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Jessica N. Welch
University of Tennessee - Knoxville, jwelch14@utk.edu

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Variation in the Abundance of Bees Across Distinct Montane Meadows

JESSICA NICOLE WELCH

Advisor: Nathan Sanders

Department of Ecology and Evolutionary Biology,
University of Tennessee, Knoxville

Across different landscapes, plant abundance and richness change. Bee distributions may vary spatially or temporally in accordance with differences in floral diversity. I used a habitat-based approach to investigate the hypothesis that the abundance of bees in assemblages varied among three distinct meadow types: dry meadow, wet meadow-Veratrum, and wet meadow-Salix. Patterns of bee abundance were sampled using bee bowls and netting around Gothic, Colorado. I sampled four triplets of sites (each consisting of the three meadow types) every other week, between June 22 and August 26, 2009. In total, I caught 2938 bees and identified each of them to family. I found that there was no significant difference in the abundance of bees across the three meadow types. Furthermore, I did not detect a difference in bee abundance within a family across the three meadow types, though there were significantly more bees of the family Apidae than either Colletidae or Megachilidae within wet meadow-Veratrum sites. There was no significant relationship between bee abundance and the mean flower abundance or rarefied richness at sites. Overall, I found no difference in bee abundance at different meadow types once divided into four sampling periods; however, bee abundance for the family Apidae depended on time and meadow type while bee abundance for the family Halictidae depended on time only. Additional experimentation over multiple years may be needed to reveal significant patterns. About 50 percent of the variation in bee abundance was accounted for by site, rarefied plant species richness, and daily rainfall. Bee distribution may also depend on nesting preference, or perhaps there are species level differences that this experiment was not able to detect.

Introduction

Pollination by insects and other animals is critical to the reproductive success of up to 90% of angiosperm species (Buchmann & Nabhan 1996). Globally, bees are among the most important and effective pollinators and are often considered to play a keystone role within

ecosystems (Kearns et al. 1998). There are an estimated 30,000 species of bees with at least 4,000 species found in North America, and most rely on flower visitation for nectar and pollen to provision their offspring (Michener 1979). Many studies have tracked whether bee foraging behavior or intensity depends on the density or number of flowers of the same species (Bullock et al. 1989, Potts et al. 2003, etc.), but few studies have examined how the diversity of flowering plants among distinct habitat types might relate to the abundance of bee species over the course of an entire season.

In bee assemblages, there is some evidence that abundance is correlated with the number of flowering plant species. For example, Heithaus (1974) found that the number of flower-visiting bees was positively correlated with the number of flower species and flower abundance in Costa Rica. Trap-nesting of solitary bees in Southern Brazil showed that abundance and diversity depended on habitat, probably in response to the associated flowering resources (Buschini 2006). Both studies suggest that habitats and their associated floral diversity can have a significant effect on bee community structure.

Pollinator abundance should be expected to vary over the course of a single growing season because of climatic variation or the phenology of flowering. For example, Pascarella (1999) found that species richness of bees fluctuated markedly over the sampling period for different families and that the fluctuations differed slightly among habitat types. Fluctuations in the abundance of bees may have been in response to the availability of food resources which is closely linked to environmental cues such as temperature and precipitation. Flowering phenology may be especially important in determining bee abundance in habitats where the flowering period is short, such as in montane meadows. According to a study performed in the Colorado Rocky Mountains where there is a distinctively narrow flowering season, floral richness peaked during the middle of the flowering season (Morales et al. 2004). If pollinator abundance is correlated with flowering richness, then pollinator abundance should also peak during the middle of the season.

In this study, I surveyed the abundance of bee species among three habitat types in south central Colorado to address four questions: 1) Does the abundance of bees differ among meadow types? 2) Are the abundance and richness of flowering plants correlated with bee abundance? 3) Does bee abundance change over the sampling period? and 4) What biotic and abiotic variables account for variation in bee abundance among sites?

