

# **Selection for early reproduction in the solitary bee *Hoplitis fulgida***

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## Abstract

Reproductive timing is an important determinant of offspring success which ultimately contributes to an individual's overall fitness. In seasonal environments with short growing seasons, organisms must time reproductive activity so that offspring experience relatively high levels of resource abundance but also have enough time to undergo sufficient ontogenetic development to successfully overwinter. The timing of other life-history events that necessarily precede reproduction such as gonadal maturation, migration, and emergence from diapause may place further constraints on reproductive timing. We investigated the effects of reproductive timing in subalpine populations of the solitary bee *Hoplitis fulgida* on individual reproductive output and offspring success. Specifically, we examined how timing of nesting in *H. fulgida* affected both individual reproductive output (given by nest construction rate and total number of brood cells constructed per nest), and offspring success (using larval development as a proxy). We also conducted surveys of *H. fulgida* floral hosts to determine temporal patterns of resource abundance. Nest construction rate significantly declined over the course of the season but was only explained by the day of the year and was not associated with floral resource abundance in our models. Similarly, the total number of brood cells per nest decreased seasonally but was only explained by the day on which the nest was initiated and not by floral resource abundance. Both results seemed to suggest that *H. fulgida* individuals are under directional selection for early reproduction; however, the selective pressures that are driving these trends have yet to be investigated.

## Introduction

The timing of life-history events such as reproduction can have considerable effects on offspring success, which ultimately contributes to an individual's overall fitness (Brommer et al. 2002; Varpe et al. 2007). Reproductive timing can have cascading effects on various factors that affect offspring viability (Einum & Fleming 2000) including competitive ability (Johnsson et al. 1999), vulnerability to predation (Brännäs 1995), access to resources (Visser et al. 1998), and ability to withstand harsh environmental conditions (Cargnelli & Gross 1995). For example, early-born offspring may have ontogenetic advantages over later-born individuals in cases where intraspecific size-dependent competition determines offspring success (Johnsson et al. 1999). In other cases, late reproduction may be favourable if offspring produced later benefit from greater predator dilution effects (Brännäs 1995).

The importance of reproductive timing is often accentuated in strongly seasonal environments in which the amount of time organisms have to reproduce is constrained by short growing seasons (Dunn et al. 2011; Varpe et al. 2007; Gruebler & Naef-Daenzer 2010). In such environments, seasonality in temperature, precipitation, and photoperiod are likely important selective agents on reproductive timing (Varpe et al. 2007). The brevity of growing seasons in seasonal environments suggests that organisms should be under strong selection to synchronize reproductive activity with peak food abundance, both so that parents can meet the energetic demands of reproduction (Benkman 1990; Perrins 1970), and so that offspring are able to grow and survive (Perrins 1970; Visser et al. 2006; Arlettaz et al. 2001). However, many organisms living in seasonal environments (i.e. high latitude or high altitude regions) have annual life-cycles that may include obligatory overwintering larval diapause stages prior to emergence in the spring (Tauber et al. 1986; Forrest 2016). This means that in addition to sufficient food, offspring may also require a certain amount of time to develop to a stage in which they are able to survive

winter conditions. The importance of this developmental period for offspring success in seasonal environments has been demonstrated in various taxa including mammals (Ransome 1989), insects (Landa 1992) and fish (Cargnelli & Gross 1995). Moreover, for some organisms, reproductive timing may also be contingent on other life-history events such as gonadal maturation, migration and mating. In the case of overwintering organisms, the timing of emergence from diapause or hibernation may place further constraints on reproductive timing.

In general, early reproduction in seasonal environments can be unfavourable since climatic conditions may be unpredictable and resources scarce (Perrins 1970; Crecco & Savoy 1985). However, reproducing early can also be advantageous, since offspring are likely to have enough time to develop and survive unfavourable environmental periods such as winter (Cargnelli & Gross 1995; Frick et al. 2010; Landa 1992; Olsson & Shine 1997; Ransome 1989). Individuals reproducing late in the season are likely to experience the opposite effects, with lower offspring mortality due to harsh early-season conditions and resource scarcity, but also less time for offspring development. Reproductive timing ultimately reflects how organisms maximize fitness while constrained by trade-offs (e.g., between resource abundance and time for offspring development) as well as other life-history events such as emergence.

