

Crab spiders show mixed effects on flower-visiting bees and no effect on plant fitness components¹

Reuven DUKAS², Animal Behaviour Group, Department of Psychology, McMaster University, 1280 Main Street West, Hamilton, Ontario L8S 4K1, Canada, e-mail: dukas@mcmaster.ca

Douglass H. MORSE, Department of Ecology and Evolutionary Biology, Box G-W, Brown University, Providence, Rhode Island 02912, USA.

Abstract: Predation on flower-visiting insects can potentially reduce pollination levels and hence plant fitness. We tested this prediction in a field experiment with 10 matched pairs of milkweed patches in which one patch in each pair contained crab spiders and the other patch was predator free. Significantly fewer honeybees were observed in the spider than no spider patches, but there was no spider effect on the two species of bumblebees. A possible explanation for this difference is that the honeybees suffered three times higher predation rates than the bumblebees. There were no spider effects on either the rate of pollinia removal from milkweed flowers or the number and mass of seeds produced. The results suggest that crab spiders may have only small effects on bees and plant fitness, at least where bees are abundant.

Keywords: bees, crab spiders, insect plant interactions, pollination, predation.

Résumé : La prédation exercée sur les insectes visitant les fleurs pourrait réduire les niveaux de pollinisation et, par conséquent, le succès reproducteur des plantes. Nous avons testé cette hypothèse à l'aide d'une expérience menée sur le terrain. Le dispositif expérimental comportait 10 paires de colonies d'asclépiades; chaque paire était constituée d'une colonie avec araignées-crabes et l'autre sans prédateur. Un nombre inférieur significatif d'abeilles a été observé au niveau des colonies contenant des araignées par rapport à celles qui en étaient exemptes, mais les araignées n'ont eu aucun impact sur les deux espèces de bourdons. On pourrait expliquer cette différence par le fait que les abeilles auraient subi des taux de prédation trois fois plus grands que les bourdons. Par ailleurs, les araignées n'ont pas eu d'influence sur le taux de prélèvement des pollinies des fleurs d'asclépiade ou sur le nombre et la masse des graines produites. La présence d'araignées-crabes n'aurait donc que peu de conséquences sur les abeilles et les bourdons ainsi que sur le succès reproducteur des plantes, du moins lorsque les abeilles et les bourdons sont abondants.

Mots-clés : abeilles et bourdons, araignées-crabes, interactions entre insectes et végétaux, pollinisation, prédation.

Nomenclature: Mitchell, 1960; Radford *et al.*, 1968; Platnick, 2005.

Introduction

Much of the research in pollination biology has focused on the ecology and evolution of flower visitors and the plants they visit for floral reward (reviewed in Real, 1983; Chittka & Thomson, 2001). Whereas the focus on flowers and potential pollinators is clearly appropriate, there has recently been increased interest in the effects of animals other than flower visitors on animal-flower interactions. The most obvious category of such animals is that of pollinators' predators. Flowers are predictable places for finding relatively high concentrations of prey. Indeed, a wide variety of animals are either obligate or facultative predators of flower visitors. Notable examples include bee-wolves (*Philanthus* spp.) and a few other taxa of sphecid wasps (Evans & O'Neill, 1988), various species of social wasps (Evans & Eberhard, 1970; De Jong, 1990), crab spiders (Thomisidae) (Morse, 1981; Morse, 1986b), predacious bugs (Hemiptera) (Balduf, 1939; Greco & Kevan, 1995), praying mantids (Mantidae) (Caron, 1990), bee eaters (Meropidae) (Fry, 1983), and Old- and New-World flycatchers (Muscicapidae and Tyrannidae) (Ambrose,

1990). In addition, parasitoids such as conopid flies (*Conopidae*) also rely on flowers for locating and laying eggs on hosts (Schmid-Hempel, 1998). Other animal categories that affect pollinator-flower interactions include foliar herbivores (Irwin *et al.*, 2003) and nectar thieves that damage flowers (Galen & Cuba, 2001).