Methods

Study Sites

I conducted this study in and around the Rocky Mountain Biological Laboratory in Gothic, Colorado (RMBL; *latitude* 38°45'N, *longitude* 106°59'W). This sub-alpine area is at approximately 2,945 meter elevation in the East River valley of the West Elk mountains. The start of the growing season is marked by the melting snowpack near the end of May and ends with the first hard frost, typically in September (Inouye et al. 2000). I focused on three meadow types: dry meadow, wet meadow-*Veratrum*, and wet meadow-*Salix* (Willow) (Panel 1, Table 1). The three meadow types were identified by a local pollination specialist as having distinct characteristics and as being common throughout the study area (Inouye 2000). The dry meadows are characterized by rocky, dry soil, with plants in the following genera being the most common: *Erigeron*, *Potentilla*, *Eriogonum*, and *Arenaria*. Wet meadow-*Veratrum* has deep soil dominated by *Veratrum californicum*, as well as plants of the genera *Potentilla*, *Erigeron*, *Senecio*, and *Delphinium*. Wet meadow-*Salix* also has deep soil with a large presence of *Salix* (Willow) species and plants of the genera *Potentilla*,

Panel 1. The three meadow types surveyed – A. Dry meadow: rocky, shallow soil with sparse vegetation; B. Wet meadow-*Veratrum*: deep soil with dense vegetation dominated by *V. californicum*; C. Wet meadow-*Salix*: deep soil with dense vegetation dominated by *Salix* (Willow) species.



Table 1. Characteristics of each site.

Times Sampled	Dates Sampled	Site Name	Site Type	Elevation	Aspect	GPS Coordinates
5	June 22 July 6 July 22 Aug 3 Aug 17	David's 401	Dry	2967.19m	West facing slope	38°57'43.646"N 106°59'12.827"W
		Willey	Wet- <i>Salix</i>	2864.38m	No slope	38°57'21.497"N 106°59'18.535"W
		Tuttle	Wet- <i>Veratrum</i>	2869.34m	No slope	38°57'17.105"N 106°59'19.334"W
4	July 1 July 16 July 29 Aug 16	Sean's	Dry	2914.37m	West facing slope	38°57'50.757"N 106°59'33.416"W
		Gothic	Wet- <i>Salix</i>	2903.03m	East facing slope	38°57'47.117"N 106°59'41.517"W
		Beaver	Wet- <i>Veratrum</i>	2901.93m	No slope	38°57'41.748"N 106°59'38.310"W
4	July 9 July 24 Aug 5 Aug 19	Marriage	Dry	2987.35m	West facing slope	38°57'58.612"N 106°59'25.168"W
		Parking	Wet- <i>Salix</i>	2989.19m	No slope	38°57'55.227"N 106°59'19.213"W
		Avery	Wet- <i>Veratrum</i>	3024.14m	No slope	38°58'25.341"N 106°59'30.883"W
4	July 14 July 27 Aug 12 Aug 24	Hill	Dry	3056.33m	South facing slope	38°58'00.376"N 106°58'12.339"W
		Copper	Wet- <i>Salix</i>	3054.86m	South facing slope	38°58'08.244"N 106°58'04.824"W
		Little	Wet- <i>Veratrum</i>	3043.72m	South facing slope	38°58'02.350"N 106°58'07.860"W

Erigeron, *Achillea*, and *Castilleja*. Due to these differences among sites, I was advised that there would probably be difference in bee abundance as well, if they exist (Inouye, personal communication). Site elevations ranged from 2864 m to 3056 m, with similar slopes. Aspects were not uniform (Table 1). Why exactly were these types of meadows chosen?

Sampling Procedures

For this study, I sampled from four blocks. Each block had one each of dry meadow, wet meadow-*Veratrum* and wet meadow-*Salix* habitat types, and each block was sampled every other week. Sampling began at Block A on June 22nd, block B on July 1st, block C on July 8th, and block D on July 14th, continuing every other week until August 26, 2009. Each triplet of sites within a block was sampled four times except for Block A which was sampled five times (Table 1). Between the hours of approximately 0800 to 1700, I randomly placed 30 bee bowls (six oz bowls filled with soapy water, 10 painted fluorescent yellow, 10 fluorescent blue, 10 left plain white) every three meters on two fixed 45-meter transects at each site (LeBuhn et al. 2003). I recorded the time that the bee bowls from each site were placed and retrieved to control for minor differences in sampling effort among sites. Maximum air temperature, cloud cover, and wind speed were obtained from the RMBL weather station for each sampling day.

