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Experience levels of individuals in natural bee populations and their ecological implications

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Abstract: Learning difficult tasks requires an extended period of experience. It is unclear, however, what level of experience is exhibited by individuals in natural populations. If many individuals are rather inexperienced at any given time, they may not possess subtle information concerning, for example, local distributions of reward and danger, which may require long acquisition periods. To quantify individual experience in field settings, we conducted a field study involving extensive marking of individual honey bees (*Apis mellifera* L., 1758) and bumble bees (*Bombus vagans* Smith, 1854 and *Bombus terricola* Kirby, 1837) visiting milkweed (*Asclepias syriaca* L.) patches that harbored crab spiders (*Misumena vatia* (Clerck, 1757)), which prey on bees. The vast majority of bees either were fully inexperienced or had little experience with the specific flower patch that they were visiting. It is likely that such inexperienced bees do not possess subtle local information involving either reward or danger. Contrary to our prediction, even the most experienced bees did not avoid experimental patches harboring crab spiders, perhaps because even these bees did not possess sufficient experience. Our results indicate that conclusions from controlled laboratory experiments may not readily generalize to natural field settings. Thus, we must gather additional data on the long-term behavior of individually marked bees in natural conditions to better understand the interactions among flowers, bees, and bees' predators.

Résumé : L'apprentissage des tâches difficiles requiert une longue période d'expérience. Il n'est pas clair, cependant, quel niveau d'expérience possèdent les individus dans les populations naturelles. Si plusieurs individus sont relativement inexpérimentés à un moment donné, ils peuvent ne pas posséder l'information détaillée concernant, par exemple, la répartition locale des bénéfices et des dangers, ce qui peut demander de longues périodes d'acquisition. Afin d'évaluer l'expérience individuelle dans des conditions de terrain, nous avons marqué un à un en nature un grand nombre d'abeilles domestiques (*Apis mellifera* L., 1758) et de bourdons (*Bombus vagans* Smith, 1854 et *Bombus terricola* Kirby, 1837) butinant des bouquets d'asclépiades (*Asclepias syriaca* L.) qui portaient des araignées crabes (*Misumena vatia* (Clerck, 1757)), des prédateurs des abeilles. La grande majorité des abeilles avaient peu ou pas d'expérience du bouquet particulier de fleurs qu'elles visitaient. Il est peu probable que de telles abeilles inexpérimentées possèdent la connaissance locale détaillée des bénéfices et des dangers. Contrairement à notre prédiction, même les abeilles les plus expérimentées n'évitent pas les bouquets expérimentaux contenant des araignées crabes et peut-être même ces abeilles n'ont pas suffisamment d'expérience. Nos résultats indiquent que les conclusions obtenues dans des expériences de laboratoire contrôlées ne peuvent pas être élargies facilement aux conditions naturelles de terrain. Il nous faut donc accumuler plus de données sur le comportement à long terme en conditions naturelles d'abeilles marquées individuellement pour mieux comprendre les interactions entre les fleurs, les abeilles, et les prédateurs des abeilles.

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Introduction

Numerous experiments over the past few decades have established that animals, including tiny short-lived insects, can learn about parameters such as the relative profitability of alternative resources, the nature and magnitude of predation risk, and a variety of other factors that affect survival and reproduction (reviewed in Papaj and Prokopy 1989; Krebs and

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Davies 1997; Dukas 1998; Lima 1998). Generally, there appears to be at least partial correspondence between a species' natural and life history and both the types of information it can typically acquire and the rates of learning. Furthermore, although some information can be acquired almost instantly, common tasks such as learning which is the best food type among a few available alternatives, learning to handle novel foods, and learning to detect cryptic objects require extensive learning. The rate of learning, or the number of trials it takes a novice animal to reach expert-level performance, depends on the task difficulty, which can be quantified a priori and independently. For example, decreasing the mean difference between cryptic items and their surrounding background increases the detection difficulty (reviewed in Shettleworth 1984; Dukas 1998; Shettleworth 1998).

There is probably high variation among species in the proportion of individuals that possess extensive knowledge about their environment at any given time and place. That variation is highly relevant for our understanding of within and between species interactions. For example, an ambush predator encountering a prey population consisting of predominately transient individuals may ignore the effect of learning by the prey, because learning may have a negligible influence on the behavior and availability of most prey individuals. In contrast, a predator hunting for experienced individuals would probably have to take measures to counter the effect of prey learning on the prey's antipredatory behavior (see Sih 1998; Lima 2002).

