

Climate Change and Parasitism: An Investigation into Parasitic Bees' Climate Responses as Compared to their Hosts

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Abstract

With an increase of research into how climate change has affected bees, only a fraction of that research has been conducted in relation to bees with parasitic life history strategies. Parasitic bees serve important ecological roles in the population management of their hosts, which comprise a variety of bee families and groups, while also providing pollination services to a variety of plants. This study analyzes the social parasitic bee species *Bombus insularis* and kleptoparasitic bee genus *Sphecodes* as well as their respective hosts near the Rocky Mountain Biological Laboratory located in Gothic, Colorado

over an 11 year and nine year period, respectively, to determine (1) if hosts and their parasites respond similarly to climate change, (2) whether host and parasite abundances are affected by the same environmental cues, and (3) which abiotic environmental factor(s) are driving these variations. To do this we calculated the yearly catch rate of each parasitic bee and their hosts across multiple long term study sites and compared them to snowmelt timing and rainfall utilizing a generalized linear mixed model. We found that *Bombus insularis* responds to environmental cues in a mismatched manner compared to its hosts while *Sphecodes* and its hosts respond in a similar way. For all parasites and hosts we found that snowmelt was the only environmental factor driving these variations. These results imply that either climate change is affecting some parasitic bee abundances differently than those of their hosts. Alternatively, the way in which climate change affects some parasitic bee abundances could allow for more parasitism of their host species.

Key Words

- ◆ *Bombus insularis*
- ◆ *Sphecodes* sp.
- ◆ Kleptoparasite
- ◆ Social Parasite
- ◆ Climate Change
- ◆ Parasite-Host Abundance

Introduction

Climate change is increasingly causing changes in the abundance and distribution of organisms worldwide. Changes in temperature cause changes in species phenologies and abundance as well as the regions in which they are found (Parmesan 2006). This is especially true of species that live at high elevations, as mountain regions are expected to experience some of the most extreme climate changes (Nogés-Bravo et al. 2007). There is evidence suggesting that species are already being impacted by the effects of climate change. For example, shifts in floral resource availability and phenology cause pollinator species to respond by changing their elevational and latitudinal ranges (Miller-Struttmann et al. 2015; Pyke et al. 2016).

Bees serve as critical pollinators within mountain regions. However, climate change is causing declines in pollinator populations worldwide (Burkle et al. 2013; Soroye et al 2020). Ogilvie et al. (2017) found that climate change is affecting bumble bees in the Colorado Rocky Mountains around the Rocky Mountain Biological Laboratory (RMBL, 9,500 feet elevation). Earlier snowmelt dates have caused the flowering season to become longer. Over the course of the 39-year study, first flowering on the community level advanced by 25 days, at a rate of 6.4 days per decade (CaraDonna et al. 2014). However, plants only create a certain number of flowers regardless of the season's length. This leads to reduced average daily floral availability across the season, resulting in an increase in low floral abundance days which makes it more difficult for pollinators such as bees to obtain nectar and pollen resources. Furthermore, earlier snowmelt dates increase the likelihood of damaging spring frosts, which can damage flowers, leading to further pollinator food shortages (Ogilvie et al. 2017). These food shortages are especially important for bumble bees early in the season when queens are establishing their nests. Furthermore, there could be reductions in the phenological match between plants and their pollinators, which over time, could lead to reductions in both plant and pollinator populations. A study found that the removal of one pollinator species reduces overall ecosystem functioning and can lead to a decrease in pollinator specialization, resulting in negative effects to plant reproduction (Brosi and Briggs 2013). Research examining plant-pollinator interactions is therefore critical to protecting pollination services.

In order to understand plant-pollinator networks and ecosystem functioning as a whole, it is critical to understand parasites and the ways in which they impact bee populations in the context of climate change. Although they are often perceived as destructive, parasites play a critical ecological role in host population management and ecosystem balance. Many parasites have closely evolved alongside their hosts and provide critical top-down control for the natural management of host populations (Forrest and Chisholm 2017). Parasitic bees nectar feed as adults, making them important pollinators. Moreover, by making at least 15% of the 20,000 bee species worldwide (Onuferko et al. 2019), parasites are important to conserve from a conservation perspective. Further research is necessary to better understand parasitic bees as well as to uncover how changes in climate may affect their ecology and host interactions.

Parasitism in bees is highly evolved. These bees often lack specialized hairs used to collect pollen to supply a brood cell with provisions. Thus, they insert their egg into the chamber of another bee species and leave it to develop there. These invading parasites are often known as "cuckoo bees," named after cuckoo birds who lay their eggs in another bird's nest to be raised. There are other types of parasitic bees, as well, such as social parasites, who kill and replace a colony's queen and enslave its workers to raise her own parasitic offspring.

Parasitic bees may be at high risk from the effects of climate change, most likely due to their dependence on certain host species or genera for survival. A long-term study on 360 bee species found a population decrease steeper than that of their hosts in kleptoparasitic bees in Belgium, especially in the Megachilidae and Anthophoridae families (Rasmont et al. 2005). This decline was most likely caused by a drop in the number of available hosts, which are essential to the

survival of kleptoparasites. The strong regression of kleptoparasites can be tied to bee decreases as a whole, which are exacerbated by climate change (Rasmont et al. 2005).

