions that life-cycle length will increase under cooler temperatures (tested for bees and beetles) and increase with greater provision sizes (tested for bees only). I couch my experimental results in observations from three years of nest excavations. In addition, I track the demographic impacts of entering prolonged dormancy by measuring the fraction of 1-year and 2-year forms that survive to emergence as adults. I expected lower survival of 2-year forms since dormancy requires maintaining physiological status for an additional year without the opportunity to acquire additional food. Moreover, this study advances our mechanistic understanding of the drivers of voltinism for diverse insect taxa, offers insight into the role of dormancy for mediating responses to environmental change, and contextualizes a growing body of knowledge on patterns of phenology and voltinism in wild pollinators.

## Methods

### Study species

*Colletes validus* Cresson 1868 (Colletidae) is a solitary, ground-nesting bee that lives in pine barrens of eastern North America. In spring, mated females dig nests underground, forming conspicuous nesting aggregations with conspecifics (1–10 nests-m$^{-2}$). The nest of a single female contains between three to five brood cells, most of which are located 20–50 cm deep (Batra 1980). Each brood cell contains an egg provisioned with a soupy mixture of pollen and nectar primarily from blueberry (Ericaceae: *Vaccinium* spp.) flowers, though females have also been observed gathering pollen from *Arctostaphylos uva-ursi* (Ericaceae), *Hudsonia ericoides* (Cistaceae), and *Prunus pensylvanicus* (Rosaceae) (N. Dorian pers. obs.). Since offspring are produced in discrete, transparent brood cells, it is straightforward to manipulate environmental conditions among individuals and to visually track development across the life cycle.

Offspring in the nests of *C. validus* exhibit both 1-year and 2-year life cycles (Fig. 1). Upon hatching in spring $t_0$, larvae progress through five instars, reaching the prepupal stage by fall $t_0$ and consuming all food provisions in the process. One-year bees pupate, diapause over the winter, and emerge as adults spring $t_1$. In contrast, 2-year bees arrest

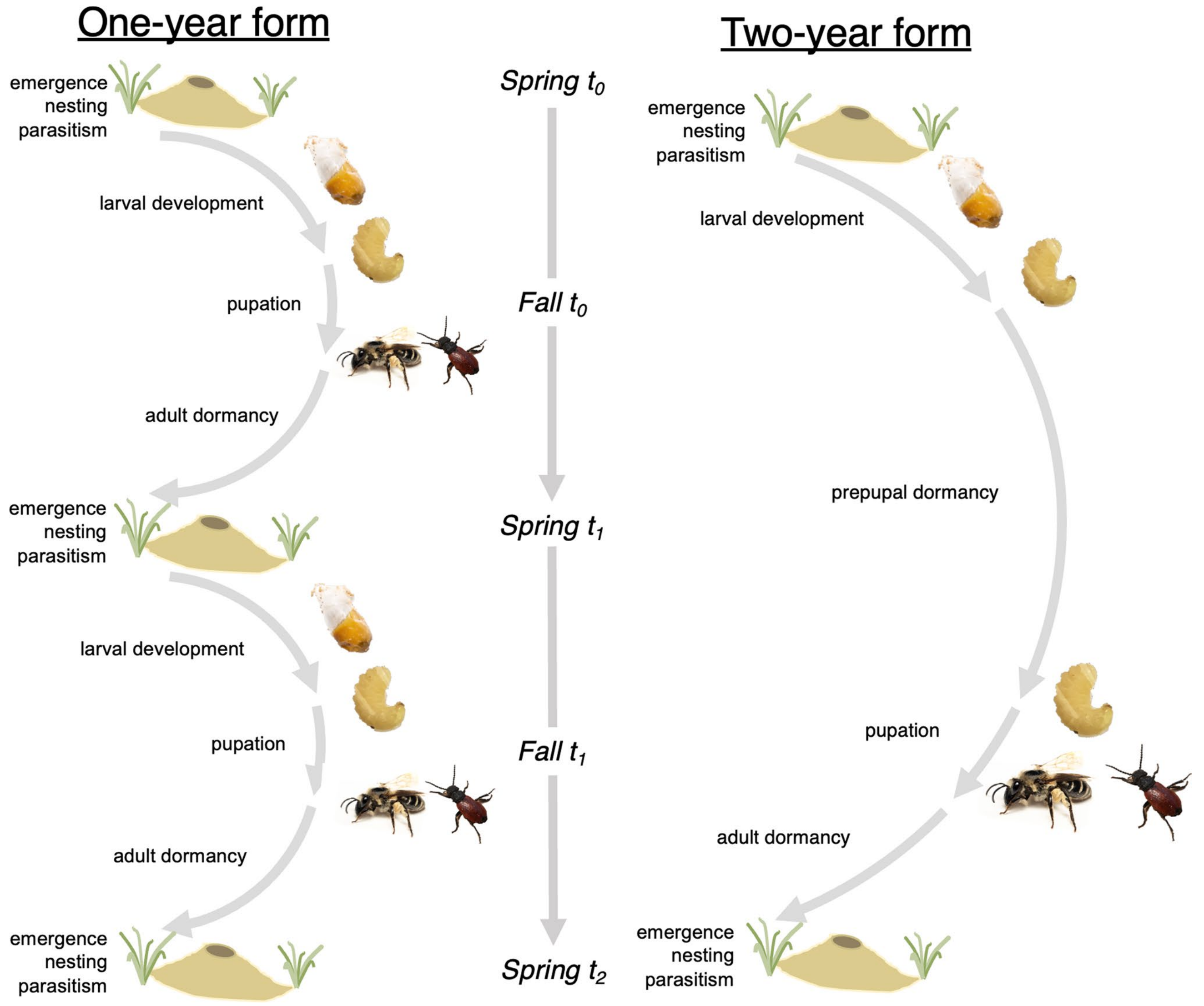

**Fig. 1** Two life-cycle lengths are observed in *Colletes validus* and *Tricrania sanguinipennis*: 1-year forms emerge after a single dormancy period, whereas 2-year forms emerge after two dormancy periods Intriguingly, 2-year forms overwinter as two different life stages, as mature larvae during their first winter, and as adults during their second winter

