

Crab spiders affect flower visitation by bees

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In a field experiment, the bumblebee, *B. ternarius*, visited milkweed patches harboring crab spiders, *Misumena vatia*, at a lower frequency than patches free of crab spiders, and honeybees showed a similar but non-significant trend. Two other bumblebee species, *B. terricola* and *B. vagans*, did not avoid the spider patches. The latter two species are larger than *B. ternarius* and honeybees and suffer lower crab-spider predation. As far as we know, this is the first field study documenting negative effects of predators on flower visitation rate by pollinator populations. Our study suggests that pollinator response to predation may influence pollinator-plant interactions.

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Ecological studies on animal-flower interactions typically neglect the possible effect of predation on flower visitors. With a few exceptions (Louda 1982, Lima 1991, Willmer and Stone 1997), researchers have assumed that predation at flowers is too rare to be of importance (Pyke 1979, Miller and Gass 1985, Morse 1986a, Schmid-Hempel 1991). Recent research in other systems, however, provides convincing evidence for substantial effects of predation in natural settings, even when observers report low predation rates. Such effects of predation include changes in temporal and spatial patterns of activity, food preference, life history, and reduced fitness (Lima and Dill 1990, Peckarsky et al. 1993, Lima 1998, Peacor and Werner 2000).

Bees in general, and social bees in particular, are among the most commonly observed flower visitors. Two common misconceptions about bees are, first, that predators avoid them due to their sting, and, second, that the non-reproducing workers of social bees may ignore predation because it would not affect colony reproduction. First, numerous animals prey on bees. These include bee eaters (Meropidae) (Fry 1983), Old and New World flycatchers (Muscicapidae and Tyrannidae) (Ambrose 1990), bee-wolves (*Philanthus*

spp) (Evans and O'Neill 1988), a few species of social wasps (Evans and Eberhard 1970, De Jong 1990), crab spiders (Thomisidae) (Morse 1981, 1986a), predacious bugs (Hemiptera) (Balduf 1939, Greco and Kevan 1995) and praying mantids (Mantidae) (Caron 1990). Second, theoretical analyses indicate that workers of social bees should consider predation risk while making foraging choices, albeit to a lesser degree than solitary bees (Clark and Dukas 1994, Dukas and Edelman-Keshet 1998).

In recent experiments using artificial flowers, honeybees 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). These results along with others documenting behavioral sensitivity of individual bees to predation risk (Cartar 1991, Craig 1994) suggest that bees, like other animals, take anti-predatory measures, which may affect animal-flower interactions (Dukas 2001b). No ecological study, however, has examined effects of predators on bees at the population and community level in natural settings. Such effects, if they do exist, may influence flower-pollinator interactions.

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To evaluate possible effects of predation on bee populations, we manipulated the density of crab spiders (*Misumena vatia*), common predators of flower-visiting insects, in adjacent plant patches. We then asked whether the local populations of bumblebees and honeybees would avoid patches harboring these spiders.

Methods

Study area and species

The experiment was conducted successively in two old fields at and near the Darling Marine Center of the Univ. of Maine, South Bristol, Lincoln County, Maine, USA. Field 1 was within the center's grounds and field 2 was approximately 1 km away. Each of the two fields contained a few thousand stems of common milkweed (*Asclepias syriaca*) before our experimental manipulation. Usually, a milkweed stem produces a few inflorescences (umbels), each containing from 30 to 75 flowers, more than half of which are at nectar producing stage simultaneously when the umbel is at peak bloom (Morse 1986b).

In our study area, milkweed umbels harbor adult female crab spiders, whose density greatly varies in time and space. In a large patch containing more than 1000 milkweed stems, the spider density ranged between 0.2% to 2.2% of the stems with a mean (\pm SE) of $1.1\% \pm 0.32\%$ over five years. Counts in much smaller patches containing 3 to 50 milkweed stems each ranged between 0% to 43.2% of the stems with a mean of $11.7\% \pm 3.29\%$ (D. H. Morse, unpubl.).

The crab spiders are sit-and-wait predators, which can reversibly adapt their color to the flowers they occupy. On milkweed, the spiders are white and UV absorbing, hence highly camouflaged to the human and bee eye (Chittka 2001, Thery and Casas 2002). The spiders may reach 12 mm in length, and the distance between the extremities of their extended raptorial forelimbs may exceed 30 mm. They capture various flower-visiting insects, including species as large as bumblebees (Morse 1979, 1981, 1986a).

