

Variation in the Structure and Dynamics of Bee Assemblages across Distinct Montane Meadows

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August 15, 2009

Advanced Undergraduate Research
Research Experience for Undergraduates

Abstract

Across different landscapes, plant abundance and richness change. Bee distributions may vary spatially in accordance to these differences in floral diversity. I used a habitat-based approach to investigate this hypothesis across three distinct meadow types: dry meadow, wet meadow-*Veratrum* and wet meadow-*Salix*. Patterns of bee species abundance and richness were sampled using bee bowls and netting around Gothic, Colorado. A triplet of sites (each consisting of the three different meadow types) was sampled every other week, for a total of eight sampling days. In total, 1084 bees were caught and identified to family. I found that there was no significant difference in the number of bees caught per hour across the three meadow types; however, there was a trend of more bees caught in the dry meadows. Furthermore, there was no difference in the number of bees caught per hour within a family, though there was a significant difference between the number of Halictids and Colletids caught in both of the wet meadows. There was no significant relationship between the number of bees caught per hour and the mean number of flowers per plot within meadow types or across all sampling sites. Additionally, I used the data set to investigate whether the number of bees caught per hour changed with subsequent samplings for one triplet of sites. There were significantly more bees caught during the first sampling than the two subsequent samplings. I also looked at whether bumble bee abundance affects the abundance of solitary bees, but no significant results were found. More sampling may be needed to reveal significant patterns, or perhaps there are other mechanisms besides meadow type and flower abundances that are driving the distributions of bees in Montane meadows.

Keywords: Hymenoptera, community structure, bowl traps, meadow type, sweep net

Introduction

Pollination by insects and other animals is critical to the reproductive success of up to 90% of angiosperm species (Buchmann and Nabhan 1996), representing one of the best known mutualisms and co-evolutionary relationships. Globally, bees are among the most important and effective pollinators (Kearns et al. 1998) as the majority of bees rely on flower visitation for nectar and pollen to provision their offspring. Because of their mutualism with plants, floral diversity has been shown to be a good indicator of bee diversity (Fontaine et al. 2006). Although they provide a vital service to flowering communities, little is known about the abundances and spatial distributions of many bee species.

The majority of research conducted on bees has been with eusocial species in the genera *Bombus* and *Apis* (Apidae) (e.g., Pyke 1982, Goulson and Darvill 2004, etc.); however, there has been heightened interest in the distribution and abundance of solitary bees as well (e.g. Hughes et al. 2000, Lonsdorf et al. 2009). Solitary bees comprise over 85% of bee species (Michener 2000); yet, comparatively few studies have explored patterns in community structure or how distributions change spatially. Steffan-Dewenter et al. (2000) found that the abundance and richness of solitary bees is closely correlated with the proportion of semi-natural habitats across three spatial scales. Additionally, Buschini (2006) showed that trap nesting solitary bees in Southern Brazil across habitat types resulted in habitat-dependent abundance and diversity. Both studies suggest that landscapes can have a significant effect on solitary bee community structure.

The goal of this study was to survey the abundance and richness of bee species using a habitat-based approach. In particular, I addressed four questions: 1) Does the abundance and

richness of bees differ among different meadow types? 2) Does the abundance and richness of flowering plants correspond with bee abundance? 3) How does bee abundance change with subsequent samplings? and 4) Does the abundance of bumble bees (genus *Bombus*) have an effect on the abundance of solitary bees? Since there are many bumble bees working towards the success of one nest as opposed to solitary bee females that singularly provisions individual nests (Michener 2000), bumble bees species may outcompete solitary bees for resources, which may drive bee distributions.

The sampling design of this study has allowed me to contribute to a two-year control study assessing the potential impacts bee sampling may have on subsequent bee abundance and diversity within and across seasons. Although standard methods for bee monitoring by bee bowls and netting in other parts of the world have not resulted in noticeable declines in bee abundance or diversity (Westphal et al. 2008, Lebuhn et al. 2003), there has not been a study designed to test this observation, per se.