Little is known about parasitic bee ecology, let alone the impacts of climate change on these bees as compared to their host species. Many parasitic bees are challenging to identify to the species level, the specific host species they parasitize are still unknown, and the plants they visit for nectaring (and perhaps pollinate) are often unrecorded. Nonetheless, parasitic bees are speculated to play a critical role in host population control similarly to how other parasites manage their host populations (Washburn 1991). We analyzed long-term bee phenology data to ask: (1) if hosts and their parasites respond similarly to climate change, (2) whether host and parasite abundances and phenology are affected by the same environmental cues, and (3) which abiotic environmental factor(s) are driving these variations. We hypothesized that there is a difference in the way climate change affects parasitic bees as compared to their hosts as demonstrated in Rasmont et al. (2005). However, in the context of declining global bee populations, we hypothesize that host and parasite abundances will be affected by similar abiotic factors (Rasmont et al. 2005).

Methods

Study Methods

We conducted a bee abundance and plant phenology observational study in the East River valley in the West Elk Mountains of southwest Colorado, USA, near the Rocky Mountain Biological Laboratory (RMBL) in Gunnison County. Our study built on a dataset beginning in 2009 consisting of seventeen study sites across an elevational gradient (**Figure 1**).

To collect data pertaining to our dependent variables (parasitic and host bee abundances) and to continue to add to the long-term dataset, we sampled each of our seventeen study sites every two weeks over the course of the 2020 summer flowering season, as described in Gezon et al. (2015). Each site consists of two 45 meter transects intersecting at approximately right angles. We sampled bees using both passive and active methods. For our passive sampling protocol, pan traps (weigh boats) were painted either fluorescent yellow, fluorescent blue, or left white, in order to attract pollinators with different flower color preferences. Traps were placed every three meters along each transect and filled with soapy water (using Dawn blue dish soap) to create a passive lethal trap. Traps were left in place all day (for a minimum of five hours, from approx. 09:00-15:00). At the end of the field day, bees were collected from the pan traps and stored in 70% ethanol for identification in the laboratory. Passive pan traps typically account for a high proportion of bees captured (Wilson, Griswold & Messinger 2008; Popic, Davila & Wardle 2013), but are primarily useful for collecting smaller-bodied bees; they are less effective for collecting larger species (i.e., *Bombus* sp.).

In order to catch a wider variety of bee species, including *Bombus* sp., we also conducted active sampling. Active sampling consisted of systematically walking through the area surrounding the

two transects for one hour each in the morning and afternoon in each site. Bumble bees (*Bombus* sp.) were netted and identified *in situ* to the species level using their pile markings, marked with indelible ink on their thorax to avoid double counting, and released. Solitary bees cannot be identified in the field and were stored in ethanol for laboratory identification. For all netted bees, the netters recorded the host-plant from which the bees are netted. The amount of time that pan traps were in the field and bees were netted for was recorded on a daily basis to control for variation in sampling effort.

In order to assess environmental and weather-related factors driving bee phenology — our independent variables — we measured floral abundance and phenology in each site. To do so, we estimated floral abundance and diversity in fixed 2 x 2 meter flower census plots every day a site was sampled for bees (see Gezon et al. 2015). To estimate floral abundance and diversity we recorded the plant species in bloom and the number of flowers per plant on 10 randomly selected plants per plot on 10 randomly selected plants per plot. To account for any plant species missed in the census plots we also recorded flowering species outside the plots in order to account for the richness of species missed in the flowering plots data.

Overall, these data allowed us to monitor parasite and host abundances over 11 years for *Bombus insularis* and nine years for *Sphecodes* sp. to determine if bee parasites and hosts responded similarly, or if they were differentially impacted, by climate change.

Environmental variables

We initially assessed five environmental factors as candidates for our independent variables: first date of bare ground (snowmelt), centimeters of snowfall, centimeters of summer rainfall, mean maximum summer temperature, and number of accumulated summer degree days. After running correlation tests in R between each of the five variables (see **Table 1**), we found that yearly mean maximum summer temperature and number of degree days were highly correlated.

Table 1: Correlations Between Abiotic Factors

	Rainfall	Degree Days	Average Maximum Temperature	Snowmelt
Rainfall	1.0			
Degree Days	0.1152	1.0		
Average Maximum Temperature	0.3448	0.8014	1.0	
Snowmelt	-0.4286	-0.4286	0.6271	1.0

To avoid multicollinearity, we limited our independent variables of interest to three environmental factors: first date of bare ground (the number of days into the year starting January 1 to when the snow melted), precipitation (calculated in cumulative centimeters of summer rainfall), and yearly mean summer maximum temperature (calculated in degrees Celsius). Summer was operationalized as April 1 to September 30. We elected to use the first bare ground date rather than centimeters of winter snowfall, as the variables are highly correlated and bare ground date is standard in the literature (Ogilvie et al. 2017; Stemkovski 2020). Further into the analysis we found that snowmelt and yearly mean summer maximum temperature yielded Variance Inflation Factors (VIFs) greater than 6 and so only snowmelt was included in analyses. As such, our final independent variables of interest consisted of the first date of bare ground (Julian days) and rainfall (centimeters). All weather data was provided by Billy Barr.