Because bee bowls typically sample smaller species of bees (Wilson et al. 2008), I also used netting to sample larger species (particularly species in the family Apidae and Megachilidae). I netted flying and flower-visiting bees for approximately one hour in the morning and one hour in the afternoon along the meadow transects and in the general vicinity at each sampling location. When I collected a bee on a flower, I recorded the flower species. If a bumble bee species was caught, I identified it in the field and released it after marking its thorax with a paint dot, so that I did not capture and count the same individuals multiple times.

In order to compare the richness of the floral community to the abundance of bees collected at each site, I also recorded flowering diversity and abundance at each site from six randomly fixed plots (each 2 m x 2 m) along the site transects. Flowering surveys were conducted by counting the number of flowering plants per plot and then counting the number of flowers on up to 10 flowering plants per species. I identified all flowering plants to species using Darrow (2006), Kershaw et al. (1998), and the RMBL herbarium.

Bee Processing

I used 95% ethanol to store the contents of the bee bowls until processing. All contents collected from a particular bowl color (fluorescent yellow, fluorescent blue or white) on a given date were stored together in one vial per site, respectively. All bees were washed, "fluffed" using a hair drier, and pinned. For each new bee species I collected (determined by eye), its proboscis was pulled prior to pinning. Bees were identified to family using Michener et al. (1994), the bee keys developed by Sam Droege on Discoverlife.org, and Rebecca Irwin's reference collection.

Statistical Analyses

Bee abundances were converted to number of bees caught per hour for each site and sampling day in order to account for unequal sampling times. All abundances were log transformed to improve normality.

To ask whether bee abundance differed among habitat types, I used a randomized block standard least squares model with bee abundance as the response variable and habitat type as the model effect. Block was chosen as a random attribute to compensate for spatial differences among sites. To ask whether bee richness at the family level varied among habitat types, I used a randomized block standard least squares model with bee abundance

for each of five families as the response variable and habitat type as the model effect. Block was chosen as a random attribute.

To assess if there was an association between bee abundance and flower abundance, I used a regression with bee abundance as the response variable and mean number of flower per site as the predictor variable. To assess if there was an association between bee abundance and floral richness, I used a regression with bee abundance as the response variable and rarefied flowering richness as the predictor variable. I rarefied flowering richness using EcoSim (Gotelli and Entsminger 2000) to take into account differences in floral abundance on estimates of the number of flowering species. Flowering species were rarefied down to the least common abundance.

To test whether bee abundance changed over the total sampling period for each meadow type, I divided samplings into four approximately three-week periods based on the number of times the blocks were sampled. I used a repeated measure ANOVA with bee abundance as the response variable and meadow type as the model effect.

To test what additional factors may predict bee abundance I first performed a multi-variate correlation using the quantitative variables rarefied richness, mean number of flowers, elevation (meters), high temperature, and rainfall (cm). Due to co-linearity among variables, mean number of flowers and high temperature were not used for model selection. Next, I performed a backwards-stepwise regression using the variables rarefied richness, rainfall (cm), elevation (m), site, meadow type, cloud cover and wind to determine which variables should be included in the model. For the final model I included the variables rarefied richness, rainfall (cm), site, cloud cover and wind.

Results

Does the abundance of bees differ among meadow types?

A total of 2,938 bees were collected over 17 sampling days. Bee abundance did not significantly differ across the three meadow types ($F_{2,45.0} = 0.12$, $p = 0.89$; Figure 1). I found bees of five families: Andrenidae, Apidae, Colletidae, Halictidae, Megachilidae (Table 2); all

Figure 1. Box plot of the number of bees caught per hour between the three habitat types (dry meadow, wet meadow-*Veratrum*, wet meadow-*Salix*).

