BUMBLE BEE PREDATORS REDUCE POLLINATOR DENSITY AND PLANT FITNESS

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Abstract. Research in pollination biology has focused on the interactions between animals and the flowers they visit for food reward. However, other selective agents, including predators, seed feeders, and herbivores, may affect pollination systems. Because flowers are predictable food sources for a variety of species, flowers are also reliable sites at which predators can locate flower-visiting animals. Prominent among pollinators' predators are beewolves (*Philanthus* spp.), common sphecid wasps (Sphecidae) that prey almost exclusively on bees. My fieldwork over three years indicates first, that an area of ~50 km^2 surrounding a single bumble bee wolf (*Philanthus bicinctus*) aggregation had a low bumble bee (*Bombus* spp.) density caused by intense predation by the wasps, and second, that fruit-set of the bumble bee-pollinated western monkshood (*Aconitum columbianum*) was significantly lower at locations and times of bumble bee wolf activity than at control locations and times with no such predatory activity. These results indicate that predation can sometimes alter plant–pollinator interactions.

Key words: Aconitum columbianum, *western monkshood; beewolf; bumble bees; flowers; insect–plant interactions;* Philanthus bicinctus; *pollination; predation; wasps.*

INTRODUCTION

The interactions between animals and flowers have been subjected to many classic studies in ecology and evolution (Real 1983, Chittka and Thomson 2001). Recently there has been increased interest in broadening the traditionally narrow focus of pollination biology to include additional trophic levels and whole-community interactions. Examples include studies examining the effects of pollinators' predators, seed predators, and herbivores on floral traits (Dukas 2001*b*, Galen and Cuba 2001, Brown 2002, Adler and Bronstein 2004, Irwin et al. 2004). Whereas it is convenient to focus on only the two obvious players, flower visitors and flowers, it is clear that other agents may sometimes shape pollination systems.

It has commonly been assumed that bees suffer little predation because of their ability to sting. Moreover, pollination studies are typically carried out at locations and times where pollinators are abundant and predators are infrequent (e.g., Pyke 1979), potentially creating a biased perception that predation on pollinators is a negligible force in pollination biology (Dukas 2001*b*). In contrast, Niko Tinbergen (1958) estimated that the honey bee wolves (*Philanthus triangulum*) at the aggregation he and his colleagues studied extensively in coastal Holland captured several thousand honey bees (*Apis mellifera*) per day. Surprisingly, however, the ecological effects of beewolves and other predators on

bees and bee-pollinated plants has not been closely examined (Dukas 2001*b*, Dukas and Morse 2003, Suttle 2003, Muñoz and Arroyo 2004). To quantify the effects of bee predation, I tested whether predatory activity by bumble bee wolves (*P. bicinctus*) was negatively correlated with (1) bumble bee density at flower patches of three common plant species and, (2) fruit production of the bumble bee–pollinated western monkshood (*Aconitum columbianum*).

METHODS

Study area and species

The research was conducted within a distance of 6 km from a single bumble bee wolf aggregation along the Snake River in northwestern Wyoming, USA, in the summers of 2002–2004. There is little elevation change (~25 m) along this section of the river, and the area supports similar plant communities with similar phenology. The forest adjacent to the river is dominated by mature Engelmann spruce (*Picea engelmannii*) and lodgepole pine (*Pinus contorta*). Western rayless cone-flower (*Rudbeckia occidentalis*) is the most common plant in bloom at numerous natural forest clearings, and western monkshood (*Aconitum columbianum*) is abundant in moist areas. Spots adjacent to the river support large patches of late-blooming goldenrods (*Solidago* spp.).

The bumble bee wolf aggregation, previously studied by Armitage (1965) and Evans and O'Neill (1988), contained a few hundred active nests spread over an open sagebrush (*Artemisia tridentata*) field a few hundred meters in diameter. Each season, the bumble bee

Fig. 1. Bumble bee wolf, *Philanthus bicinctus*, stinging a bumble bee (*Bombus* spp.) on a coneflower. After grasping the bee's dorsal side, the wasp turns the bee onto its ventral side, curves its own abdomen, and stings the bee in the thorax. Then the wasp tightly holds the paralyzed bee with the bee's ventral side up against its own thorax and flies to her burrow.

wolves were active from late July to late August, capturing small and medium-sized worker and male bumble bees at flowers (Fig. 1). With a single exception, I observed beewolves only within 3.7 km of the center of the wasp aggregation. Hence I defined near- and far-flower patches as patches <4 km to and >5 km from the wasp aggregation, respectively.

