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An examination of synchrony between insect emergence and flowering in Rocky Mountain meadows

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Abstract. One possible effect of climate change is the generation of a mismatch in the seasonal timing of interacting organisms, owing to species-specific shifts in phenology. Despite concerns that plants and pollinators might be at risk of such decoupling, there have been few attempts to test this hypothesis using detailed phenological data on insect emergence and flowering at the same localities. In particular, there are few data sets on pollinator flight seasons that are independent of flowering phenology, because pollinators are typically collected at flowers. To address this problem, we established standardized nesting habitat (trap nests) for solitary bees and wasps at sites along an elevational gradient in the Rocky Mountains, and monitored emergence during three growing seasons. We also recorded air temperatures and flowering phenology at each site. Using a reciprocal transplant experiment with nesting bees, we confirmed that local environmental conditions are the primary determinants of emergence phenology. We were then able to develop phenology models to describe timing of pollinator emergence or flowering, across all sites and years, as a function of accumulated degree-days. Although phenology of both plants and insects is well described by thermal models, the best models for insects suggest generally higher threshold temperatures for development or diapause termination than those required for plants. In addition, degree-day requirements for most species, both plants and insects, were lower in locations with longer winters, indicating either a chilling or vernalization requirement that is more completely fulfilled at colder sites, or a critical photoperiod before which degree-day accumulation does not contribute to development. Overall, these results suggest that phenology of plants and trap-nesting bees and wasps is regulated in similar ways by temperature, but that plants are more likely than insects to advance phenology in response to springtime warming. We discuss the implications of these results for plants and pollinators, and suggest that phenological decoupling alone is unlikely to threaten population persistence for most species in our study area.

Key words: climate change; elevational gradient; Hymenoptera; phenology; pollination; reciprocal transplant experiment; Rocky Mountain Biological Laboratory; solitary bees; trap nests; trophic mismatch.

Introduction

Numerous authors suggest that climate change may lead to trophic mismatch, or phenological decoupling of interacting organisms (e.g., Price and Waser 1998, Inouye et al. 2000, Menzel et al. 2006, Cleland et al. 2007, Høye and Forchhammer 2008). Such effects could arise if, for instance, the springtime emergence of an herbivorous insect is triggered by different cues than those used by its host plant, and if climate warming differentially affects those cues. In this case, insects might fail to time their emergence to correspond with maximum food availability. There is now abundant evidence of shifts in phenology of individual species in response to climate change (Parmesan 2007, Rosenzweig et al. 2007), and a small but growing number of documented cases of climate-change-driven asynchrony between adjacent trophic levels (e.g., Edwards and Richardson 2004, Winder and Schindler 2004, Both et al. 2006, Visser et al. 2006). However, there is still little beyond anecdotal evidence for temporal mismatches between plants and insect pollinators (Hegland et al. 2009; but see Thomson 2010).

The lack of evidence may reflect a real absence of asynchrony, because phenologies of both plant and insect species are frequently well correlated with air temperatures in the months before emergence or flowering. On the other hand, long-term phenological data suggest that insects may be more responsive to temperature changes than are many plants (Gordo and Sanz 2005, Parmesan 2007). Therefore, if we have not yet observed phenological decoupling of plants and pollinators, this may merely reflect a shortage of long-term observations of most pollinator taxa. However, it is difficult to draw conclusions about the likelihood of

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asynchrony on the basis of global generalizations about plants and insects, because species in different environments are likely to have evolved different types of responses to environmental cues. In addition, to realistically assess the threat posed by climate change to plant–pollinator relationships, we will need to go beyond simple correlations between temperature and dates of first flowering or first insect sighting, and begin to test the ability of alternative models to predict phenology of interacting species (e.g., Visser and Holleman 2001). Long-term data and historical records, although valuable as a starting point, are often insufficiently detailed to achieve this more mechanistic goal; so, in many systems, we must use shorter time series and existing spatial variation in phenology, together with high-resolution climate data, to develop robust phenology models.

Determinants of flowering phenology

Flowering phenology has been relatively well studied, both in model organisms and in the field. Many plants respond strongly to photoperiod, with either short or long days promoting bud formation (Glover 2007). However, temperature also has a strong effect on development rate, and interacts with the photoperiod response to determine the actual timing of flowering (Billings and Mooney 1968, Wilczek et al. 2010). Studies using long-term data on flowering phenology in temperate-zone plants frequently emphasize the temperature effect, showing good correlations between springtime temperatures and dates of first or peak flowering (e.g., Fitter et al. 1995, Miller-Rushing et al. 2007, Miller-Rushing and Primack 2008).

For some species, phenology models have been developed to predict the date of flowering as a function of thermal units (e.g., growing degree-days, the cumulative amount of time spent above a particular threshold temperature), so that warmer years, in which the requisite amount of heat accumulates more quickly, are expected to show earlier flowering (Jackson 1966, Diekmann 1996, Wolfe et al. 2005, Hülber et al. 2010). However, there is another important aspect of plant responses to temperature: many plants require the passage of a period of cold temperatures before development can proceed, or develop more rapidly if a greater amount of chilling has occurred (Murray et al. 1989, Henderson et al. 2003). The chilling requirement for flowering, in particular, is known as vernalization. The need for chilling complicates interpretation of temperature effects on phenology; in some cases, springtime phenology may even be delayed by warming temperatures because of the reduction in chilling (cf. Zhang et al. 2007, Morin et al. 2009, Yu et al. 2010).

Finally, in high-altitude and high-latitude environments, flowering time is often strongly correlated with snowmelt (Inouye and Wielgolaski 2003, Kudo 2006, Ellebjerg et al. 2008). It is unclear whether snowmelt truly acts as a cue for plant phenology or whether it simply sets a lower limit on the date of initiation of growth, with the rate of subsequent development then more directly regulated by air and soil temperatures. Field studies that have examined the explanatory power of both snowmelt date and temperature in regulating flowering phenology have not reached consistent conclusions about which factor is of primary importance (Thórhallsdóttir 1998, Dunne et al. 2003, Hülber et al. 2010). Thus, in spite of the wealth of knowledge about flowering induction in model species such as *Arabidopsis thaliana*, we are still a long way from understanding what regulates flowering time of other taxa in the field.

Determinants of insect phenology

In many insects, development rate is closely tied to temperature (Tauber et al. 1986, Gullan and Cranston 2000). More specifically, the expected stage of development at a given time can often be predicted from the degree-days, above some estimated or assumed threshold temperature, accumulated up to that point (reviewed by van Asch and Visser 2007). Such degree-day models are commonly used to determine the appropriate time for application of pest control measures (Delahaut 2003).

Although temperature is likely to influence development rate in most insects simply through its effect on biochemical reaction kinetics, this does not tell the complete story about timing of adult emergence, which also typically involves the termination of seasonal diapause. Diapause termination may occur in response to an external stimulus (e.g., photoperiod, temperature) (Tauber et al. 1986) or, more rarely, to an internal biological clock (Blake 1959). Frequently, diapause is broken more readily if insects have experienced a sufficiently long chilling period (Kimberling and Miller 1988, Gomi 1996, Bosch and Kemp 2003, 2004). This is clearly analogous to the chilling requirements of many plants. In addition, insect activity is temperature dependent (de Jong et al. 1996, Willmer and Stone 2004, Saastamoinen and Hanski 2008), so that even if development is complete and diapause has been broken, insects are unlikely to be observed if the weather is cool and overcast.

The available long-term phenology records also reinforce the importance of temperature for insects: springtime air temperatures are good correlates of the first appearances of insects such as honey bees (Gordo and Sanz 2006) and butterflies (Sparks and Yates 1997, Roy and Sparks 2000, Gordo and Sanz 2006). One study, at an Arctic site, found date of snowmelt to be a better predictor than temperature of the timing of arthropod appearance in pitfall traps (Høye and Forchhammer 2008); however, the temperature data used for comparison were monthly means from a weather station 100–600 m from the sampling plots, so the predictive value of temperature may have been underestimated.

Unfortunately, phenology of pollinating insects, specifically, is difficult to monitor in an unbiased way. If records come from insects at flowers, where most pollinators are captured, the data cannot be independent of the phenology of the plants. Documenting a temporal mismatch between plants and pollinators is impossible using data collected in this way, unless one makes numerous assumptions (e.g., Memmott et al. 2007). Fortunately, there are laboratory data on one group of pollinators (bees in the genus *Osmia* [Megachilidae], some of which are important pollinators of orchard crops), and these reinforce the conclusion that temperature is a key determinant of phenology. *Osmia* spp. overwinter as adults and emerge in spring, so temperature dependence of larval development in the previous summer is essentially irrelevant to emergence phenology. However, bees do emerge earlier when incubated at warm post-wintering temperatures (Pitts-Singer et al. 2008, White et al. 2009) and after having experienced a sufficiently long chilling period (Bosch and Kemp 2003, 2004). Growth chamber experiments with overwintering *O. cornifrons*, in particular, demonstrate that a certain number of degree-days, rather than a specific temperature threshold, is needed to break diapause (White et al. 2009).

We therefore expect temperature to be of primary importance in regulating phenology of most temperate-zone insects, including pollinators, with other factors playing a secondary role. This is similar to the expectation for plants, although timing of snowmelt may be a more important factor in some environments. However, because temperature requirements for insect development and activity may differ from those of plants, it does not follow that temperature dependence in both taxa would ensure synchrony. Furthermore, laboratory studies typically manipulate a single environmental variable in isolation, and hold that variable constant throughout the experiment. This approach is useful for determining appropriate rearing conditions for managed populations, but results from such experiments cannot be used on their own to confidently predict phenology (or synchrony with other taxa) in the field, where temperature variability and other environmental factors come into play (Bosch and Kemp 2000, Gullan and Cranston 2000, Watt and McFarlane 2002). Field studies are also needed to test the applicability of the laboratory results to natural communities.

Objectives of this study

We studied insect phenology in subalpine habitats in the Rocky Mountains of Colorado, USA, where several studies have shown that plant phenology is strongly influenced by timing of snowmelt (Inouye et al. 2002, Dunne et al. 2003, Inouye et al. 2003), but where there is so far little information on the determinants of pollinator phenology. Plants and one group of insects in particular, the cavity-nesting Hymenoptera, seem potentially vulnerable to phenological decoupling. This is because these insects overwinter in trees, above ground, and therefore seem less likely than plants to be influenced by the date of bare ground. We therefore asked (1) which weather variables are most closely correlated with insect emergence, (2) do the same variables predict timing of plant flowering, and (3) to what extent do plant and insect phenology covary? To answer these questions in the absence of a long-term data set on insect phenology, we used spatial variation as a proxy for temporal variation in climate. Over three years, at sites along an elevational gradient, we collected data on air temperatures, insect emergence phenology, and flowering phenology. Emergence traps on insect nests allowed us to document pollinator phenology independently of flowering phenology (cf. Minckley et al. 1994). We experimentally verified that local environmental conditions, rather than local genotypes, were the main determinants of insect phenology by conducting a reciprocal transplant. We then evaluated various phenology models for several species of plants and insects to determine whether both groups have similar phenological responses to climatic variation.

Methods

Study system

Many species of flower-visiting wasps and bees nest in preexisting tunnels in wood and will readily occupy artificial structures ("trap nests"). Of these insects, only the bees are wholly and directly dependent on flowers for larval provisioning; the wasps are either predators of other arthropods or brood parasites of other cavity nesters (Table 1). However, as adults, all of these cavity-nesting species are flower visitors and use floral nectar as their main source of energy, and both bees and their brood parasites require pollen for larval growth. Trap nests provide standardized overwintering conditions and can be monitored for insect emergence in spring.

