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The effects of predation risk from crab spiders on bee foraging behavior

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Recent studies have suggested that top–down effects of predation on plant–pollinator interactions may not be, as previously thought, rare and/or weak. In this paper, we explore the effects of crab spiders (Araneae: Thomisidae) on the behavior of 2 species of bee (Hymenoptera: Apidae) foraging for nectar and pollen on 3 different plant species in central Portugal. In 2 experiments, we found that the eusocial bee *Apis mellifera* was significantly less likely to inspect and accept a flower or inflorescence if it harbored a spider. In contrast, we found no such effects of spiders on the behavior of the solitary bee *Eucera notata*. Further experiments showed that the effects of environmental cues associated with predators on flower visitation by *A. mellifera* were detectable even when no spider was present at the moment a flower was encountered. Such indirect effects were only identified, however, in bees foraging on 1 of 2 plant species studied. In a final experiment, *A. mellifera* was shown to respond negatively to the presence of the corpses of conspecifics glued to flowers. This suggests that prey corpses left exposed on petals or bracts by spiders provide an obvious cue that bees can use to avoid predators. These results add to a growing body of evidence that plant–pollinator interactions are not immune to the effects of predation and suggest that the strength of such effects vary both between and within species. *Key words: Apis mellifera, Eucera notata,* flower visitation, inflorescence, pollination, top–down effects. *[Behav Ecol 17:933–939 (2006)]*

Studies of the foraging behavior of pollinators often ignore the effects of predators (Schmid-Hempel 1991; Dukas 2001b), partly because it is commonly assumed that predation is too rare to be of general ecological or evolutionary significance in plant–pollinator systems (Pyke 1979; Morse 1986; Schmalhofer 2001). There is, however, strong evidence from a wide range of animal species that the lethal (see, e.g., Crawley 1992) and behaviorally mediated nonlethal effects (reviewed in Lima 1998a, 1998b; Lind and Cresswell 2005) of predation have important consequences for fitness and the nature of interactions between species. The increasingly well-established consensus that top–down effects on consumer–resource interactions are widespread in terrestrial ecosystems has prompted a reevaluation of the role of predation in plant–pollinator systems (Suttle 2003).

Recent studies exploring the effects of predators on visitation rates to plants by insect pollinators have produced mixed results. There is evidence that the presence of crab spiders (Araneae: Thomisidae) (Dukas and Morse 2003, 2005; Suttle 2003; Dukas 2005; Robertson and Maguire 2005) and lizards (Muñoz and Arroyo 2004) on or near flowers can reduce visitation rates and that seed production may be reduced as a result (Suttle 2003; Muñoz and Arroyo 2004; Dukas 2005). However, in the relatively well-studied interaction between crab spiders and bees (Hymenoptera: Apidae), the effects of predation risk seem to vary among pollinator species (Dukas and Morse 2003, 2005), and in some situations, there appear to be no detectable effects at all (Morse 1986; Dukas et al. 2005). Such results, and the general dearth of studies of interactions other than those between spiders and bees, mean that it is as yet unclear if top–down effects of predators in plant–pollinator systems are of widespread importance.

The apparent inconsistency in the results of studies of the responses of insect pollinators to predation risk may reflect the fact that very little is known about the mechanisms by which predation risk is detected. For example, studies of bee–spider interactions that have failed to find consistent effects of predation risk on pollinator activity have often focused on the effects of predator density at a patch level (where a patch contains many plants or flowers) (Dukas and Morse 2003; Dukas 2005; Dukas et al. 2005), but it is quite possible that pollinators respond to risk through the modification of behavior only at the scale of the individual plant or flower (Dukas 2001a; Dukas and Morse 2003).

If predators are detected at the scale of the individual flower, it is not clear whether risk is assessed by pollinators before landing, immediately after landing, or while collecting nectar or pollen. Previous studies have tended to collect data only on the frequency of visits to focal flowers or patches (e.g., Dukas and Morse 2003, 2005; Robertson and Maguire 2005) and have not considered explicitly how predation risk affects the sometimes complex decision-making process used by insects when they encounter a potential food resource. Before and during a "visit," pollinators must assess the benefits and costs (which might be expected to include the risk of predation) in order to decide whether to spend time and energy landing on a flower and collecting resources before flying off in search of the next flower (e.g., Duffield et al. 1993; Higginson and Barnard 2004). Observed effects of predation risk on the duration of visits to flowers by pollinators (Suttle 2003; Muñoz and Arroyo 2004), which sometimes occur in the absence of effects on visit frequency (Muñoz and Arroyo 2004), suggest that decisions being made after a visit has begun may have subtle effects on plant–pollinator interactions.