Bumble bee census on goldenrod and coneflower

I compared bumble bee activity near and far from the beewolf aggregation on goldenrod (*Solidago* spp.) in August 2002 and on western rayless coneflower (*R. occidentalis*) in August 2003. For each plant species, I carried out 12 days of observations, one each in six pairs of haphazardly chosen patches containing similar numbers of plants in bloom. Each pair of patches included one patch within 4 km of the beewolf aggregation and one patch >5 km from the aggregation. All plant patches were within the Snake River valley and well matched in flower phenology. To minimize temporal effects, observations were always carried out in blocks of two days in which one day was devoted to a near patch and the other day to a far patch of the same species.

Each observation day consisted of 18 observation periods between the hours of 10:00 and 15:00 in each goldenrod patch and 12 observation periods between the hours of 12:00 and 14:00 in each coneflower patch. Each observation period lasted ~7 min and consisted of averaging bumble bee counts from three successive scans, each involving a systematic counting of all individual bumble bees observed in the patch. I did not identify individual bumble bees to species in the field because of the enormous within-species color variation. Later identification of captured bumble bees revealed that the dominant species at flowers and common beewolf prey was *Bombus rufocinctus*.

Bumble bee activity and fruit-set in monkshood

Western monkshood (*A. columbianum*) is a self-incompatible (Bosch and Waser 1999), classic bumble bee–pollinated plant (Laverty 1980). I observed only bumble bees visiting monkshood flowers at my study site. In 2003, I individually marked 100 monkshood plants near and 100 monkshood plants far from the beewolf aggregation and counted all flowers and flower buds on these plants. There were 12.9 ± 0.8 (mean $\pm$ SE) and 11.7 ± 0.95 flowers and buds per plant near and far from the wasp aggregation, respectively ($F_{1, 198} = 0.9$, $P > 0.3$). Three weeks later, I counted the number of mature fruits on the marked plants. In addition, I haphazardly chose 100 near and 100 far monkshood plants at early bloom and counted the number of mature fruits on each plant at the fruiting stage. Statistical analyses were conducted on arcsine-transformed and log-transformed data for the first and second data sets, respectively.

In 2004, I conducted two sets of comparisons. The first set was carried out in July, before the start of bumble bee wolf activity, which occurred in late July. The second set was conducted during peak bumble bee wolf activity in August. Each set of comparisons involved (1) a census of bumble bees in six pairs of monkshood patches near and far from the wasp aggregation, following the methods described above for coneflower, and (2) monitoring of monkshood fruit production. In each set, I haphazardly chose 100 near and 100 far monkshood plants and counted all open flowers on these plants. The near and far monkshoods had 8.34 ± 0.28 and 8.28 ± 0.31 open flowers, respectively ($F_{1, 198} = 0.02$, $P > 0.8$). I marked two flowers at a female stage on each of the 100 near and 100 far monkshood plants and recorded the proportion of flowers that produced fruits two weeks later. The fruit data were arcsine transformed for statistical analyses. All monkshood patches were within the Snake River valley
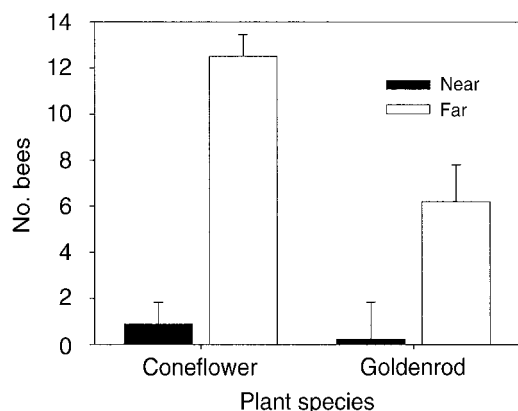
FIG. 2. The number of bumble bees observed (mean + SE) at six pairs of patches of coneflower (*Rudbeckia occidentalis*) and goldenrod (*Solidago* spp.) near and far from the bumble bee wolf aggregation.

and well matched in flower phenology, as indicated by the similar number of flowers per plant close and far from the aggregation. To minimize temporal effects, observations were always carried out in blocks of two days, in which one day was devoted to a near patch and the other day to a far patch.

Activity and hunting success of bumble bee wolves

I followed focal wasps engaged in hunting behavior on coneflower. The wasps were not marked for individual identification because of the large number of individuals in the aggregation and the difficulty of reading individual tags on swiftly moving wasps. Nevertheless, each year, there were up to eight individuals in the patch simultaneously, indicating that I recorded data on a minimum of 24 distinct individuals over three seasons. For each focal wasp observed, I recorded all encounters with bumble bees and classified each as either a success or a failure. To supplement the focal observations, I also recorded the rate of prey delivery to the wasp aggregation during a 1-h period in 6 days. This recording involved two observers continuously watching two distinct sections of the aggregation and counting all wasps descending to their nest holes with prey within a circular area with a radius of $\sim$20 m. We could readily identify wasps carrying bumble bees because of their characteristic slow, almost vertical descents toward their burrows. When feasible, I also approached the wasps and identified their prey.