Study sites

In May of 2007 and 2008, we set out experimental trap nests at a total of 14 sites in the West Elk Mountains of central Colorado, USA (Table 2). At each site, we deployed trap nests at a height of ~1 m from the ground by attaching them to trunks of trees located at the edge of a meadow or clearing. The four sites with the highest occupancy rates in 2007 were used again in 2008; we also added six new sites in 2008. Although the sites span an elevational gradient of only 350 m, they encompass substantial variation in climate and phenology: the highest and lowest sites used in 2007 differed by 43 days in the date at which nests became snow-free in spring 2008, and differed by 2.5°C in June mean temperatures.

Field methods

Trap nests.—Details of trap-nest construction differed slightly between years (Fig. 1). In 2007, we placed four nest blocks at each site (eight at the reciprocal transplant

TABLE 1. Trap-nesting Hymenoptera investigated in this study.

Family and species	Larval food source	RT	NH	PM
A) Wasps				
Gasteruptiidae				
Gasteruption kirbii	larvae of trap-nesting bees or sphecoid wasps	×		×
Chrysididae				
Chrysis coerulans	prey of *Ancistrocerus* or *Symmorphus* spp.	×	×	×
Omalus aeneus	prey of *Passaloecus cuspidatus*	×		
Vespidae				
Ancistrocerus albophaleratus	moth caterpillars			×
Symmorphus cristatus	larvae of chrysomelid beetles	×		×
Sphecidae				
Passaloecus cuspidatus	aphids	×		
Trypoxylon frigidum	spiders			
B) Bees				
Colletidae				
Hylaeus annulatus	multiple plant species	×		×
Megachilidae				
Hoplitis fulgida	multiple species, mainly Rosaceae	×		×
Osmia coloradensis	Asteraceae		×	
Osmia iridis	plant species unknown		×	×
Osmia lignaria	multiple plant species	×		
Osmia tersula	multiple plant species			×
Megachile relativa	multiple species, mainly Asteraceae		×	
Stelis montana	nest stores of *Osmia* spp.		×	

Notes: Food source records of wasp larvae are from Krombein (1967) except *G. kirbii* (Townes 1950). Food sources of bees are from Rust (1974), Michener (1947), Mitchell (1960, 1962), Torchio (1989), Strickler et al. (1996), Sheffield et al. (2003), and J. R. K. Forrest (*personal observations*). Note that *Gasteruption*, *Chrysis*, *Omalus*, and *Stelis* are brood parasites; the other species are primary nest occupants. All 15 species consume floral nectar as adults, and all bees consume nectar and pollen as larvae. An "×" indicates that the species was sufficiently abundant for inclusion in a particular analysis (RT, reciprocal transplant; NH, nest height experiment; PM, phenology modeling). See the Appendix for a full list of taxa recorded in trap nests.

sites), each block consisting of a 22 cm section of 14 × 14 cm untreated softwood lumber. Blocks were prepared as described by Cane et al. (2010), except that we used four different diameters for nest holes (3.2–7.9 mm) and different types of hole lining (paper or cardboard straws, or no lining) in an effort to attract a range of insect species. Fifty holes, 14 cm deep, were drilled in each block. Asphalt roofing shingles provided some protection from rain.

In 2008, for each individual nest, we used a single 14 cm long section of 4 × 4 cm lumber with a hole drilled lengthwise through the middle. Ten of these nests were bound into a single unit ("nest block"), to which an overhanging hardboard roof was attached. At each site, 10 of these nest blocks (20 at the "401 Trail" site) were attached to trees, as in 2007. On average, we used larger nest holes in 2008: hole diameters ranged from 6.4 mm to 9.5 mm, again with different types of paper liners.

TABLE 2. Sites used in the study, showing year(s) in which each site was used.

Site name	Latitude (° N)	Longitude (° W)	Elevation (m)	2007–2008	2008–2009	2009–2010
Cement Creek	38°49′17.8″	106°52′9.8″	2682		×	×
Brush Creek 1†	38°51′39.8″	106°55′10.2″	2729	×		
Brush Creek 2	38°51′47.9″	106°54′54.0″	2743		×	×
Mt. Crested Butte	38°53′21.1″	106°57′44.3″	2889		×	
Rosy Point	38°55′57.6″	106°58′12.6″	2900	×		
South Gothic	38°57′16.6″	106°59′6.7″	2926		×	
Research Meadow	38°57′21.5″	106°58′55.7″	2929	×		
Marmot Meadow	38°58′40.4″	106°59′57.1″	2938		×	×
Kebler Clearing	38°51′30.9″	107°3′37.7″	2958	×	×	×
Splain's Gulch	38°51′24.2″	107°4′28.4″	2967	×	×	×
401 Trail‡	38°57′41.7″	106°59′5.6″	2970	×	×	×
Snodgrass	38°55′15.6″	106°58′16.3″	2999		×	×
Irwin Junction	38°51′21.7″	107°5′22.6″	3009	×		
Kebler Pass†	38°51′5.0″	107°6′0.0″	3034	×	×	×

† Sites used in reciprocal transplant experiment.
‡ Site used for nest height study.



FIG. 1. Examples of trap nests used in (A) 2007–2008 and (B) 2008–2010 for solitary bees and wasps at sites along an elevational gradient in the Rocky Mountains, Colorado, USA. Photo credit: J. Forrest.

In mid-August 2007, when most nesting activity was finished, emergence traps were attached to all nest blocks. Each trap consisted of a durable mesh panel supported by a wooden frame with a plugged access hole. A LogTag air temperature logger (MicroDAQ.com, Contoocook, New Hampshire, USA; accurate to ±0.5°C) was attached to the underside of one nest at each site to record temperatures hourly throughout the winter and following summer.

For the trap nests established in 2008, we attached emergence traps in the following May. These consisted of transparent vials attached to the front of each occupied nest hole, so that insects could emerge into the vials. A HOBO pendant temperature/light data logger (Onset Computer Corp., Bourne, Massachusetts, USA; accurate to ±0.5°C) was attached to the underside of one centrally located nest block at each site (two at the 401 Trail site) and took hourly readings from July 2008 to July 2010 at all but two sites. At the remaining two sites, data loggers were removed in September 2009 because of damage to the nest blocks.

Reciprocal transplant experiment.—In 2007, we established twice as many trap nests at the highest- and lowest-elevation sites as at the remaining sites. These two sites are separated by ~15 km and 350 m in elevation, without major barriers to dispersal. In late summer, after emergence traps had been attached, four of eight nest blocks at the highest site were switched with four blocks at the lowest site, so that insects occupying these nests would experience overwintering and springtime conditions at the transplant site. Because nests of different insect species were unevenly distributed among nest blocks, we assigned blocks nonrandomly to the transplant and control treatments in an effort to achieve a balanced design for as many species as possible.

Nest height study.—In 2008, at the 401 Trail site, we also deployed a double set of trap nests. The objective of this study was to decouple the effects of snowmelt date and spring–summer air temperature on insect phenology by having nest blocks experience differing durations of snow cover in an otherwise similar microenvironment. To do this, we used a paired design: lower blocks were attached at 50 cm above ground level, and upper blocks were attached to the same 10 trees at 125 cm. Maximum snowpack commonly exceeds 150 cm in this area (b. barr, *personal communication*), and we have observed bees occupying or searching for natural nests from ~0.15 to >2 m above ground level. One lower and one upper block were outfitted with HOBO data loggers. Nest blocks were assigned to heights before nesting began, and insects were allowed to select their own nest height "treatments." It is therefore possible that

differences in emergence phenology between upper and lower nests could be due to nonrandom nest selection, if, for instance, mothers of high-condition, rapidly developing larvae tend to select lower nests. However, because we consider such correlations unlikely, we treat nest position effects in this study as the result solely of environmental differences between high and low nests.

Nest monitoring and flower censuses.—Starting in early May of 2008 and 2009, and continuing until late July, trap nests were monitored every 2–4 days for emerging insects. Nests at all sites were monitored less frequently (1–2 times per week) during August 2008 and 2009. We also monitored nests approximately weekly between early May and mid-July 2010 because we observed that many nesting *Osmia* had remained in diapause through 2009. In 2008 and 2009, insects that were alive when we checked traps were assumed to have emerged on that date; dead insects were assigned an emergence date two days earlier. In 2010, dead insects were assumed to have emerged four days earlier, because of the reduced sampling frequency. Bees and wasps were preserved and identified to species, if possible, using keys in Krombein (1938), Sandhouse (1940), and Bohart and Menke (1976) for Sphecidae; Bohart and Kimsey (1982) for Chrysididae; Bequaert (1943), Carpenter and Cumming (1985), Cumming (1989), and Buck et al. (2008) for Eumeninae (Vespidae); Townes (1950) for Gasteruptiidae; Sandhouse (1939) and Michener (1947) for Megachilidae; and Snelling (1970) for *Hylaeus* (Colletidae). Voucher specimens are deposited in the Royal Alberta Museum (Edmonton, Alberta, Canada), the USDA–ARS Pollinating Insect Research Lab (Logan, Utah, USA), and the RMBL (Rocky Mountain Biological Laboratory, Crested Butte, Colorado, USA) insect collection.

On each day from May to late July 2008 and 2009 that we checked a site for emerging insects, we also monitored flowering plants. We established three or four 100-m permanent belt transects at each site, radiating out from the trap nests in approximately the four cardinal directions. Some transects were truncated if they encountered a barrier such as a road, cliff edge, or dense forest. The choice of a 100 m radius is somewhat arbitrary, and very likely underestimates resources available to newly emerged insects: typical natal dispersal distances are unknown, but *Osmia*-sized solitary bees can fly distances of several hundred meters (Gathmann and Tscharntke 2002, Greenleaf et al. 2007). However, preferred foraging ranges are certainly less than this in several species (see, e.g., Peterson and Roitberg 2006, Greenleaf et al. 2007, Zurbuchen et al. 2010). In any case, as the purpose of the transects was to estimate phenological progression of the flowering plant community rather than to quantify resource availability, a 100 m radius provides a reasonable index. Transect widths ranged from 10 to 200 cm, depending on the size and population density of the species being counted. For most plant species, we counted the number of open flowers, or capitula (Asteraceae), found on the transects. For species with many flowers per plant (*Mertensia* spp. [Boraginaceae], *Viola praemorsa* [Violaceae]), we instead counted the number of whole plants that had at least one open flower. Plant taxonomy follows Hartman and Nelson (2001). *Mertensia fusiformis* and *M. brevistyla* are morphologically and phenologically very similar (and frequently synonymized; Hartman and Nelson 2001), so we treated these as a single taxon here, called "*M. fusiformis*" for convenience (*M. brevistyla* occurred only at the Kebler Pass site).

Data analysis

Estimating snow cover from weather data.—We assumed that a recorded daily temperature range of <5°C indicated insulation of nest blocks by snow. In the 2008–2009 and 2009–2010 winters, when data-loggers recorded light as well as temperature, we were able to confirm that these periods of low temperature variability corresponded with periods of low daily maximum light intensities (<1000 lux, compared to typical maxima of $\sim$30 000 lux on sunny summer days). Duration of snow cover was therefore estimated as the interval between the first and last days with daily ranges <5°C (excluding brief, isolated periods of low temperature variability).

Response variables.—For the reciprocal transplant experiment and the nest height study, we wished to make inferences about treatment effects on mean, or median, emergence dates of insects. We did this by treating individual insects (or entire species) as replicates and each individual's date of emergence (or the mean date of emergence for a species at one site) as the response variable. For developing predictive phenology models, however, we used emergence and flowering data from each sampling date, while treating sites and years as the units of replication. This allowed us to make inferences about climate effects on the entire distribution of emergence and flowering dates (not only on first or peak dates). These analyses will be described in more detail.