Predation risk may influence pollinator activity via a direct effect on pollinator population density (Dukas 2005) or via behavioral changes that cause a reduction in visitation rates

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(Dukas and Morse 2003; Muñoz and Arroyo 2004; Robertson and Maguire 2005). Pollinators may respond to direct visual cues indicating the presence of a predator on a flower (Robertson and Maguire 2005), but the role of nonvisual cues remains unclear. It is also possible that individuals with prior experience of failed attacks learn to associate a particular flower or patch with the presence of a predator (Dukas 2001a, 2001b; Dukas and Morse 2003) in the same way that they learn to associate environmental cues such as spider webs with predation risk (Craig 1994a, 1994b). Predators have evolved strategies to combat attempts by their prey to avoid risky flowers. For example, crab spiders evade detection by mimicking petal colors (e.g., Théry and Casas 2002) and even exploit preexisting preferences in pollinators for particular visual cues to attract potential victims (Heiling et al. 2003).

In this paper, we report results from a series of experiments and observations that explore the interaction between crab spiders and bees in 3 systems that had not been previously studied in this context. We had 3 main objectives: 1) to discover if spiders influenced plant–bee interactions at the scale of an individual flower/inflorescence, 2) to determine at what stage in a bee's decision-making process any effects of predation risk on bee behavior occurred, and 3) to determine whether bees could assess predation risk in the absence of direct visual (or other) cues from a spider.

METHODS

Study system

The effects of the presence of crab spiders (Araneae: Thomisidae), and of cues associated with the presence of spiders, on the foraging behavior of bees were investigated in a series of field observations and experiments. Data were collected describing the behavior of an introduced strain of honeybee that originates from Italy (*Apis mellifera lingustica* L.) and a solitary bee (*Eucera notata* L.) foraging on lavender (*Lavandula stoechas* L.), crimson spot rockrose (*Cistus ladanifer* L.), and sage-leaf rockrose (*Cistus salvifolius* L.). Observations and one experiment (Experiment 2) were conducted at the Quinta de São Pedro research station near Lisbon in Portugal (38°33′67″N, 009°11′34″W) in April 2004. Two experiments (Experiments 1 and 4) were conducted at the same field site in March 2005. One experiment (Experiment 3) was conducted in the nearby Paisagem Protegida da Arriba Fossil da Costa da Caparica in March 2005.

In all observations and experiments, the responses of bees when they encountered an individual flower of *Cistus* spp. or an inflorescence (group of flowers) of *L. stoechas* were recorded by an observer standing in close proximity (~1 m) to the plant in question. A flower/inflorescence was assumed to have been encountered if a bee had flown to within 2 cm of it. Two distinct decision-making phases were then recognized for each bee. First, bees decided whether to "inspect" an encountered flower/inflorescence. On *L. stoechas*, where only *A. mellifera* visits were recorded, a bee was deemed to have made an inspection if it hovered next to an inflorescence for a few seconds (sometimes touching it with its forelegs) (Duffield et al. 1993). Such hovering behavior was easily distinguished from the alternative scenario, in which an encountered inflorescence was apparently ignored (see also Gonzalez et al. 1995; Higginson and Barnard 2004). Neither *A. mellifera* nor *E. notata* performed obvious inspections while hovering near flowers of *Cistus* spp. and, instead, often alighted on a flower for a few seconds before either leaving or commencing feeding. Thus, a flower of *Cistus* spp. was deemed to have been inspected when a bee alighted on it. The second decision made by a bee was whether to "accept" an inspected flower/inflorescence or to reject it and fly away. A bee was deemed to have accepted a *L. stoechas* inflorescence if it alighted on it (after which feeding almost always commenced). A bee that had alighted on a flower of *Cistus* spp. was deemed to have accepted the flower if it began probing for nectar or collecting pollen.