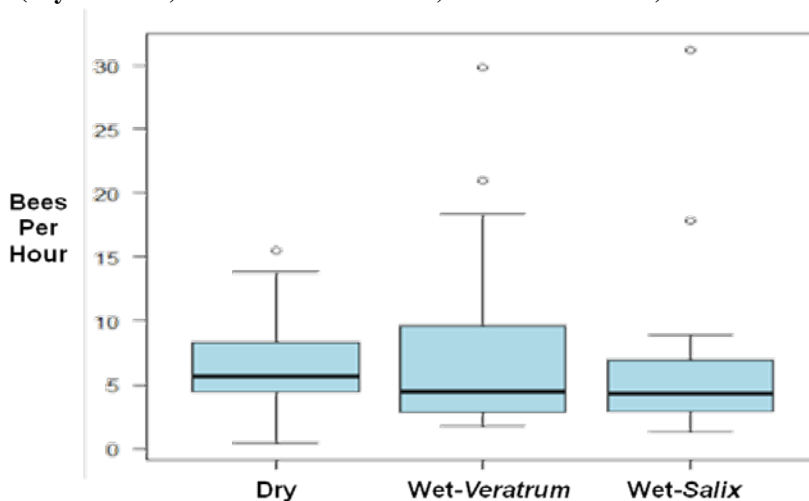
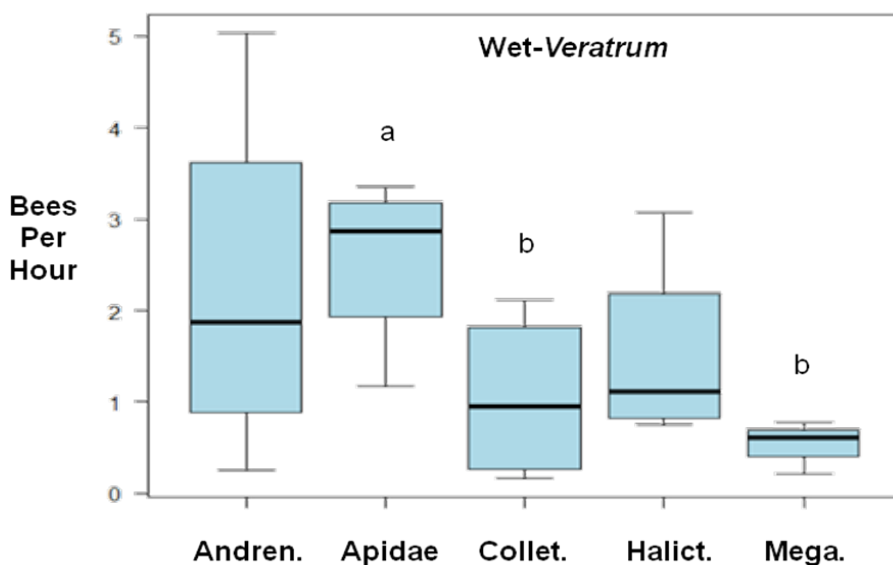


Table 2. Mean±SE of bees per hour of five families caught across three meadow types.

	Dry	Wet <i>Veratrum</i>	Wet Willow	Total
Andrenidae	1.57±0.39	2.42±1.12	1.88±0.95	1.96±0.50
Apidae	1.50±0.33	2.58±0.45	1.56±0.31	1.88±0.22
Colletidae	0.77±0.21	1.01±0.59	0.95±0.48	0.91±0.23
Halictidae	2.28±0.80	1.60±0.59	1.89±0.48	1.92±0.36
Megachilidae	0.70±0.12	0.55±0.14	0.67±0.13	0.64±0.07
	1.36±0.20	1.63±0.30	1.39±0.24	1.46±0.14