Our interest in the magnitude of experience in a natural prey population was inspired by our recent findings. On the one hand, in recent controlled experiments using a few artificial flowers, honey bees showed sensitivity to perceived danger by selecting apparently safe flowers over equally rewarding alternatives harboring either a dead bee or a spider, and avoiding revisitation of a site where they have escaped a simulated predation attempt (Dukas 2001a). On the other hand, in a field experiment, we documented relatively weak antipredatory responses by bees to crab spiders, which are ambush predators hunting bees at flowers. Specifically, in a replicated set of 10 pairs of experimental patches of common milkweed (*Asclepias syriaca* L.), in which each pair had one patch harboring crab spiders and the other patch containing no spiders, we recorded significantly fewer workers of *Bombus ternarius* Say, 1837 in the spider patches. We found, however, no significant differences in the numbers of individual honey bees (*Apis mellifera* L., 1758) and bumble bees (*Bombus vagans* Smith, 1854 and *Bombus terricola* Kirby, 1837) (Dukas and Morse 2003). We suggested that perhaps the bees visiting the milkweed flowers consisted of primarily inexperienced individuals that did not have the opportunity to learn about the local abundance and exact location of crab spiders.

To quantify the level of experience and its effect on antipredatory behavior in natural prey populations, we conducted a follow-up field study involving extensive individual marking of bees visiting milkweed patches in an old field habitat. We asked two questions. First, what is the frequency distribution of experience levels in natural bee populations? Second, would the most experienced bees show selective avoidance of milkweed patches harboring crab spiders?

Methods

General protocol

The experiment was conducted at an old field in South Bristol, Lincoln County, Maine, during July 2003. The field contained several thousand stems of common milkweed in early bloom. The dominant visitors to milkweed in our study area were two species of bumble bees (*B. ternarius* and *B. vagans*) and honey bees (*A. mellifera*); hereinafter, also collectively referred to as bees. As far as we know, the honey bees belonged to a feral colony. The crab spiders, *Misumena vatia* (Clerck, 1757), were all adult females collected within 10 km of the experimental site.

In two successive replicates, we removed milkweed stems to create two matched patches each containing 20 milkweed stems. The patches were separated from each other by 5 m of clearing and from the remainder of the field by 3 m of clearing. The two replicates were carried out approximately 100 m apart. On the morning of day 1 of both replicates, we introduced seven crab spiders to one of the randomly chosen patches. We refer to that patch as the spider patch and to its matched patch as the no-spider patch. Because of some spider movement away from the patch, we expected the actual spider density to be approximately 0.25 per stem, which is well within the range of natural spider densities in small natural milkweed patches (Dukas and Morse 2003).

On the morning of day 1, we also began capturing all bees arriving in both patches. We chilled the bees in an ice chest, recorded their species identity, attached to each individual a tag with a unique number and color combination, and released them at a spot equidistant from the two patches. Starting on the morning of day 2, two people continuously recorded the presence of marked bees in each patch using handheld computers. Another team caught and marked all unmarked bees. Depending on the weather, we conducted either five or six 1-h observation periods between 0900 and 1600 each day, the peak period of bee activity (Dukas and Morse 2003). The observations and bee marking were terminated at the end of day 5 in replicate 1 and at the end of day 4 in replicate 2. The premature termination of replicate 2 was caused by an extended period of rain followed by the end of milkweed blooming.

Overall, we marked 873 bees (343 *A. mellifera*, 327 *B. ternarius*, and 203 *B. vagans*) in the two replicates over 9 days and recorded visits by marked bees to the milkweed patches over 7 days. Only 6 bees marked in replicate 1 were observed in replicate 2, which was initiated 1 day after the end of replicate 1. These 6 bees were excluded from the analyses.

During data collection, we recorded each marked bee observed in a patch. This involved scouting the patch and reading each bee tag, meaning that we could not continuously follow each individual bee in the patch. Although we attempted to avoid double-counting of a single bee visit to a patch, a long bee visit could be counted more than once. For example, a bee could be recorded just when it entered the patch and then again 5 min later. To eliminate such multiple counting of a single patch visit, we removed from the data set any record of a bee within 15 min since its last recorded visit. The choice of the somewhat arbitrary 15-min period reflected our expectation that no two distinct bee trips be-

tween the colony and milkweed patches were likely to occur within less than 15 min. Although this data editing eliminated most multiple counting, it probably also removed some independent bee re-entries to a patch within single foraging trips. This compromise reflected our preference to avoid pseudoreplication over losing a small number of independent data points.