Four species of crab spider were studied in total. In all experimental manipulations, the locally abundant species *Synaema globosum* Fabricius was used. When spiders were needed for manipulations, *S. globosum* individuals were collected from various plant species at the field sites. They were trapped and stored in Perspex tubes and handled using a small paintbrush. Three other species (*Misumena vatia* Clerck, *Heriaeus hirtus* Latreill, and *Xysticus* sp.) were present in small numbers (<10% of crab spiders encountered) at our field sites. Because we did not distinguish between species when making observations, our nonexperimental data should therefore be taken as being representative of the particular community of crab spiders present at our field sites and not as being representative of any one particular spider species.

Effects of spider presence on bee behavior

One set of observations and one experiment were conducted to investigate the effects of the presence of spiders on flowers/inflorescences on bee foraging behavior. The observations made were of the behavior of *A. mellifera* toward *L. stoechas* inflorescences. Between 1000 and 1700 over a period of 6 days, bees foraging on a large patch of *L. stoechas* (>1000 inflorescences) were selected opportunistically as they entered the patch and followed until they had encountered 5 inflorescences. Four observers, each of whom moved to a new, haphazardly chosen location around the periphery of the patch every 20 min, were employed to minimize observer bias affecting the identity of the bees and inflorescences being observed. Each time an inflorescence was encountered, the bee's decision and the presence or absence of a crab spider were recorded.

In Experiment 1, the responses of *A. mellifera* and *E. notata* to flowers in a patch of 15 *C. ladanifer* plants were recorded over 2 days. All flowers of *Cistus* spp. at our field site were renewed each day by the plant, with no flower remaining intact for more than about 8 h (petals typically dropped in the late afternoon). On any one day, approximately 70 flowers were open in the patch. A total of 16 crab spiders were collected and placed on randomly selected, newly opened *C. ladanifer* flowers at 1000 each morning. The behavior of bees toward these flowers, and toward 24 randomly chosen control flowers that did not harbor spiders, was then observed between 1100 and 1600 each day. Observations were not taken during the hottest part of the day (1230–1430) when pollinator activity was minimal. Observations of individual flowers ceased if the status of a flower (spider vs. control) changed owing to the departure or arrival of a spider. Although 32 spiders were placed on flowers over the 2 days, some spiders left the flowers on which they had been placed before observations could begin. In total, 20 flowers with spiders and 46 control flowers were observed over the 2 days.

Effects of cues associated with spiders on bee behavior

Three experiments were conducted to test for effects of cues associated with the current or previous presence of spiders on flowers/inflorescences on bee behavior. Over the course of 3 days, Experiment 2 examined the behavior of *A. mellifera* when offered individual *C. salvifolius* flowers, some of which had previously been exposed to a crab spider. The day before they opened, 379 flowers on a large *C. salvifolius* bush were randomly assigned to 1 of 4 treatments: "bagged control," "unbagged control," "bagged treated," and "unbagged treated." Treated flowers were each exposed to a crab spider immediately before being offered to a bee, whereas untreated flowers were not exposed to spiders. In order to expose a flower to a spider, a captive spider was transferred to the flower and allowed to walk around for 1 min before being removed. During this process, it was noted that silk was often produced by the spider and deposited on the flower. The night before they opened, bagged flowers were individually isolated in a muslin bag to prevent any foraging insects or crab spiders from visiting them before they were offered to a bee, whereas the unbagged flowers were left uncovered so that they could be visited freely in the hours before they were used in the experiment. We included this manipulation because preliminary studies and other published work on *A. mellifera* foraging behavior (e.g., Williams 1998) indicated that the probability of acceptance of a flower by a bee was likely to be influenced strongly by previous visits from other pollinators.

Between 1100 and 1600, flowers in each of the 4 treatments were cut from the bush in a random order and offered to opportunistically selected foraging bees. It was observed that bees foraging on *C. salvifolius* typically moved systematically from flower to flower on a bush, traveling a few centimeters at a time. Therefore, each cut flower was held with forceps within a few centimeters of a flower on which a bee was already feeding, in a position chosen to coincide with the anticipated flight path of the bee. If, having left its original flower, the bee encountered the offered flower (i.e., flew in the anticipated direction), its decision was recorded. If the bee left its original flower in a different direction from the offered flower, nothing was recorded. Each flower was discarded once a decision had been recorded.