development as prepupae in fall $t_0$, diapause until spring $t_1$, pupate in fall $t_1$, and emerge in spring $t_2$ 2 years after being laid (Fig. 1). One-year bees and 2-year bees can be visually differentiated as early as fall $t_0$ (Fig. S1). Longer life cycles in this species, e.g., 3-year bees, have neither been observed in the wild nor recorded in the lab.

*Tricrania sanguinipennis* Say, 1824 (Meloidae) is a parasitic blister beetle that develops inside the brood cells of *C. validus* (Parker and Böving 1925; Batra 1980). Adult *T. sanguinipennis* beetles emerge in early spring and mate, and females lay eggs in the soil near *C. validus* nests. Eggs hatch into highly mobile, first instar larvae called triungulins which gain access into a nest by hitchhiking on the body of the female bee, possibly vectored by the male during copulation (Parker and Böving 1925; Vereecken and Mahe 2007). Once in the nest, larval beetles kill the host bee egg and each other, until just one triungulin remains (Parker and Böving 1925). The triungulin develops on the pollen provisions until it becomes a pseudopupa, which is a life stage adapted to persist through long periods of suboptimal conditions (Shintani et al. 2017). Beetles either pupate in the fall of their first year (1-year beetle) or arrest development as a pseudopupa and pupate one year later in the fall of their second year (2-year beetle). Life-cycle length of *T. sanguinipennis* can also be determined in fall $t_0$. Throughout the text, dormancy is used to mean prolonged periods of inactivity, which includes both diapause (which both 1- and 2-year forms undergo) and quiescence (Wilsterman et al. 2021).

## Field methods

I conducted fieldwork at Montague Plains Wildlife Management Area, Montague, Massachusetts (42.568, −72.536, hereafter Montague Plains). At this site, adult *C. validus* and *T. sanguinipennis* are active along a sandy powerline right-of-way for about 6 weeks each year, from mid-April through the end of May.

From 2020–2022, I marked active *C. validus* nests in spring with uniquely numbered metal tags (Forestry Suppliers, Jackson, MS). In 2020 and 2021, I returned in mid-June to excavate brood cells for lab experiments. Since nests occur in aggregate, I excavated clusters of nests (range = 2–6 nests per cluster). Recovered brood cells were placed into individual wells of a sterile 48 well plate (Corning, Glendale, AZ) and kept in a cooler for transport back to the lab (Fig. S1). In 2020, I excavated 387 brood cells from 121 nests, and in 2021, I excavated 283 brood cells from 91 nests. Upon return to the lab, I scored intact brood cells as live larval bee, live larval blister beetle, or dead. All living larvae were actively feeding with visible provision remaining; none had already developed into prepupae. Brood cells were frequently parasitized by blister beetles (parasitism rates: 5.6% of brood cells in 2020 and 7.7% of brood cells in 2021). Damaged brood cells were removed from the experiment.

From 2020–2022, I returned to Montague Plains in mid-September to measure the fraction of 2-year forms in natural populations. I conducted a second round of nest excavations by excavating nests built in spring $t_0$. Nest markers from the previous year were left in the ground at the site, allowing me to be sure that I was only excavating nests built that growing season. Therefore, the fraction of one and 2-year forms recovered from these nests could be used to estimate the rate of prolonged dormancy in the population produced in that year. I scored recovered brood cells as either 1-year bee (adult), 2-year bee (prepupa), or parasitized. In 2 out of 3 years, brood cells also contained parasitic bombyliid (*Bombylius* spp.) fly larvae; in 2020 and 2021, respectively, 26 and 11% of brood cells were parasitized by bombyliid flies. After scoring, I re-buried brood cells to reduce impact on the local population.

In 2021 and 2022, I buried temperature loggers (precision ± 0.5 °C; iButton, Whitewater, WI) to measure soil temperatures during bee development. Two temperature loggers were deployed 50 cm deep from May through October. Temperatures were recorded every 2 h.

## Lab experiments: solitary bees

In 2020 and 2021, I conducted 2 × 2 factorial experiments to determine the influence of temperature and provision size on *C. validus* voltinism. Temperature treatments consisted of warm (24 ± 0.5 °C) vs. cool (18.5 ± 0.5 °C), and food treatments consisted of no supplemental provision vs. supplement (+ 20% ± 5% additional provision by mass). Brood cells containing live larval bees were weighed to the nearest 0.01 g and then randomly assigned to one of four treatments: warm-no supplement ($n_{2020} = 61$, $n_{2021} = 30$), cool-no supplement ($n_{2020} = 59$, $n_{2021} = 36$), warm-supplement ($n_{2020} = 37$, $n_{2021} = 36$), and cool-supplement ($n_{2020} = 24$, $n_{2021} = 40$). Experimental treatments were chosen to simulate the natural variation in temperature and provision sizes experienced by larvae. The temperature treatments simulate roughly 20 and 80% quantiles of soil temperatures at Montague Plains. The supplemented provision treatment simulates the difference in weight of the upper quartile of brood cells compared to the median brood cell.