Bee behavior and spider predation

Of the 873 bees we marked during the study, 360 (41%) revisited the patches over the observation periods. All these bees were included in the analyses unless otherwise specified. To quantify the overall frequency of revisitation by individual bees, we included in the analyses only the 351 bees that were marked on days 1 and 2 in replicate 1 and on day 1 in replicate 2. We chose these bees because they all had the opportunity to revisit the patches for at least 3 additional days following the day of marking. Only 140 out of these 351 bees revisited the patches. Hence, the analyses of visit frequencies included only these 140 bees.

In addition to recording all visits to the patches by marked bees, we randomly chose focal bees that had just entered a patch and followed them until they left the patch. We collected individual behavioural data for 23 *A. mellifera*, 52 *B. ternarius*, and 19 *B. vagans*. Finally, we also recorded all bees captured by the crab spiders.

Inexperienced versus experienced bees

To compare the proportions of inexperienced and experienced bees, we counted on each day the number of (*i*) unmarked bees that were caught, marked, and released, and (*ii*) all bees that were marked on all previous days. Preliminary analyses indicated no effects of either patch or day, variables that were not included in the final ANOVA because of the small number of independent datum points.
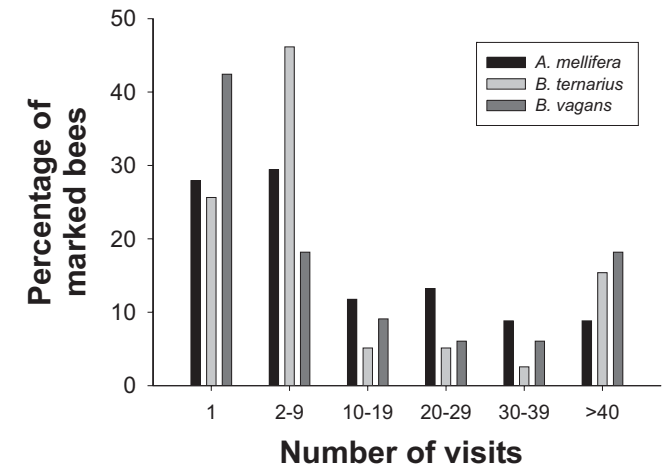
Do experienced bees avoid the spider patches?

For this analysis, we selected the 18 bees (6 individuals of each species) that visited the patches at least 40 times (Fig. 1) and considered only the first 40 visits by each of these bees to obtain a balanced data set. All of these bees visited both the spider and the no-spider patches. For each bee, we calculated the proportion of visits to the spider patch out of all visits to the spider and no-spider patches over 4 blocks of 10 visits each. The data were then arcsine-transformed for statistical analyses. We also conducted another analysis similar to the one just described but including the 50 bees that visited the patches at least 20 times.

Results

Bee behavior and spider predation

Of all the bees that were marked early in the experiment (*n* = 351), an average (±1 SE) of 28% ± 5%, 20% ± 4%, and 15% ± 3% were observed 1, 2, and 3 days after the day of marking, respectively. The decline in return rates of experienced bees over the 3 days was significant and there was no significant difference among the three bee species (repeated measures ANOVA on arcsine-transformed proportions; $F_{[1,6]}$ = 15.8, P < 0.01 and $F_{[1,6]}$ = 0.08, P > 0.9, respectively). Of the bees that were marked early in the experiment

Fig. 1. The frequency distribution of patch visits by marked bees that revisited the milkweed (*Asclepias syriaca*) patches. Only the 140 bees that had the opportunity to revisit the patches for at least 3 additional days following the day of marking were included in the figure (i.e., bees that were marked on days 1 and 2 of replicate 1 and day 1 of replicate 2).

and revisited the patches (*n* = 140), 32% of the individuals were recorded only once and 63% visited fewer than 10 times (Fig. 1). The median number of patch visits by these revisiting marked bees (*n* = 140) was 6.5 for *A. mellifera*, 3 for *B. ternarius*, and 2 for *B. vagans*, respectively. The difference between the species in frequency of visits was not significant (Kruskal–Wallis test, χ^2 = 0.96, df = 2, P > 0.5).