To date, only a few studies have examined the effect of predation risk on flower visitors and plants (reviewed in Dukas, 2001). In a recent field experiment, Dukas and Morse (2003) documented that fewer worker bumblebees (*Bombus ternarius*) visited experimental milkweed (*Asclepias syriaca*) plots harbouring crab spiders (*Misumena vatia*) than matched plots with no crab spiders. Suttle (2003) also reported that fewer insects visited inflorescences of ox-eye daisy (*Leucanthemum vulgare*) harbouring crab spiders (*M. schlingeri*) than inflorescences with no spiders. Furthermore, an experiment comparing seed sets of 16 matched ox-eye daisy plants suggested 17% fewer seeds on spider-harbouring compared to spider-free inflorescences (Suttle, 2003). Finally, lizard predation (*Liolaemus bellii*) significantly reduced visitation rates and visit durations by satyrid butterflies (*Cosmosatyrus chilensis*) and syrphid flies (*Scaeva melanostoma*) to flowers of *Chuquiraga oppositifolia* (Asteraceae) in the Chilean Andes (Muñoz & Arroyo, 2004). Moreover, plants

¹Rec. 2004-11-02; acc. 2005-01-06.

Associate Editor: Josep Escarré.

²Author for correspondence.

exposed to lizards had lower seed set compared to lizard-excluded plants (Muñoz & Arroyo, 2004).

To further evaluate the effects of predators on pollinators and plants, we extended our previous work with milkweed (Dukas & Morse, 2003). We conducted a replicated, controlled field experiment to test two central predictions. The first prediction was identical to the prediction in our previous paper (Dukas & Morse, 2003), namely that experimental milkweed patches harbouring crab spiders would have fewer bee visitors than matched, spider-free, control patches. The second prediction was that the rate of pollinia removal and seed production per milkweed stem, measures that are related to male and female fitness respectively, would be lower in patches with spiders than without them. We used patches as the experimental units because our earlier work indicated significant spider effects at the level of patches but not individual umbels (Dukas & Morse, 2003).

Methods

STUDY AREA AND SPECIES

The experiment was conducted at an old field in South Bristol, Lincoln County, Maine in July 2003. The field contained several clones of common milkweed (*Asclepias syriaca*) in early bloom, collectively consisting of more than 10,000 flowering stems. Typically, each milkweed stem produces a few inflorescences (umbels), each containing between 30 and 75 flowers, more than half of which are at the nectar-producing stage when at peak umbel bloom (Morse, 1986a). Milkweeds are the preferred hunting ground of crab spiders (*Misumena vatia*), which are ambush predators that prey on various flower-visiting insects, including bumblebees (Morse, 1979; Morse, 1981; Morse, 1986b).

The dominant visitors to milkweed in our study area were two species of bumblebees, *Bombus ternarius* and *B. vagans*, and honeybees (*Apis mellifera*). All crab spiders used in the experiment were adult females collected within 10 km of the experimental site.

THE MATCHED-PATCHES AND STATISTICAL ANALYSES

In early July, we cleared milkweed stems to create 10 matched pairs of patches. Each patch contained 20 stems in bud stage and 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 randomly assigned one patch in each matched pair to be the spider patch. We then covered all 400 stems with bags made of fine-mesh nylon tricot to exclude insect visits. The experiment commenced after all stems started to bloom.

Our experimental protocol involved 10 matched patch-pairs. Hence, all the statistical analyses consisted of repeated measures ANOVAs, which treated the matched pairs as 10 independent experimental units.

BEE AND SPIDER CENSUS

On the morning of day 1, we removed all the bags and placed one crab spider on each of 7 stems in each of the 10 spider patches, a density within the normal range of abundance of this species (Dukas & Morse, 2003). We also examined the 10 matched no-spider patches to verify

that they were indeed free of crab spiders. Each day from day 1 through day 7, we conducted six bee counts in each of the 20 patches every 30 min between 1100 and 1400, the peak visitation times of the bees. In addition, we also scanned each spider patch twice a day to monitor spider presence and the identity of prey species the spiders were observed to consume.

MILKWEED FITNESS COMPONENTS

POLLINIA REMOVAL

On day 4, we randomly selected five stems in each of the 20 patches. On each of these stems, we chose an umbel with few or no opened flowers and marked with a permanent marker one sepal on each of the open flowers. On each of the succeeding five days, we used a unique colour scheme to mark all the newly opened flowers on that umbel. On either day 7 or 8, once all the flowers on the first umbel had opened, we switched to a new umbel on the same stem and repeated the procedure just described. On each afternoon from day 7 to day 11, we picked one 3-d-old flower from each of the 100 umbels and counted under a dissecting microscope the number of pollinia missing in each of the flowers. The majority of pollinia are removed from flowers within the first 3 d of blooming (Morse, 1987). Overall, we counted five flowers in each of the 20 patches on each of 5 d, for a total of 500 flowers.