Understanding the underlying mechanisms that impose selection on life-history stages is becoming increasingly critical as changes in climate alter the timing of biological events such as flowering (Inouye 2008), budburst (Murray et al. 1989) and migration (Butler 2003). For many organisms, changes in the timing of such events can in turn alter how reproductive timing affects offspring success. Specifically, there has been a recent surge of interest in the effects of climate change on pollinators due to concerns over phenological decoupling between pollinators and their floral hosts. Numerous studies have attributed changes in flowering time to climate change (Abu-Asab et al. 2001; Anderson et al. 2012; Dunne et al. 2003; Fitter & Fitter 2002); however, few studies have actually documented the fitness consequences of plant-pollinator decoupling to date (Rafferty & Ives 2011). Whether the evolved timing of life-history events such as reproduction in pollinators remains optimal as environmental conditions change remains unclear.

In this study, we investigated the effects of variation in emergence and nesting phenology among individuals of the solitary bee *Hoplitis fulgida* on reproductive output and offspring success as proxies of individual fitness. We also explored the factors that impose selection on *H. fulgida* life-history timing including floral resource abundance and time required for larval development. Specifically, we asked the following questions: (1) How does reproductive timing in *H. fulgida* reflect the constraints of trade-offs such as temporal patterns of floral resource abundance and time required for offspring development?, and (2) what are the effects of emergence and nest initiation date on *H. fulgida* offspring production and survival (i.e. individual fitness)?

## Methods:

### *Study sites*

Fieldwork was conducted in the summer of 2017 over a 10-week period in four subalpine sites located in the Rocky Mountains of Colorado, USA (Figure 1). Sites span an elevational gradient of approximately 300 meters. Each site contains pre-established wooden trap-nests attached to the trunks of trees located at the edge of a meadow or clearing which have been used in previous

studies (Forrest & Thomson 2011; Spear et al. 2016, Forrest & Chisholm 2017). Trap-nests consist of wooden blocks containing ten 14 cm deep holes of three different diameters (4.5, 6.1 and 8.2 mm) that attract a range of insect species including *H. fulgida*. Each hole is lined with a paper straw allowing nests to be temporarily removed from trap-nests and inspected.

### *Study organism*

*Hoplitis fulgida* (Apoidea: Megachilidae) is a solitary bee occurring throughout western North America and is commonly found nesting in pre-existing cavities in dead trees and stumps (Tepedino & Parker, 1984). *H. fulgida* adults typically emerge starting mid-June (personal observation) and mate. Females then seek out suitable nesting cavities and construct nests which consist of a linear series of brood cells partitioned by walls made of mud, pebbles and masticated leaf material (Tepedino & Parker 1984). Each cell contains a mass of pollen and nectar upon which a single egg is deposited (Tepedino & Parker 1984). Data from previous observations at our study sites suggest that *H. fulgida* are pollen generalists (polylectic), collecting pollen from multiple plant families including Rosaceae (*Potentilla* spp.), Plantaginaceae (*Penstemon strictus*), Violaceae, and Boraginaceae (unpublished data). Once the nest is complete, females seal it with a thicker wall comprised primarily of small pebbles (Tepedino & Parker 1984).

Upon progressing through several instars and consuming pollen provisions, larvae initiate cocoon spinning in which they spin salivary strands onto fecal particles until they are completely encased in several cocoon layers which are attached to brood cell-wall surfaces (Torchio 1989; Torchio 1980). Following cocoon construction, larvae overwinter as pre-pupae (late-instar larvae) before pupating in the spring. They then molt into adult form, and emerge (Torchio 1989).

Because they readily occupy the artificial nest blocks set up at our four sites, the emergence and nesting phenology, as well as floral-host usage of *H. fulgida* can be easily observed. Moreover, data collected from 2013 to 2016 from six study sites (including the four used in 2017) suggest that there is considerable variation in the timing of *H. fulgida* nesting even within sites (e.g. first nesting from mid-June to mid-July). The variation in *H. fulgida* phenology makes this species an ideal candidate for our study.