Methods

Study sites

This study was conducted at the Rocky Mountain Biological Laboratory (RMBL) in Gothic, Colorado (2730 meters), and nearby areas. We focused on three meadow types (dry meadow, wet meadow-*Veratrum*, and wet meadow-*Salix*; Table 1). The dry meadows are characterized by rocky, dry soil, with plants in the following genera dominating: *Potentilla*, *Eriogonum*, *Erigeron*, and *Arenaria*. Wet meadow-*Veratrum* is a mix of wet meadow dominated by *Veratrum californicum*, as well as plants of the genera *Potentilla*, *Ligusticum*, *Valeriana*, and *Geranium*. Wet meadow-*Salix* is wet meadow with a large presence of *Salix* species and plants

of the genera *Potentilla*, *Achillea*, *Draba*, and *Linum*. Site elevations ranged from 2864 m to 3056 m, with similar slopes. Aspects were not uniform (Table 1).

Sampling procedures

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 (LeBuhn et al. 2003). Sampling was conducted on relatively sunny, warm, calm days; temperature and wind speed were obtained from the RMBL weather station on each sampling day. I recorded the exact time that the bee bowls from each site were placed and picked up to control for minor differences in sampling effort among sites. 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. Block A sampling began on June 22, 2009. Block B sampling began a week after Block A's initial sampling (July 1st) and also continued every other week. Block C and Block D followed similar patterns (sampling beginning July 8th and July 14th, respectively; Table 1). Due to time constraints, the data presented in this paper ended on July 24th with Block B sites for a total of eight sampling days; however, the sampling will continue through the end of August, 2009, and the data will be available for my senior thesis at UTK.

Because bee bowls have been shown to typically collect smaller species of bees (Wilson et al. 2008), I also used netting to collect 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. When I collected a bee feeding on a flower, I recorded the flower species. If a bumble bee

species was caught, it was identified in the field and released 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 diversity of the floral community to the abundance of bees, I also recorded flowering richness and abundance at each site from six randomly fixed plots (each 2 m x 2 m) along the site transects within a day of bee bowl sampling. 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.

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 approximately each new bee species we 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. As part of my honors thesis, I will continue to identify the bees to species during Fall 2009. I identified all flowering plants to species using Darrow (2006), Kershaw et al. (1998), and the RMBL herbarium.

Statistical analyses

All bee abundances were converted into the number of bees caught per hour for each site and sampling day in order to account for unequal sampling times. All abundances were then log transformed to fit a normal distribution.

To ask whether bee abundance differed among habitat types, I used a randomized block ANOVA with bee abundance as the response variable and habitat type as the independent variable. Habitat type was tested over the nested block term. To ask whether bee richness at the family level varied among habitat types, I used an ANOVA.

To assess if there was an association between bee abundance and floral diversity, I used a regression with bee abundance as the response variable and the number of flowers per plot and rarefied flowering richness as independent variables for each meadow type and across all habitats. 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 look at how bee abundance changes with subsequent sampling, I used ANOVA for the Block A meadows only. Block A was used because it was the only triplet of sites that had been sampled three times by the time I analyzed these results. I used a correlation to assess if there was a relationship between *Bombus* species abundance and overall solitary bee abundance across all sites and sampling days.

Results

Does the abundance and richness of bees differ among different meadow types?

I collected a total of 1084 bees over the eight sampling days. Species abundance was not significantly different across the three meadow types ($F_{2,8.38} = 2.73$, $p = 0.12$; Figure 1). I found bees in five families: Andrenidae, Apidae, Colletidae, Halictidae, Megachilidae; all five families occurred in all habitat types (Table 2). There was no difference in the number of bees caught per hour within families across the different meadow types (Andrenidae: $F_{2,21} = 0.84$, $p = 0.44$;

Apidae: $F_{2,21} = 0.78$, $p = 0.47$; Colletidae: $F_{2,21} = 2.28$, $p = 0.13$; Halictidae: $F_{2,21} = 0.28$, $p = 0.76$; Megachilidae: $F_{2,21} = 0.96$, $p = 0.40$); however, there was a difference between families (Figure 2). At the wet meadow-*Veratrum* and wet meadow-*Salix* sites, there was a significant difference between the number of Colletids and Halictids caught (wet meadow-*Veratrum* $F_{4,35} = 3.00$, $p = 0.03$; Wet meadow-*Salix*: $F_4 = 3.66$, $p = 0.01$) but not in the dry meadows ($F_{4,35} = 2.31$, $p = 0.077$).

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

There was no association between the number of bees caught by the average number of flowers per plot within meadow types (Dry meadow: $r^2=0.02$, $p=0.72$; Wet meadow-*Veratrum*: $r^2=0.12$, $p=0.39$; Wet meadow-*Salix*: $r^2=0.02$, $p=0.75$) or across all sites and sampling days ($r^2=0.02$, $p=0.47$; Figure 3). There was also no association between number of bees per hour and rarefied flowering richness ($r^2=0.03$, $p=0.60$).