Experiment 3 was carried out in an attempt to identify any indirect cues used by bees to identify flowers/inflorescences that have recently been visited by spiders. Specifically, we wanted to distinguish between the possible effects of olfactory cues (scent deposited by spiders) and visual cues (silk deposited by spiders). Inflorescences in a large patch of *L. stoechas* were randomly allocated to 1 of 3 treatments: "control," "spider," or "silk." The spider treatment was achieved by exposing each inflorescence to a crab spider (as in Experiment 2). For the silk treatment, silk was harvested by repeatedly making a spider "abseil" on a strand of silk from one end of a Perspex tube to the other (inverting the tube after each run). When approximately 20 strands had been generated, a paintbrush was used to collect the silk from the tube and transfer it on to the target inflorescence. The amount of silk transferred was chosen to be equal to the maximum amount deposited on inflorescences by spiders in the spider treatment. It should be noted that the silk may itself carry spider scent, but alternative treatments to exclude scent altogether were not feasible in our study system, and we considered our silk treatment to be the next best option. Control flowers were not manipulated. All decisions made by bees were recorded at a total of 79 experimental inflorescences observed between 0930 and 1700 for 5 days.

During preliminary observations of *C. ladanifer* and *L. stoechas* at our field site in 2004, it was noticed that the "mummified" corpses of prey (most commonly *A. mellifera*) killed by crab spiders were often attached by silk to conspicuous parts of flowers/inflorescences. Experiment 4 sought to investigate whether a corpse could serve as an indirect visual cue to the presence of a spider on a flower. Forty-one flowers in a patch of 27 *C. ladanifer* plants were randomly allocated to 1 of 2 treatments: "control" and "dead bee." On the morning of the experiment, before these flowers had opened, 22 *A. mellifera* were caught using a sweep net while foraging on various species of plant nearby and placed in a freezer at −18 °C for 45 min until they were dead. For the dead bee treatment, corpses were attached using superglue to the center of arbitrarily selected petals on target flowers. Control flowers had glue added but no corpse. All decisions made by foraging *A. mellifera* and *E. notata* encountering experimental flowers were recorded between 1100 and 1600 (but not between 1230 and 1430) on 1 day.

Observations of spider behavior

Observations of spider behavior on *L. stoechas* inflorescences were made with the aim of quantifying the risks taken by *A. mellifera* when foraging on inflorescences that harbored spiders. Observations of 60 inflorescences known to harbor spiders were carried out for 20-min periods between 1000 and 1700 over a period of 6 days. Four observers were employed, each of whom watched about 15 inflorescences at a time. When a bee encountered an inflorescence with a spider, the actions of the spider were categorized as follows: "emerged"—the spider left its resting/hiding place (often among the sterile terminal bracts of the inflorescence), "attacked"—the spider made an attempt to capture the bee with its front legs, and "killed"—the spider captured and killed a bee.

Statistical analysis

Bee decision data from experiments and observations were analyzed with appropriate generalized linear models (GLMs) or generalized linear mixed models (GLMMs) with binomial (inspect vs. ignore and accept vs. reject) error structures. Repeated measures models were employed for Experiments 1, 3, and 4, where multiple observations were made from each individual flower, inflorescence, or bee. All analyses were conducted in R 1.9.0 (The R Development Core Team 2004). Models were implemented following Crawley (2002).

RESULTS

Observations of spider behavior

On 39 occasions in 16 h of observations, *A. mellifera* was observed alighting on an inflorescence harboring a spider. On 30 (79%) of these occasions, the spider emerged from its resting/hiding place, and on 16 occasions (41%), an attack was attempted. Three successful attacks were observed, meaning that a bee alighting on an inflorescence harboring a spider had on average a 7.7% chance of being captured and killed.

Effects of spider presence on bee behavior

There was a significant effect of the presence of a spider on the behavior of *A. mellifera* observed foraging on *L. stoechas* inflorescences (Figure 1). Although there was no significant effect of spider presence on the decision to inspect an inflorescence (GLMM: $F_{1,907} = 1.089$, $P = 0.297$), with the vast majority being inspected regardless, *A. mellifera* was only about half as likely to accept an inflorescence after inspection if it harbored a spider ($F_{1,834} = 16.544$, $P < 0.001$).