FRUIT AND SEED CHARACTERISTICS

On day 12, we removed all crab spiders from the spider patches and put back the mesh bags on all stems in all patches. We removed the bags once all blooming ended in mid-August. At the end of August, we counted and removed all pods from all the plants. We then randomly chose 10 pods from each of the 20 patches and measured *i*) the total number and total mass of all the seeds per pod and *ii*) individual mass of five randomly chosen seeds from each pod. Aborted and broken seeds were avoided except in a few cases where no other seeds were available.

Seed production may be affected by both seed predators and crab spiders who prey on some seed predators (Louda, 1982; Romero & Vasconcellos-Neto, 2004). We observed, however, no seed predation in our samples. The major seed predators of common milkweed in our geographic area, milkweed bugs (*Lygaeus kalmii*: Lygaeidae) and milkweed beetles (*Tetraopes tetraophthalmus*: Cerambycidae) appeared infrequently at our study sites and, when encountered, were at low densities (D. H. Morse, pers. observ.).

Results

BEE CENSUS

We counted approximately twice as many worker honeybees in the spider-free as in the spider patches (repeated measures ANOVA, $F_{1,9} = 8.1$, $P < 0.05$, Figure 1). That pattern was consistent over all days ($P > 0.1$ for the spider \times day interaction). In eight of the matched pairs of patches, we recorded more honeybees in the spider-free patch than the spider patch but there was significant between-pair variation in the magnitude of difference ($P < 0.01$ for the spider \times patch-pair interaction). In contrast to the honeybees, workers of the two bumblebee species

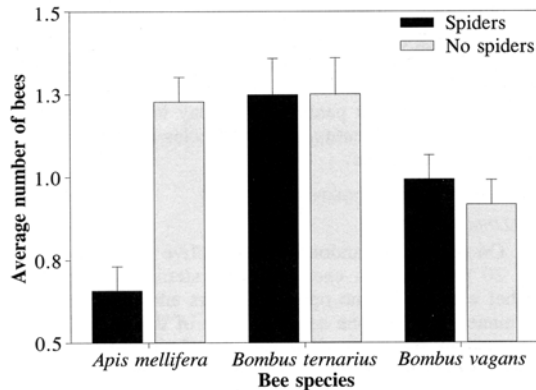


FIGURE 1. The average (+ SE) number of individual honeybees and two species of bumblebees in 10 spider and 10 no spider milkweed patches over 7 d.

were about equally distributed between the spider and no spider patches ($F_{1,9} = 0$, $P = 1$ for *B. ternarius*, $F_{1,9} = 0.3$, $P > 0.5$ for *B. vagans*, Figure 1). All three bee species showed a large increase in the number of individuals during the 7-d census period ($P < 0.01$ for each of the three species).

SPIDER CENSUS

We spotted an average of 4.4 ± 0.3 (mean \pm SE) spiders per spider-patch each day. The daily average of bee prey observed while being consumed by spiders in these patches was 7.1 ± 2.2 honeybees, 2.3 ± 0.5 *B. ternarius*, and 2.3 ± 0.4 *B. vagans*.

MILKWEED FITNESS COMPONENTS

POLLINIA REMOVAL

The average number of pollinia removed from flowers in the spider and no spider patches was virtually identical: 2.27 ± 0.12 and 2.30 ± 0.12 , respectively (repeated measures ANOVA, $F_{1,9} = 0.08$, $P > 0.5$). There was a large increase in the number of pollinia removed during the 5-d census period ($P < 0.01$), but all interactions were non-significant ($P > 0.2$).

FRUIT AND SEED CHARACTERISTICS

We compared four components of female fitness: the number of pods per plant, number of seeds per pod, total seed mass per pod, and average seed mass. All of the four measures indicated nearly identical female fitness components in the spider and no spider patches. The values in the spider and no spider patches, respectively, were 3.2 ± 0.4 and 3.18 ± 0.5 pods \cdot plant⁻¹ (repeated measures ANOVA, $F_{1,9} = 0.2$, $P > 0.8$), 179 ± 2.7 and 178 ± 2.7 seeds \cdot pod⁻¹ ($F_{1,9} = 0.1$, $P > 0.5$), 0.38 ± 0.01 and 0.36 ± 0.01 g total seed mass \cdot pod⁻¹ ($F_{1,9} = 0.29$, $P > 0.5$), and 2.16 ± 0.06 and 2.11 ± 0.06 mg average seed mass ($F_{1,9} = 0.08$, $P > 0.5$).