How does bee abundance change with subsequent samplings?

For the Block A sites, there was a significant difference between the number of bees caught during the first sampling versus the two subsequent samplings ($F_{2,6} = 11.32$, $p = 0.01$; Figure 4). Between the first and second samplings, bee abundance declined by 8.5 bees per hour. The number of bees caught per hour was the same for the second and third samplings.

Does the abundance of bumble bees have an effect on the abundance of solitary bees?

There was no correlation between the number of solitary bees caught and the number of bumble bees caught across all samplings ($r = -0.30$, $p = 0.15$; Figure 5).

Discussion

Overall, my results do not provide significant insight to the mechanisms driving bee distributions around Gothic, Colorado. In comparison to other bee surveys, the data presented here was over a shorter time span so that the results may not provide an accurate description of the overall bee abundance and richness within a season. Furthermore, my results did not support the results of other studies that suggest that habitat types are biologically meaningful for bee distributions (Hughes et al. 2000, Buschini 2006, etc.). Significant patterns may be revealed with subsequent sampling and once the bees collected are identified to species.

My results did not indicate that there were any statistically significant differences in the number of bees across the three meadow types; however, there was a trend of catching more bees in the dry meadows than either of the wet meadows. After performing a power analysis, I found that about 24 replicates would be needed to produce significant results. This is an encouraging prediction, considering that it is not outside the realm of possibilities. If there is indeed a difference in bee abundance among meadow types, it may be due to the fact that many solitary bees are ground nesters (Michener 2000), and the dry sites might offer the best nesting opportunities. In concurrence to my findings, other studies have revealed a low abundance of Colletids across the sampling period (Pascarella et al. 1999, Giles and Ascher 2006). There may have been less Colletids and more Halictids because of temporal patterns within the sampling period; additional samplings may better reveal these patterns.

Although I thought that bee distributions might be driven by the flowering community, my results did not support this prediction. This lack of an association may be due to the fact that the bees around Gothic are preferential visitors to only certain types of flowers, thus, high

flowering diversity does not significantly affect bee distributions. More likely, however, there is a significant association that cannot be detected because of too few sampling days. Once the bees are identified to species, I predict an association between bee and flowering richness as shown by previous studies.

There was a significant difference in the number of bees caught over the sampling period. In particular, bee abundance was significantly higher in the first sampling period than in subsequent sampling periods. However, I do not think that this decline in bee abundance was due to the negative effects of sampling, but rather, I think that this was due to the weather patterns. The first day that Block A was sampled was the first warm, sunny summer day in Gothic. I hypothesize that due to the favorable weather conditions, all the bees were emerging and beginning to collect resources to provision their nests.

Though there was no strong correlation between the abundances of solitary and bumble bees, there was a slightly negative correlation. With further sampling, significant patterns may be revealed which may imply that the two groups of bees compete for resources. Bumble bees are social; each nest has one breeding female and several worker females that are responsible to care of the brood and collection of resources (Michener 2000). Since there is such a high abundance of bumble bee workers collecting resources during the season, they may collect pollen and nectar more efficiently than single, solitary bee females, which would decrease solitary bee abundances.

This project is important not only because it provides insight to the community interactions 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 (Westphal et al. 2008, LeBuhn et al. 2003).

There is evidence to support the notion that flowering communities are in the midst of a “pollination crisis” due to anthropogenic sources resulting in declines of pollinator species, especially honey bees and bumble bees, 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 plants that rely on specialist pollinators. Furthermore, due to the increasing interest in the effects of climate change on pollinators and the services they provide (Hegland et al. 2009), 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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Table 1. Characteristics of each site.