Bees assigned to supplement treatments were given additional pollen provisions containing 30% pollen to sugar solution (1:1 solution of refined sugar to distilled water by mass). I sliced open the top of each brood cell with a sterile scalpel and placed additional provision on the existing pollen mass, taking care not to disturb the feeding larva. Although *Vaccinium* pollen is preferred by *C. validus,* it is not commercially available and collecting sufficient

*Vaccinium* pollen for lab experiments is prohibitively labor-intensive since flowers have poricidal anthers. Therefore, I used honey bee collected pollen as the supplement in 2020, and I used single-source plum pollen (*Prunus* spp.) as the supplement in 2021 (Firman Pollen, Yakima, WA). To test whether opening the brood cell influenced survival of bees, I measured survival of un-opened brood cells in both temperature treatments in 2020 ($n = 181$). Survival to fall $t_0$ did not differ between the cells that were opened vs. the cells that were left intact (Binomial GLM $\chi^2 = 0.13$, df = 1, $p = 0.72$). Therefore, I combined opened and un-opened treatments for analyses of 2020 data.

All brood cells were stored in warm, dark conditions (24C, 0L: 24D) upon return from the lab. Within 48 h of collection, brood cells were processed and assigned to treatments, after which I stored brood cells in individual wells in sterile, capped 48 well plates. Well plates were buried in moistened sand in a plastic box to maintain sufficient humidity during rearing. I reared bees in 24-h darkness (to simulate below-ground nesting) in Percival I-30L environmental chambers (Percival Scientific, Perry, IA). I visually scored development of bees every 3–5 days during the experiment according to the following: larva, prepupa, pupa, adult, and dead. The transition from larva to prepupa was accompanied by a noticeable darkening of the brood cell indicating that the larva had finished consuming the provision. During scoring, bees were removed from their temperature treatments (scoring all bees within a single well plate took less than fifteen minutes) and examined under red light.

On 15-October, all surviving bees were scored as either 1- or 2-year bee and removed from experimental treatments. Surviving bees were placed in "winter conditions" (4 °C, 0L:24D) for 6 months. On 15-April, I measured survival of 1-year bees to emergence and 1-year bees were removed from the experiment. Two-year bees were transferred to "summer conditions" (24 °C, 0L:24D), regardless of initial rearing treatment.

In both experiments, I scored development and survival of 2-year bees from spring $t_1$ until emergence. On 15-October of the second year (fall $t_1$), 2-year bees were transferred to winter conditions for the second time. Then, on 15-April of the second year (spring $t_2$), I evaluated survival of 2-year bees to emergence by counting all alive adult bees.

## Lab experiments: blister beetles

In 2020, I placed beetle-parasitized brood cells ($n = 21$) into a single warm treatment, and in 2021, I partitioned beetle-parasitized brood cells ($n = 17$) among warm and cool temperature treatments (same conditions as the bees). Beetles were not partitioned among provision size treatments. I scored beetle life-cycle length in fall $t_0$ when 1-year beetles had pupated into adults and 2-year beetles had arrested development as pseudopupae. I also monitored survival of beetles to fall $t_0$ and to emergence (spring $t_1$ for 1-year beetles and spring $t_2$ for 2-year beetles), following the same summer- and winter-rearing regimes as bees.

## Data analysis

All analyses were performed in R version 4.1.2 (R Core Team 2023). Except where indicated, I built separate models for 2020 and 2021 experiments and all binomial generalized linear models (GLMs) were run with a logit link. The two years were analyzed separately given that the food provision treatments differed across the two experiments. Marginal hypothesis tests to determine significance of model predictors were conducted using the Anova() function in the *car* package (Fox and Weisberg 2019); type II tests were used for additive models and type III tests were used for models with interaction terms.

## Solitary bees

I determined how prolonged dormancy rate and survival to fall $t_0$ were influenced by temperature, provision size, and their interaction using binomial GLMs. For 1-year bees, I estimated survival to emergence using two binomial GLMs: (1) an intercept-only model to estimate an average survival rate among all 1-year bees and (2) a model including temperature, provision size, and their interaction as predictors. For 2-year bees, I estimated the average survival rate of bees from fall $t_0$ to three time points—spring $t_1$, fall $t_1$, and spring $t_2$—using separate intercept-only binomial GLMs. To determine the influence of rearing treatment on survival to emergence, I used binomial GLMs with provision size as the only predictor; temperature was not included as a predictor since there was insufficient variation among treatments (i.e., nearly all 2-year bees occurred in the cool treatments; see *Results*). I determined significance between survival estimates by assessing overlap of 83.4% confidence intervals (MacGregor-Fors and Payton 2013). Comparing the overlap of 83.4% confidence intervals (whether the lower interval of one estimate overlaps the upper interval of the other estimate) can be used to assess statistical significance between estimates not included in the same model at $\alpha = 0.05$ (MacGregor-Fors and Payton 2013).