The dominant visitors to milkweed in our study area were three species of bumblebees (*Bombus ternarius*, *B. terricola* and *B. vagans*) and honeybees (*Apis mellifera*). We observed only workers of *B. ternarius* and *B. terricola*, but more than half of the *B. vagans* visits were by males. Honeybees were observed only in field 2. Although worker bumblebees greatly vary in size, we could readily distinguish between two distinct size categories of relatively large (*B. terricola* and *B. vagans*), and small (*B. ternarius* and honeybees) bees. The average fresh body mass (mean \pm SE) of bees that were caught in the field and immobilized by chilling was, *B. terricola*: 184.28 ± 9.459 mg ($n = 25$ bees), *B. vagans*: 109.39 ± 6.768 mg ($n = 18$), *B. ternarius*: $81.55 \pm$

2.794 mg, and honeybees: 85.44 ± 3.948 mg ($n = 36$). In addition to the four bee species on which we focus, the milkweed was visited by two species of yellow jacket (*Vespa* spp) and various species of flies and moths, the latter mostly at night. We did not notice predatory activity besides that of crab spiders during this study, but did observe a few conopid parasitoids (Conopidae).

Matched-patch comparison

One day before the start of the experiment, we cleared milkweed stems to create ten matched pairs of patches, each containing 25 stems in or just before peak bloom. Four of the matched pairs were in field 1 and six in field 2. Each patch was surrounded by 2–3 m of clearing, which separated the patch from its matched pair and other plants not included in the experiment. We examined all the milkweed stems in the patches and removed all crab spiders.

On day 1, we counted the number of bees visiting the patches to verify that the matched patches were similar in their attractiveness to bees. We performed two counts at each of the 4 time periods: 8:00, 10:00, 12:00 and 14:00. Each count involved starting in a randomly chosen patch, recording the number and species of bees observed on each stem, then moving to the matched pair and so on until completion of all the patches. Immediately afterwards, the count was repeated for the second time. Overall, we had a total of 8 counts from each patch.

On the morning of day 2, we introduced the crab spiders, all adult females that had been collected on flowers within several km from the study site and numbered with indelible ink for individual identification. One randomly chosen patch of each patch pair received 10 crab spiders. We placed each spider on a milkweed umbel at peak bloom and put a small piece of tape indicating the spider's identity under a leaf at the bottom of the stem. After placing the spiders, we allowed them and the bees to adjust to the new settings for the rest of the day.

On days 3, 4 and 5, we counted the number of bees in each patch at 8:00, 10:00, 12:00, 14:00 and 16:00. At each of the bi-hourly counts, we began at a randomly chosen patch, recorded the number and species of bees observed on each stem, then moved to the matched pair and so on until completion of all the patches. Immediately afterwards, the count was repeated for the second time. Overall, for each of the 3 days, we had a total of 10 bee counts per patch.

The bee visitation data were log transformed for the statistical analyses. The results of the preliminary census conducted on day 1 were analyzed with a separate repeated measures ANOVA for each bee species. The ANOVA model included future spider presence (2 values) and time of day (4 values) as fixed factors, and

patch-pair (10 pairs) as a random factor. The results on patch visitation over the whole experiment were analyzed with one repeated measures ANOVA for each bee species. The ANOVA model included spider presence (2 values), day (4 values), and time of day (5 values) as fixed factors, and patch-pair (10 pairs) as a random factor. In short, the dependent factor in the repeated measures ANOVA's was always the average number of individual bees observed at each of the five bi-hourly counts in each of the 10 matched pairs of patches; the total number of experimental units was 10 pairs in which repeated counts were made over four days.

Matched-umbel comparison

Instead of avoiding the entire spider-occupied patch, bees could selectively by-pass either the stems or umbels on which spiders resided. To test for this possibility, we conducted the matched-umbel comparison. Within the spider-occupied patches, we selected a milkweed umbel with an active crab spider and a nearby umbel on another milkweed stem; the matching stems and umbels were at similar blooming stages. We recorded the number and species identity of all bee visitors to each umbel for a period of 30 min. We repeated this comparison with 23 matched pairs of umbels. The data were log transformed and analyzed with a matched-pair t-test.