Dates Sampled	Site Name	Site Type	Elevation	Aspect	GPS Coordinates
June 22, July 6, July 22, 2009	David's 401	Dry	2967.19m	West facing	38°57'43.646"N 106°59'12.827"W
	Willey	Wet-Willow	2864.38m	No slope	38°57'21.497"N 106°59'18.535"W
	Tuttle	Wet-Veratrum	2869.34m	No slope	38°57'17.105"N 106°59'19.334"W
July 1, July 16, 2009	Sean's	Dry	2914.37m	West facing	38°57'50.757"N 106°59'33.416"W
	Gothic	Wet-Willow	2903.03m	East facing	38°57'47.117"N 106°59'41.517"W
	Beaver	Wet-Veratrum	2901.93m	No slope	38°57'41.748"N 106°59'38.310"W
July 8, July 24, 2009	Marriage	Dry	2987.35m	West facing	38°57'58.612"N 106°59'25.168"W
	Parking	Wet-Willow	2989.19m	No slope	38°57'55.227"N 106°59'19.213"W
	Avery	Wet-Veratrum	3024.14m	No slope	38°58'25.341"N 106°59'30.883"W
July 14, 2009	Hill	Dry	3056.33m	South facing	38°58'00.376"N 106°58'12.339"W
	Copper	Wet-Willow	3054.86m	South facing	38°58'08.244"N 106°58'04.824"W
	Little	Wet-Veratrum	3043.72m	South facing	38°58'02.350"N 106°58'07.860"W

Table 2. Number of bees caught per hour for five families across three meadow types.

	Dry	Wet Veratrum	Wet Willow	Total
Andrenidae	14.4	6.6	6.8	27.8
Apidae	8.1	10.5	6.5	25.1
Colletidae	3.7	0.9	0.7	5.3
Halictidae	25.1	18.9	15.6	59.6
Megachilidae	6.1	4	5	15.1
Total	57.4	40.9	34.6	132.9

Figure 1. Number of bees caught per hour (log transformed) did not vary between the three habitat types (dry meadow, wet meadow-*Veratrum*, wet meadow-*Salix*). Data are means $\pm$ SE.