### *Emergence phenology*

At each site, where *H. fulgida* had been recorded nesting in 2016, we attached emergence traps consisting of transparent snap-cap vials stapled to the front of nest entrances (cf. Forrest & Thomson 2011). This allowed for the date on which individuals emerge to be approximated. Traps were then monitored every 3 – 5 days for emergence. We removed trap vials and extracted and inspected nesting straws whenever emerged insects (live and dead) or nest wall debris (indicating that an insect had been active) were found in the emergence vials. Individuals found alive in emergence vials were assumed to have emerged the day before the site was visited, while individuals found dead in vials were assigned an emergence date three days earlier. Individuals found alive in nesting straws were assumed to have emerged the day the straw was opened, and individuals found dead in nesting straws were not assigned an emergence date. In order to track individuals over the course of the summer, we applied a paint mark to the mesosoma of all live individuals emerging from trap nests (Testors hobbyist's paint: Vernon Hills, Illinois, USA) with the expectation that some of the marked individuals would nest in the trap-nests at their site of

emergence (Steffan-Dewenter & Schiele 2004). Marked individuals generally flew away after being marked.

### *Nesting phenology*

Trap nests were also monitored every 3-5 days to locate newly constructed *H. fulgida* nests and monitor progress in existing nests. To quantify nesting progress, we temporarily extracted nesting straws (each nest consists of the contents of a single straw) and marked the location of the outermost pollen provision on the outer surface of the straw to the nearest 0.1 cell each time sites were visited (cf. Forrest & Chisholm 2017). When possible, we also caught and marked nesting females so that the reproductive output and offspring success of each individual could be quantified. We counted the total number of brood cells once nests had been sealed and completed.

### *Determining H. fulgida floral hosts*

Pollen samples were taken from the innermost and outermost cells of each completed nest to determine the identity of floral host-plants being used by *H. fulgida*. To do this, we temporarily removed nests and cut small windows in the paper straw so that a sample of pollen from the brood cell could be collected using fine forceps. Pollen samples were then melted on a slide with fuchsin stain, examined under a compound microscope, and compared with a pre-existing local reference collection to determine their identity (Kearns & Inouye 1993). Samples were then qualitatively scanned to note the major and minor pollen constituents. Pollen sources were considered major constituents if they made up greater than 25% of the sample while sources that made up less than 25% of the sample were considered minor (Table 1). However, all taxa found in pollen samples were considered important floral hosts for *H. fulgida* and were surveyed during floral abundance surveys.

### *Floral resource availability*

To determine the seasonal patterns in floral resource availability, we estimated the density of *H. fulgida* host plants each time sites were checked for emergence and nesting. To achieve this, we adopted the same protocol used by Forrest & Chisholm (2017) in which observers walked in progressively larger circles from a central point and counted open flowers until a total of 100 flowers of each species or a distance of 100 meters (straight-line distance) from the center was reached, whichever came first. The distance ( $r$ ) to the 100<sup>th</sup> flower was then measured so that floral density could be calculated as  $100/\pi r^2$ .

### *Larval success*

Towards the end of the season when most nesting activity had finished, we temporarily removed nests and cut small windows in the paper straw at every brood cell to determine if larvae had started constructing cocoons. Larvae that had initiated cocoon construction were considered “successful” and we assumed these individuals would successfully survive winter conditions.

### *Data Analysis*

Seasonal patterns of floral abundance:

Floral density data were collected every year from 2013 to 2017. To estimate floral density on each day of the season (including days on which we did not sample), we fitted a cubic spline with the R package “stats” (R Core Team 2015) to the observed floral densities (cf. Forrest &

Chisholm 2017). To evaluate seasonal patterns in *H. fulgida* resource abundance, we used Pearson correlations to evaluate the association between the day of the year and the interpolated combined floral density of all relevant floral-hosts. We also ran linear models with the squared day of the year as a predictor of floral density, to accommodate curvilinear (U- or hump-shaped) patterns in the data. Floral density was fourth root power-transformed to improve normality.

#### Reproductive activity:

Data on *H. fulgida* nesting progress was collected from 2013 to 2015 (compiled in a single dataset) and in 2017. To characterize when the most rapid nesting progress occurs during the season, we analyzed the effect of day of the year and average floral density on cell construction rate using the R package “lme4” with year and study site included as fixed categorical effects and nest identity as a random factor. Cell construction rate was calculated for each observation of each nest as the number (or fraction) of brood cells completed since the last site visit divided by the number of days elapsed between the current observation date and the previous observation date. For each nest, we estimated nest initiation date by subtracting the number of brood cells completed since the last site visit from the date at which nesting was first observed. This was based on the assumption that individuals construct one brood cell per day. To obtain an estimate of average floral density during nesting, we summed daily floral density estimates across all host-plant taxa used by *H. fulgida*, and averaged the total over the number of days elapsed between the current observation date and the previous observation date.