five families occurred at all sites. There was no difference in the abundance of bees within a family across the different meadow types (Andrenidae: $F_{2,45.1} = 0.06$, $p = 0.94$; Apidae: $F_{2,44.9} = 2.43$, $p = 0.10$; Colletidae: $F_{2,44.9} = 0.04$, $p = 0.96$; Halictidae: $F_{2,45.1} = 0.33$, $p = 0.72$; Megachilidae: $F_{2,45.0} = 0.54$, $p = 0.59$). For wet meadow-*Veratrum* there were significantly more Apidae bees than either Colletidae or Megachilidae bees ($F_{4,77.0} = 4.75$, $p = 0.002$; Figure 2) but not in dry meadow ($F_{4,76.9} = 2.32$, $p = 0.06$) or wet meadow-*Salix* ($F_{4,76.9} = 2.31$, $p = 0.07$). Approximately 33% of bees collected at wet meadow-*Veratrum* sites were of the family Apidae, while about 12% and 11% were of the family Colletidae and Megachilidae, respectively. There was no significant difference between the abundance of Colletids and Megachilids versus Andrenids and Halictids at wet meadow-*Veratrum* sites. Regardless of meadow type there were significantly fewer Colletids or Megachilids than bees of other families over the entire sampling period ($F_{4,247} = 8.38$, $p < 0.0001$).

Figure 2. Number of bees per family caught at each meadow type. Box plots with different lower case letters indicate significant difference based on Tukey HSD test at $p < 0.05$. Differences were only observed at the wet meadow-*Veratrum* sites.



Does the abundance and richness of flowering plants correspond with bee abundance?

There were no significant associations between bee abundance and flower abundance for each meadow type (dry: $r^2 = 0.05$, $F_{1,16} = 0.83$, $p = 0.38$; wet meadow-*Veratum*: $r^2 = 0.004$, $F_{1,16} = 0.06$, $p = 0.82$; wet meadow-*Salix*: $r^2 = 0.0009$, $F_{1,16} = 0.01$, $p = 0.91$). There was no association between bee abundance and flower abundance independent of meadow type ($r^2 = 0.0004$, $F_{1,49} = 0.02$, $p = 0.88$; Figure 3). There was no association between bee abundance and rarefied flowering richness for each meadow type (dry: $r^2 = 0.00009$, $F_{1,16} = 0.0013$, $p = 0.97$; wet meadow-*Veratum*: $r^2 = 0.207$, $F_{1,16} = 3.93$, $p = 0.07$; wet meadow-*Salix*: $r^2 = 0.025$, $F_{1,16} = 0.39$, $p = 0.54$). There was no association between bee and flower abundances within each meadow type ($r^2 = 0.05$, $F_{1,49} = 2.50$, $p = 0.12$; Figure 4).

Figure 3. Relationship between bee abundance and the mean number of flowers. Each point represents a sampling day and a site.

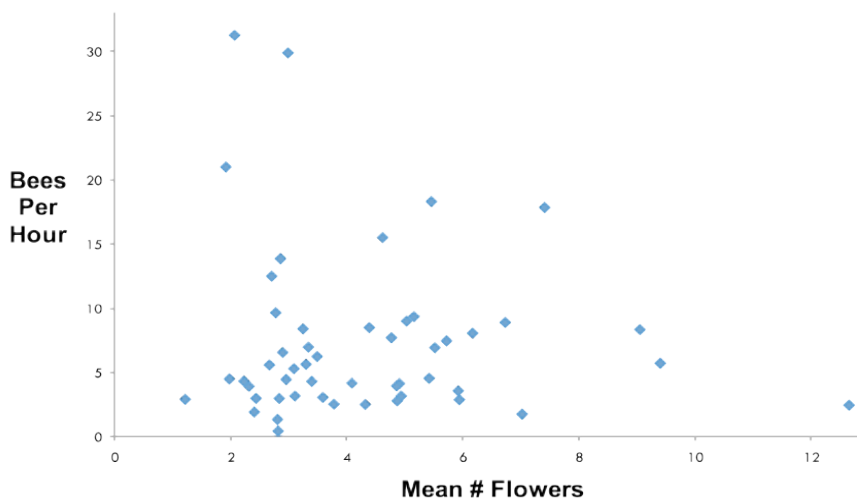
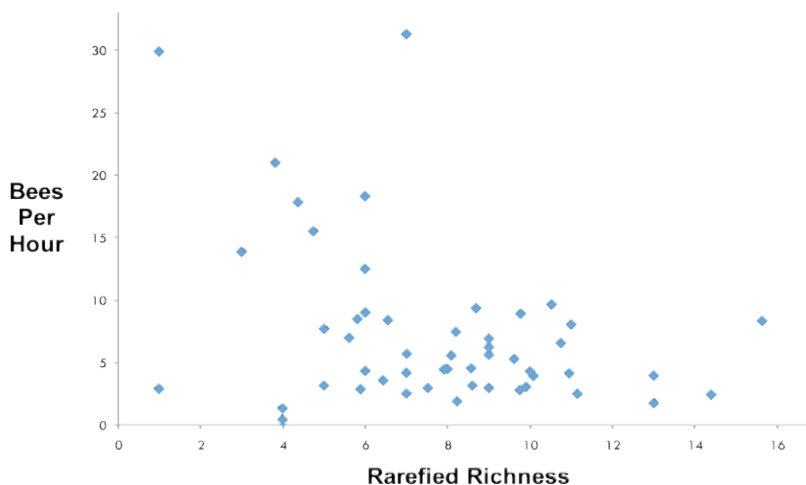