Spider and bee behavior

To supplement the experimental data, we conducted behavioral observations on spiders and bees throughout the experiment (days 2–5). The observations involved watching a spider-occupied umbel and recording the number and species of visiting bees, whether the bee was attacked, and the bee's response to an attack. An attack typically involved movement of the spider in an attempt to position its forelimbs around the bee. A successful attack culminated with a bite, which almost instantly immobilized the bee. To calculate the frequency of visits ending in attacks for each bee species, we included only the spider-occupied umbels that received visits by that bee species.

Each observation period lasted for a maximum of 2 hours but some observations terminated early due to prey capture, the spiders leaving the umbel or the observer's conflict with other duties. Overall, we recorded data on 45 spiders over 74 hours, an average of 100 min per spider. We observed only spiders that appeared to be in an active mode, meaning that the spiders were positioned at the flowers with their front legs extended and were not engaged in either feeding or resting away from the flowers.

In addition to the direct behavioral observations, we also surveyed all the spiders every 3 hours from approx-

imately 08:30 to 17:30 h. On average, a crab spider feeds on a bee for a few hours (Morse 1981). Hence our surveys allowed us to record most of the bee captures during the experiment.

We provide only descriptive statistics for the behavioral information because we could not control for several variables such as the spider's location, time of day, and the type and timing of the spider's most recent meal. In addition, the data on bees' responses to attacks were from unmarked bees of unknown age and experience.

Results

Matched-patch comparison

On day 1 (before spider introduction), bees of all four species visited at similar frequencies the patches assigned to be occupied by spiders and the patches assigned to be spider-free (repeated measures ANOVA, $p > 0.3$ for all four bee species; Fig. 1). In contrast, two out of the four bee species showed a decrease in relative visitation frequency to the spider patches throughout the experiment. That trend was statistically significant only with *B. ternarius* (repeated measures ANOVA, $F_{3,27} = 4.9$, $p < 0.01$; Fig. 1). By day 5, we recorded an average of less than half as many *B. ternarius* workers in the spider than spider-free patches. *B. terricola*, which was the least common bee in our study area (note difference in scale for that species in Fig. 1), showed an ambiguous daily visitation pattern insufficient for statistical interpretation. *B. vagans* showed no significant change in relative visitation throughout the experiment ($P > 0.9$). Finally, although honey bees were

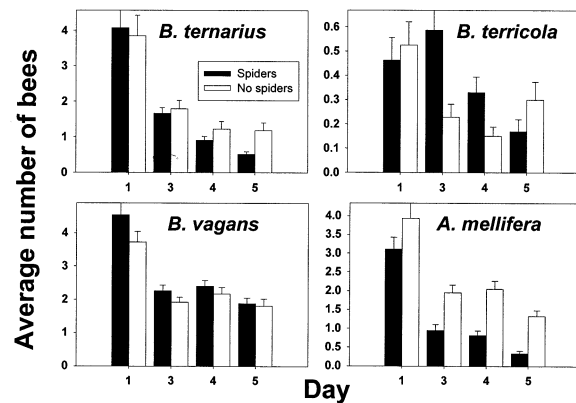


Fig. 1. The average number (+SE) of bees observed in 10 matched pairs of milkweed patches in each census over 5 days. One patch of each matched pair was randomly assigned to harbor 10 crab spiders, while its twin patch remained free of crab spiders during the preliminary census on day 1. Data were not collected on day 2, during which spiders could settle and bees adjust to the new conditions.

4 times less likely to visit the spider patches by day 5, the increase in their avoidance of the spider patches during the experiment was not statistically significant ($P > 0.3$). The statistical power of the repeated measures ANOVA was high (i.e. the probability of rejecting the null model given a 50% reduction in visitation to the spider patches was larger than 0.8). All bee species showed significant between-day variation in visitation frequency ($P < 0.01$; Fig. 1) and visited some patch-pairs more often than others ($P < 0.01$). The variation in visitation rate throughout the day (time effect) was statistically significant only with *B. vagans* ($P < 0.05$), which showed a gradual increase in visits throughout the day.

Matched-umbel comparison

Visitation rates to the spider umbel were either similar or slightly lower than to the spider-free umbel (Fig. 2). That difference approached statistical significance only with *B. ternarius*, which showed a 10% lower frequency of visits to the spider umbels (matched pairs t-test, $t_{22} = -2.03$, $P = 0.055$).