Calculating Bee Abundance

We conducted two separate analyses: one for the social parasitic bee *Bombus insularis* compared to two hosts over an 11 year period at nine different sites and one for the kleptoparasitic bee *Sphecodes* sp. compared to two hosts over a nine year period at 15 different sites. Our independent variables were environmental and weather-related factors impacting bee abundance. Our dependent variables were the abundances of host bee species as compared to parasitic species.

For the social parasitic bee *B. insularis*, we isolated the data collected on all *Bombus* sp. for the past 11 summers and calculated the yearly catch rate of *B. insularis* (see **equation 1**) at nine sites, all close to the RMBL and similar in elevation (2877-3069 m).

$$\frac{\text{\# of bees caught}}{\text{sampling effort}} \quad 1.$$

For catch rate, the number of bees caught at each site in a given year was divided by the number of sampling hours (netting only) spent at the same site during that year. We did the same for the five most common *Bombus* hosts; *B. appositus*, *B. fervidus*, *B. flavifrons*, *B. nevadensis*, and *B. occidentalis*. However, due to a lack of data in many years across multiple sites for *B. fervidus*, *B. nevadensis*, and *B. occidentalis*, our final analysis only utilized the catch rates calculated for *B. appositus* and *B. flavifrons*. Since *Bombus* sp. are physically large in comparison to solitary bee species and thus almost exclusively captured via netting, in this analysis we controlled for netter bias among years (given that different years had different research assistants collecting the data). To control for this bias, we calculated the ratio of *B. insularis* compared to the total number of *Bombus* sp. excluding *B. insularis* caught each year (**equation 2**).

$$\frac{\text{\# of } B. \textit{insularis} \text{ caught}}{\text{\# of all other } Bombus \text{ sp. caught}}^2.$$

The number of *Bombus insularis* caught at each site in a given year was divided by the number of all other *Bombus* species caught at the same site during that year. This allowed us to ascertain the ratio of *B. insularis* caught in relation to all other *Bombus* sp. We used this ratio as our response variable for our *B. insularis* analysis.

For the kleptoparasitic bee *Sphecodes* sp., we used the data collected on all solitary parasitic bees for the summers from 2009-2017 (the solitary bee species from the 2018 and 2019 data are not yet completely identified). Using these nine years of data, we calculated the yearly catch rate of *Sphecodes* sp. (see **equation 1**) at 15 separate sites across the elevation gradient. We did the same calculations for *Sphecodes*' six most common hosts: *Agapostemon* sp., *Andrena* sp., *Calliopsis* sp., *Colletes* sp., *Halictus* sp., and *Lasioglossum* sp. We restricted the host analysis to *Halictus* sp. and *Andrena* sp. because those genera had the best representation across sites and years for analysis. We restricted our kleptoparasite analysis to the genus rather than the species level due to the difficulty of identifying *Sphecodes* and many of its hosts past their genera. This does not substantially impact the catch rate analysis because many *Sphecodes* species share the same genera of hosts. Unlike the *B. insularis* analysis, the bees collected for our solitary analysis, including *Sphecodes* sp., were primarily caught in passive pan traps due to their small body size. Controlling for netter bias was not necessary for the *Sphecodes* sp. analysis owing to the passive nature of pan traps, thus we simply used the yearly catch rates of *Sphecodes* sp. and their hosts in this analysis.

Analysis

Analyses were conducted in R and SAS. For our analyses of the parasites, we used the first spring date of bare ground and centimeters of rainfall in the summer as our fixed independent variables, and site as our random effect. However, due to widely varying abundances of *B. appositus* and *B. flavifrons*, catch rate was calculated across all sites each year for *Bombus insularis* hosts, removing site as a random effect for these analyses. For the same reasons, this yearly catch rate was utilized for *Sphecodes* hosts as well. We conducted separate generalized linear mixed models (one for each parasite) with gaussian error distribution using the lme4 package (Bates et al. 2015) in R (R Core Team 2020). We compared a full model containing all of our fixed variables to reduced models for parasites and hosts for both *B. insularis* and *Sphecodes* sp., for a total of four models. We then conducted ANOVAs between each of these reduced models and our full models to determine the best fit model. For *Bombus insularis* and *Sphecodes* sp., the full models held the best fit. For the hosts for each of the parasites, we conducted a simpler analysis in SAS in which we calculated the total host catch rate in each site-

year and then calculated the mean catch rate across all sites in each year (yielding one datapoint per year). We then used multiple regression to assess how host catch rate related to the dependent variables, retaining the model for each species that yielded the lowest AICc values (by 2 units).