## Blister beetles

I estimated prolonged dormancy of 2-year beetles in the 2021 experiment using a binomial GLM with temperature as a predictor. For both experiments, I used binomial GLMs to estimate survival of 1-year beetles from fall $t_0$ to emergence in spring $t_1$ and survival of 2-year beetles from fall $t_0$ to emergence in spring $t_{2.}$

### Solitary bee voltinism and temperature in the field

Soil temperatures during bee development at Montague Plains were estimated by averaging measurements from a logger placed 50 cm deep (1-May through 15-September) in 2021 and 2022. Soil temperatures were 21.03 °C in 2021 (SD = 4.11) and 21.57 °C in 2022 (SD = 3.36). In 2020, no loggers could be deployed, so I used average air temperatures from a nearby weather station as a proxy (South Deerfield, MA, ~ 10 km away). In 2021 and 2022, average air temperatures from South Deerfield and soil temperatures at Montague Plains during the growing season fell within 0.7 °C of each other, suggesting that it was reasonable to make this extrapolation for 2020. In 2020, average soil temperatures during bee development at Montague Plains were estimated from air temperatures in Deerfield, MA (~ 10 km miles away) to be 21.37 °C (SD = 5.56).

The proportion of 2-year bees at Montague Plains was estimated with a binomial GLM, where events were the number of brood cells containing a 2-year bee, trials as the total number of excavated brood cells containing a live bee, and a fixed effect of year. To assess the relationship between temperature and dormancy rate, including both field and lab estimates, I used Pearson's correlation between average temperature during development and the fraction of 2-year bees.

## Results

### Solitary bees

In both years, 2-year bees were more likely to occur under cool developmental temperatures than under warm temperatures, irrespective of provision size (Fig. 2a–b; Table 1). I found no significant effects of provision size, or provision size × temperature interactions on the prolonged dormancy rate (Table 1). In 2020, the proportions of 2-year bees in the cool treatments were 0.50 (cool-no

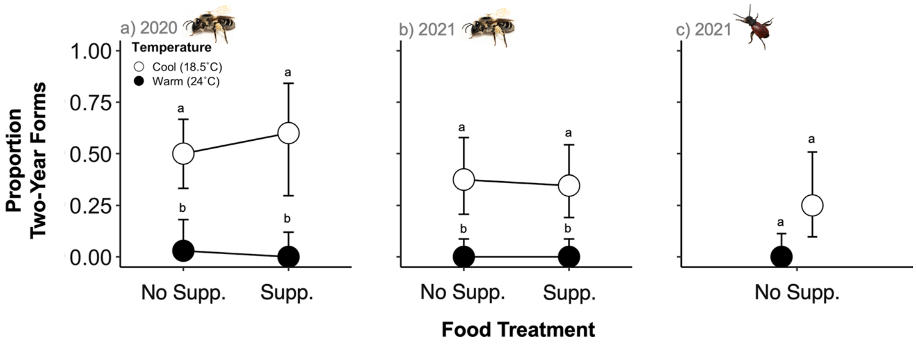

**Fig. 2** Proportion of 2-year forms of solitary bees (panels **a**, **b**) and parasitic beetles (panel **c**) was strongly influenced by temperature. Data shown are means ± 95% confidence intervals; statistical significance is denoted by differing letters within each panel

**Table 1** Marginal hypothesis test statistics for linear models assessing the effects of temperature and provision size on the proportion of 2-year forms (dormancy) and survival to fall of the first year (fall $t_0$)

| Species | Vital rate transition | Year | n | Model term | $\chi^2$ | df | *p* value |
|---|---|---|---|---|---|---|---|
| Solitary bee (*Colletes validus*) | Dormancy | 2020 | 91 | Temp | 21.92 | 1 | < 0.01 |
| | | | | Food | 0.31 | 1 | 0.58 |
| | | | | Temp × Food | 0.95 | 1 | 0.33 |
| | | 2021 | 90 | Temp | 13.80 | 1 | < 0.01 |
| | | | | Food | 0.11 | 1 | 0.74 |
| | | | | Temp × Food | 0 | 1 | 1 |
| | Survival to fall $t_0$ | 2020 | 181 | Temp | 0.07 | 1 | 0.79 |
| | | | | Food | 0.64 | 1 | 0.42 |
| | | | | Temp × food | 0.11 | 1 | 0.74 |
| | | 2021 | 144 | Temp | 0.27 | 1 | 0.60 |
| | | | | Food | 0.01 | 1 | 0.92 |
| | | | | Temp × food | 1.27 | 1 | 0.26 |
| Beetle (*Tricrania sanguinipennis*) | Dormancy | 2021 | 16 | Temp | 3.06 | 1 | 0.08 |
| | Survival to fall $t_0$ | 2021 | 17 | Temp | 1.33 | 1 | 0.25 |

supplement, $CI_{95} = 0.33–0.67$) and 0.60 (cool-supplement, $CI_{95} = 0.30–0.84$), and in the two warm treatments were 0.03 (warm-no supplement, $CI_{95} = 0.00–0.18$) and 0.00 (warm-supplement, $CI_{95} = 0.00–0.09$; Fig. 2a, Table 1). In 2021, the proportions of 2-year bees in the two cool treatments were 0.38 (cool-no supplement, $CI_{95} = 0.21–0.58$) and 0.35 (cool-supplement, $CI_{95} = 0.19–0.54$), and in the two warm treatments were 0.00 (warm-no supplement, $CI_{95} = 0.00–0.09$) and 0.00 (warm-supplement, $CI_{95} = 0.00–0.09$; Fig. 2b, Table 1).