Spider and bee behavior

In the spider surveys we conducted 4 times a day, we found an average of 6.7 ± 0.3 (mean \pm SE) spiders per spider patch. Thirty of the 45 spiders observed (67%) attacked bees. *B. ternarius* ($n = 402$ visits) and *B. terricola* (102 visits) were attacked on approximately 7.5% of their visits to umbels harboring spiders (Fig. 3). Male and worker *B. vagans*, which were the most frequent visitors (779 visits), were attacked at the lowest frequency of approximately 5% of the visits, while

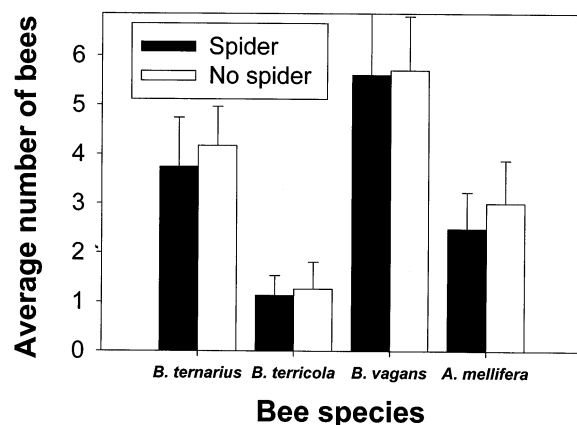


Fig. 2. The average number (\pm SE) of bees observed visiting 23 matched pairs of milkweed umbels in 30 min. One milkweed umbel harbored a crab spider, while the other umbel, on a nearby stem, was free of crab spiders.

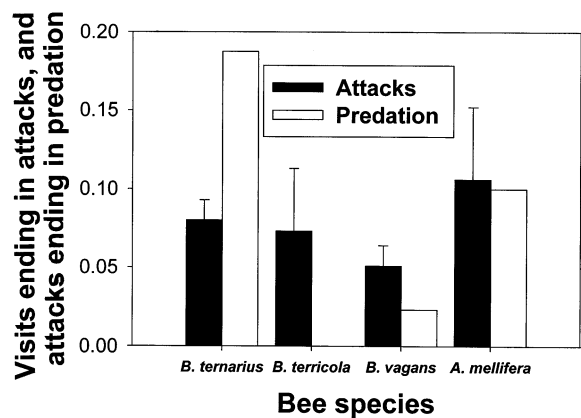


Fig. 3. The average proportion (\pm SE) of visits to milkweed umbels harboring crab spiders that ended in the spider attacking the bee, and the average proportion of the attacks that were successful. The data are based on observations of 45 spiders and total visits of 402 *B. ternarius*, 102 *B. terricola*, 779 *B. vagans* and 327 honey bees.

honey bees (327 visits) were the most likely to be attacked (11%; Fig. 3). Note that we provide here only descriptive statistics for the behavioral information because we could not control for several variables such as the spider's location and time of day.

Our data on bees' responses to attacks by crab spiders included 17 *B. ternarius*, 43 *B. vagans* and 10 honey bee visits. In approximately 80% of the visits, the bees left the umbel immediately after the attack without visiting any additional flower. Among the bees that left the umbel, about 25% stayed on the same stem, 65% left the stem but stayed to visit other stems within the same patch, and the remaining 10% left the patch altogether. The different bee species responded in a similar manner, but the limited data set is not sufficient for a thorough between-species comparison. Moreover, the data on bees' responses to attacks must be compared to a proper control in which one records bees' "response" to a randomly timed "no-attack".

We directly observed a total of 6 bee captures, which suggested a higher success rate with the smaller *B. ternarius* and honey bees than with the larger *B. vagans* (Fig. 3). We further observed spiders feeding on a total of 4 *B. ternarius*, 2 *B. terricola*, 2 *B. vagans* and 10 honey bees.

Discussion

Bee response to crab spiders

The bumblebee, *B. ternarius*, visited milkweed patches harboring spiders at a lower frequency than patches free of crab spiders, and honeybees showed a similar non-significant trend (Fig. 1). *B. ternarius* and honeybees also showed slight avoidance of umbels with spi-

ders compared to spider-free umbels (Fig. 2). As far as we know, this is the first data set documenting that predators negatively affect flower visitation rate of pollinator populations in natural settings. That is, our data suggest that predation on pollinators may affect population and community-level interactions among pollinators and between pollinators and plants.