Reciprocal transplant experiment.—A balanced three-way ANOVA, with species, site of emergence, and site of origin as factors predicting mean emergence date, would be desirable but was not possible because each species was absent or rare in at least one of the four treatment combinations. We therefore treated species, rather than individual insects, as replicates, and tested for an effect of site of emergence (high or low) and site of origin (high or low) using two separate paired t tests in which each pair consisted of a species' mean emergence dates at the two sites. Differences between sites in mean emergence dates for each species were approximately normally distributed. For species represented by at least five individuals per treatment in at least two treatments, we were also able to test for treatment effects on emergence date for each species, using the emergence date of each individual as a replicate. Here, we tested for effects of site of origin and site of emergence separately, using

Kruskal-Wallis (Mann-Whitney) tests because emergence dates of individuals were non-normally distributed.

Nest height study.—Species that were represented by at least five individuals in both the upper (1.25 m) and lower (0.5 m) nests were used for analysis. Emergence dates of individual insects were not normally distributed, so we tested the effect of nest height using Kruskal-Wallis tests.

Estimating temperature effects on emergence and flowering.—We wished to determine the most likely phenology model for each plant and insect species that was well represented in our data set. Preliminary analyses showed that peak dates of flowering and insect emergence at different sites in 2008 were predicted well by degree-days above a base temperature between 0° and 10°C in the preceding months; for most species, degree-days were better predictors than snowmelt date, various candidate threshold air temperatures, or mean temperatures in the preceding months. Consequently, for the remainder of the analysis, we focused on developing degree-day models for each species and seeing whether plants and insects responded similarly.

We focused on the eight insect species (Table 1) for which we had collected at least 50 individuals across all sites and years (range 51–540) and that were present at a minimum of four sites. All but two (*Hylaeus annulatus* and *Osmia tersula*) were adequately represented in at least two years of the study. The six focal plant species were those that were abundant at a majority of sites and for which our monitoring had captured most or all of the flowering period at each site. For the two focal species for which we had missed the end of flowering (*Linum lewisii* [Linaceae] and *Helianthella quinquenervis* [Asteraceae]), we fitted sine curves to the existing data (following Malo 2002) to allow us to estimate flower densities on later (hypothetical) sampling dates. In all cases, these estimates indicated that our sampling had captured more than 95% of all flowering. Using the actual or estimated flower counts, we calculated the cumulative proportion of flowering for a given species by a given date as the sum of all flower counts of that species prior to and including that sampling date, divided by the sum of all counts of that species over all sampling dates (in a fixed sampling area).

For each sampling date or estimated emergence date, we calculated accumulated degree-days until that date using the hourly air temperature data from each site (see Supplement). We calculated degree-days (DD) since 1 January using a range of base temperatures (0–15°C in 1°C increments), because the lower threshold temperature for development or activity was unknown for these taxa and had to be estimated from the data. For each species, we fit generalized linear mixed models, with binomial error and logit link, to the cumulative proportion of emergence or flowering that had occurred by a given date. Initially, we used degree-days above a particular base temperature, and site (a random factor) nested within year (fixed), as predictor variables. However, the year effect could not be tested for all species (some were recorded in only one year), and it was nonsignificant in many, but not all, of the others. We therefore created a single, composite, random variable, "site–year," to encompass all site + year combinations. For simplicity and consistency, we report only the results of analyses using site–year instead of site nested within year. Similarly, we allowed random variation in regression intercepts for each site–year, but slopes were fixed because inclusion of a random slope term did not significantly improve model fit for most species. Logistic models are commonly used for phenology modeling (e.g., Kemp and Onsager 1986, Manel and Debouzie 1997, Meagher and Delph 2001, Régnière et al. 2007), and although they will not produce the best fit in cases where phenological events are not normally distributed (Brown and Mayer 1988), we found that they generally provided a good fit to our data (see Figs. 2 and 3). Data transformations did not improve model fit, so we used untransformed data. We used the lme4 package in R (R Development Core Team 2007) to fit logistic models, using each possible base temperature for DD accumulation. Because models did not differ in the number of parameters, models were compared simply on the basis of their log likelihoods.

Because we found highly significant effects of site–year in these models ($P < 0.0001$ for all species, according to likelihood ratio tests against models with site–year omitted), we attempted to explain these effects as a consequence of among-site and among-year variation in the amount of chilling. We defined "chill days" as hours between 1 October and 31 March in which local temperature was below 5°C, divided by 24. (We tested alternate definitions, such as higher or lower threshold temperatures and greater ranges of dates, and found that these gave qualitatively similar, although typically weaker, results. Low, but not subzero, temperatures are required for vernalization in *Arabidopsis thaliana* [Kim et al. 2009] and are regularly used for housing *Osmia* over winter [e.g., Kemp and Bosch 2005, White et al. 2009] because they hasten subsequent springtime emergence [Bosch and Kemp 2004].) We then tested, using linear regression, whether the site–year-specific intercepts of the best-fit logistic regressions could be predicted by chill days. As an alternative, we also tested whether start dates for DD accumulation later than 1 January improved model fit. Later start dates have the effect of discounting any heating that occurs early in the year, effectively penalizing lower elevation or earlier warming sites for their head start in DD accumulation, and producing an effect similar to the incorporation of chill days in the model (Fig. 4). Specifically, we tested start dates between 22 March and 10 June (or the latest possible date prior to the onset of each species' emergence or flowering), in 10-d increments. We chose 22 March because little heating occurs before this date at any site.

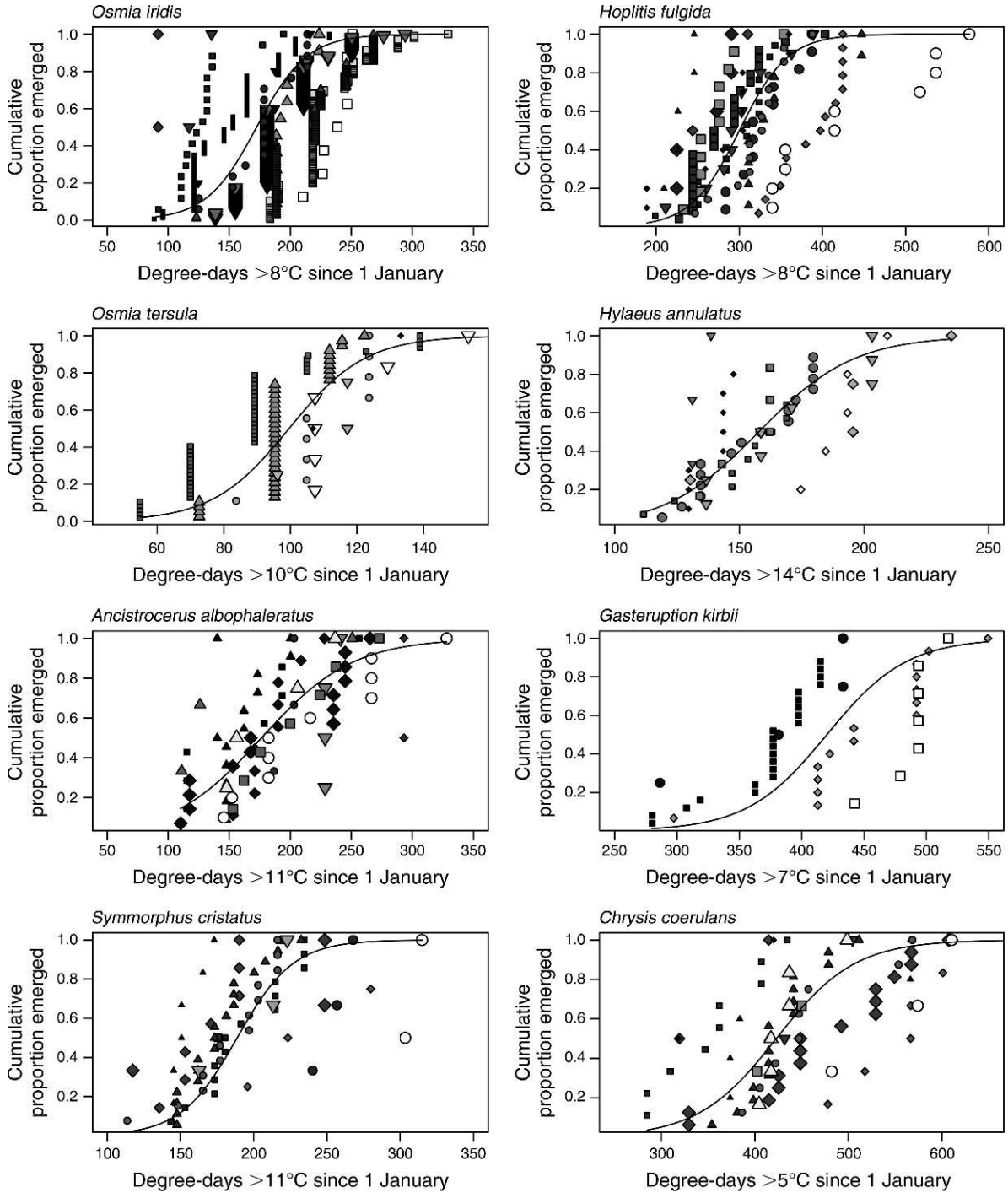

FIG. 2. Emergence phenology of eight species of trap-nesting Hymenoptera at subalpine meadow sites. The cumulative proportion of emergence having occurred on each sampling date at each site is plotted against the number of degree-days accumulated up to that date. Note that different base temperatures are used for each species; these are the base temperatures that provide the best model fits across all sites and years. Different site–year combinations are indicated by different symbols. Symbol shading corresponds to the number of chill days (see *Methods: Data analysis: Estimating temperature effects on emergence and flowering*) experienced at each site in the preceding winter (lighter shading represents fewer chill days); sites experiencing less chilling tend to be found farther to the right in each plot, indicating that they require more heat accumulation for emergence. Note that there were 27 different site–year combinations; only a subset are shown in each panel. Symbols and shading were chosen for within-panel clarity and contrast; thus they are not completely consistent across all panels. Lines show the best-fit logistic regressions for each species over all site–years combined (regressions for individual site–years are omitted for clarity).