The spider and no-spider patches received similar average numbers of visits by the marked bees throughout the experiment (4 ± 0.4 and 3.7 ± 0.4, respectively; $t_{[1,359]}$ = 0.9, P > 0.3). There was no significant difference either among the bee species or between the replicates in the proportions of visits to the spider patches (ANOVA on arcsine-transformed proportions; $F_{[2,354]}$ = 2.6, P > 0.07 and $F_{[1,354]}$ = 2.9, P > 0.09, respectively).
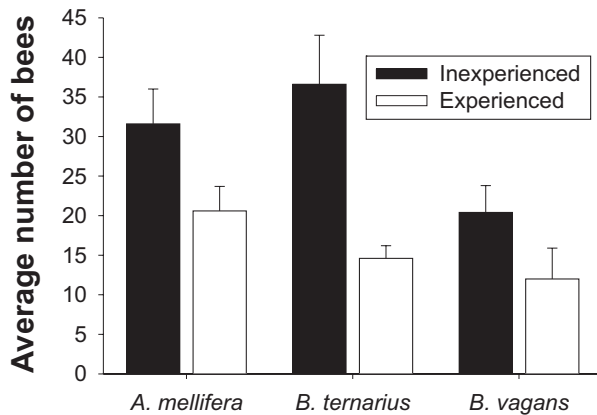
Our observations on focal bees indicated that the average number of umbel visits per patch was similar among the three bee species: 9.1 ± 1.2, 9.3 ± 1.3, and 9 ± 1.8 for *A. mellifera*, *B. ternarius*, and *B. vagans*, respectively (ANOVA, $F_{[2,91]}$ = 0.1, P > 0.9). The average duration in a patch was also similar among the three bee species: 254 ± 42, 188 ± 25, and 218 ± 50 s for *A. mellifera*, *B. ternarius*, and *B. vagans*, respectively (ANOVA, $F_{[2,91]}$ = 1, P > 0.3). The maximum patch durations recorded were 12, 12, and 11 min for *A. mellifera*, *B. ternarius*, and *B. vagans*, respectively.

The overall predation on bees by crab spiders in the two experimental spider patches was 7 marked and 4 unmarked *A. mellifera*, 2 marked and 3 unmarked *B. ternarius*, and 3 marked *B. vagans*. These numbers amounted to approximately 3.2% of the *A. mellifera*, 1.5% of the *B. ternarius,* and 1.5% of the *B. vagans* that we marked in the patches.

Inexperienced versus experienced bees

On average, twice as many inexperienced as experienced bees visited the milkweed patches on each day (ANOVA, $F_{[1,36]}$ = 17.6, P < 0.001; Fig. 2). There was a significant difference among the bee species in the total number of indi-

Fig. 2. The average (+1 SE) number of inexperienced and experienced bees observed in the milkweed patches on each day.

Fig. 3. The proportion (mean + 1 SE) of visits to the spider patch out of the first 40 visits to the spider plus no-spider patches by the 18 most experienced bees (*n* = 6 for each species).

viduals visiting the patches ($F_{[2,36]}$ = 3.8, $P < 0.05$; Fig. 2), but there was no significant interaction between experience and bee species ($F_{[2,36]}$ = 1.6, $P > 0.2$).

Do experienced bees avoid the spider patches?

The 18 most experienced bees did not reduce their proportions of visits to the spider patches over their first 40 patch visits (repeated measures ANOVA, $F_{[3,39]}$ = 0.08, $P > 0.9$; Fig. 3). There was no significant difference either among the three bee species ($F_{[2,13]}$ = 2.4, $P > 0.1$) or between the two replicates ($F_{[1,13]}$ = 1.3, $P > 0.2$). Finally, inspections of the individual curves for each of the 18 bees revealed no consistent patterns. The analysis of the 50 bees that visited the patches at least 20 times also revealed no significant reduction in the proportions of visits to the spider patches over 4 blocks of 5 patch visits (repeated measures ANOVA, $F_{[3,135]}$ = 0.3, $P > 0.8$).

Discussion

Levels of experience

On any given day, most bees visiting the milkweed patches under natural field conditions possessed either no or little experience with these patches (Figs. 1, 2). The fact that similar patterns were exhibited by three different bee species adds generality to the results. The important implication of our finding is that such inexperienced bee populations are less likely to learn about subtle patch-specific information involving either differential reward distribution among individual plants or predation risk posed by camouflaged predators, for which substantial experience may be required. For example, the bee populations are unlikely to bypass a patch with a high density of crab spiders if extensive experience is necessary for learning such information.