Figure 4. Relationship between bee abundance and rarefied flowering richness. Each point represents a sampling day and a site.



How does bee abundance change over the sampling period?

There was no difference in total bee abundance across meadow types over the four designated sampling periods ($F_{6,14} = 0.52, p = 0.51$; Figure 5). There were some differences in bee abundance across the sampling divisions once bees were divided by family. For Apids, there was a significant interaction for time (Wilks Lambda: $F_{3,7} = 3.64, p = 0.01$) and time*meadow (Wilks Lambda: $F_{6,14} = 0.20, p = 0.05$). For Halictids, there was a significant time interaction (Wilk Lambda: $F_{3,7} = 6.81, p = 0.002$; Figure 6). There were no significant interactions for the other three families.

Figure 5. Bee abundance for each meadow type over four sampling periods. The first sampling period was between June 22 - July 14; sample period 2: July 6 - July 27; sample period 3: July 22 - August 12; sample period 4: August 3 - August 26, 2009.

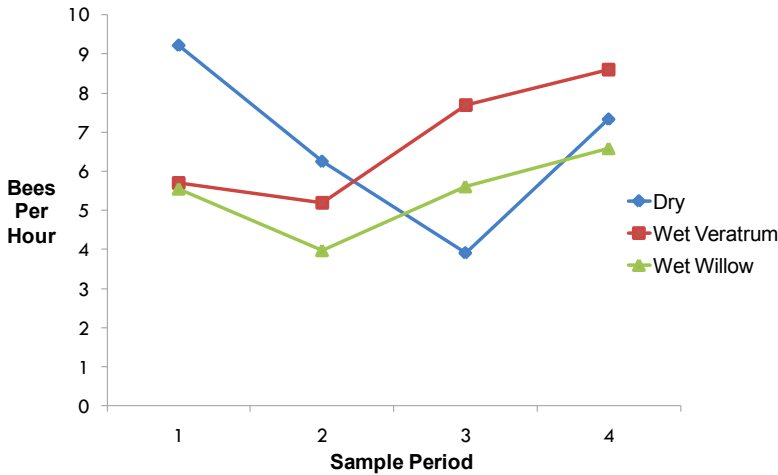
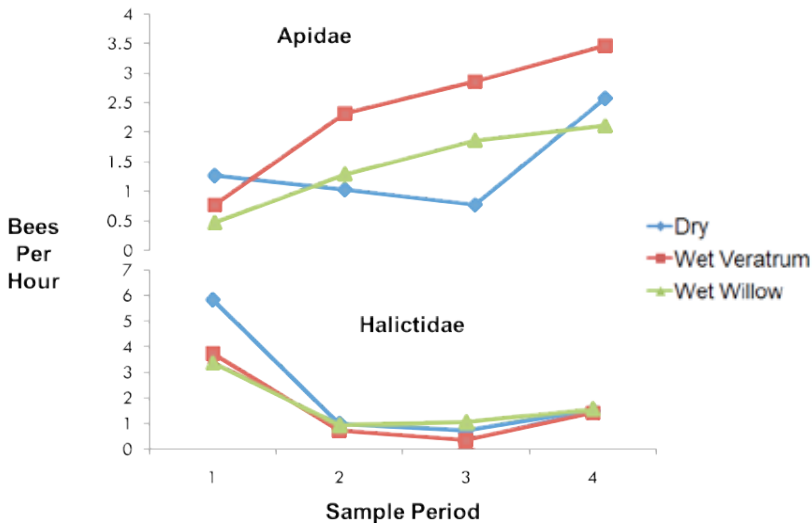