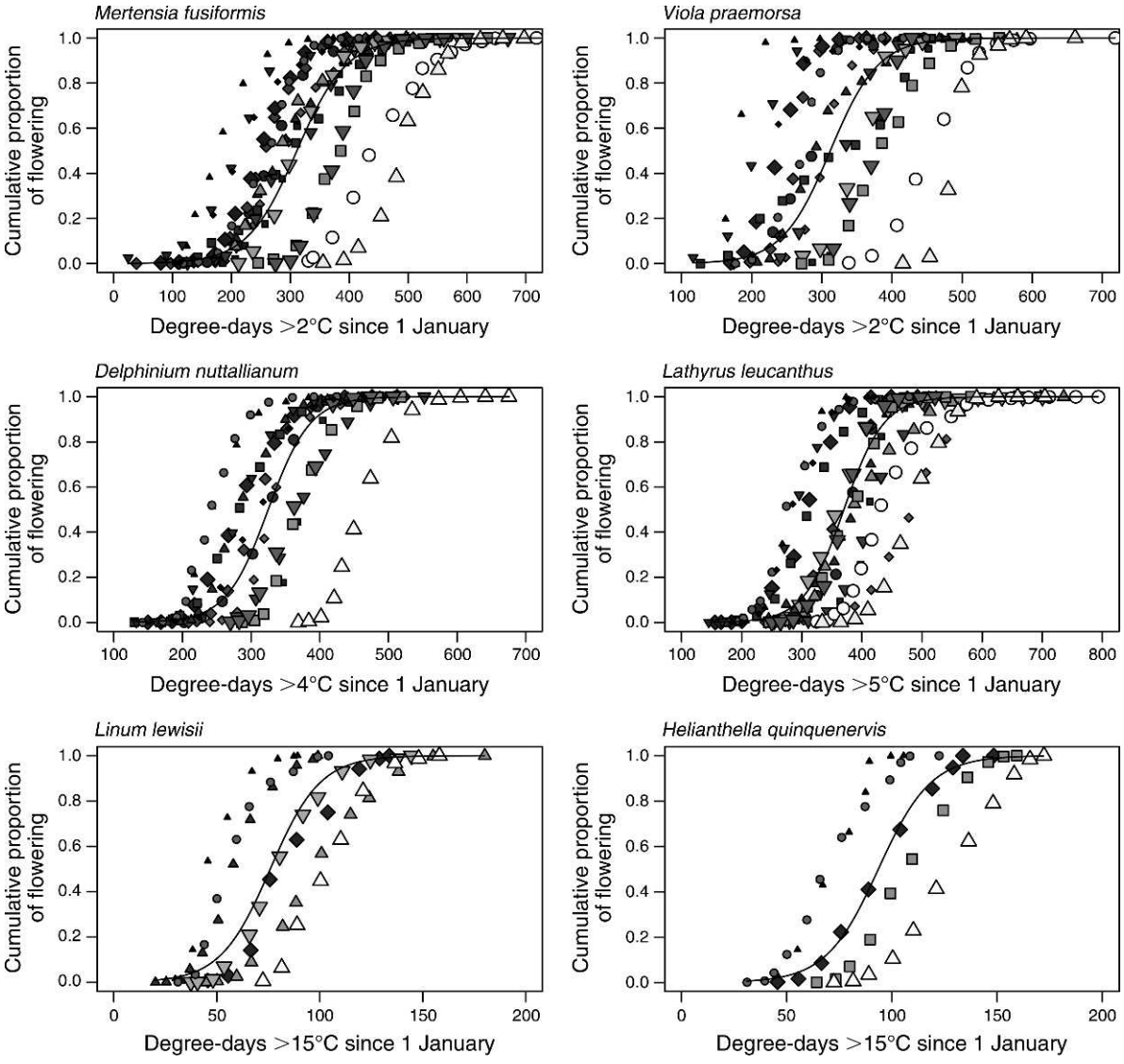

FIG. 3. Flowering phenology of six plant species at sites along an elevational gradient. Lines and shading are as in Fig. 2.

Decoupling of plants and pollinators.—Finally, to evaluate whether differences in the temperature responses of bees and plants could result in their phenologies coinciding in some sites or years, but not others, we plotted median emergence dates of *Hoplitis fulgida*, the best represented bee species in our 2008–2009 samples ($N = 142$), against median flowering dates of two plant species it is known to visit, for each site–year. Points falling along the 1:1 line in these plots would indicate site–years with perfect synchrony between insect emergence and plant flowering. Points lying above the line represent site–years in which flowering was past its peak by the time of peak insect emergence; such a scenario would presumably make that resource largely unavailable to the insects. In contrast, points below the line represent site–years in which insect emergence precedes flowering; if the precedence is not too great (i.e., does not exceed a bee's life span or its ability to survive without food), these floral resources are likely to be available to foraging bees. *Lathyrus lanszwertii* var. *leucanthus* (henceforth *Lathyrus*; Fabaceae) is the plant species in our data set with a phenology most similar to that of *H. fulgida*. However, *Potentilla hippiana* × *gracilis* (henceforth *Potentilla*; Rosaceae) is a species on which *H. fulgida* females are frequently seen collecting pollen, and it may be a more important resource for this bee. Both plant species are visited by other insects; neither is dependent on *H. fulgida* for cross-pollination. We did not include *Potentilla* in previous analyses, because our sampling did not capture its full flowering period at most sites, and it has an indeterminate and frequently bimodal flowering curve that defied all attempts to fit parametric models. (This may be because this taxon encompasses multiple hybrid

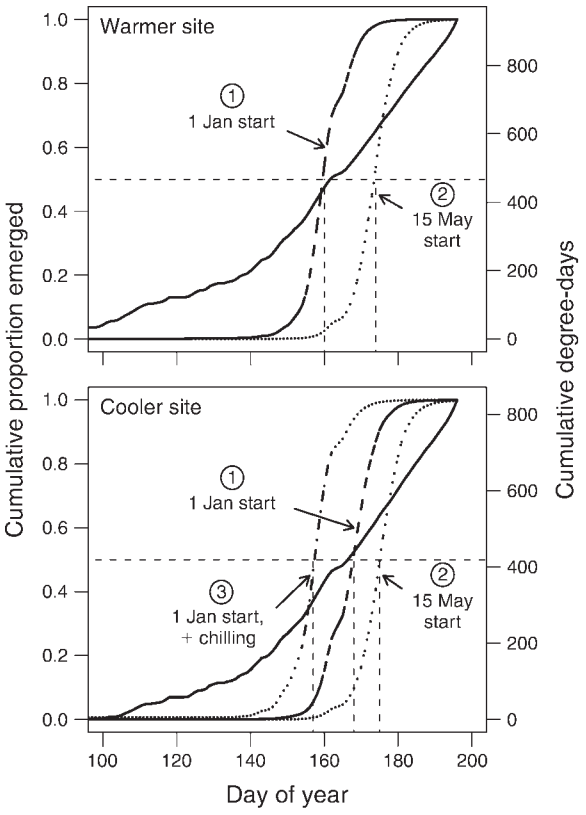

FIG. 4. Proposed relationship between heat accumulation, chilling, and phenology, illustrated for two hypothetical sites with different weather patterns. In both cases, cumulative emergence (or flowering), y, is a logistic function of accumulated degree-days, x; i.e., $y = 1/(1 + e^{-a-bx})$, where a is the intercept of the logistic function and b is its slope. The right-hand axes and solid curves represent cumulative degree-days from 1 January (day of year = 1). The left-hand axes and broken curves represent cumulative emergence under different (numbered) scenarios. Median emergence dates are indicated by the intersection of the horizontal dashed line and the emergence curves. In scenario (1), degree-day accumulation begins on 1 January and organisms are not exposed to chilling temperatures; in this scenario, median emergence occurs later at the cooler site. Scenario (2) is the same as (1) except that degree-day accumulation does not begin until 15 May (day 135) at either site; this has the effect of making median emergence dates more similar between sites. Scenario (3) is the same as (1) except that greater exposure to chilling temperatures at the cooler site is hypothesized to raise the value of the intercept, a, such that emergence occurs earlier for a given amount of heating. The figure demonstrates that changing either the start date for degree-day accumulation or the intercept of the logistic function shifts the position of the phenology curve along the x-axis. Parameter values are: $b = 0.023$ for all three scenarios; $a = -10$ for (1) and (2), and $a = -5$ for (3).

strains, with slightly different phenologies, that could not be distinguished in the field.) Here, for illustrative purposes, we treated the data as though we had captured the full flowering curve at each site. It should be noted that doing so biases estimates of peak flowering toward earlier dates, particularly at late-flowering sites; however, it does not affect the earlier part of the flowering curve, with which *H. fulgida* emergence coincides.

RESULTS

In total, 412 insects representing 25 species of Hymenoptera, excluding Ichneumonoidea, emerged from our trap nests during the 2008 season; 731 insects (27 species, of which 18 were also present in 2008) emerged in 2009, and 963 insects (eight species) had a two-year life cycle, emerging in 2010 (see Appendix). *Osmia iridis* and *O. tersula* were present in all three years, indicating that these species are parsivoltine in our study area (i.e., capable of a one- or two-year life cycle; Torchio and Tepedino 1982); but the latter was represented by only a single individual in 2009. Most species were rare (<50 individuals across all three years), but those that were sufficiently numerous for analysis are listed in Table 1.

Reciprocal transplant experiment

Nine insect species occurred in at least two of the four reciprocal transplant treatments (two sites of origin × two transplant sites). Considering all of these together, there was no indication of a site-of-origin effect on mean emergence date (paired t test, $t_5 = 0.42$, $P = 0.69$; Fig. 5). The difference in mean emergence dates between insects originating at high- and low-elevation sites would have had to exceed 9.8 days to be detectable with 90% power; the observed mean difference was only 1.0 d (low-site insects emerging slightly later than those from the high site). In contrast, there was a significant effect of overwintering site on mean emergence date: insects overwintering at the high-elevation site emerged, on average, 18.2 d later than those at the low-elevation site (paired t test, $t_8 = 8.20$, $P < 0.0001$; Fig. 5). To check that the significance of the latter test was not solely due to its larger sample size, we ran the test again with all possible subsets of $N = 6$ species; the highest P value obtained was 0.0034, suggesting that the result is robust.

These overall patterns were consistent with those obtained from the two species (both bees) that we were able to test individually: *Osmia lignaria* occurred naturally only at the low-elevation site, where it emerged in mid-to-late May, but it emerged from transplanted nests at the high site, on average, 34 days later (Kruskal-Wallis $\chi^2 = 13.7$, $P = 0.00021$, $N = 10 + 9$). *Hoplitis fulgida* individuals originating at the high site also emerged 16 days later at that site than when transplanted to the low site (Kruskal-Wallis $\chi^2 = 10.7$, $P = 0.0011$, $N = 14 + 5$); conversely, bees overwintering at the high site emerged at approximately the same time (18 or 20 July, on average), regardless of site of origin (Kruskal-Wallis $\chi^2 = 0.047$, $P = 0.83$, $N = 5 + 5$). (In comparison, snow melted from high-elevation nests 43 days later than from low-elevation nests.) Thus, overall, any genetic effect on insect phenology is weak compared with the effect of local environmental conditions.