B. ternarius and honeybees showed a stronger response to crab spiders than did either *B. terricola* or *B. vagans*. We think the reason for this difference is the higher vulnerability of the two smaller bee species to crab-spider predation (Fig. 3). Our behavioral observations indeed indicated that the crab spiders had difficulties capturing the larger bumblebees. Previous data on three of the bee species observed in our study also indicated a higher proportion of successful attacks by crab spider on honeybees than on either *B. terricola* or *B. vagans* (Morse 1986a).

Finally, all four bees showed an overall decline in visitation rate to all patches (Fig. 1). We think this was caused by our experimental manipulation, which significantly reduced plant density, and by a seasonal change. An additional possibility, however, is that predation resulted in the bees avoiding the experimental fields altogether, rather than only the spider patches.

The effects of predation

The lower visitation rate by *B. ternarius* to the milkweed patches that contained spiders may be explained either by direct or indirect effects of predation. Direct effects simply mean that spider predation reduced the number of bees visiting the patches with spiders. Direct effects of predation would be most plausible if an individual bee confined its foraging to a single patch. This, however, was not the case in our experiment, where each patch contained only 25 milkweed stems and we commonly observed inter-patch movement. Furthermore, we documented only four captures of *B. ternarius*, the only species that showed statistically significant avoidance of the patches with spiders. This number is too small relative to the total population of that species in our site (which our counts revealed to be larger than 100 individuals) to explain the change in visitation rate we noted. Nevertheless, direct effects of crab-spider predation on patch visitation rate by pollinators may be important where the predation rate is high relative to the visitation rate.

Indirect effects of predation mean that bees learn to avoid the patches with spiders. The most obvious information available to bees is being attacked by crab spiders. Because most spider attacks fail, attacks provide highly reliable data on danger. Indeed it appears that many of the bees that had been attacked by crab spiders on a milkweed umbel abruptly departed the umbel. We do not know, however, what the bees

perceived about the attack and to what extent a single attack caused them to subsequently avoid the attack location. That is, we defined an attack as any spider attempt to enclose a bee with its raptorial forelegs, resulting in body contact between the spider and the bee. Attacks varied from a light body contact to a “close call”, in which the bee was seized by the spider but escaped. It is possible that bees perceived only the latter as predatory behavior, mostly because bees may occasionally be touched or even hit by other foragers or wind-blown plants. Although the bees may possess a generic leaving response to such hits, perhaps only obvious attacks or repeated attacks on the same umbel would prompt them to avoid that umbel or patch.

Avoidance learning has been documented in honeybees (Abramson 1986, Gould 1987, Smith et al. 1991). Furthermore, in a recent experiment, honeybees showed strong avoidance of a site where they had experienced a simulated predation attempt (Dukas 2001a). However, there is currently no published information on avoidance learning in bumblebees except for a report by Thomson (1989) indicating that bumblebees (*Bombus* spp) avoided flowers where they had experienced aggressive interactions with wasps (*Vespula* spp). In a follow up experiment, we individually marked 10 pairs of *B. ternarius* at a milkweed patch and hit one randomly chosen bee of each pair with a model spider 30 mm in diameter within a few hours after marking. We subsequently spotted 100% of the control bees but only 70% of the “attacked” bees. This suggests that bumblebees show weak avoidance of the sites where they have been attacked, an assertion requiring further empirical evaluation.

Expected and observed response to crab spiders

The average natural density of adult female crab spiders in our area is approximately 1 per 100 milkweed stems (Morse 1986a). Would such predator density affect stem or patch choice by bees? This question may be addressed at two levels. At the evolutionary level, one may ask whether bees should possess anti-predatory behavior at flowers. If predation on bees at flowers were rare, as some researchers have suggested (Pyke 1979, Miller and Gass 1985, Morse 1986a, Schmid-Hempel 1991), then no anti-predatory behavior would be necessary at all (but see Dukas 2001b). Our data, however, indicate that 80% of the bees that were attacked by spiders left the umbel following the attack. Moreover, previous experiments have documented high sensitivity of honeybees to perceived danger at flowers (Dukas 2001a) and avoidance of spider webs by stingless bees (*Trigona fluviventris*) (Craig 1994). Hence we can conclude that bees do possess anti-predatory behavior at and on the way to flowers.