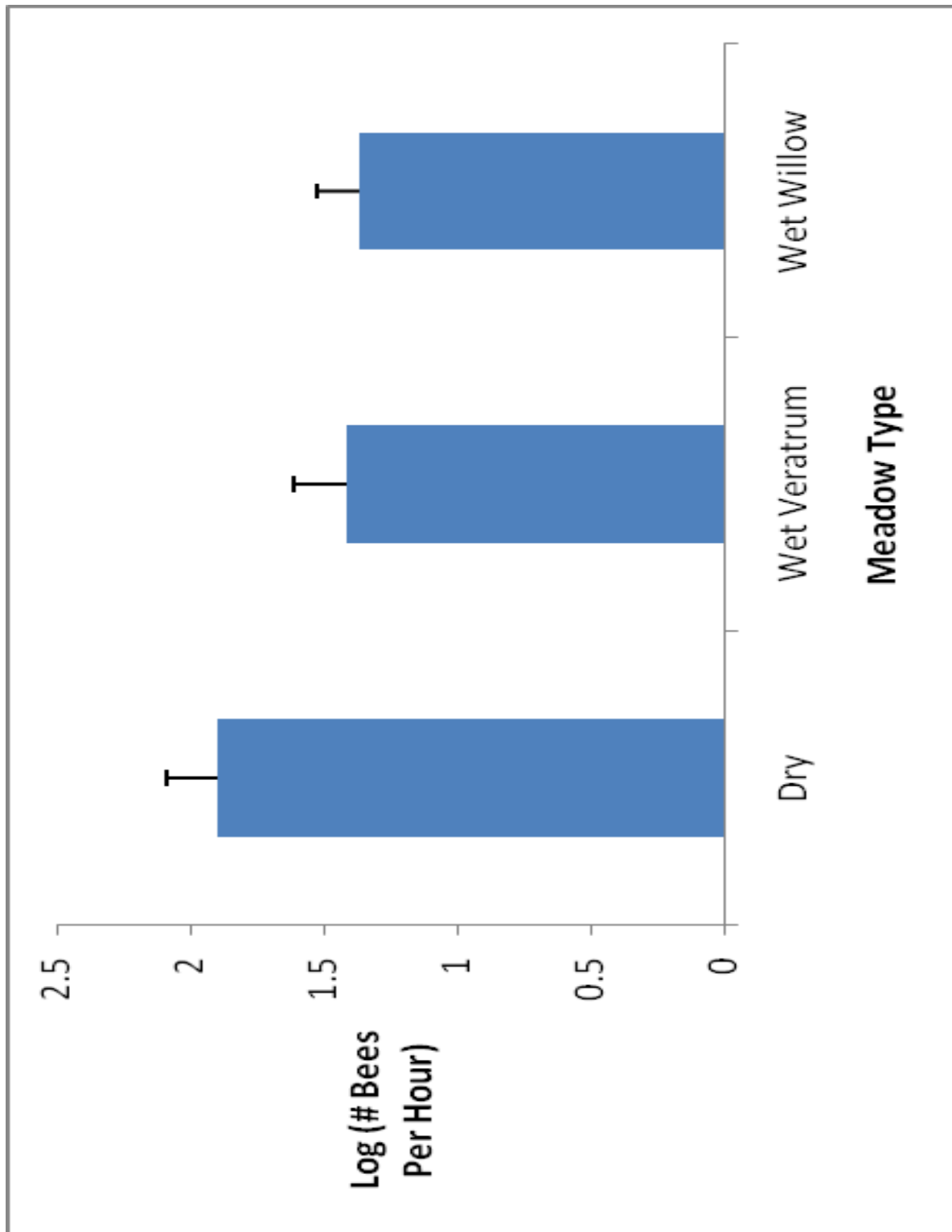


Figure 2. Number of bees per family caught at each meadow type. Data are means $\pm$ SE. Bars with different lower case letters indicate significant difference based on Tukey test at $p < 0.05$. Differences were only observed in the wet meadow-*Veratrum* and we meadow-*Salix* sites.