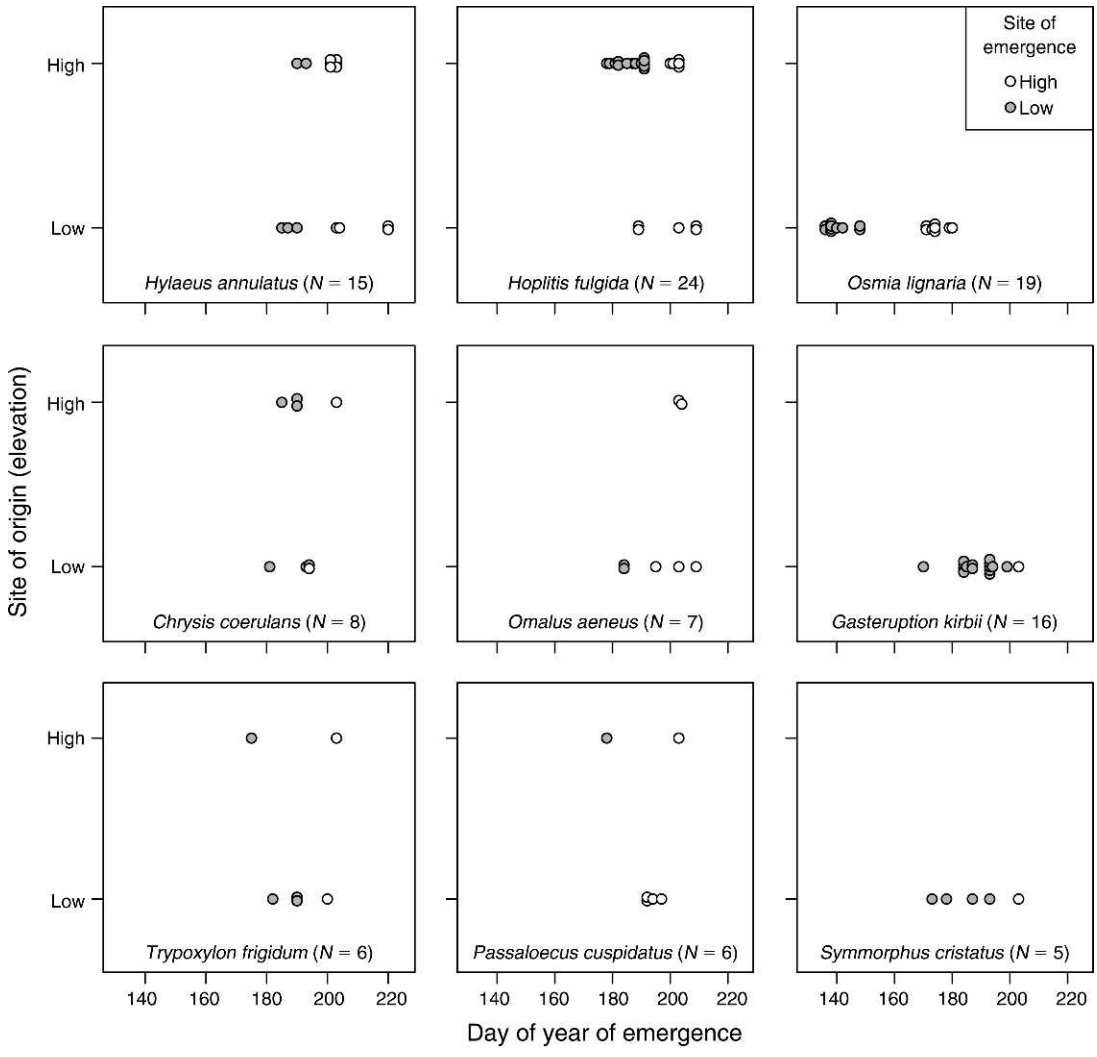

FIG. 5. Emergence dates for nine species of trap-nesting Hymenoptera occurring in the reciprocal transplant experiment, as a function of site of origin and site of emergence. Each circle represents one insect. Shaded circles represent insects emerging at the low-elevation site; open circles represent the high-elevation site. Data points have been jittered for clarity. Sample sizes (number of individuals) are indicated in each panel.

Nest height study

The upper (1.25 m) nests were not snow covered during either the 2008–2009 or the 2009–2010 winters, whereas the lower (0.5 m) nests were snow covered, except for brief thaws, from 16 December 2008 to 8 April 2009 and from 22 January to 8 March 2010. Upper and lower nests experienced nearly identical temperatures after snowmelt, but earlier in the spring, upper nests experienced much greater temperature variation, and, consequently, had accumulated many more heating units between 1 January and 1 May (e.g., degree-days >5°C: 213 vs. 38 in 2009, and 178 vs. 35 in 2010).

Five insect species occurred in both upper and lower nests in sufficient numbers for analysis (Table 1). For each species, we analyzed the sexes separately, either because one sex did not occur at one or both of the nest heights, or because strong covariances between sex ratio and nest position would have biased results: males emerge before females in all of these species, and in our nests, one sex or the other was always underrepresented at one nest height. For the one species (*Osmia iridis*) that emerged in both years of the study, there was no difference in phenology between years, so data from both years were combined for analysis.

Emergence dates of *Megachile relativa* and *Stelis montana* were unaffected by nest height ($P > 0.3$); *M. relativa* individuals even tended to emerge later from the upper nests (although not significantly so). For the two other bee species (*O. coloradensis* and male and female *O. iridis*) and the wasp *Chrysis coerulans*, timing of emergence was significantly affected by nest position (Kruskal-Wallis $\chi^2 > 4.0$, df = 1, $P < 0.05$; Fig. 6). A significant nest position effect remains for *C. coerulans*

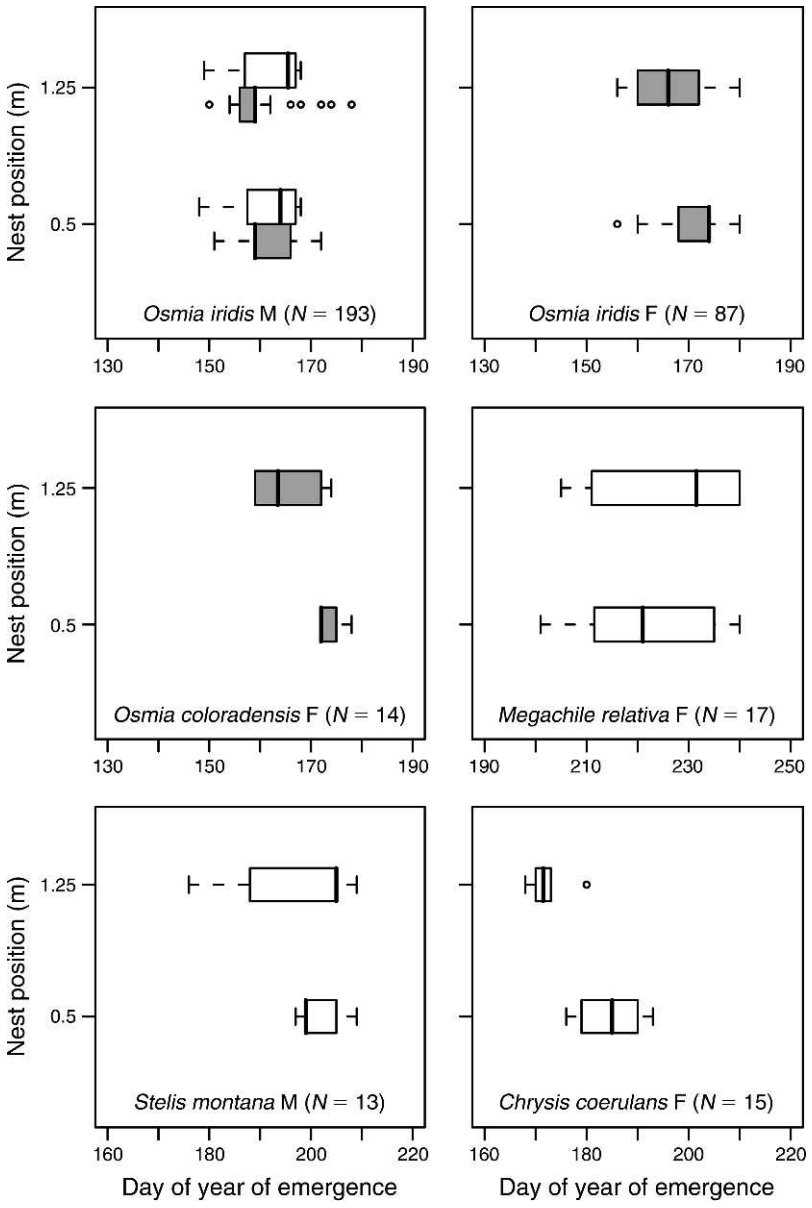

FIG. 6. Tukey boxplots showing the effect of nest position (meters above ground level) on emergence phenology of five species of trap-nesting Hymenoptera. Shaded boxes represent insects emerging in 2010; unshaded boxes represent 2009 emergence. Nests at 0.5 m were snow covered each winter; those at 1.25 m were not. Sample sizes (number of individuals) are indicated in each panel. "M" denotes males; "F" denotes females. Insects emerged significantly earlier from upper nests in *O. coloradensis*, *O. iridis* (both sexes), and *C. coerulans*. Boxes show medians and interquartile ranges; whiskers extend to the most distant point that is within 1.5 times the interquartile range from the end of the box. Open circles represent outliers that are >1.5 times the interquartile range beyond the box.

and *O. iridis* even after applying a Bonferroni-corrected α of 0.01; note, however, that it is the magnitude of the effect, rather than its significance, that is of most interest. Individuals of both *Osmia* species and the wasp emerged only 2–12 days later, on average, from the lower nests than the upper ones. Even the 12-d delay seen in *C. coerulans*, the species showing the largest effect of nest height, amounted to an increment of only 105 DD >5°C, according to the low-nest temperature readings from that period of June–July 2009. This amount does not make up the difference in January–May heat accumulation between upper and lower nests.

Temperature effects on emergence and flowering

Regressions of cumulative emergence or flowering against accumulated degree-days were well fit by logistic functions specific to each site–year for all species (Figs. 2 and 3). Assuming a 1 January start date for degree-day