Results

Our response variable for the *Bombus insularis* analysis, the ratio of *B. insularis* catch rate to the catch rate of other *Bombus* sp., ranged from 0 to 0.75 (mean=0.0751, SD=0.1249). The response variable for the two *B. insularis* hosts analyzed, *B. appositus* and *B. flavifrons*, was the combined summer catch rate of *B. appositus* and *B. flavifrons*, which ranged from 0 to 25.052 (M=3.4795, SD=4.1101) host bees caught per hour. Our response variable for the *Sphecodes* sp. analysis, the summer catch rate of *Sphecodes* sp., ranged from 0 to 1.0646 (M=0.1079, SD=0.1816) *Sphecodes* sp. collected per hour. The response variable for the two genera of *Sphecodes* sp. hosts analyzed, *Andrena* sp. and *Halictus* sp., was the combined summer catch rate of *Andrena* sp. and *Halictus* sp., which ranged from 0 to 2.9523 (M=0.7155, SD=0.6578) host bees caught per hour. The environmental variables we used in the models exhibited wide variation. Day of bare ground, our first fixed independent variable for all analyses, ranged from 114 (April 24th) to 162 (June 11th) days to bare ground after January 1, while centimeters of summer rain, our second fixed independent variable for all analyses, ranged from 10.41 to 34.60 (M=22.6799, SD=7.5753) cm of rain between April 1 and September 30.

Our generalized linear mixed model revealed differential effects of snowmelt date on parasite and host abundances. For *Bombus insularis*, earlier snowmelt was associated with higher *B. insularis* abundance ($X^2=20.39$, $p < 0.0001$; **Figure 2**). In contrast, however, the parasite's hosts, *Bombus appositus* and *Bombus flavifrons*, showed the opposite trend and were more abundant in years with later snowmelt ($F_{(1,10)}=6.98$, $p=0.0296$; **Figure 3**). *Sphecodes* sp. parasites were also more abundant in early snowmelt years ($X^2=4.91$, $p=0.03$; **Figure 4**), as were their hosts ($F_{(1,8)}=22.07$, $p=0.003$; **Figure 5**).

Rainfall was not found to significantly affect *Bombus insularis* abundance ($p>0.05$), nor did it impact *Bombus* hosts, ($F_{(1,10)}=1.40$, $p=0.2701$; **Figure 6**). The impacts of rainfall were also not significant for *Sphecodes* sp. ($p>0.05$) or their hosts ($F_{(1,8)}=3.82$, $p=0.098$; **Figure 6**).

Discussion

The overall goal of this study was to expand the understanding of the relationship between climate factors, parasitic bees and their hosts. We predicted that the populations of both parasite and host species would decrease in response to climate change. However, we found that there was not a similar response to climate change between our social parasite and its hosts. There are more *Bombus insularis* in earlier snowmelt years and more of our *Bombus* hosts, *B. appositus* and *B. flavifrons*, in later snowmelt years. As for the solitary bees, we found that there was a similar response to climate change between parasites and their hosts. *Sphecodes* sp., our solitary parasite, catch rates are higher with earlier snowmelt, and *Sphecodes* hosts, *Andrena* sp. and

Halictus sp., are more abundant with earlier snowmelt. Our results were consistent with our hypothesis that host and parasite abundances would be affected by similar environmental cues. We found that the abiotic factor driving these parasite and host variations were snowmelt timing, which is correlated with temperature. This makes sense because earlier snowmelt would require warmer temperatures. However, we found that rainfall was not significantly associated with either parasites or host variations. From these results we can conclude that populations of some parasitic bees and their hosts benefit from earlier snowmelt years while other parasitic bee populations respond in a mismatched manner as compared to their hosts. The mechanisms driving these variations deserve further study.

This study has provided us with a stronger understanding of how snowmelt and, by correlation temperature, affects parasitic bees and their hosts. Our results also support related studies that found similar climate factors directly and indirectly affect abundance (Bergman et al. 1996, Ogilvie et al. 2017). We are not sure if the higher abundance of *B. insularis* is affecting the host abundances or if early snowmelt and higher summer temperatures are having an effect. Further research is needed to understand what about earlier snowmelt allows *B. insularis* to be more abundant.

There are many hypotheses that could explain the results we found for *B. insularis* and *Sphecodes*; these hypotheses are not mutually exclusive. *B. insularis* and *Sphecodes* could be more abundant in earlier snowmelt years due to their physiology. Studies have shown that certain species of bumble bees have a greater physiological tolerance to cold temperatures than lower elevation bees (Oyen et al. 2016) and that smaller bees are less able to thermoregulate during higher temperatures (Bergman et al. 1996). Another explanation could be that in earlier snowmelt years, *B. insularis* host queens are out earlier to forage, allowing more opportunity for *B. insularis* to infiltrate the hive, similar to how early emergence of ground nesting bumble bees could be caused by an increase in soil temperature due to early snowmelt (Kudo & Ida 2013). Another explanation could be that early snowmelt years are often associated with lower flower days early in the season (Ogilvie et al. 2017) which could put added stress on queens starting hives, making them more vulnerable to attack and usurpation by *B. insularis*. Overall, the biggest question stemming from these results is whether it is the parasite or the environmental factor causing the reduced host abundances. Studies that manipulate floral abundance and assess how good social parasites are usurping queens would provide important ecological insights.