Apis mellifera also changed its behavior toward *C. ladanifer* flowers when they harbored spiders in Experiment 1 (Figure 2). Bees were less likely to inspect a flower (GLMM: $F_{1,61} = 10.061$, $P = 0.002$) and inspected flowers were less likely to be accepted ($F_{1,59} = 5.573$, $P = 0.022$) in the presence of a spider. In contrast, *E. notata* was not significantly less likely to inspect or accept flowers with spiders (inspections: $F_{1,51} = 1.345$, $P = 0.252$; acceptances: $F_{1,47} = 1.420$, $P = 0.239$).

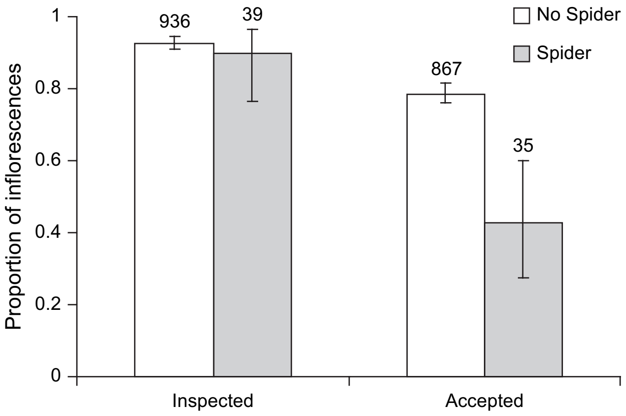

Figure 1
Proportion of *Lavandula stoechas* inflorescences with and without naturally occurring crab spiders that were inspected and accepted by *Apis mellifera*. The number above each bar indicates the sample size. Error bars are 95% confidence intervals calculated using the binomial distribution.

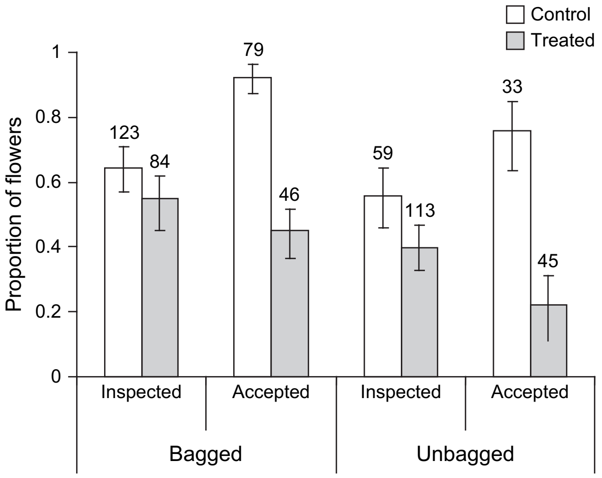

Figure 3
Proportion of treated (previously exposed to a crab spider) and control *Cistus salvifolius* flowers that were inspected and accepted by *Apis mellifera*. Flowers were either bagged prior to opening to prevent visits by other pollinators and spiders or left unbagged. The number above each bar indicates the sample size. Error bars are 95% confidence intervals calculated using the binomial distribution.

Effects of cues associated with spiders on bee behavior

The results of Experiment 2 suggested that *A. mellifera* could detect and respond to cues indicating the recent presence of a crab spider on a *C. salvifolius* flower, even if the spider was no longer on the flower (Figure 3). Overall, bees were significantly less likely to inspect a flower (GLM: $F_{1,367} = 4.699$, $P = 0.030$), and less likely to accept a flower after inspection ($F_{1,193} = 12.597$, $P < 0.001$), if that flower had previously been exposed to a spider. Overall, bees were also significantly less likely to inspect ($F_{1,368} = 7.809$, $P = 0.005$) or accept ($F_{1,194} = 8.876$, $P = 0.003$) a flower if it had not been protected from other invertebrates by a muslin bag prior to opening, but there was no interaction between the effects of exposure to spiders and bagging (inspection: $F_{1,366} = 0.481$, $P = 0.488$; acceptance: $F_{1,192} = 0.010$, $P = 0.920$).