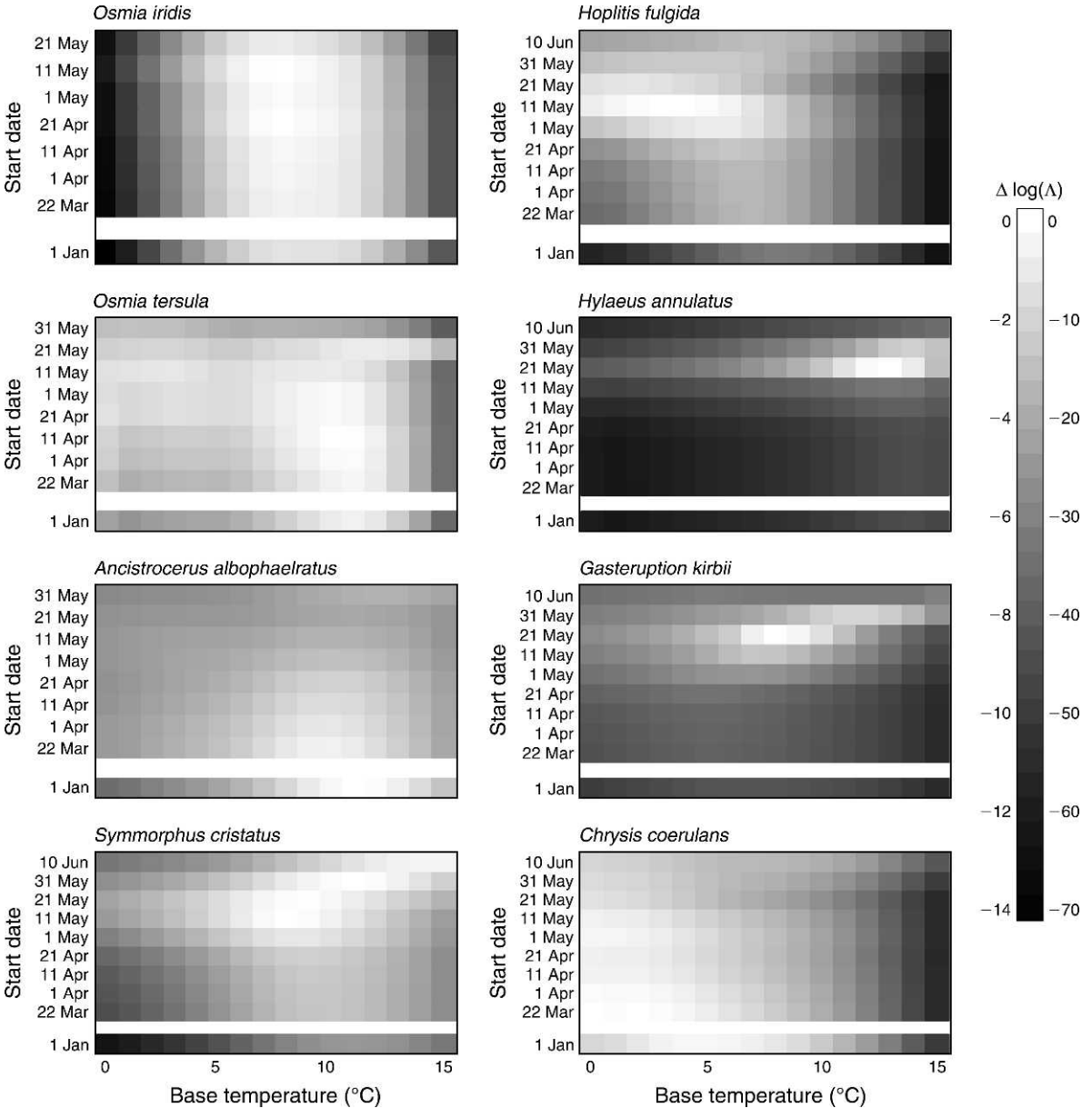

FIG. 7. Relative log likelihoods, $\Delta \log(\Lambda)$, of different phenology models for eight insect species. Each model requires a specified base temperature for degree-day calculation and start date for degree-day accumulation; each shaded square in the figure represents the log likelihood of a single model and therefore a single combination of base temperature and start date. All combinations of base temperatures between 0° and 15°C (in 1°C increments) and start dates between 22 March and 10 June (or as late as possible, in 10-day increments), plus 1 January, were used for fitting logistic regressions to emergence data (as in Fig. 2). Squares are shaded according to the difference in log likelihood between that model and the most likely model for that species. The square representing the most likely model is completely unshaded; darker shading indicates worse fit. The key translates differences in shading to differences in log likelihoods. Values to the right of the key apply to *Osmia iridis*, which showed greater differentiation among models and therefore a greater range of log likelihoods; values to the left of the key apply to all other species. All models use the same number of parameters, so model fits can be assessed by comparison of log likelihoods, with a difference of much greater than 1 indicating substantially less support for the inferior model (Burnham and Anderson 2002). The fact that models using start dates later than 1 January tend to have greater support suggests that high temperatures occurring early in the season are less effective at hastening development.

accumulation, the best-fit models for the eight insect species used degree-days above a base temperature between 5° and 14°C, depending on the species (Figs. 2 and 7). For most species, these most likely base-temperature estimates are robust, within 1°C, to the decision not to include site-specific slopes (i.e., a random slope effect) in the regression model for cumulative emergence vs. accumulated degree-days. For two species

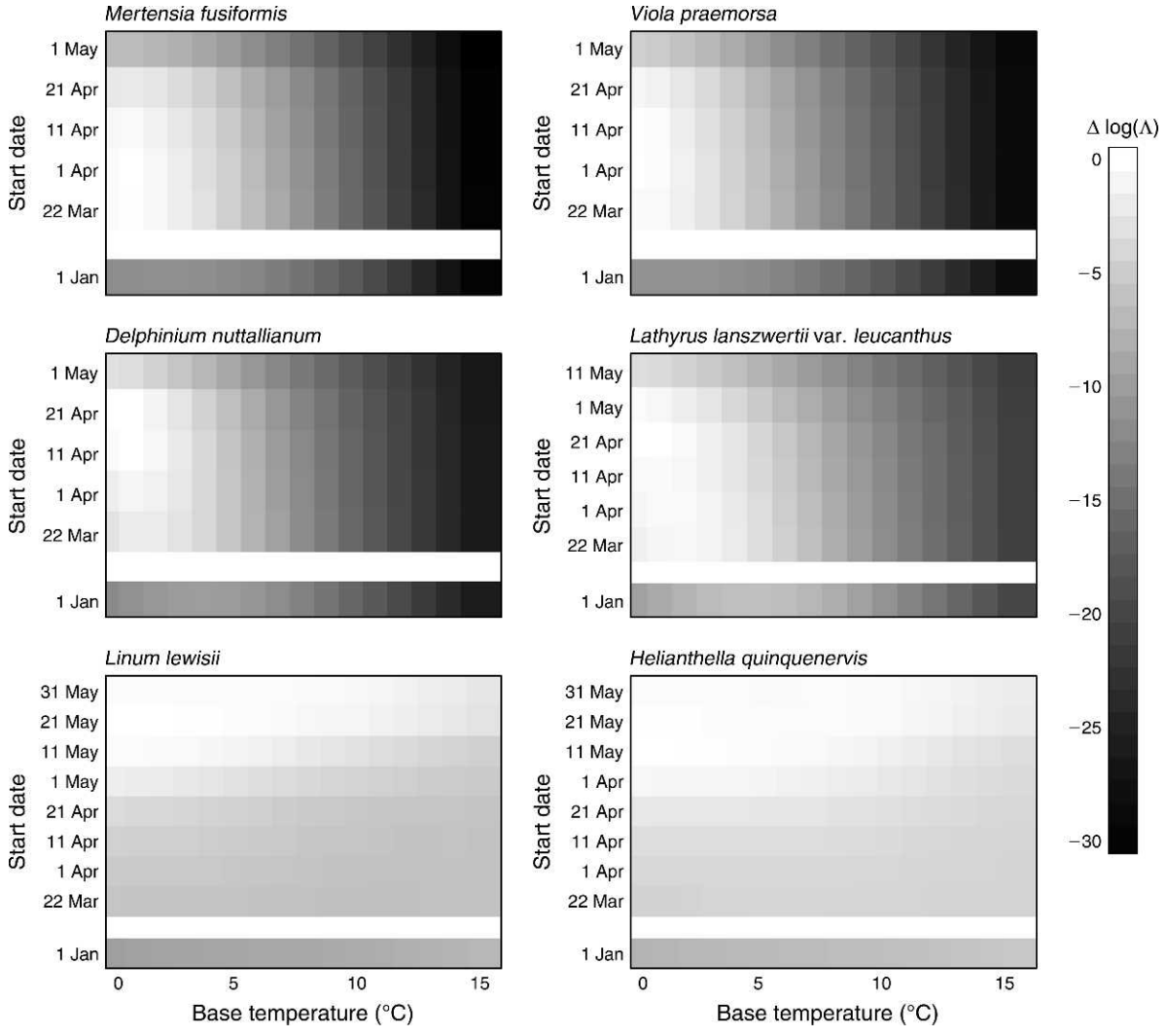

FIG. 8. Relative log likelihoods of phenology models for six plant species. See Fig. 7 for an explanation.

(*Chrysis coerulans* and *Osmia iridis*), however, allowing slopes to vary among site–years produces significantly more likely models with higher base-temperature estimates (10°C and 11°C, respectively, instead of 5°C and 8°C).

For four out of six plant species investigated, the best model fits were obtained for base temperatures between 2°C and 5°C, again assuming a 1 January start date for degree-day accumulation (Figs. 3 and 8). For the remaining two (*L. lewisii* and *H. quinquenervis*, the two latest-flowering species we considered), model support increased with increasing base temperature at least up to 15°C; however, there was little difference in log likelihood (<3) over the full 15°C range, indicating only weak relative support for a model with such a high base temperature (Fig. 8). For all six species, the base temperature estimate is robust within 1°C to the exclusion of site-specific (random) slopes. In general, plants seem to have lower base temperatures.

Although models based on degree-days accumulated from 1 January fit well for individual site–years, there was substantial remaining variation among sites in degree-days required for 50% emergence or flowering (i.e., the site–year intercept term remained highly significant for all species). Specifically, organisms at lower-elevation or earlier-melting sites tended to require more degree-days than those at higher, later-melting sites. Indeed, for most species, the number of "chill days" experienced in a given site–year was a good predictor of the position of the phenology curve (i.e., the regression intercept): more chilling tended to shift the curve to the left (Figs. 2 and 3). This was true of all six plants, three bee species, and *Gasteruption kirbii* (Figs. 9 and 10). For the remaining four insect species, the trend was in the same direction but nonsignificant (Fig. 9). Similarly, for all plants and most insects, model fits were greatly improved by the use of start dates for DD accumulation later than 1 January (Figs. 7 and 8). This

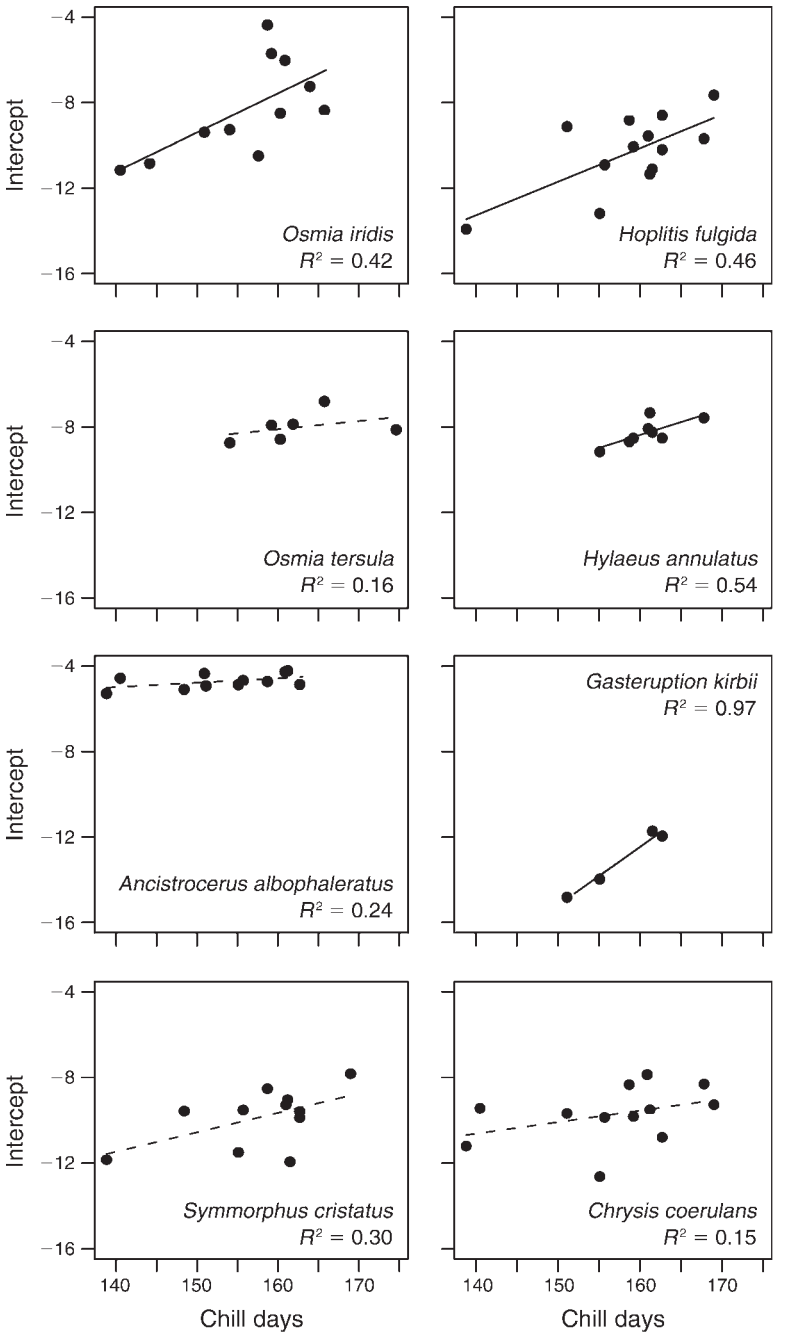

FIG. 9. Intercepts of phenology models (logistic regressions of emergence vs. degree-days since 1 January), plotted against days of chilling temperatures, for eight insect species. Each circle represents one site and/or year ($N = 4$–13). Significant linear relationships ($P < 0.05$) are plotted as solid lines; nonsignificant relationships are plotted as dashed lines.

suggests that high temperatures occurring early in the season are ineffective at hastening development in most species. The best models incorporating later start dates explained, on average, 82% of the deviance for each species, with little difference in explanatory power between insects and plants (Table 3). For several species, using later start dates also changed the estimate of the best base temperature, shifting estimates downward in all six plant species and in a majority of the insects (Figs. 7 and 8). The pattern of generally higher base temperatures for insects, compared to plants, remains (Table 3).