Two caveats are important to consider in this study. First, our analysis does not consider how lag effects of environmental conditions may affect the abundance of hosts and their parasites. Lag effects explain how previous years' climate influence some organisms in the present. Due to their generational life histories, this likely would only be seen in the solitary species of our study. Due to time constraints we were unable to include this in our analysis. Second, our analyses only considered environmental variables associated with the abiotic environment and we did not consider floral abundance and phenology in our analyses. Doing so would have required more complicated analyses teasing apart the direct and indirect effects of abiotic factors on flowers and

hosts (akin to Ogilvie et al 2017) and would have required that we know who the floral host plants are for the solitary parasites, of which little is known.

Research into parasitic bees' general ecological roles is lacking and therefore necessary. Research into parasitic bees as population control for hosts is critical to understanding how host-parasite interactions influence and interact with ecosystem functioning. More so, further research on the potential and relative importance of parasitic bees as pollinators is warranted. Parasitic bees, though they lack the means to collect pollen, feed on nectar and get covered with pollen in the process. Thus, we believe they are active pollinators, but further research is needed to elucidate which flowers they pollinate. In addition, the pollination ability of parasitic bees compared to other species in their community is unknown and should be investigated to assess the degree to which they are efficient pollinators.

Figures

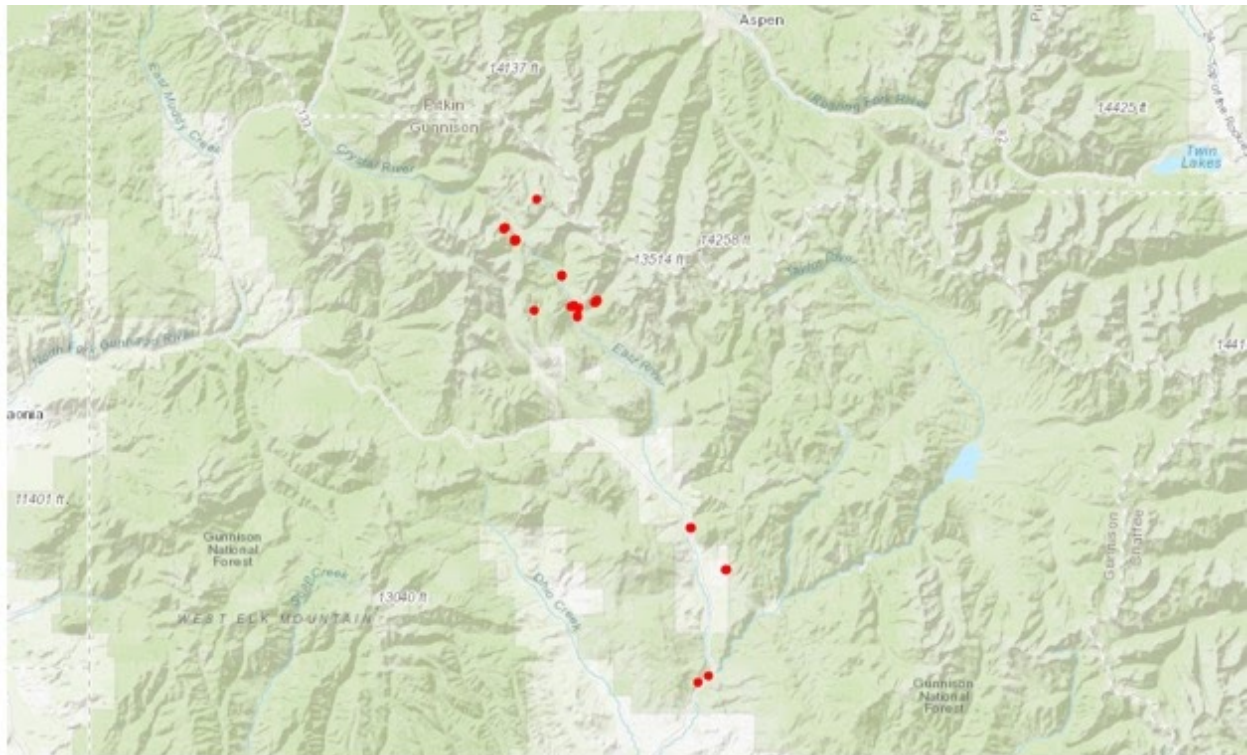


Figure 1: Study Sites Located in the East River valley near the Rocky Mountain Biological Laboratory in Gunnison County. Pictured are the 17 study sites across an elevational gradient from Almont to Mexican cut.