At the behavioral and life history level, we may ask how a focal bee that has survived a spider attack should respond. We will assume that the focal bee regularly visits an area with 100 milkweed stems and one crab spider. This assumption agrees with numerous observations on marked honeybees and bumblebees, which indicate that workers usually restrict their visits to a moderate number of plants (Free 1966, Heinrich 1976, Thomson and Chittka 2001). Our data (Fig. 3) indicate that a bee's probability of being captured on her next visit to the same spider umbel may be as high as 0.01 (Morse 1986a). If the bee avoids the stem harboring the spider, which amounts to avoiding only 1% of the available milkweed stems, it would experience negligible energetic loss but potentially large benefit, measured as increased lifetime food collection by that bee due to longer life span (Clark and Dukas 1994, Dukas and Edelman-Keshet 1998, Dukas 2001b).

If theoretical considerations suggest that bumblebees and honeybees should avoid milkweed stems harboring spiders, why did not the bees show a much stronger avoidance of our experimental spider-enriched patches, which contained spiders on approximately one third of the stems? It is possible that a large transient bee population masked strong responses by a small number of constant bees. We do not know about the turnover rate of bees in our field site but limited data from other studies suggest that bee turnover rate may have been rather high. Heinrich (1976), also working in Maine (Franklin county), marked all *B. vagans* foragers on *Aster novae-angliae* and recorded a daily increase of approximately 10% in the proportion of unmarked conspecific bees over the successive 12 days. In another study, Williams and Thomson (1998) videotaped all visits to a single *Penstemon strictus* plant in a patch of 27 plants visited by individually marked bumblebees (*B. flavifrons*). They found that four individual bumblebees made over half of the visits, while 23 marked bees and additional unmarked bees made a few visits each. Furthermore, it is possible that bees show interspecific difference in site constancy or traplining (J. D. Thomson, unpubl.). In our study, perhaps some individuals that repeatedly visited the experimental patches learned to avoid the spider patches, while other bees visited these patches only occasionally and hence failed to avoid the spider patches.

In summary, our field experiment indicates that bumblebees and honeybees may visit with lower frequency flower patches that harbor predators. The realistic possibility that predation on pollinators influences interactions between plants and floral visitors requires further evaluation.

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References

- Abramson, C. I. 1986. Aversive conditioning in honey bees (*Apis mellifera*). – *J. Comp. Psychol.* 100: 108–116.
- Ambrose, J. T. 1990. Birds. – In: Morse, R. A. and Nowogrodzki, R. (eds), *Honey bee pests, predators, and diseases*. Cornell Univ. Press, pp. 243–160.
- Baldur, W. V. 1939. Food habits of *Phymata pennsylvanica americana* Melin (Hemip.). – *Can. Entomol.* 71: 66–75.
- Caron, D. M. 1990. Other insects. – In: Morse, R. A. and Nowogrodzki, R. (eds), *Honey bee pests, predators, and diseases*. Cornell Univ. Press, pp. 156–176.
- Cartar, R. V. 1991. Colony energy requirements affect response to predation risk in foraging bumble bees. – *Ethology* 87: 90–96.
- Chittka, L. 2001. Camouflage of predatory crab spiders on flowers and the colour perception of bees (Aranida: Thomisidae/Heymenoptera: Apidae). – *Entomol. Gener.* 25: 181–187.
- Clark, C. W. and Dukas, R. 1994. Balancing foraging and antipredator demands: an advantage of sociality. – *Am. Nat.* 144: 542–548.
- Craig, C. L. 1994. Limits to learning: effects of predator pattern and colour on perception and avoidance-learning by prey. – *Anim. Behav.* 47: 1087–1099.
- De Jong, D. 1990. Insects: hymenoptera (ants, wasps, and bees). – In: Morse, R. A. and Nowogrodzki, R. (eds), *Honey bee pests, predators, and diseases*. Cornell Univ. Press, pp. 135–155.
- Dukas, R. 2001a. Effects of perceived danger on flower choice by bees. – *Ecol. Lett.* 4: 327–333.
- Dukas, R. 2001b. Effects of predation risk on pollinators and plants. – In: Chittka, L. and Thomson, J. (eds), *Cognitive ecology of pollination*. Cambridge Univ. Press, pp. 214–236.
- Dukas, R. and Edelman-Keshet, L. 1998. The spatial distribution of colonial food provisioners. – *J. Theoret. Biol.* 190: 121–134.
- Evans, H. E. and Eberhard, J. W. 1970. *The wasps*. – Univ. of Michigan Press.
- Evans, E. E. and O'Neill, K. M. 1988. *The natural history and behavior of North American beewolves*. – Cornell Univ. Press.
- Free, J. B. 1966. The foraging behaviour of bees and its effect on the isolation and speciation of plants. – In: Hawkes, J. G. (ed.), *Reproductive biology and taxonomy of vascular plants*. Pergamon Press, pp. 76–92.
- Fry, C. H. 1983. Honeybee predation by bee-eaters, with economic considerations. – *Bee World* 64: 65–78.
- Gould, J. L. 1987. Honey bees store learned flower-landing behaviour according to time of day. – *Anim. Behav.* 35: 1579–1581.
- Greco, C. F. and Kevan, P. G. 1995. Patch choice in the anthophilous ambush predator *Phymata americana*: improvement by switching hunting sites as part of the initial choice. – *Can. J. Zool.* 73: 1912–1917.
- Heinrich, B. 1976. The foraging specialization of individual bumblebees. – *Ecol. Monogr.* 46: 105–128.
- Lima, S. L. 1991. Energy, predators and the behaviour of feeding hummingbirds. – *Evol. Ecol.* 5: 220–230.
- Lima, S. L. 1998. Nonlethal effects in the ecology of predator-prey interactions. – *BioScience* 48: 25–34.
- Lima, S. L. and Dill, L. M. 1990. Behavioral decisions made under the risk of predation: a review and prospectus. – *Can. J. Zool.* 68: 619–640.
- Louda, S. M. 1982. Inflorescence spiders: a cost/benefit analysis for the host plant, *Haplopappus venetus* (Asteraceae). – *Oecologia* 55: 185–191.