In contrast to the findings from Experiment 2, the results from Experiment 3 suggested that the effect of spiders on *A. mellifera* foraging on *L. stoechas* did not extend beyond the time for which a spider was actually present on an inflorescence (Figure 4). Overall, compared with controls, the likelihood that a bee would inspect or accept a flower was slightly higher for flowers that had been treated with silk and slightly lower for flowers that had been exposed to spiders, but in neither case was the effect of treatment significant (GLMM for inspection: $F_{1,65} = 0.894$, $P = 0.414$; for acceptance: $F_{1,63} = 0.409$, $P = 0.666$).

There was a strong effect of the presence of the corpses of conspecifics on *A. mellifera* behavior when foraging on *C. ladanifer* in Experiment 4 (Figure 5). Overall probabilities of inspection (GLMM: $F_{1,39} = 7.928$, $P = 0.008$) and acceptance ($F_{1,37} = 27.874$, $P < 0.001$) were much lower when flowers harbored corpses. In contrast, any effects of *A. mellifera* corpses on *E. notata* were weak and not significant (inspection: $F_{1,28} = 0.577$, $P = 0.454$; acceptance: $F_{1,24} = 0.761$, $P = 0.392$).

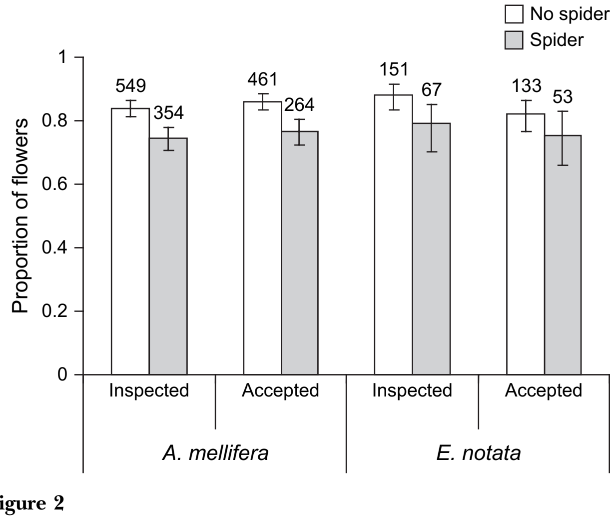

Figure 2
Proportion of *C. ladanifer* flowers with and without artificially added crab spiders that were inspected and accepted by *Apis mellifera* and *Eucera notata*. The number above each bar indicates the sample size. Error bars are 95% confidence intervals calculated using the binomial distribution.

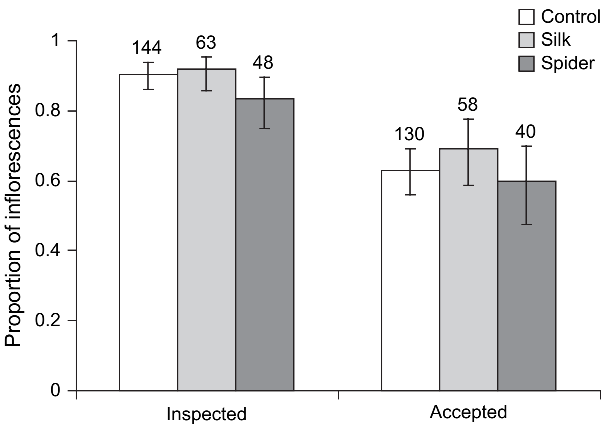

Figure 4
Proportion of *Lavandula stoechas* inflorescences in 3 experimental groups that were inspected and accepted by *Apis mellifera*. Inflorescences had crab spider silk added (silk), were exposed to a spider (spider), or were subjected to no manipulation (control). The number above each bar indicates the sample size. Error bars are 95% confidence intervals calculated using the binomial distribution.

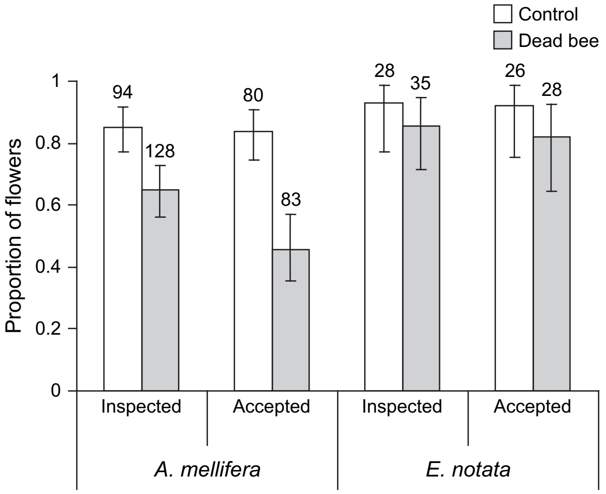

Figure 5
Proportion of *Cistus ladanifer* flowers, with and without artificially added dead *Apis mellifera*, that were inspected and accepted by *A. mellifera* and *Eucera notata*. The number above each bar indicates the sample size. Error bars are 95% confidence intervals calculated using the binomial distribution.