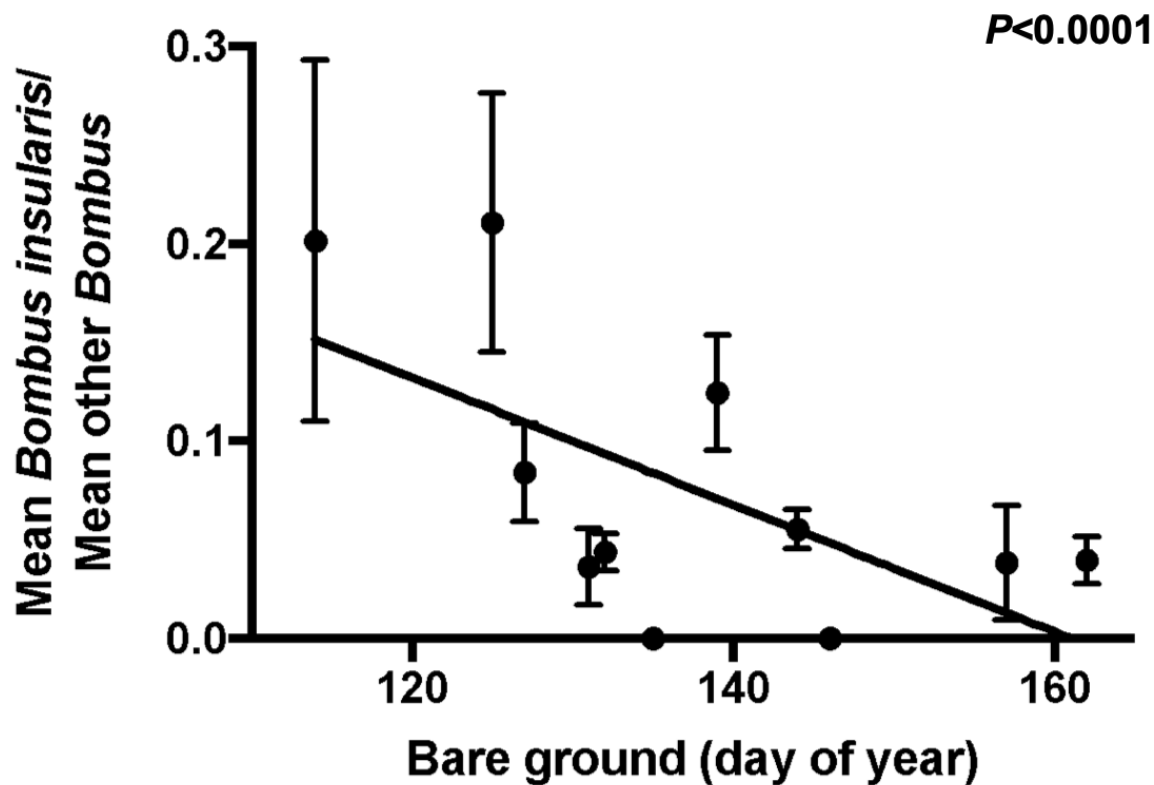


Figure 2: Effect of snowmelt on *Bombus insularis* abundance

Bare ground represents the number of days after January 1st when bare ground was first seen. Dots represent the mean across all sites and error bars are standard error.