On average, about half of all bees survived until fall $t_0$ (Fig. S2). The proportion of bees that survived to fall $t_0$ was 0.50 in 2020 ($CI_{95} = 0.43–0.56$, $n = 181$) and 0.63 in 2021 ($CI_{95} = 0.54–0.70$, $n = 144$). Survival to fall $t_0$ did not differ among treatments in either year (Table 1).

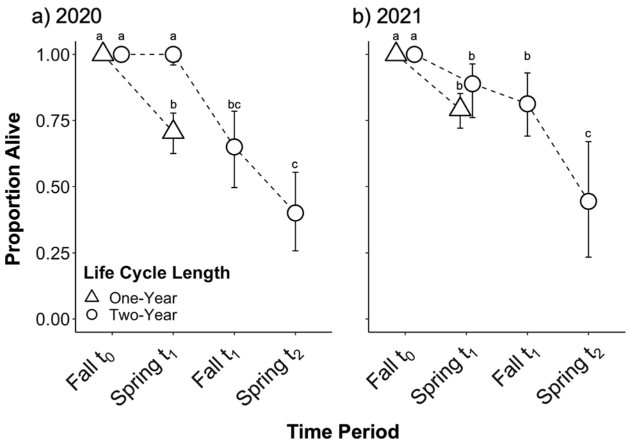

**Fig. 3** Survival of 1- and 2-year bees from fall of $t_0$ until emergence in **a** 2020 and **b** 2021 experiments. Time points indicate: fall $t_0$, when all bees are transferred to identical rearing conditions; spring $t_1$, when 1-year bees emerge and 2-year bees remain as prepupae; fall $t_1$, when 2-year bees pupate into adults; and spring $t_2$, when 2-year bees emerge. Data presented are means ± 83.4% confidence intervals. Differing letters within a panel denotes statistical significance; significance was assessed by whether confidence intervals overlapped. Some points are jittered horizontally to enhance readability

Over the first winter, 2-year bees had higher survival than 1-year bees (Fig. 3). In 2020, significantly more 2-year bees survived to spring $t_1$ (1.00, $CI_{83.4} = 0.96–1.00$, $n = 23$) than 1-year bees (0.71, $CI_{83.4} = 0.63–0.78$, $n = 68$) and in 2021, 2-year bees had slightly higher survival to spring $t_1$ (0.89, $CI_{83.4} = 0.76–0.96$, $n = 18$) than 1-year bees (0.79, $CI_{83.4} = 0.72–0.85$, $n = 72$), though this difference was not statistically significant.

For 1-year bees, survival to emergence (spring $t_1$) varied across treatments (Fig. S3; Table 2). In 2020, 1-year bees developing under cool conditions had significantly higher overwinter survival to spring $t_1$, regardless of provision treatment (cool: 0.95, $CI_{95} = 0.72–0.99$ vs. warm: 0.60, $CI_{95} = 0.46–0.73$; Table 2). In 2021, there was a significant interaction between temperature and provision size on 1-year bee survival to spring $t_1$ (Table 2). Bees developing in warm-no supplement (0.95, $CI_{95} = 0.73–0.99$, $n = 21$) and cool-supplement treatments (0.94, $CI_{95} = 0.94$, $CI_{95} = 0.68–0.99$, $n = 17$) had higher survival than warm-supplement (0.5, $CI_{95} = 0.29–0.71$, $n = 20$) and cool-no supplement treatments (0.79, $CI_{95} = 0.51–0.93$, $n = 14$). For 2-year bees, survival to spring $t_1$ did not vary across treatments in either year (2020: 1.00 in both provision treatments; 2021: no supplement = 0.89, $CI_{95} = 0.50–0.99$, $n = 9$ vs. supplement = 0.89, $CI_{95} = 0.50–0.99$, $n = 9$; Fig. 3).

Two-year bees had lower survival to emergence than 1-year bees (Fig. 3). Survival to fall $t_1$ of 2-year bees was 0.65 in 2020 ($CI_{83.4} = 0.50–0.79$, $n = 20$) and 0.83 in 2021 ($CI_{95} = 0.58–0.96$, $n = 18$) and did not significantly differ among provision treatments in either year (Fig. 3; Table 2). In 2020, the proportion of 2-year bees that survived to emergence was 0.40 ($CI_{83.4} = 0.26–0.55$, $n = 20$) which was significantly lower than survival of 1-year bees to emergence (0.71, $CI_{83.4} = 0.63–0.78$; Fig. 3a). Survival to spring $t_2$ was significantly higher for bees that did not receive a