- Miller, R. S. and Gass, C. L. 1985. Survivorship in hummingbirds: is predation important? – *Auk* 102: 175–178.
- Morse, D. H. 1979. Prey capture by the crab spider *Misumena calycina* (Araneae: Thomisidae). – *Oecologia* (Berlin) 39: 309–319.
- Morse, D. H. 1981. Prey capture by the crab spider *Misumena vatia* (Clerck) (Thomisidae) on three common native flowers. – *Am. Midl. Nat.* 105: 358–367.
- Morse, D. H. 1986a. Predation risk to insect foraging at flowers. – *Oikos* 46: 223–228.
- Morse, D. H. 1986b. Inflorescence choice and time allocation by insects foraging on milkweed. – *Oikos* 46: 229–236.
- Peacor, S. D. and Werner, E. E. 2000. Predator effects on an assemblage of consumers through induced changes in consumer foraging behavior. – *Ecology* 81: 1998–2010.
- Peckarsky, B. L., Cowan, C. L., Penton, M. A. and Anderson, C. 1993. Sublethal consequences of stream-dwelling stoneflies on mayfly growth and fecundity. – *Ecology* 74: 1836–1846.
- Pyke, G. H. 1979. Optimal foraging in bumblebees: rule of movement between flowers within inflorescences. – *Anim. Behav.* 27: 1167–1181.
- Schmid-Hempel, P. 1991. The ergonomics of worker behavior in social hymenoptera. – *Adv. Study Behav.* 20: 87–134.
- Smith, B. H., Abramson, C. I. and Tobin, T. R. 1991. Conditional withholding of proboscis extension in honey bees (*Apis mellifera*) during discriminative punishment. – *J. Comp. Psychol.* 105: 345–356.
- Thery, M. and Casas, J. 2002. Visual systems: predator and prey views of spider camouflage. – *Nature* 415: 133.
- Thomson, J. D. 1989. Reversal of apparent feeding preferences in bumble bees by aggression from *Vespula* wasps. – *Can. J. Zool.* 67: 2588–2591.
- Thomson, J. D. and Chittka, L. 2001. Pollinator individuality: when does it matter? – In: Chittka, L. and Thomson, J. D. (eds), *Cognitive ecology of pollination*. Cambridge Univ. Press, pp. 191–213.
- Williams, N. M. and Thomson, J. D. 1998. Trapline foraging by bumble bees. III. Temporal patterns of visitation and foraging success at single plants. – *Behav. Ecol.* 9: 612–621.
- Willmer, P. G. and Stone, G. N. 1997. How aggressive antguards assist seed-set in *Acacia* flowers. – *Nature* 388: 165–167.