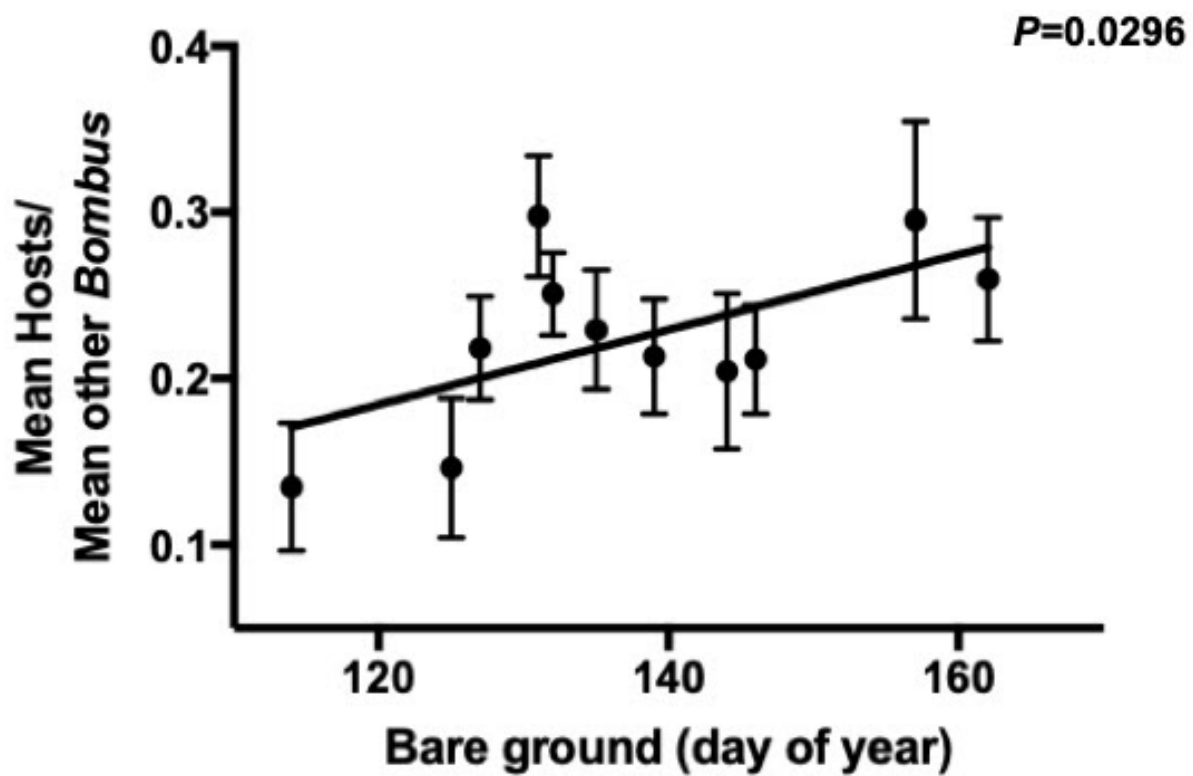


Figure 3: Effect of snowmelt on *Bombus* host abundance

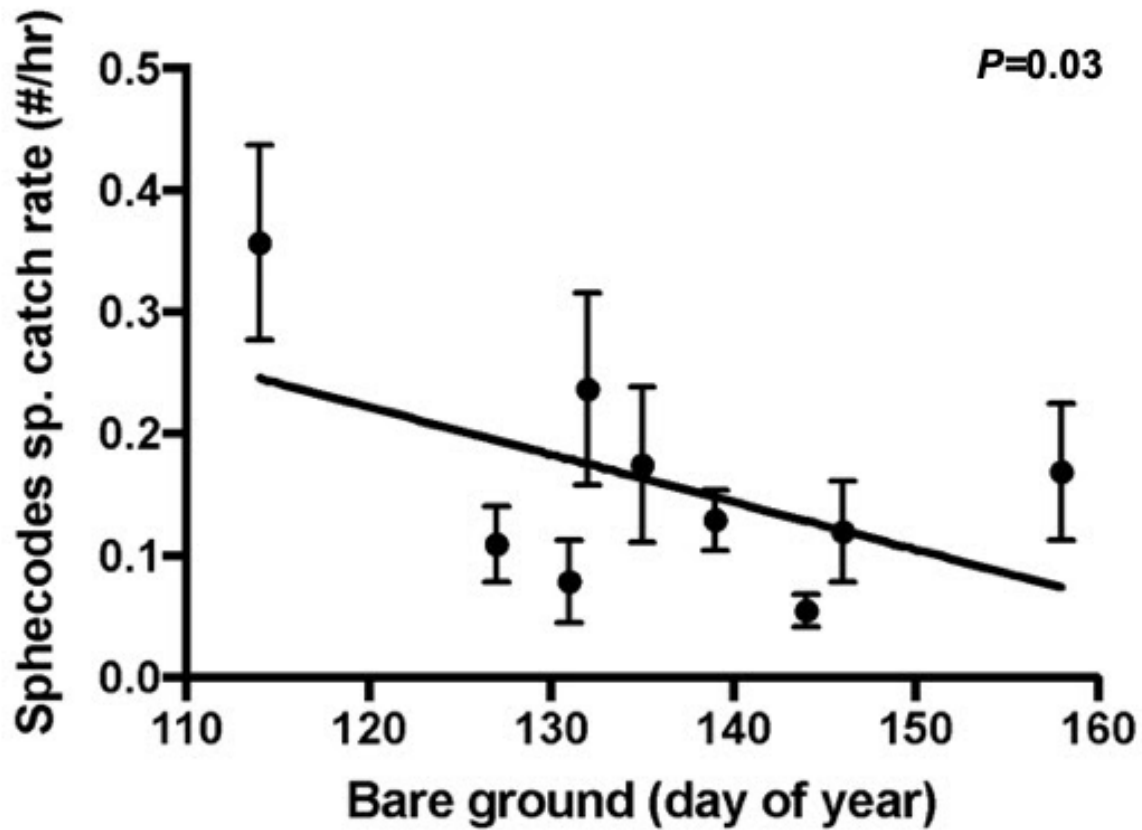


Figure 4: Effect of snowmelt on *Sphecodes* sp. abundance

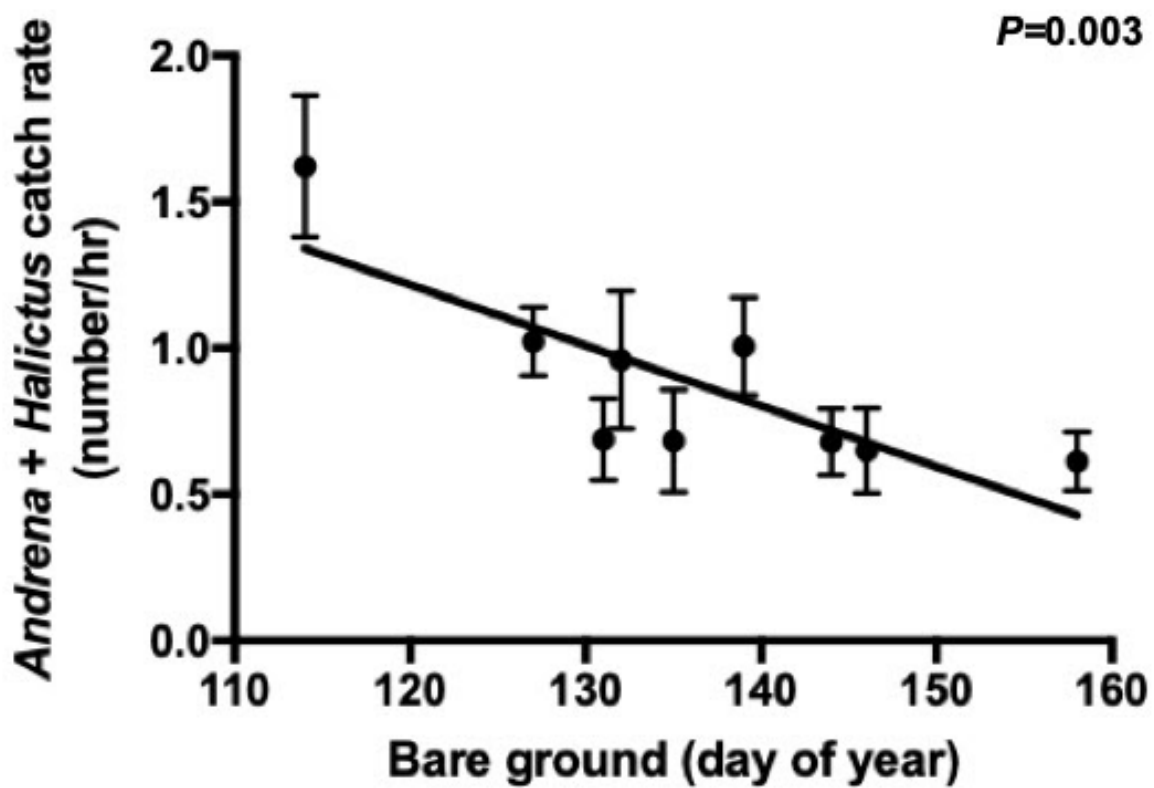