We tested the effects of reproductive timing on reproductive success (i.e. fitness) with linear models using the “lm” function in R with nest initiation date and average floral density as predictors for the total number of brood cells per nest. Floral density was summed across all host-plant taxa and averaged over the number of days elapsed during the construction period of the nest. We also ran a similar model with the total number of brood cells per individual bee as a response but only used data collected from 2013 since that was the only year *H. fulgida* were individually marked. The total number of cells constructed per individual was determined by summing the number of brood cells completed for each marked bee regardless of whether or not those cells were from the same nest (some individuals built more than one nest). Floral density was averaged over the number of days in which the individual was observed to be nesting. In both models (total cells per nest and total cells per individual), year and site were included as categorical fixed effects.

Since the number of completed brood cells was not recorded in 2016, we used the number of emerged bees observed in 2017 as an indicator of offspring success for each nest. We estimated nest initiation date by taking the mid-point between the date at which the nest was first observed and the date of the subsequent site visit. We then ran linear models with nest initiation date and floral density during the nest-construction period as predictors of the number of emerged bees per nest with site included as a categorical fixed effect.

For all models, we checked that model assumptions were met with diagnostic plots, and we note cases where data could not be transformed to meet model assumptions.

## Results

Over the course of this 5-year study, seasonal patterns of floral density varied from year to year and across sites. From 2013 to 2015, floral density and day of year were positively correlated ( $r = 0.295$ ). In 2016 and 2017, floral density and day of year were negatively correlated ( $r = -0.386$ ;  $r = -0.308$  for 2016 and 2017 respectively). Similarly, our regression analyses on the 2013 to 2015 dataset showed positive relationships between the day of the year (squared) and floral density, while our analyses for 2016 and 2017 resulted in negative relationships between the day of the year (squared) and floral density. In general, visual inspection of scatter diagrams (Figure 2) suggest that floral density behaves bimodally, exhibiting both an early- and a late-season peak in abundance. However the magnitudes of early peaks relative to late peaks vary by year and site. For example, for most sites in 2014 and 2015, late season peaks tended to exceed early season peaks while the opposite was true for most sites in 2016 and 2017.

Throughout the season, we recorded emergence from a total of 36 *H. fulgida* individuals from nests constructed in 2016 across three of our sites. Of these, 15 emerged alive and we were able to mark and release them. However, none of these individuals were subsequently observed nesting in our trap-nests so we were not able to test the effects of emergence time on individual reproductive success.

In total we observed 9 *H. fulgida* nests in 2013, 22 nests in 2014, 38 nests in 2015, 37 nests in 2016, and 19 nests in 2017. In 2013, all nest occupants were marked and in 2017, 14 out of 18 individuals observed nesting were marked.

In general, for all years in which data were collected on nesting progress (2013 to 2015, 2017), we found significant negative relationships between nest initiation date and bee reproductive performance (i.e. nest construction rate and cells per nest; Figure 3). Nesting progress was most rapid early in the season and significantly decreased over the course of the season ( $F_{3, 186} = 18.29$ ,  $p < 0.001$ ; Figure 3A). Similarly, individuals with earlier nest initiation dates had more brood cells per nest while those that started nesting later had fewer cells per nest ( $-0.117$  nest cells per day;  $F_{10, 57} = 4.359$ ,  $p < 0.001$ ; Figure 3B). Nest initiation day was not a significant predictor of total cells per individual, likely because very few individuals were actually marked in our dataset resulting in a small sample size for this test. Surprisingly, average floral density during nesting was not a significant predictor for either nesting rate or number of cells per nest ( $p = 0.196$  and  $p = 0.227$  respectively). Nest initiation date and floral density were also not significant predictors of the number of emerged bees per nest (based on nests constructed in 2016). However, this result was likely the result of the sample size used for in this test since emergence was observed from very few nests in 2017.

## Discussion

Our results indicate that *H. fulgida* individuals that begin nesting earlier in the season are both able to construct nests more rapidly, and have greater reproductive output. While this may suggest that floral resource abundance play a weak selective role on *H. fulgida* reproductive timing, we recognize that our initial presumptions concerning seasonal patterns of floral abundance may have overlooked more complex nuances (i.e. bimodality), and that there are likely other factors that were not tested here but that may be important in understanding *H. fulgida* reproductive timing (i.e. weather and correlative effects of parental quality).