**Table 2** Marginal hypothesis test statistics for linear models assessing the effects of temperature and provision size on the survival of 1- and 2-year forms to emergence

| Vital rate transition | Life-cycle length | Year | n | Model term | $\chi^2$ | df | *p*-value |
|---|---|---|---|---|---|---|---|
| fall $t_0$–spring $t_1$ (emergence) | One-year | 2020 | 68 | Temp | 7.90 | 1 | < 0.01 |
| | | | | Food | 0.46 | 1 | 0.49 |
| | | | | Temp × food | 0.32 | 1 | 0.57 |
| | | 2021 | 72 | Temp | 2.29 | 1 | 0.13 |
| | | | | Food | 1.69 | 1 | 0.19 |
| | | | | Temp × food | 9.33 | 1 | < 0.01 |
| fall $t_0$–spring $t_1$ | Two-year | 2020 | 23 | Food | 0 | 1 | 1 |
| | | 2021 | 18 | Food | 0 | 1 | 1 |
| fall $t_0$–fall $t_1$ | Two-year | 2020 | 20 | Food | 0.83 | 1 | 0.36 |
| | | 2021 | 18 | Food | 0.28 | 1 | 0.59 |
| fall $t_0$–spring $t_2$ (emergence) | Two-year | 2020 | 20 | Food | 7.8 | 1 | < 0.01 |
| | | 2021 | 18 | Food | 0 | 1 | 1 |

supplement compared to those that did receive a supplement (no supplement 0.57, $CI_{83.4} = 0.35–0.72$; supplement 0.0, $CI_{83.4} = 0.00–0.15$; Table 1). In 2021, 2-year bee survival to emergence was 0.44 ($CI_{83.4} = 0.23–0.67$, $n = 18$), which was significantly lower than survival of 1-year bees to emergence (0.79, $CI_{83.4} = 0.72–0.85$, $n = 72$; Fig. 3b). Survival of 2-year bees to spring $t_2$ did not differ significantly among provision treatments with both treatments having identical survival rates (no supplement: 0.44, $CI_{83.4} = 0.24–0.67$, $n = 9$; supplement: 0.44, $CI_{83.4} = 0.24–0.67$, $n = 9$; Table 1).

### Blister beetles

In the lab, blister beetles exhibited both 1-year and 2-year life cycles (Fig. 2c). In 2020, when reared only under warm conditions, all beetles exhibited a 1-year life cycle (1.00, $CI_{95} = 0.00–0.01$, $n = 19$). In 2021, when partitioned across temperature treatments, beetles exhibited 2-year life cycles in the cool treatment (0.25, $CI_{95} = 0.06–0.62$, $n = 8$), but not the warm treatment (0.00, $CI_{95} = 0.00–0.21$, $n = 8$), though this difference between treatments was not significant (Fig. 2c, Table 1).

In 2020, the proportion of blister beetles that survived to fall $t_0$ was 0.91 ($CI_{95} = 0.68–0.97$, $n = 21$) and, of those, nearly all survived to emergence (0.95, $CI_{95} = 0.71–0.99$, $n = 19$; Fig. S4). In 2021, the proportion of blister beetles that survived to fall $t_0$ was 0.94 ($CI_{95} = 0.77–0.99$, $n = 17$) and there was no difference in survival among treatments (Fig. S4). Both 1 and 2-year beetles had perfect survival to emergence in 2021 (1-year beetle: 1.00, $CI_{95} = 0.89–1.00$, $n = 15$; 2-year beetle: 1.00, $CI_{95} = 0.38–1.00$, $n = 2$).

### Relationship between temperature and solitary bee voltinism

The proportion of 2-year bees produced in the field ranged from 0.07–0.16, but did not differ significantly among years (2020: 0.09, $CI_{95} = 0.04–0.18$, $n = 77$; 2021: 0.16, $CI_{95} = 0.08–0.30$, $n = 43$; 2022: 0.07, $CI_{95} = 0.02–0.23$, $n = 30$; year $\chi^2 = 2.03$, df = 1, $p = 0.36$; Fig. 4). The proportion of 2-year bees was negatively correlated with temperature during development when data were pooled across all conditions (field and lab) in this study ($r = -0.92$, $t = -5.13$, df = 5, $p < 0.01$; Fig. 4).

## Discussion

Temperature strongly influenced voltinism in *C. validus*. In both experiments, the proportion of 2-year bees increased under cooler developmental temperatures. Notably, developmental decisions of bees were plastic in that larvae from different nests could be induced to arrest development as prepupae under cooler lab temperatures. These temperature effects may be conservative, in that bees were collected as larvae (not eggs) from the field, and therefore experienced the same field conditions up until the start of the experiment. A strong effect of temperature on voltinism agrees with past work in parsivoltine bees. For example, the proportion of 2-year forms of *Osmia californica* increased from 0 to 0.5 moving down a temperature cline of 6–8 °C (Tepedino et al. 2022) and the proportion of 2-year forms of *Osmia iridis* increased from 0.25 to 1 while dropping along a 7 °C temperature cline (Forrest et al. 2019). These responses from montane environments are strikingly similar to my findings from temperate New England (roughly 0 to 0.5 over a 6 °C gradient), and suggests an emerging pattern of how wild bee voltinism responds to temperature.