Figure 5: Effect of snowmelt on *Sphecodes* sp. host abundance

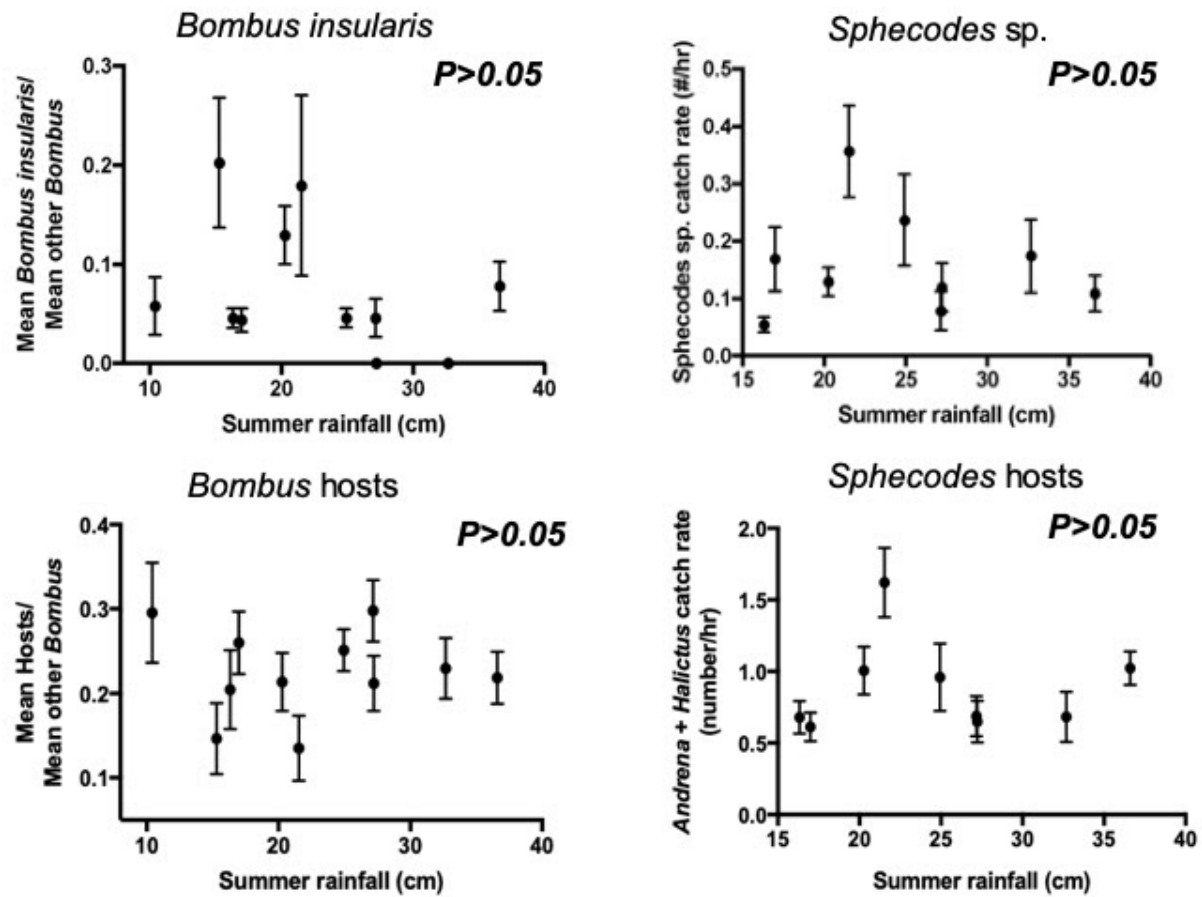


Figure 6: Effect of rainfall on parasite and host abundances

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