Figure 6. Bee abundance for two families at each meadow type over four sampling periods. The first sampling period was between June 22 - July 14; sample period 2 July 6 - July 27; sample period 2 July 22 - August 12; sample period 4 August 3 - August 26, 2009.



What additional variables predict bee abundance?

According to the model with the least amount of collinearity, 50% of the variation in bee abundance can be explained by the site, rarefied richness on a given day at a site and rainfall ($r^2 = 0.51$, $F_{13,37} = 2.97$, $p = 0.005$). According to standard betas, rainfall was the most important variable in the model.

Discussion

Taken as a whole, my results did not support my hypotheses and contradicted the findings of similar studies. Bee abundance did not differ among meadow types or depend upon the number of flowering species. One possible explanation for these results is that the meadow types did not differ significantly in their flowering vegetation, although they appear to be distinct based on observation alone. For instance, at all sites regardless of meadow type, flowers of *Potentilla pulcherrima* were observed in high numbers and bees from nearly every family were observed on this plant (although it is unknown if they were actively feeding upon the flowers). I hypothesized that the characteristic vegetation at different meadows would result in differing bee abundances, but this pattern is unrealistic if the meadows are floristically homogenized. In a similar study, Heithaus (1979) found significant differences in bee abundances across different meadow types; however, the vegetation within the three habitats was considerably discrete. There were, however, some plant species that appeared to be abundant at only one type of meadow, though these particular plant species may not have been an important bee resource. Perhaps vegetation type does matter as with Heithaus (1979), but only when the sites differ from one another more dramatically than in my study. That is, it is likely that the abundance of bees varies among forests and meadows, but not different kinds of meadows.

Colletid and Megachilid bees had the smallest abundances over the sampling period independent of meadow type. In particular, these two families had exceptionally low numbers at wet meadow-*Veratrum* sites relative to the abundance of Apidae bees. These patterns may be due to the overall low abundance of Colletids and Megachilids and the high abundance of Apids at these sites; while not significant, there were observably more Apids at wet meadow-*Veratrum* sites where the flowers of *Delphinium barbeyi* were abundant. Apids are known to visit these flowers in high numbers (Pyke 1978). Additionally, the collection method may have introduced error by reducing catch rates for Colletids and Megachilids, as these are typically high and fast flying and catching them within a bee bowl may be unlikely (Giles and Ascher 2006). It would be interesting to analyze bee abundances across the meadows with the bees identified to species level to see if more significant patterns arise.

Although I hypothesized that abundance of bees might be driven by the flowering community, my results did not support this prediction. Wet meadow-*Veratrum* sites had the highest mean abundance of bees, but it also had the highest variation. Interestingly, wet meadow-*Veratrum* sites also had the highest overall rarefied flowering richness; however, there was no association between the abundance of bees and abundance of flowers at these sites. In addition, dry meadow sites had the highest mean number of flowers, though there was no association between bee abundance and flower abundance at these sites. These results suggest that floral resources within particular meadows do not effectively predict bee abundance. The lack of an association may be due to the fact that the bees around Gothic are generalists and not tightly linked with any particular flowering species (Mommott et al. 2004). Bees within the different meadows may be present due to other important factors

that structure bee communities such as nesting availability (Potts 2005). Generalist behavior may be reinforced by the narrow foraging season at Gothic (Waser et al. 1996); thus, high flowering diversity may not significantly affect bee abundance or distributions. Future studies of this type should focus on the guild nature of the community in order to reveal if bees are behaving as generalist or specialists within this system.