Surprisingly, we know little about the frequency distribution of experience levels among bees at particular flower patches under natural settings. One would expect, however, a large variation in levels of experience among habitats, plant and bee communities, and seasons. Whereas there have been many reports about some marked bees faithfully returning to certain flower patches over time, most older studies did not include proper quantification of the degrees of experiences by all individuals at a patch over time (reviewed in Ribbands 1953; Free 1970). That is, there may have been a strong bias
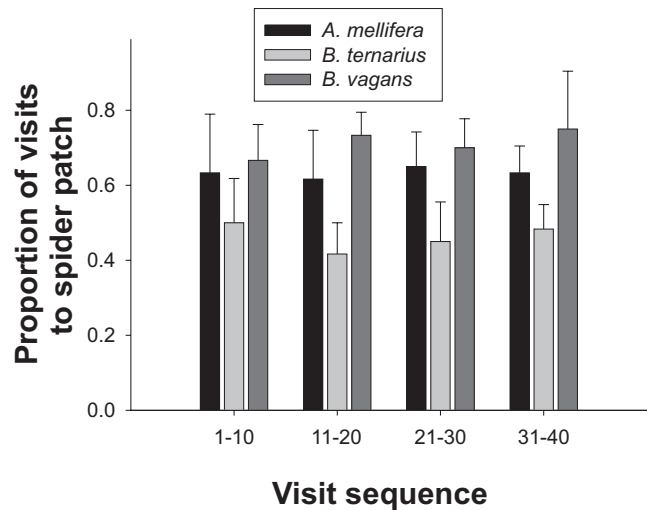
in the literature towards assuming that most individual bees visit the same individual plants for many days. At least two studies, however, fall somewhere between the traditional view and our findings. First, Heinrich (1976) marked all *B. vagans* foragers at a large patch of *Aster novae-angliae* L. One day after marking, 75% of the bees observed were marked. The proportion of marked bees decreased by approximately 10% per day, approaching zero after 12 days. This information and additional data on marked bees provided by Heinrich (1976) suggested moderate turnover rates. Second, Williams and Thomson (1998) videotaped all visits to a single *Penstemon strictus* Benth. plant by bumble bees (*Bombus flavifrons* Cresson, 1863), which were marked on previous days. Whereas 28 marked bees contributed 84% of the 553 recorded plant visits, an unknown number of individuals provided additional 88 visits. This data set probably indicates a smaller proportion of inexperienced individuals than in our study.

In summary, in many cases it appears that a moderate to large proportion of bees have little experience with the flower patches they visit under natural field settings. Further detailed field studies on individually marked bees are necessary to clarify the importance of experience for interaction among bees, between bees and plants, and between bees and other species, including predators and parasitoids (see Thomson and Chittka 2001). We should caution, however, that it is tempting to conduct marking studies where there are relatively few flowers and few bees, because no massive marking and following of hundreds of individuals is necessary. Obviously, such research bias may translate into a misunderstanding of the ecology of natural bee communities.

The effect of experience and possible explanations

In our field settings, even the most experienced bees did not learn to avoid the spider patches (Fig. 3). This result is somewhat puzzling. The estimated total predation by crab spiders during the experiment ranged between 1.5% and 3.2% of the marked bees of the three species. Both general

theoretical considerations and specific calculations using realistic parameters for the bee – crab spider system suggest that bees which learn to avoid the locations harboring predators would incur significant fitness advantage (Clark and Dukas 1994; Dukas and Edelstein-Keshet 1998; Dukas 2001*b*; Dukas and Morse 2003). Furthermore, experiments with *A. mellifera* indicate that, at least under simple artificial conditions, they are highly sensitive to perceived danger at flowers (Dukas 2001*a*). Whereas we do not understand the discrepancy between our prediction and results, we will briefly provide a few possible explanations.