We were not aware of the non-linear patterns characterizing the specific floral-hosts we identified for *H. fulgida* *a priori*; however, bimodal patterns of *total* flower abundance have been documented in this area in a study by Aldridge et al. (2011). In that study, the authors conclude that increasing mean mid-summer temperatures are driving shifts from the typical unimodal peaks in seasonal floral abundance to bimodal peaks. In the case of our study, this pattern may suggest that there are actually two possible reproductive strategies available to *H. fulgida* individuals with regards to resource abundance since early-nesters may benefit from early resource peaks and late-nesters may benefit from late peaks. However, this was not reflected in our analysis of *H. fulgida* nesting since relationships between reproductive activity (i.e. nest construction rate and total cells per nest) and average floral density were relatively weak.

While it is tempting to associate the advantages of early nesting seen in our results to the cumulative benefits of both relatively high resource abundance early in the season and ample time for offspring development, we did not find a strong relationship between reproductive output (i.e. nesting rate and cells per nest) and average floral density. Moreover, as of now, data collected on the effect of reproductive timing on offspring development (i.e. cocoon spinning) remains to be analyzed. The lack of relationship between reproductive output and floral density was unexpected and confounds our initial presumptions in which early-nesters are resource-limited. Here we present several speculative reasons for why individuals nesting earlier may have had higher nesting rate, and reproductive output:

First, warm seasons in the Rocky Mountains are characterized by an annual monsoon system in which the region experiences a pronounced increase in stormy conditions and rainfall that typically lasts from July to mid-September (Higgins et al. 1997; Adams & Comrie 1997). The increased frequency of storm events during this period may have significant consequences specifically for flying insects since flight (and therefore foraging activity) is highly dependent on weather conditions (Kingsolver 1989). Separate studies on honey bees (*Apis mellifera carnica*; Riessberger & Crailsheim 1997), stingless bees (*Melipona marginata*; Kleinert-Giovannini & Imperatriz-Fonseca 1986), and wasps (*Vespula germanica*; Kasper et al. 2008) all showed either reduction or cessation of foraging activity during rain events. Similarly, an experimental study found that the bumblebee *Bombus terrestris* L. had difficulties landing on flowers in strong wind conditions (Wolf et al. 1999). For these reasons, nesting earlier in the season before the monsoonal rains may have been advantageous for *H. fulgida* individuals since weather conditions were likely more favourable for foraging. Since HOBO pendant temperature/light data loggers (Onset Computer Corp., Bourne, Massachusetts, USA) are attached to the underside of one centrally located nest block at each site, future work may involve determining the effects of weather variables on *H. fulgida* reproduction. However, whether monsoonal conditions are actually promoting selection for early nesting in is questionable since reproductive activity (i.e. nest construction rate and total cells per nest) declined gradually over the course of the season (Figure 3) while monsoon season tends to start abruptly.

Secondly, how factors such as resource abundance and offspring developmental constraints impose selection on reproductive timing can be confounded by intrinsic parental qualities that are important in determining offspring success but that are only correlated with reproductive timing (Lande & Arnold 1983; Price et al. 1988). For example, in dwarf surfperch (*Micrometrus minimus*), females that breed earlier are often also larger individuals that have greater lipid

reserves compared those that breed later (Schultz et al. 1991). In this case, early-breeders may have greater reproductive output not because they breed earlier, but because they are in better physical condition to begin with. In our study, early-nesters may also tend to be individuals that develop and pupate faster, emerge earlier, and are therefore able to begin nesting earlier. Those that nest later may be individuals that take longer to develop and are of poorer physical condition when they begin nesting. Notably, while our results suggest that selection favours early nesting in *H. fulgida*, we still observed nesting activity relatively late in the season (mid- to late-July). This variation in nesting time may be reflective of the constraints of the timing of other life-history events such as pupation and emergence which likely vary across individuals.

## Conclusion

While the results of our study indicate that *H. fulgida* individuals are under directional selection for early reproduction, as of now, we can only speculate as to why we saw these trends. The underlying mechanisms driving these patterns including offspring developmental constraints, weather conditions, and maternal quality have yet to be investigated. Understanding these mechanisms may prove to be important as changes in environmental conditions due to climate change can potentially have significant effects on the factors that drive selection on reproductive timing in *H. fulgida*.