Overall, there was no significant difference in bee abundance among different meadows and bee abundance did not peak during the middle of the flowering season. However, it appears that the wet meadow sites are more similar to each other than to the dry meadow sites. Interestingly, bee abundance at dry meadow sites plummeted during the third sampling period but recovered by the fourth. It is unclear why such a precipitous decline, followed by a rebounding abundance, should occur. For the family Apidae there was a significant interaction term for time and meadow type, indicating that the abundance of Apidae differed among meadow types, but this difference varied with time. The Halictidae family had a significant interaction for time only, which means that the abundance of Halictids changed over time and the variation was the same for each of the three meadow types. I hypothesize that these results may be due to either phenological shifts for the bees or in response to flowering phenology. Future studies should aim at comparing phenological changes of flowering plants that are observably preferred by certain bee species.

Taken as a whole, my results do not support other studies that suggest that habitat types are biologically meaningful for pollinator distributions (Hughes et al. 2000, Loyola & Martins 2009, etc.). Model selection revealed, however, that the factors most important in determining bee abundance is the particular site, rarefied richness at those sites on sampling days and rainfall. Since rainfall was correlated with high temperature, cloud cover and wind, it appears that the weather during a given sampling day is a large determinant of bee activity. This result coincides with personal observations that bee abundance was highest on the clearest, sunniest days and very low on days that it was cloudy or that it rained. Unfortunately, it was not possible to sample only on “nice” days because the weather could change very rapidly at these montane sites and it was important to sample at every available opportunity because the summer season is so short. In order to determine if these results are, indeed, insignificant or if they are contingent upon the particular sampling year, this experiment should be replicated over several years.

This project is important not only because it provides insight to the distribution of a community of a very diverse, yet poorly known group of organisms, but also because it contributes to the global monitoring efforts of bee populations and offers a useful dataset. Since I used sampling methodology recommended by global bee monitoring programs, the data are comparable with other studies. According to experimentation by Westphal et al. (2008), the bee bowl method of bee collection is the least biased, most successful technique for sampling. Standardized transect walks to collect bee by netting is also recommended, though it has significant collector bias. In order to effectively monitor the status of bee populations, LeBuhn et al. (2003) advise that pollination researchers should adopt a standardized method for bee monitoring so that data are comparable. The data collected for this experiment adhere to LeBuhn and Westphal’s recommendations and can be used by other pollination researchers in the future to identify potential locations and times associated with particular bees around Gothic, Colorado.

Global bee monitoring is important because there is evidence to support that flowering communities are in the midst of a “pollination crisis” due to anthropogenic sources resulting in declines of pollinator species around the world (Kearns et al. 1998). It has been proposed that bee declines and extinctions will produce negative cascading effects in

pollination networks (Memmott et al. 2004). For example, Biesmeijer et al. (2006) showed that a decline in pollinators is correlated with a decline in the plants they pollinate, especially among pollinator specialists. Furthermore, due to the increasing interest in the effects of climate change on pollinators and the services they provide (Hegland et al. 2008), exploring the relationships between bee and plant species distributions are vital to our understanding of plant-pollinator mutualisms and how community structure might be altered with environmental change.

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About the Author

Jessica Nicole Welch recently graduated with honors from the University of Tennessee and was named the 2010 Outstanding Undergraduate in the Department of Ecology and Evolutionary Biology. As a student, she assisted in a number of research labs before completing her own independent research project at the Rocky Mountain Biological Laboratory. Jessica currently works for a non-profit organization, Island Conservation, as a database specialist and occasionally as a research assistant within the Department of Ecology and Evolutionary Biology. In the future, Jessica hopes to attend graduate school in order to study island bat conservation.

About the Advisor

Dr. Nathan Sanders is an associate professor in the Department of Ecology and Evolutionary Biology and the Faculty Fellow for Research for the UTK Honors Programs. His research and teaching interests center on the causes and consequences of biodiversity, and he carries out field research in Colorado, Argentina, Spain, Arizona, China, Sweden, and even Tennessee, mostly on ant biodiversity.