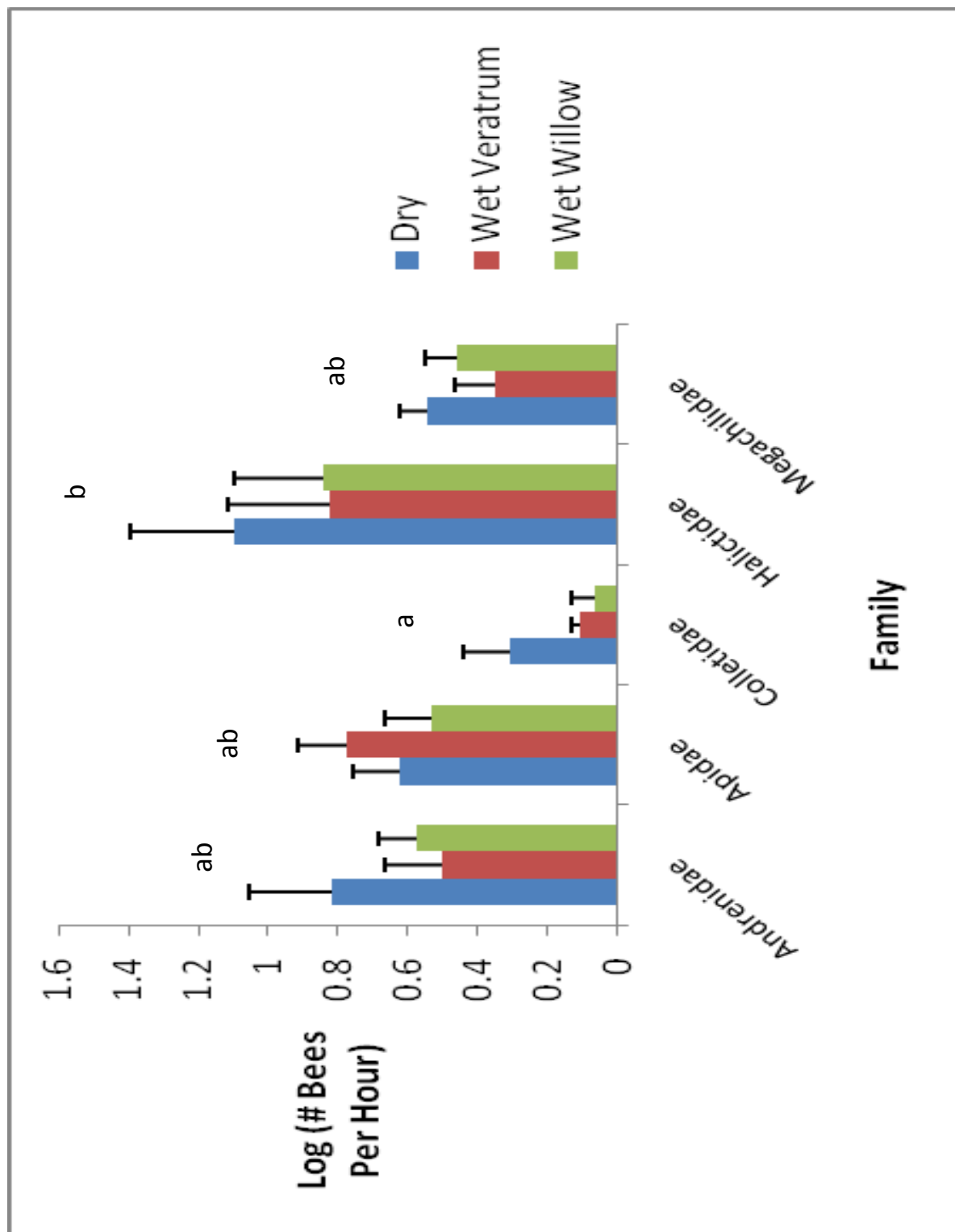


Figure 3. Relationship between number of bees caught per hour (log transformed) by the mean number of flowering plants per plot. Each point represents a sampling day and a site.

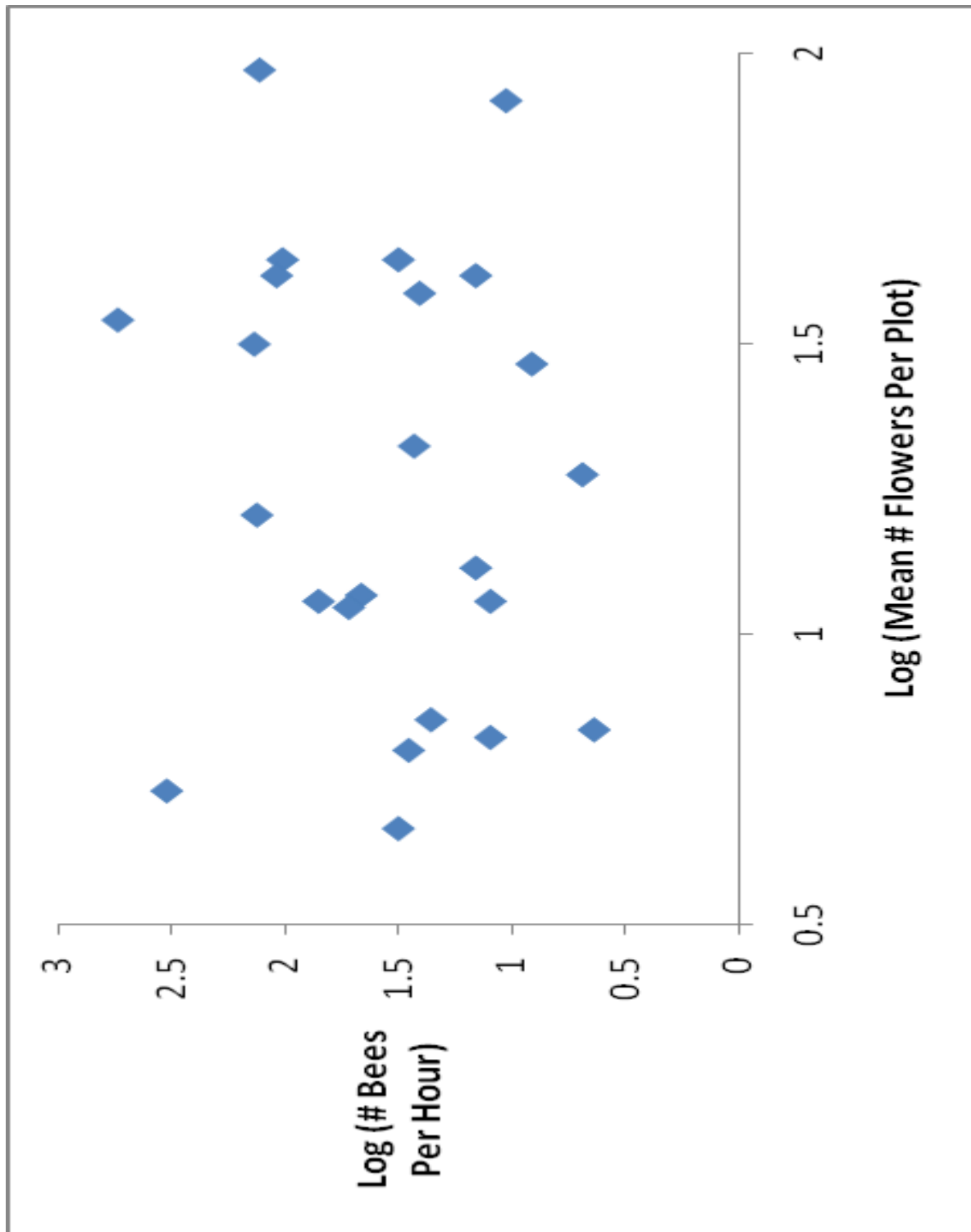


Figure 4. Number of bees caught per hour for Block A over three sampling days. Data are means $\pm$ SE. There were significantly more bees caught on the first sampling day than the second and third sampling days ($p = 0.0092$).