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## Appendix

TABLE 1. Number and percentage of nests containing each pollen taxon used by *H. fulgida* as major and minor constituents.

| Pollen taxon                                                        | Number of nests found as major constituent | % nests found as major constituent | Number of nests found as minor constituent | % nests found as minor constituent |
|---------------------------------------------------------------------|--------------------------------------------|------------------------------------|--------------------------------------------|------------------------------------|
| <i>Allium</i> spp.                                                  | 13                                         | 81%                                | 2                                          | 13%                                |
| <i>Arctostaphylos uva-ursi</i>                                      | 0                                          | 0%                                 | 2                                          | 13%                                |
| <i>Rosaceae</i><br>( <i>Fragaria</i> spp. & <i>Potentilla</i> spp.) | 10                                         | 63%                                | 11                                         | 69%                                |
| <i>Phacelia</i> spp.                                                | 1                                          | 6%                                 | 1                                          | 6%                                 |
| <i>Polemonium</i> spp.                                              | 0                                          | 0%                                 | 3                                          | 19%                                |
| <i>Vicia americana</i>                                              | 0                                          | 0%                                 | 1                                          | 6%                                 |
| <i>Wyethia amplexicaulis</i>                                        | 0                                          | 0%                                 | 1                                          | 6%                                 |

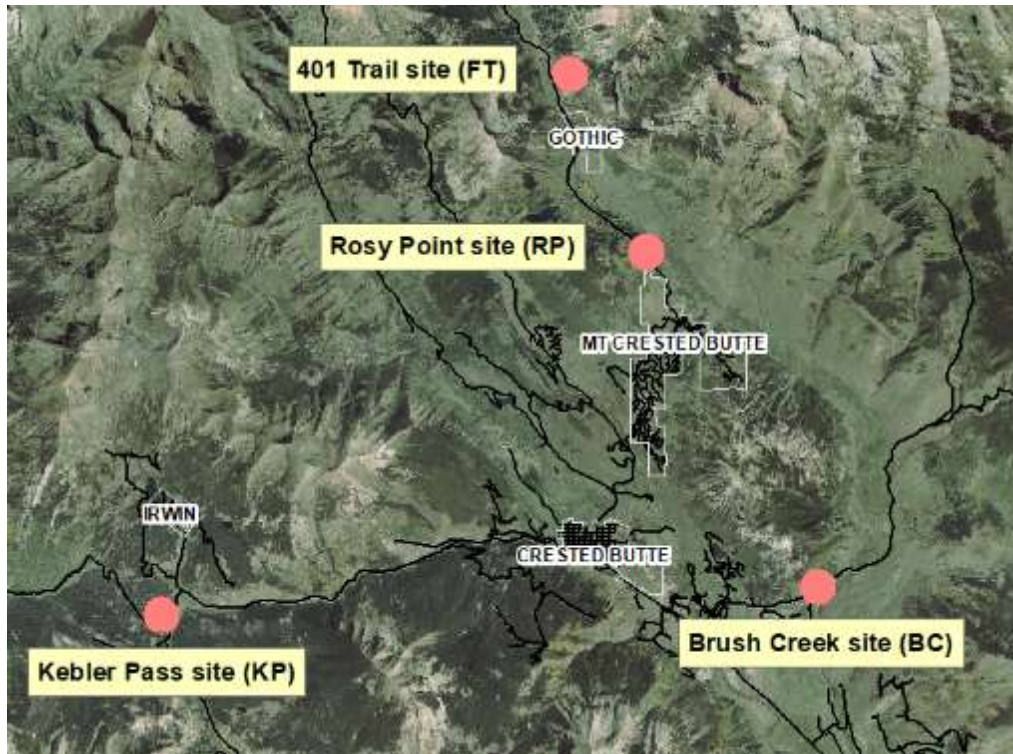
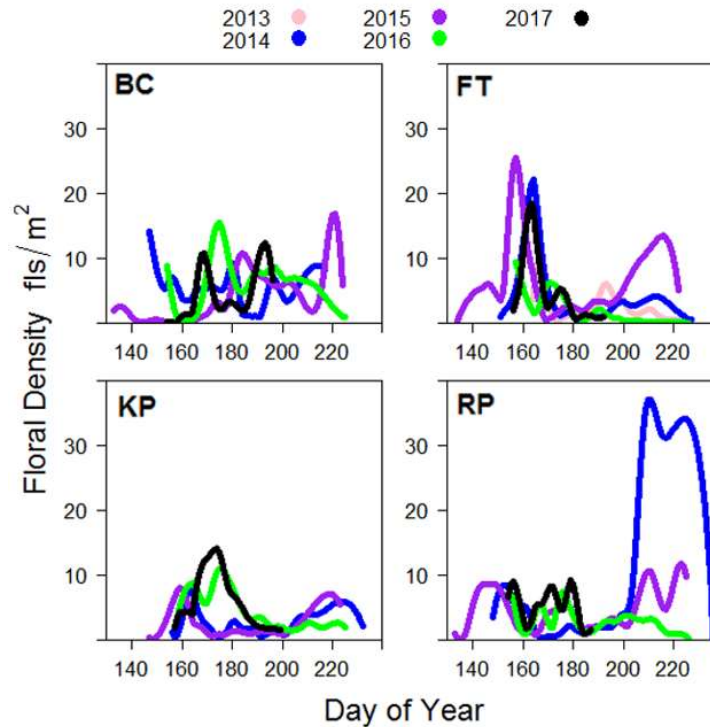
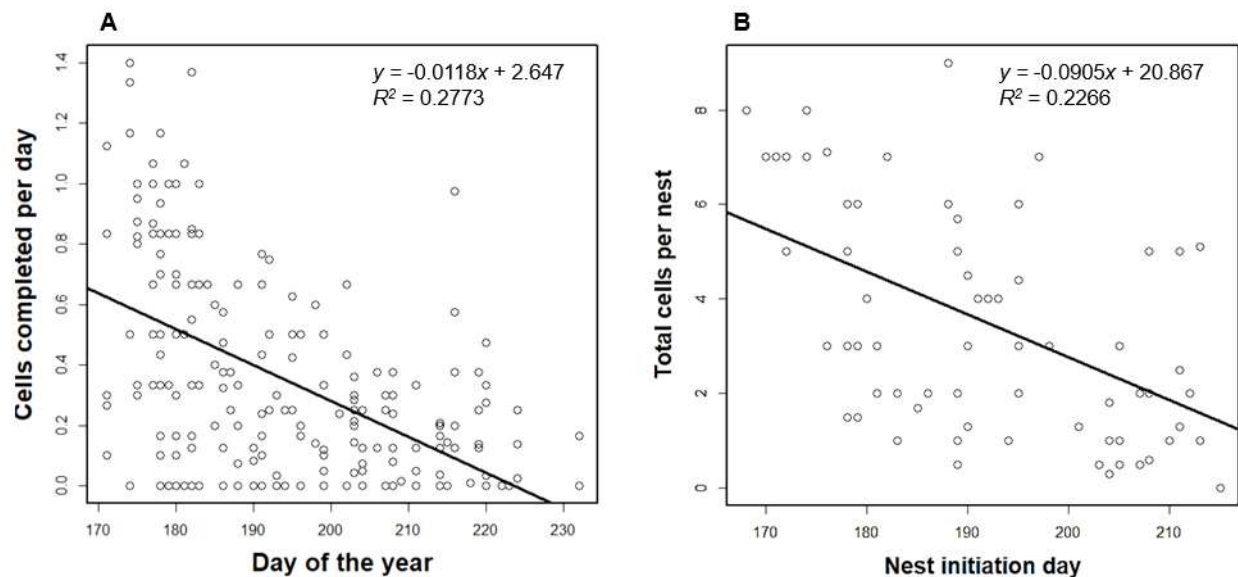


Figure 1. Map of four study sites used in 2017 data collection



**Figure 2.** Floral densities over the sampling season at four sites (i.e. those included in data collection in 2017) from 2013 to 2017. Lines are cubic splines fitted using the R package “stats” to the observed floral densities.



**Figure 3.** (A) Rate of nesting progress (number of nest cells per day) as a function of the day of the year for 227 observations of 83 *H. fulgida* nests from data collected over four years (2013-2015, 2017) across six study sites. (B) Total number of brood cells per nest as a function of when that nest was first initiated for 68 *H. fulgida* nests from data collected over three years (2013-2015) across six study sites.