DISCUSSION

Our results add to a growing body of evidence that top–down effects have a significant influence on plant–pollinator interactions. In particular, predation risk from spiders appears to have widespread consequences for bee behavior (our results and Théry and Casas 2002; Dukas and Morse 2003, 2005; Heiling et al. 2003; Suttle 2003; Robertson and Maguire 2005) and population density (Dukas 2001b, 2005) and ultimately for plant reproduction and therefore fitness (Suttle 2003; Dukas 2005). It is clear, however, that the effects of predators on pollinators vary qualitatively and quantitatively between and even within pollinator species. For example, we found significant effects of predation risk in *A. mellifera* but not (where tested for) in *E. notata*, and our results suggested that although *A. mellifera* was about 50% less likely to accept *L. stoechas* inflorescences harboring spiders, it was only about 10% less likely to accept risky *C. ladanifer* flowers. Variations in sample sizes and experimental design are likely to influence observed effect sizes and significance, and we cannot rule out confounding effects in all our experiments. Nevertheless, the inter- and intraspecific differences in the effect of spiders on visitation probabilities appear to indicate variations across plant and pollinator species in the ease with which spiders can be detected or in the balance between the costs associated with predation risk and the benefits provided by nectar and pollen rewards. Such variations may help to explain inconsistencies observed in the results of other studies (e.g., Dukas and Morse 2003, 2005).

Levels of predation risk in some plant–pollinator systems appear to be so low that the impacts on pollinator population density, and the strength of selection pressure on pollinators to modify their behavior in order to reduce predation risk, are likely to be minimal (Pyke 1979; Morse 1986; Schmalhofer 2001). However, the level of risk faced by pollinators in our study system (if they do not modify their behavior to reduce risk) is relatively high. For example, if *A. mellifera* workers foraging on *L. stoechas* at our field site visit 1000 inflorescences at random each day (in fact they probably visit many more than this—Higginson 2005), and spiders occupy 0.1% of inflorescences (Higginson 2005), the mean probability of accepting an inflorescence is about 0.6 (see Results) and the probability that a spider will launch a successful attack on a visiting bee is 0.077 (see Results); the probability (x) that a bee will be killed on any given day is given by

$$x = 1 - [1 - (0.001 \times 0.6 \times 0.077)]^{1000} = 0.045.$$

This figure is likely to be nontrivial from the point of view of colony fitness. Indeed, a model of *A. mellifera* behavior specific to our *L. stoechas* study system predicts that significant modifications to bee foraging decisions at a patch scale are likely at observed spider densities (Higginson and Gilbert 2004), and this prediction is supported by the results of field experiments (Higginson 2005).

Little is known about the exact nature of the mechanisms that generate top–down effects on plant–pollinator interactions. Our data support the suggestion that some bees can assess predation risk from spiders at the scale of the individual flower (Suttle 2003; Robertson and Maguire 2005) and suggest that (at least in the case of *A. mellifera* foraging on *Cistus* spp.) behavioral responses to that risk can be made both before and after a flower has been deemed worth visiting. Because the decision about whether to inspect a flower occurs before a bee has landed, our results also suggest that bees act on information about predation risk that is available both while in flight and while in contact with the flower. Thus, direct physical contact with a spider cannot alone explain the reluctance of *A. mellifera* to visit potentially risky *Cistus* flowers. Recent studies have shown that visual cues associated with crab spiders that are detected before a bee alights on a flower can have strong effects on visitation rates (Heiling and Herberstein 2004; Heiling et al. 2005). Interestingly, these effects are not always negative—spiders may attract bees to flowers, apparently by exploiting preexisting preferences of bees for particular color patterns (Heiling et al. 2003, 2005). Especially in the light of such findings, it seems likely that visual cues associated with predation play an important role in honeybee foraging behavior at our study sites.