Decoupling of plants and pollinators

Lathyrus and *H. fulgida* showed broad overlap in phenology at most sites in 2008 (Fig. 11), in spite of the

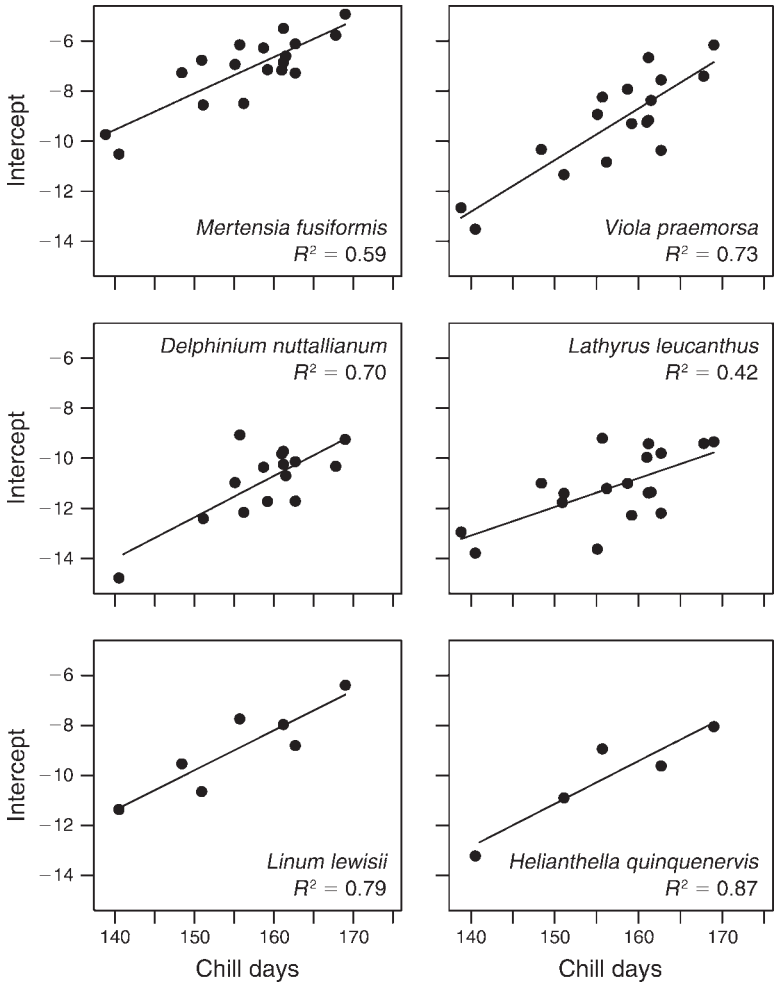

FIG. 10. Intercepts of phenology models vs. days of chilling temperatures for six plant species. Lines are as described in Fig. 9. $N = 5$–18 site–years.

TABLE 3. Summary statistics of maximum-likelihood degree-day models for each focal species.

Species	Base temperature (°C)	Start date	Deviance explained (%)
A) Insects			
Ancistrocerus albophaleratus	11	1 Jan	62.5
Chrysis coerulans	0	22 Mar	70.2
Gasteruption kirbii	8	21 May	87.1
Hoplitis fulgida	3	11 May	76.7
Hylaeus annulatus	13	21 May	87.9
Osmia iridis	8	11 May	89.2
Osmia tersula	10	11 Apr	79.7
Symmorphus cristatus	8	11 May	76.8
B) Plants			
Delphinium nuttallianum	1	11 Apr	86.8
Helianthella quinquenervis	0	11 May	95.1
Lathyrus leucanthus	0	21 Apr	81.1
Linum lewisii	0	21 May	94.0
Mertensia fusiformis	1	1 Apr	84.5
Viola praemorsa	1	1 Apr	70.8

Note: Parameters listed are the combinations of base temperature and start date for degree-day accumulation that explained the greatest proportion of deviance in the data for each species, across all sites and years.

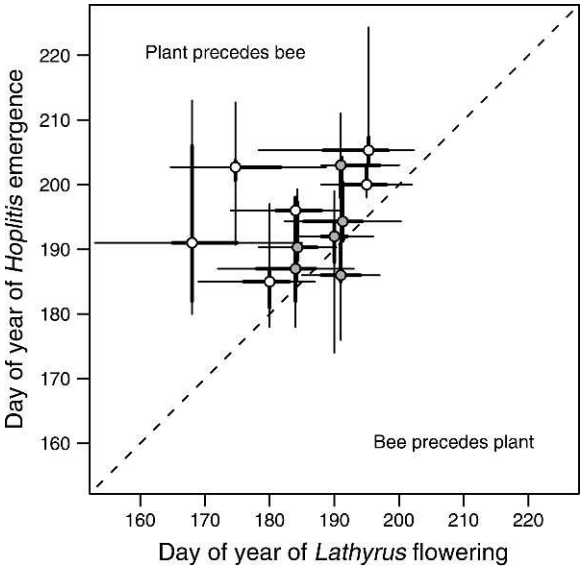

FIG. 11. Phenology of *Hoplitis fulgida* (Hymenoptera: Megachilidae) and *Lathyrus lanszwertii* (Fabaceae), plotted as median emergence or flowering dates, respectively (circles), interquartile range (thick lines), and 5–95% range (thin lines) for each site–year. Shaded circles represent data from 2008; open circles represent 2009. The dashed line is the 1:1 line, representing perfect synchrony between *Lathyrus* flowering and *H. fulgida* emergence. Circles above the line indicate that flowering occurred earlier than bee emergence. Circles below the line indicate that bee emergence (although not necessarily bee foraging and nesting activity) preceded flowering. Some values have been jittered by ±0.3 d for clarity.

two species showing modest differences in temperature responsiveness in the previous analysis. However, they showed, at best, only slight overlap at any site in 2009, such that, at all sites, *Lathyrus* had finished or almost finished flowering by the time of peak *H. fulgida* emergence (Fig. 11). This was due, in part, to generally earlier flowering by this species at warmer, low-elevation sites in 2009 compared to 2008, without a corresponding advance in phenology of the bees.

In contrast, emergence phenology of *H. fulgida* corresponded reasonably well with that of *Potentilla* in both study years (Fig. 12). At one site in 2009, peak bee emergence did not occur until late in the *Potentilla* flowering period; but for most other site–years, emergence matched or preceded peak flowering by several days, a sequence that should ensure that pollen is locally available to female bees while they are provisioning nests. Note that this qualitative result would be unchanged even if we assumed that our median flowering dates for this species are underestimated at the later-flowering sites.

DISCUSSION

Environmental determinants of phenology

Insects in our study showed no sign of local adaptation in timing of emergence. Although sample sizes were small in the reciprocal transplant experiment, we were able to detect a strong effect of local conditions at the emergence site on emergence time, but no effect of site of origin, suggesting that environmental effects on emergence time outweigh any genetic differentiation among sites. Interestingly, we detected no tendency for insects from the high-elevation site to develop more rapidly than low-elevation insects at a given emergence site, a pattern that is often observed along latitudinal and elevational gradients (counter-gradient variation; Conover and Schultz 1995). The geographic scale of our study may have been too small to have produced local adaptation, particularly considering the substantial interannual variation in season length in these habitats. A similar result was reported by Krombein (1967), who noted, anecdotally, that conspecific insects in trap nests from various localities along a latitudinal gradient in the eastern United States emerged at approximately the same time in a common rearing environment in Washington, D.C., likewise suggesting no local adaptation in phenology.

In fact, there may be little selection for earlier emergence in high-elevation insect populations if season length is sufficiently long to complete a generation. Also, if the resources on which insects depend similarly show no differentiation over the elevational gradient in their responses to environmental cues, there may be no advantage to insects in getting a more rapid start to the season at higher sites. We did not test for local adaptation in phenology of the plants in this study, but an earlier common-garden experiment with *Potentilla*

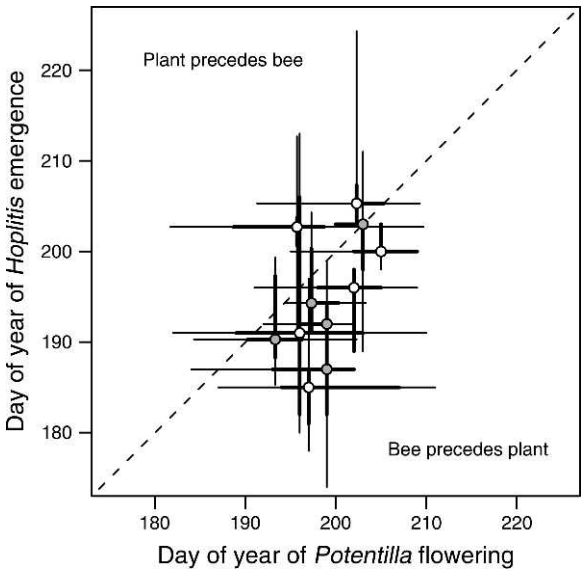

FIG. 12. Phenology of *Potentilla hippiana* × *gracilis* and *H. fulgida*, represented as in Fig. 11, except note that plant sampling ended on day 202–203 in 2008 and on day 209–210 in 2009, so the end of flowering was missed at most sites. This tends to bias data points (especially those representing later sites, in the upper right of the graph) to the left.

gracilis ("*P. pulcherrima*"; Hartman and Nelson 2001) in our study area around the Rocky Mountain Biological Laboratory provides relevant information. That study showed no genetic difference in time to flowering among populations that spanned a greater elevational range (1000 m) than did our study sites; and, furthermore, selection on phenology in that species was similar at all sites, favoring a shorter prefloration interval regardless of elevation (Stinson 2004). If *P. gracilis* is representative of plants in the area, we would not expect local adaptation in phenology in our study species, although transplant tests with all of them would be required to confirm this.

Given that, in general, phenology of insects and plants is primarily determined by the local environment, which aspects of the environment are most important? Photoperiod can be ruled out as being the sole cue, because it does not covary with season length along an elevational gradient. Snowmelt also must not be a critical factor, at least for insects: all trap nests were snow covered in the heavy winter of 2007–2008, but this was not the case in the next two winters, when snowpack under trees did not reach 1 m at most sites. We do not have site-specific data on the date of snowmelt at ground level, so it is possible that this would have provided a good predictor of plant flowering even though the date at which snow melted off the trap nests (in 2008) generally did not. In the two species (*Mertensia fusiformis* and *Viola praemorsa*) for which the 1 m snowmelt date was a better predictor of peak flowering than degree-days in the preceding months ($r^2 = 0.90$ vs. 0.88 for *M. fusiformis*, $r^2 = 0.69$ vs. 0.64 for *V. praemorsa*; $N = 7$ sites), the slopes of the relationships were much less than 1 (95% CI: 0.29–0.60 for *M. fusiformis*, 0.15–0.76 for *V. praemorsa*), indicating that elapsed time between snowmelt and flowering is not uniform across sites. This lack of uniformity must be accounted for by other factors that vary among sites: if not alleles at phenologically relevant loci (which we have tentatively ruled out), then other components of climate.