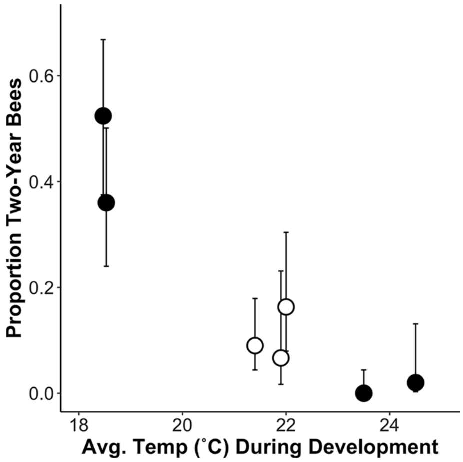

**Fig. 4** The proportion of 2-year forms of *Colletes validus* decreases with increasing developmental temperatures. Bees experienced temperatures during development in the field (open circles) that were intermediate to those experienced by lab cohorts (filled circles). Note that lab-reared bees were subjected to temperature treatments part way through development as larvae, not from the beginning of development as eggs. Data shown are mean estimates ± 95% confidence intervals of dormancy rates from bees developing in the field and the lab. Left-most two points are jittered slightly to improve readability; both correspond to a temperature of 18.5 °C. Point at 21.5 °C represents development temperature interpolated from a nearby weather station (South Deerfield, MA, ~ 10 km away)

Field observations were consistent with my experimental results, in the sense that both temperatures and the proportion of 2-year bees in the field were intermediate between the lab treatments (Fig. 4). There are two ways in which variation in voltinism between 1- and 2-year forms could be generated by natural variation in temperature. First, variation in temperature could be generated through variation in the depth at which brood cells were laid. In other insects, voltinism can be influenced by the depth at which larvae burrow, with longer life cycles occurring in offspring that develop in brood cells placed in deeper, cooler sites (Battisti 1994; Menu and Desouhant 2002). At Montague

Plains, I recovered *C. validus* brood cells from between 20 and 50 cm deep, and temperature loggers recorded soil temperatures of 20.5–22.0 °C over this range. Depending on the shape of the dormancy reaction norm to temperature in *C. validus*, it is plausible that this observed variation in temperature, mediated by nesting depth, could contribute to variation in life-cycle length (Fig. 4). Had I accounted for soil depth and temperatures at each depth, this hypothesis means that I would have observed differences in voltinism between "lower" and "upper" bees in the soil within a single year. An interesting line of future research would be to more rigorously test whether voltinism patterns of bees vary depending on nesting depth.

Second, temperature could vary in the field due to variation in the date on which eggs were laid. One possibility is that the date of egg laying is related to the number of suitable days for development within the growing season. My observations of *C. validus* from a separate nesting site in New Hampshire suggest that nesting occurs for about 45 days per year (N. Dorian *unpubl.*), meaning the earliest laid offspring could experience temperatures suitable for growth for more than 6 weeks longer than the latest laid offspring. Under this hypothesis, eggs laid latest in the season would be more likely to become 2-year bees than eggs laid earliest in the season; my field excavations did not account for the age of the nest, so I was unable to test this possibility. An alternative is that the date of egg laying underpins developmental decisions by interacting with photoperiod, which is a mechanism reported from several other insect taxa (Norling 1984; Hairston and Kearns 1995; Crowley and Hopper 2015). For solitary bees, photoperiod experienced by eggs and larvae is unlikely to play a role in voltinism since eggs and larvae occur in constant darkness. However, photoperiod may indirectly influence voltinism via maternal control (Forrest et al. 2019). It is possible that mothers who experience certain light conditions at the time of egg laying may transmit that information to offspring, which in turn would predispose offspring to either 1- or 2-year life cycle. Intriguingly, Forrest et al. (2019) found that eggs of the solitary bee *Osmia iridis* laid late in the season were more likely to exhibit 2-year life cycles, irrespective of temperature, hinting at the potential role of calendar date in governing life-cycle decisions of wild bees. Anecdotally, I observed a similar time-keeping phenomenon in *C. validus*: prepupae returned to "summer conditions" (suitable for growth) in April did not pupate until August—the date when 1-year bees pupate in wild populations—despite no obvious external way of keeping track of time (N. Dorian pers. obs.).

For blister beetles, past studies have shown that voltinism is sensitive to temperature (Shintani et al. 2017), however, as far as I am aware, my study is the first to report semivoltinism from this group. Although I did not detect a statistically significant impact of temperature on beetle voltinism in my experiment, blister beetles *Tricrania sanguinipennis* reared under cool conditions exhibited the expected pattern of fewer generations per year than those reared under warmer temperatures. This suggests that beetles have a capacity for developmental flexibility like their solitary bee hosts, as has been found for sapygid wasps *Sapyga* spp. that parasitize the solitary bee *Osmia iridis* (Forrest et al. 2019). My findings with beetles raise many more questions than they answer, and one worthwhile line of future work would be confirming whether or not prolonged dormancy occurs in wild beetles, and if so, how differences in rates of prolonged dormancy in bees and beetles shapes the relative balance of their interactions across years.

Unlike temperature, provision size did not influence solitary bee life-cycle length. An effect of provision size on developmental decisions has been found in past studies with solitary bees (Fischman et al. 2017; Helm et al. 2017). One possible explanation for the absence of an effect in my experiment is food quality. Although bees in my study were fed primarily food provisions from their mother, bees in the supplemental treatment were not supplemented with their preferred blueberry *Vaccinium* spp. pollen source due to logistical constraints. My field observations indicate that a small number of females gather non-*Vaccinium* pollen (specifically, *Prunus* spp. and *Hudsonia ericoides*), justifying this experimental decision, but the fate of offspring provisioned with these alternative pollen sources is unknown. In addition, larvae supplemented with *Prunus* spp. pollen in the lab had lower survival to emergence suggesting that supplemental non-host pollen may not have been suitable (Table 2). In some insects, food quality is known to influence diapause incidence (Short and Hahn 2023). For example, in a phytophagous tortricid moth (*Choristoneura rosaceana*), diapause incidence varies among host trees, with larvae feeding on red maple or black ash exhibiting a higher rate of diapause entry than those feeding on chokecherry (Hunter and McNeil 1997). Future work is needed to clarify the role of nutrition—both food quantity and quality—on life-cycle length in wild bees.