Discussion

EFFECTS OF CRAB SPIDERS ON BEES

Fewer honeybees visited the spider than no spider patches. Similar numbers of the two species of bumblebees, however, were observed in the spider and no spider

patches (Figure 1). These mixed results resembled the mixed results obtained in a similar experiment conducted in 2001. In the 2001 experiment, we documented fewer *B. ternarius* but not *B. vagans* in the spider than the no spider patches. In 2001, honeybees exhibited a highly suggestive though non-significant pattern of fewer workers in the spider than the no spider patches. Our statistical power for honeybees, however, was low in 2001 because the honeybees visited only 60% of the matched patches (Dukas & Morse, 2003). In sum, in two distinct experiments, we documented a similar pattern of fewer honeybees in spider than no spider patches, fewer individuals of *B. ternarius* in spider than no spider patches in 2001 but not in 2003, and no spider effect on *B. vagans* in either year.

It is easy to explain the crab spiders' negative effect on honeybees and lack of effect on *B. vagans*. In both 2001 and 2003, approximately three times more honeybees than individual *B. vagans* were killed by crab spiders. This difference reflected higher attack and predation rates on the small honeybees than on the large-bodied *B. vagans* (Dukas & Morse, 2003). We do not, however, have sufficient information to explain the difference between years in the effect of crab spiders on *B. ternarius*.

We did not attempt to differentiate between direct and indirect crab spider effects because either can potentially decrease plant fitness. We can, however, estimate the relative direct effect on honeybees based on data from a simultaneous study in the same field, in which we marked all individual honeybees visiting two pairs of matched milkweed patches, each consisting of one spider patch and one no spider patch. Only seven out of a total of 343 marked individuals (2%) were killed by the crab spiders over a 9-d period. This indicates that indirect predator effects were dominant. It is noteworthy that in honeybees, which communicate about floral resources (von Frisch, 1967; Dyer, 2002), the death of a few scouts may be magnified into a strong effect on recruitment rate to flowers.

EFFECTS OF CRAB SPIDERS ON MILKWEED FITNESS COMPONENTS

Crab spider presence did not reduce either male or female fitness components in milkweed, as both the rates of pollinia removal from flowers and several measures of seed production were nearly identical in the spider and no spider patches. One might argue that crab spiders may have negative impacts on milkweeds at either smaller or larger spatial scales than that of a patch. We focused on patches, however, because our earlier work indicated significant spider effects at the level of patches but not individual umbels (Dukas & Morse, 2003). Unfortunately, experimental logistics precluded using fields as the experimental units because of insufficient sample sizes.

Our experiment suggests that the effect of crab spiders may be negligible when pollinator abundance and visitation rates are relatively high. The most likely explanation for the insignificant effect of crab spiders is their low rate of predation. A crab spider that has captured a bee spends several hours on feeding and digestion (Morse, 1979). Hence, digestive constraints may limit per capita hunting rate by mature female crab spiders to less than one bumblebee per day (Fritz & Morse, 1985) even when prey is readily available.