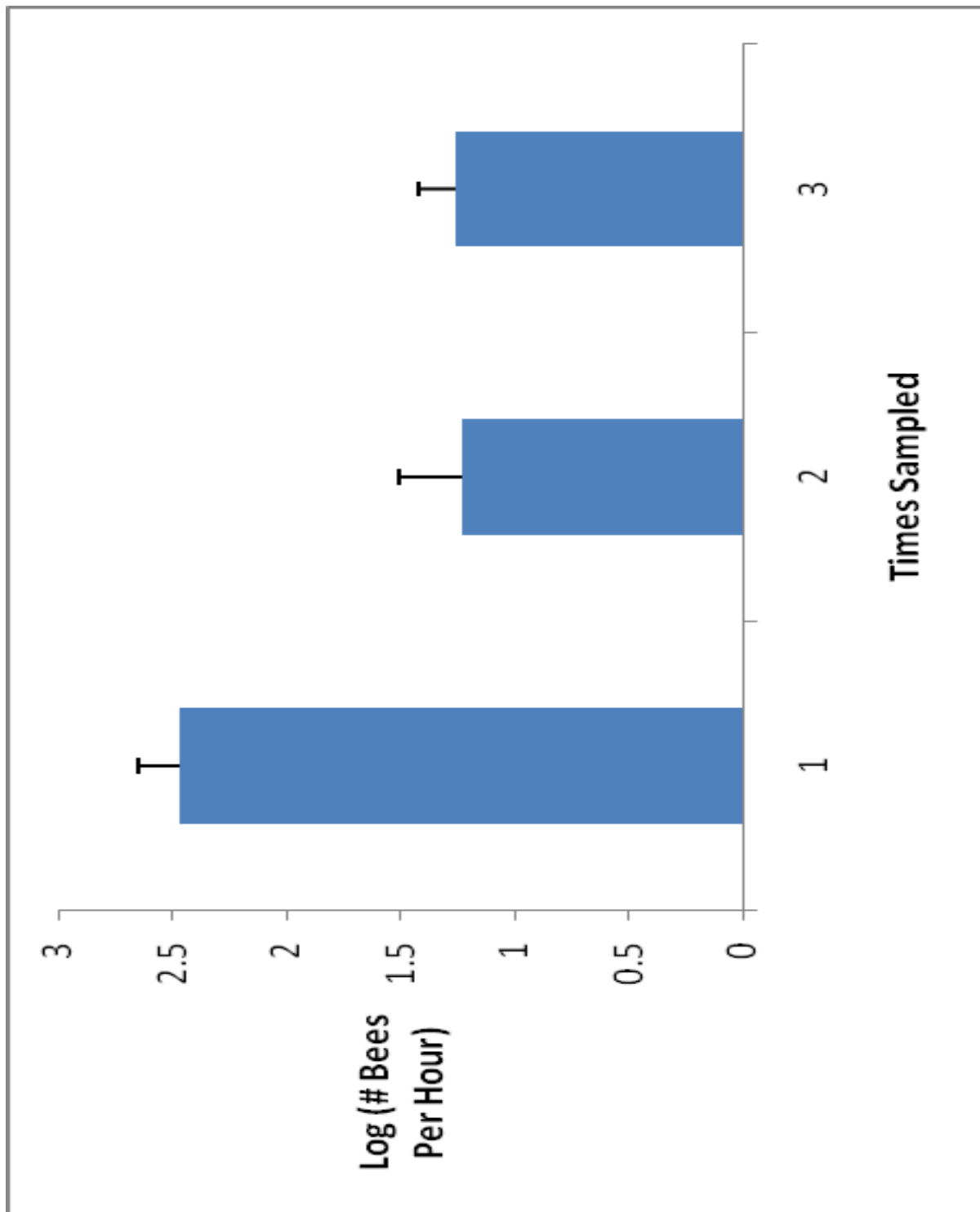


Figure 5. Correlation between the number of solitary bees caught per hour by the number of bumblebees caught per hour (each log transformed). Each point represents a sampling day and a site.