Life-cycle length influenced survival to emergence for bees, but not beetles. First, survival over the first winter was higher for both 2-year forms of bees and beetles (at this point, mature larvae) than 1-year forms (at this point, adults) (Fig. 3). This finding is consistent with the notion that the prepupal stage of solitary bees is adapted to persist during unfavorable conditions via a thicker cuticle and lower metabolic rate than adults (Kemp and Bosch 2000). However, after this first year, 2-year bees had significantly lower survival to emergence than 1-year bees (Fig. 3). Since bees do not have access to more food once they reach the prepupal stage, 2-year bees must survive twice as long as 1-year bees on the same energetic budget. Experimentally prolonged prepupal dormancy has been shown to decrease survival in the solitary mason bee *Osmia lignaria* due to depletion of metabolic reserves (Sgolastra et al. 2011), and lower survival of 2-year bees compared to 1-year bees has been found in *Osmia* spp. (Forrest et al. 2019; Tepedino et al. 2022). Despite the high survival costs incurred by 2-year bees, prolonged dormancy is widespread among wild bee species (Table S1), suggesting that there might be an advantage to developmental flexibility. Intriguingly, in contrast to bees, both 1- and 2-year beetles had perfect survival to emergence, despite presumably having to contend with similar energetic constraints.

Given the high mortality experienced by 2-year bees (even under protected lab conditions), why might this life cycle persist in natural populations? In some organisms, diversified life cycles—that is, producing offspring that emerge across multiple years—can provide demographic benefits by "averaging out" strong environmental variation among years via bet-hedging (Starrfelt and Kokko 2012; Gremer et al. 2016). In order for bet-hedging to evolve, the demographic costs of producing 2-year forms must be outweighed by the benefits of reducing among-year variance in fitness. Although theoretical basis for bet-hedging is strong, limited supporting evidence exists from natural populations (with the exception of desert annual plants Venable 2007; Gremer et al. 2016). One study in desert bees (*Perdita portalis*) provides observations of adult emergence phenology consistent with a bet-hedging life cycle (Danforth 1999), and another test with *C. validus* provides demographic evidence consistent with bet-hedging life cycle under some environmental conditions (Dorian 2023). Another non-mutually-exclusive explanation for the maintenance of 2-year forms is a developmental constraint. In temperate bees, pupae are unable survive winter, so there is a strong selective pressure to arrest development if there is insufficient time to complete pupation. The decision of whether or not to pupate must occur well before the growing season actually ends, and based on this study and others, seems to be based in part on temperature experienced during early development (Forrest et al. 2019). Therefore, an alternative hypothesis regarding cohort-splitting in solitary bees is that maintenance of both 1- and 2-year forms in nature is an emergent property of the physiological constraint that bees are able to survive the winter as one of two life stages—prepupae or adults—but not pupae (i.e., "not a strategy, but an outcome" sensu Tepedino et al. 2022).

My study comes with two important takeaways. First, this study corroborates temperature as a key factor shaping voltinism in solitary bees and contributes to a growing body of knowledge on the relative impacts of climate and food availability on wild pollinators (González-Varo et al. 2013; Kelemen and Rehan 2021; Kammerer et al. 2021). Within the context of rapid climate warming, it is interesting to consider how voltinism of *C. validus* might change into the future. By 2050, annual temperatures are expected to increase in New England between 1.4 and 5.0 °C (Kunkel et al. 2022), meaning that *C. validus* in Massachusetts may soon produce fewer 2-year forms under warmer conditions, and possibly none at all. All else being equal, an increase in the average number of generations produced per year (i.e., a shift from a mix of 1- and 2-year bees to all 1-year bees) increases average population growth rates, so the outcome of fewer 2-year bees may not necessarily be negative. However, if 2-year forms buffer against environmental variation (e.g., the bet-hedging hypothesis), then loss of 2-year bees may undermine *C. validus* long-term population growth rates. The second takeaway is that responses of cryptic life stages can have an outsized, if easily overlooked, impact on life-cycle length. This study is the first to report prolonged dormancy in *C. validus* and *T. sanguinipennis* in the field, and given the large gaps in our knowledge of bee nesting (Orr et al. 2022) and the life cycles of their parasites, it is possible that variation in life-cycle length may be more common than we currently appreciate. Although prolonged life cycles have been reported from at least 26 bee species, spread across four taxonomic families, most of these records are anecdotal and warrant further investigation (Table S1). Looking forward, efforts to interpret large-scale patterns of shifts in phenology and voltinism will be helped by focused experiments motivated by natural history observations throughout the life cycle. In particular, studies that consider cryptic, underground life stages, as well the impact of multiple cues simultaneously on life-cycle timing, will be key to a fuller understanding of how organisms respond to environmental change.

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**Data availability** All data and code associated with this project will be made available at: https://osf.io/htuq3/?view_only=e40a271c98fc4b7badf6e97ebc7b247e

## Declarations

**Conflict of interest** I declare no conflict of interest.

**Ethical approval** Ethics approval was not required for this study.

**Highlighted student research statement** This study builds our mechanistic understanding of the biotic and abiotic drivers behind shifts in insect voltinism, and demonstrates the potential of cryptic life stages to mediate responses to environmental change.

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