To understand the lack of crab spider avoidance, we estimated the attack rate on the most experienced *A. mellifera* and *B. ternarius*, the two species most susceptible to crab spider predation in our study area (Dukas and Morse 2003). A total of 10 marked *A. mellifera* and *B. ternarius* were killed by the crab spiders. The success rate of the crab spiders is approximately 10% (Morse 1986; Dukas and Morse 2003), so we assumed that there were approximately 100 attacks on marked *A. mellifera* and *B. ternarius*. We recorded a total of 973 visits by marked *A. mellifera* and *B. ternarius* to the spider patches, of which 304 visits (31%) were by the 12 most experienced *A. mellifera* and *B. ternarius*. Hence the estimated number of attacks on the most experienced bees was 31, which is equivalent to an average of 2.5 attacks per each of the 12 most experienced *A. mellifera* and *B. ternarius* over the 4 or 5 days that they visited the patches. This sums to an average of approximately one attack per bee per 2 days, which may be too low to allow for learning to avoid the spider patches. Furthermore, some spider attacks may not be perceived by the bees as such because of the low resolution of the bee eye combined with good spider camouflage (Chittka 2001; Théry and Casas 2002). Finally, bees are occasionally touched by either foliage moving in the wind or various male insects searching for mates. If such harmless touches are much more common than similar touches by attacking crab spiders, bees may be less likely to respond negatively to a spider attack.

A possible alternative explanation for our results involves our focus on the whole spider patch as the spatial unit of importance. Bees, however, could respond to the threat posed by crab spiders by either avoiding only the individual plants harboring spiders or leaving the entire field. We chose the 20-plant patch based on our experience in the same system in which we documented significant spider effects in a single bumble bee species (*B. ternarius*) at the patch but not stem level (Dukas and Morse 2003). Additionally, proper experimental design prevented us from using the whole field as the experimental unit because of the lack of a well-matched control. Nevertheless, we cannot reject the possibility that the marked bees responded at spatial scales other than at the patch level we examined here.

Another alternative explanation for our results involves the fact that only 41% of the bees we marked revisited the patches. It is likely that bees perceive the marking process as a major threat because it involves their capturing, holding in a vial, and chilling over ice. Perhaps there is individual variation among bees so that only the more resilient individuals, the ones least likely to avoid either the marking site or the predatory cues, kept visiting the patches. Such possible confounding factors could reduce our chance of detecting a difference between the number of visits by marked bees to the spider and no-spider patches. Indeed, two butterfly studies indicated that individuals selectively avoided the location of capturing and marking (Singer and Wedlake 1981; Mallet et al. 1987). Heinrich (1976), however, marked bumble bees with quick drying paint while they were perching at flowers. Heinrich suggested that this marking technique, which involved negligible disturbance, resulted in similar return rates of the marked bees as the standard technique involving capture and anesthesia (Heinrich 1976). The possibility of marking effects on return rates by bees should be subjected to the necessary critical empirical test. Such a test can readily be conducted by marking young bees at the hive and later comparing the return rates of randomly chosen marked bees that will either be captured at a flower patch for simulated marking or merely observed at the same patch.

Finally, the indifference of bees to predators in the present study is consistent with results from another recent study, which examined the effect of predation by bumble bee wolves (*Philanthus bicinctus* Mickel, 1916) on bumble bees. Observations on bumble bees that escaped failed bumble bee wolf attacks indicated that, in 59% of the cases, the bees resumed foraging in the flower patch. That is, the bees responded as if they experienced a minor disturbance rather than a predation attempt, which indicates imminent threat (Dukas 2005).

In two other experiments conducted in the same area, we documented significantly fewer worker *B. ternarius* in spider than no-spider patches in 2001 (Dukas and Morse 2003) and significantly fewer worker honey bees in spider than no-spider patches in 2003 (Dukas and Morse 2005). It seems that factors such as the phenology of the bee and plant species influence the relative attractiveness of milkweed relative to alternative flowers and this may determine bees' rates of recruitment to and abandonment of milkweed patches. The relatively small effects of crab spiders might cause more bees to desert crab spider patches when alternative flowers are more readily available. In other words, the combined conclusion from our present and previous two studies (Dukas and Morse 2003, 2005) is that, at our site, the effect of crab spiders is small and unpredictable.

In summary, the majority of honey bees and bumble bees either were fully inexperienced or had only little experience with the specific flower patch that they were visiting. Such inexperience implies that, in bee communities such as ours, most bees may not have the opportunity to learn about subtle local information involving either reward or danger. That is, conclusions from highly controlled laboratory settings may not generalize to field settings such as the ones experienced by our bees.

Acknowledgements

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