For all species that we studied, we were able to develop simple degree-day models that explained much of the variation in phenology among sites and years. For most insects, the base temperatures that provided the best fit in these models were higher than for most plants. This accords reasonably well with previous studies that have used base temperatures between 4°C (Kimberling and Miller 1988) and 18°C (Kemp and Onsager 1986) to predict insect phenology (see also Campbell et al. 1974, Nealis et al. 1984), and base temperatures of 0–1°C (e.g., Ladinig and Wagner 2005, Larl and Wagner 2005, Hülber et al. 2010) for plants. If this is a general pattern, it suggests that increases in average temperatures will hasten phenologies of both insects and plants; but the details of when warming occurs will determine the potential for differential effects on insects and plants. For example, an increase in early-morning temperatures in spring from 0°C to 4°C would be expected to promote plant development without affecting insect phenology. It is possible that we observed such an effect in 2009, when June temperatures were cooler than usual in our study area (mean maximum daily temperature in June 2009 = 18.2°C at a weather station near the RMBL, compared with an average of 21.7°C [SD = 1.7] for the same period in 2000–2008; b. barr, *personal communication*). This may explain the lack of correspondence between *Hoplitis fulgida* and *Lathyrus* at most of our study sites in that year. With earlier snowmelt in 2009 than 2008, plants at low-elevation sites were able to start growth earlier in the season, while phenology of the bees remained unchanged (Fig. 11).

Although there was a general tendency for our best insect models to require higher base temperatures than did our plant models, there was also substantial variation among insects in both the base temperature estimates and the effects of chilling on emergence phenology. In particular, three wasp species (*Ancistrocerus albophaleratus*, *Symmorphus cristatus*, and *Chrysis coerulans*) showed less effect of chilling on emergence than did plants, most bees, and the bee parasite *Gasteruption kirbii*. This is intriguing, because these wasp species are not closely related but are connected ecologically: *C. coerulans* is a brood parasite of the other two, frequently emerging from the same nest on the same day as individuals of the host species (J. Forrest, *personal observation*; also Krombein 1967). We might expect *C. coerulans* to have evolved to use similar emergence cues to those used by its hosts. However, phenology models for these three species are otherwise dissimilar (Fig. 7), so the mechanism by which *C. coerulans* maintains (or fails to maintain) synchrony with its hosts requires additional study. One possibility is that the parasite may have a longer flight season than its hosts. *Chrysis coerulans* also parasitizes nests of other eumenine wasps, some of which occurred at our study sites, so the need for synchrony with *A. albophaleratus* and *S. cristatus* is not absolute (although the other eumenines have similar phenologies).

Interspecific variation in responsiveness to chilling may also have played a role in our nest height experiment. For all five species occurring in that experiment (four bees and one wasp), the difference in phenology between upper and lower nests is less than what we would predict based on the difference in degree-day accumulation (and is absent entirely in two of the bees). This suggests that the longer chilling period experienced by insects in lower nests compensated, at least partially, for the delay they experienced in springtime warming. This compensation appears to have been especially incomplete in *C. coerulans*, which showed the greatest difference in phenology between upper and lower nests, supporting the notion that this species is less influenced than others by chilling.

Our results do not prove that chilling affects emergence phenology, although they are consistent with such an effect. Another possible explanation for among-

site differences in phenology is that both insects and plants might use a photoperiod cue as an indicator of when heating units begin to "count." Such a mechanism could also easily explain the lack of nest height effect seen in *Megachile relativa*, a species that emerges in late summer and could use photoperiod to determine a start date for degree-day accumulation that would fall after even a late snowmelt. Our data cannot distinguish between these possibilities, and in fact the two are not mutually exclusive (and may be employed by different species). We favor the chilling explanation, largely based on previous research on insects and the well-known vernalization requirement of many plants. The existence of a significant or marginally significant "year" effect in the phenology models of a few of our study species also implicates a factor that, unlike photoperiod, varied between years; however, we cannot rule out a year effect deriving from slight differences among years in our experimental methods or in the sex ratios of emerging bees. Photoperiod also seems an unlikely cue for insects overwintering deep inside wood (although perhaps not impossible; Tauber et al. 1986). The relative importance of photoperiod and chilling could be evaluated using a transplant experiment similar to the one we describe here, but with an additional treatment in which nesting bees are transplanted in spring, after overwintering (and experiencing chilling conditions) at the site of origin. If chilling is important, bees transplanted from low to high sites in spring should emerge later than bees that spent the winter at the high elevation. Conversely, if chilling is unimportant, but photoperiod determines the starting point for heat accumulation, bees at high sites should emerge at the same time regardless of when they were transplanted, provided that the spring transplant occurred before the critical day length.

Implications for phenology modeling

Our data set is not appropriate for testing the effects of more than a small number of interacting variables, so our tentative conclusions await testing under controlled conditions. In reality, factors such as moisture availability, competition, predation, and extreme weather events could affect phenology as well, potentially modulating the effects of cumulative heat units or photoperiod. Even the effect of heat on development rate might be nonlinear (see discussion in van Asch and Visser 2007) or might vary according to the life stage of the insect (Nealis et al. 1984, Manel and Debouzie 1997). The most promising way of untangling these effects probably involves an iterative series of field studies and complementary laboratory or growth chamber experiments, the results of each (in)validating and informing the other.

Nevertheless, the data that we have so far tentatively suggest a major effect of cool overwintering temperatures on phenology. Chilling or vernalization effects have been clearly documented in plants (Murray et al. 1989, Henderson et al. 2003) and insects (Kimberling and Miller 1988, Bosch and Kemp 2003, 2004), but this fact seems to be underappreciated by many ecologists monitoring phenology and making projections about climate change impacts (the process-based models such as those reviewed by Chuine [2010] are a notable exception). Simple, single-parameter degree-day models of phenology may fit well for organisms at one location, but these ostensibly "mechanistic" models will have little power to predict phenology under new conditions, when chilling temperatures (not to mention other factors) also vary. Greater awareness of these possible complexities should permit better forecasts of the phenologies of individual species and the possibility of phenological asynchrony between interacting species.

Implications for plant and insect populations

If we are correct in concluding that plants and insects use similar, but not identical, environmental cues to regulate phenology, what are the likely consequences? Our results suggest that, under novel climate conditions, some changes in temporal co-occurrence patterns are possible in our study area. These are more likely to be quantitative effects, with species experiencing reduced or increased overlap with other species, rather than qualitative changes involving complete decoupling of formerly interacting organisms. This is particularly true because our sampling included only plants within 100 m of nest sites; more remote populations with different phenologies might be accessible to insects with longer flight distances. This is especially likely in mountainous habitats with rugged topography. Also, as far as we know, none of the pollinator species in our study is specialized on a single plant species. Hence, these species are unlikely to be strongly affected by shifts in the plant communities with which their phenologies overlap. For example, although *Hoplitis fulgida* missed *Lathyrus* flowering at several sites in 2009, it maintained fairly good synchrony with *Potentilla*, a commonly used pollen source for this bee. However, even in generalist bees, larval growth and survival can vary significantly according to the pollen species in the diet, even if these are pollens that adult females are willing to collect for their offspring (Williams 2003). Studies monitoring the consequences for bee populations of changes in resource use will therefore be an important, but challenging, future step.

The only insect species in our samples that might have been at risk of emerging before *any* plants were available were the early-emerging species of *Osmia*. *Osmia lignaria*, the blue orchard bee, was the earliest species to emerge from our trap nests in 2008 (mid-May at the low-elevation site; mid-June at the high-elevation site in nests transplanted from the low site). Interestingly, emergence of these bees at both sites coincided with the opening of the earliest flowers at each site: the first bees appeared 0 and 5 days after we recorded the first *Mertensia fusiformis* flowers at the low and high sites, respectively. The earliest bee to emerge in 2009 was

Osmia pikei, a polylectic species (Cripps and Rust 1985), of which the first individuals appeared 1–2 weeks after the first *M. fusiformis* flowers at each site. Thus, we have no indication that any bee species is emerging "too early" under current conditions, although it remains possible that future climates could produce such a scenario.

From the plant perspective, these observations indicate that flowering before the emergence of any trap-nesting pollinators is a real possibility. This might be especially so in the future, if more rapid snowmelt, followed by temperatures in the 0–5°C range, means that plants get an earlier start to the season without a corresponding advance in insect phenologies. Earlier snowmelt is indeed likely: the proportion of precipitation falling as snow is generally dwindling in the southern Rocky Mountains (Knowles et al. 2006), and, in addition, dust transported from the increasingly arid Southwest can decrease surface albedo and increase the melt rate of what snow there is (Painter et al. 2007). However, trap-nesting Hymenoptera are not the only (or even necessarily the most effective) pollinators active early in the season in the Rockies. Ground-nesting bumble bee queens (*Bombus* spp., Apidae) and males of some *Andrena* spp. (Andrenidae) are often observed before the first *Osmia*; the former are regular visitors to *M. fusiformis* and both taxa frequent other early-flowering species. Earlier flowering of species normally visited by *Osmia* might mean a reduction in the total number of pollinator visits or a change in identity of the main pollinators, but it might not entail a complete loss of pollinator services.

In general, we suspect that organisms inhabiting naturally variable environments such as these subalpine habitats will have evolved strategies for coping with that variability. The parsivoltine, or facultatively semivoltine, life cycle that we document here in *Osmia iridis*, *O. tersula*, and *O. tristella* may serve as just such a strategy. The risk-spreading advantage of this life history was suggested by Torchio and Tepedino (1982), who noted that both 1- and 2-year forms could be found in a single *Osmia* nest (this was also the case in our study). At present, we do not know what determines whether an individual spends a second season in diapause, or whether diapause through a third winter can occur as well. In our study, some species failed, or all but failed, to emerge in 2009 (*O. tristella*, *O. tersula*), despite having emerged in numbers from 1-year-old nests in 2008. It is tempting to hypothesize that the cooler, overcast weather of June 2009 might have caused bees to stay in, or resume, diapause. However, in other parsivoltine *Osmia* species, 2-year bees diapause as larvae in the first winter and do not develop to adulthood until the second summer (Torchio and Tepedino 1982). In these species, at least, an individual bee's developmental schedule must be determined genetically or maternally, or by environmental cues experienced before the first winter. In any case, the parsivoltine strategy clearly buffers the insect population against catastrophic reproductive failure in any single year. The major threat to such a strategy would be the occurrence of a succession of bad years. In our study area, warmer and drier years in the last several decades have been associated with periods of midsummer floral scarcity (Aldridge et al. 2011), and some plant species, in particular, have experienced a recent series of bad flowering years caused by spring frost damage to developing flowers (Inouye 2008). These overall reductions in flowering, which are apparently being exacerbated by climate change, may pose a greater threat to both plants and insects than phenological asynchrony.

Where an organism's survival is closely tied to the phenology of another species, there should be strong selection for the two to use the same cues, or at least cues that have historically been strongly correlated. In the desert bee *Perdita portalis* (Andrenidae), for example, emergence happens in response to increased soil moisture, similar to many desert plants that germinate in response to rainfall (Danforth 1999). This presumably prevents bees from emerging in years when no flowers bloom, although it does not guarantee that the seasonal timing of flowering and bee activity will exactly coincide. In our system, where most species are generalists, reliance by insects on temperature cues similar to those used by plants may be adequate for ensuring sufficient synchrony with the flowering community as a whole. However, further tests will be necessary not only to corroborate our results but also to determine the extent to which they apply to other members of the plant and insect communities. After that, the next step will be to determine whether the diffuse and imperfect synchrony that we have observed is sufficient for maintaining plant and insect populations in the long run.

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APPENDIX

Numbers of all species of Hymenoptera (excluding Ichneumonoidea) emerging from trap nests in 2008–2010 (*Ecological Archives* M081-016-A1).

SUPPLEMENT

Temperature and light data recorded at trap-nest sites, 2007–2010 (*Ecological Archives* M081-016-S1).