It has been suggested that bees can avoid flowers harboring spiders if they have learned to associate such flowers with predation risk as a result of previous failed attacks by spiders (Dukas 2001b; Dukas and Morse 2003). There are examples in the literature of bees learning to associate environmental cues with predation risk and modifying their behavior as a result (e.g., Craig 1994b). In a laboratory study, *A. mellifera* workers learned to avoid artificial feeders at which they had previously experienced a simulated predator attack (Dukas 2001a). With the results from Experiment 2, however, we can rule out an effect of learning that is flower specific because treatments were applied at random to newly opened flowers that were then discarded. The bees that we observed avoiding potentially dangerous flowers in this experiment must have been responding on the basis of environmental cues that indicated predation risk. The response to these cues may be "hardwired" or learned through experience of attacks in the presence of similar cues, but they do not appear to be specific to individual flowers.

Because *A. mellifera* was less likely to inspect and accept a *C. salvifolius* flower that had been exposed briefly to a spider prior to the bee's arrival, we can conclude that the environmental cues used when the decision to avoid a flower is made must include some that are not related to the current presence of a spider. It is possible that spiders are detectable by their scent. Previous studies have shown that visitation rates in *A. mellifera* are strongly influenced by scent cues deposited by the sometimes distantly related species with which it competes (e.g., Cameron 1981; Stout and Goulson 2001; Reader et al. 2005). However, from the results of Experiment 3 alone, it is impossible to rule out the use of nonolfactory cues, such as those associated with spider silk.

Although they do not spin webs (Roberts 1995), crab spiders hunting on flowers use silk, and on several occasions when an attempted attack was observed during this study, it was only the presence of a silk tether that prevented spiders being carried away from flowers by their much larger prey. Because any flower or inflorescence inhabited by a spider therefore has strands of silk deposited on it and because *A. mellifera* is known to be able to see and avoid spider silk (Craig 1994a), bees may have avoided flowers in Experiment 3 because they associated the presence of silk with an elevated predation risk. Interestingly, however, the behavior of *A. mellifera* toward inflorescences of *L. stoechas* that had previously been exposed to spiders and silk in Experiment 4 was not consistent with that observed when bees were foraging on *C. salvifolius* (there was in fact no effect of treatment on inspection or acceptance rates). Thus, the exact identity of the cues used by *A. mellifera* to assess predation risk in our study systems remains unclear.

Spiders hunting on *L. stoechas* and *C. ladanifer* that had successfully captured a bee often left their mummified victims attached to petals or bracts with silk and in full view of other foraging pollinators. We do not know whether prey were attached deliberately by spiders or if they simply became accidentally entangled in spider silk. The storage of immobilized prey may be necessary for the spider while it waits for its digestive enzymes to act (Roberts 1995), but research on the effects of prey dehydration on crab spider feeding behavior makes this seem unlikely (Pollard 1989). Whatever the reason for its retention on a flower, a bee corpse provides an obvious visual and olfactory indicator of the predation risk associated with a flower harboring a spider. Results from Experiment 4 show clearly that such an indicator can influence bee decision making, at least in conspecifics. These findings support those of a laboratory study that showed that the presence of *A. mellifera* corpses led to reduced visitation rates to artificial flowers (Dukas 2001a).

Our results underline the degree of variation present in the strength of top–down effects on plant–pollinator interactions, even within individual study systems. One generalization it is possible to make about such effects is that (where they exist) they are negative, with both pollinators (e.g., this study) and plants (Suttle 2003; Muñoz and Arroyo 2004; Dukas 2005) having reduced survival or fitness in the presence of predators. Thus, although plants may have evolved mechanisms to facilitate predation and parasitism of herbivores (De Moraes et al. 1998; Ode 2006), it is likely that both plants and pollinators are under selective pressure to minimize the effectiveness of natural enemies such as crab spiders. This study and others have shown how pollinator behavior may be adapted as a result of this selective pressure, but we know almost nothing about the extent to which predation of pollinators shapes the evolution of plant strategies. Given the general level of interest in trophic cascades mediated by top–down effects in terrestrial systems (Schmitz et al. 2000; Halaj and Wise 2001), this is an obvious target for future research in pollination ecology.

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