- Johnson, J. B. & K. S. Omland, 2004. Model selection in ecology and evolution. *Trends in Ecology and Evolution*, 19: 101-106.
- Jönsson, K. I., 1997. Capital and income breeding as alternative tactics of resource use in reproduction. *Oikos*, 78: 57-66.
- Kirk, J. J., 1979. *Thamnophis ordinoides*. Catalog of American Amphibians and Reptiles 249.1-249.4. Society for the Study of Amphibians and Reptiles, Salt Lake City, Utah.
- Law, R., 1983. A model for the dynamics of a plant population containing individuals classified by age and size. *Ecology*, 64: 224-230.
- Lomnicki, A., 1988. *Population Ecology of Individuals*. Princeton University Press, Princeton, New Jersey.
- Lourdais, O., X. Bonnet, R. Shine, D. Denardo, G. Naulleau & M. Guillon, 2002. Capital-breeding and reproductive effort in a variable environment: A longitudinal study of a viviparous snake. *Journal of Animal Ecology*, 71: 470-479.
- Lourdais, O., X. Bonnet, R. Shine & E. M. Taylor, 2003. When does a reproducing female viper (*Vipera aspis*) 'decide' on her litter size? *Journal of Zoology*, 259: 123-129.
- Macartney, J. M. & P. T. Gregory, 1988. Reproductive biology of female rattlesnakes (*Crotalus viridis*) in British Columbia. *Copeia*, 1988: 47-57.
- Madsen, T. & R. Shine, 1992. Determinants of reproductive success in female adders, *Vipera berus*. *Oecologia*, 92: 40-47.
- McNamara, J. M. & A. I. Houston, 1996. State-dependent life histories. *Nature*, 380: 215-221.
- Nie, N. H., C. H. Hull, J. G. Jenkins, K. Steinbrenner & D. H. Bent, 1975. *SPSS - Statistical Package for the Social Sciences*, 2nd Edition. McGraw-Hill, New York, New York.
- Olsson, M. & R. Shine, 1996. Does reproductive success increase with age or with size in species with indeterminate growth? A case study using sand lizards (*Lacerta agilis*). *Oecologia*, 105: 175-178.
- Partridge, L. & P. H. Harvey, 1988. The ecological context of life history evolution. *Science*, 241: 1449-1455.
- Policansky, D., 1983. Size, age and demography of metamorphosis and sexual maturation in fishes. *American Zoologist*, 23: 57-63.
- Quinn, G. P. & M. J. Keough, 2002. *Experimental Design and Data Analysis for Biologists*. Cambridge University Press, Cambridge.
- Reznick, D., L. Nunney & A. Tessier, 2000. Big houses, big cars, superfleas and the costs of reproduction. *Trends in Ecology and Evolution*, 15: 421-425.
- Roff, D. A., 1992. *The Evolution of Life Histories - Theory and Practice*. Chapman & Hall, New York, New York.
- Sauer, J. R. & N. A. Slade, 1985. Mass-based demography of a hispid cotton rat (*Sigmodon hispidus*) population. *Journal of Mammalogy*, 66: 316-328.
- Schluter, D., T. D. Price & L. Rowe, 1991. Conflicting selection pressures and life-history trade-offs. *Proceedings of the Royal Society of London, B*, 24: 11-17.
- Schwarzkopf, L., 1996. Decreased food intake in reproducing lizards: A fecundity dependent cost of reproduction? *Australian Journal of Ecology*, 21: 355-362.
- Seigel, R. A. & N. B. Ford, 1987. *Reproductive ecology*. Pages 210-252 in R. A. Seigel, J. T. Collins & S. S. Novak (eds.). *Snakes - Ecology and Evolutionary Biology*. MacMillan, New York, New York.
- Shine, R., 1980. 'Costs' of reproduction in reptiles. *Oecologia*, 46: 92-100.
- Shine, R., 1995. A new hypothesis for the evolution of viviparity in reptiles. *The American Naturalist*, 145: 809-823.
- Shine, R. & S. J. Downes, 1999. Can pregnant lizards adjust their offspring phenotypes to environmental conditions? *Oecologia*, 119: 1-8.
- Stearns, S. C., 1980. A new view of life-history evolution. *Oikos*, 35: 266-281.
- Stearns, S. C., 1989. Trade-offs in life-history evolution. *Functional Ecology*, 3: 259-268.
- Stearns, S. C., 1992. *The Evolution of Life Histories*. Oxford University Press, Oxford.
- Stewart, J. R., D. G. Blackburn, D. C. Baxter & L. H. Hoffman, 1990. Nutritional provision to embryos in a predominantly lecithotrophic placental reptile, *Thamnophis ordinoides* (Squamata: Serpentes). *Physiological Zoology*, 63: 722-734.
- Tuomi, J., T. Hakala & E. Haukioja, 1983. Alternative concepts of reproductive effort, costs of reproduction, and selection in life-history evolution. *American Zoologist*, 23: 25-34.
- Wang, M.-H. & F. S. vom Saal, 2000. Maternal age and traits in offspring. *Nature*, 407: 469-470.
- Waye, H. L., 1999. Size and age structure of a population of western terrestrial garter snakes (*Thamnophis elegans*). *Copeia*, 1999: 819-823.
- Waye, H. L. & P. T. Gregory, 1998. Determining the age of garter snakes (*Thamnophis* spp.) by means of skeletochronology. *Canadian Journal of Zoology*, 76: 288-294.
- Werner, P. A. & H. Caswell, 1977. Population growth rates and age versus stage-distribution models for teasel (*Dipsacus sylvestris* Huds.). *Ecology*, 58: 1103-1111.