RESULTS

I recorded 14 times more bumble bees at coneflower patches far from than near the beewolf aggregation (repeated-measures ANOVA, $F_{1,10} = 74$, $P < 0.001$; Fig. 2), and 26 times more bumble bees at far than at near goldenrod patches (repeated-measures ANOVA, $F_{1,10} = 7$, $P < 0.05$; Fig. 2). In monkshood, I recorded twice as many bumble bees far from than near the

bumble bee wolf aggregation during peak wasp activity in August (repeated-measures ANOVA, $F_{1,10} = 7$, $P < 0.05$; Fig. 3a). In contrast, I counted similar numbers of bumble bees at monkshood patches far from and near the beewolf aggregation site before the onset of beewolf activity in mid-July (repeated-measures ANOVA, $F_{1,10} = 0.02$, $P > 0.9$; Fig. 3a).

Predatory activity of bumble bee wolves was negatively associated with fruit-set of the predominately bumble bee–pollinated monkshood. In 2003, the percentage of monkshood flowers that produced fruits was twice as high far from rather than near the beewolf aggregation ($F_{1,191} = 20.8$, $P < 0.001$; Fig. 4, left bars). The other 2003 comparison also revealed significantly higher fruit-set far from than near the wasp aggregation ($F_{1,198} = 12.3$, $P < 0.001$; Fig. 4, right bars). In 2004, I recorded significantly higher fruit-set in monkshoods far from than near the bumble bee wolf aggregation during peak wasp activity in August (ANOVA, $F_{1,196} = 15$, $P < 0.001$; Fig. 3b). In contrast, similar proportions of monkshood flowers set fruit far from and near the beewolf aggregation before the onset of beewolf activity in July (ANOVA, $F_{1,195} = 0.9$, $P > 0.3$; Fig. 3b).

Thirty-two percent of the 257 wasp attacks I observed were successful. I recorded bumble bee responses to failed wasp attacks in 61 encounters. In 59% of these encounters, the bumble bees merely flew to
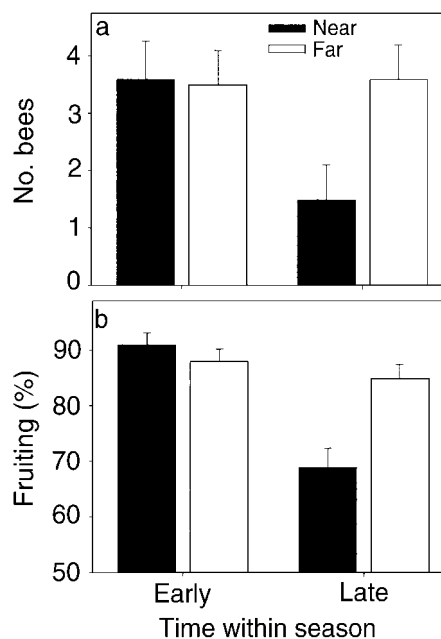

FIG. 3. Bumble bee visitation and fruit production in monkshood, 2004: (a) the number (mean + SE) of bumble bees observed on monkshood, and (b) the percentage (mean + SE) of marked monkshood flowers that produced fruits near and far from the bumble bee wolf aggregation early in the season (before bumble bee wolf activity) and late in the season (at peak bumble bee wolf activity).
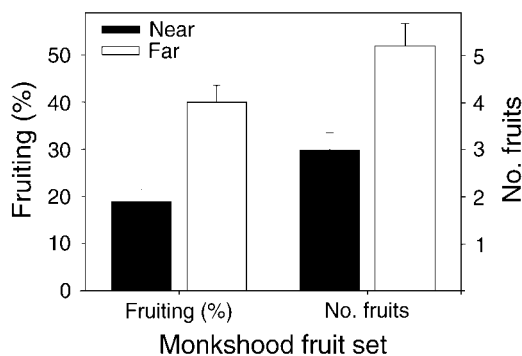
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FIG. 4. Fruit-set in monkshood, 2003: the percentage (mean + SE) of marked monkshood flowers that produced fruits (left-hand histograms) and the total number (mean + SE) of fruits on haphazardly chosen monkshood plants (right-hand histograms) near and far from the bumble bee wolf aggregation.

nearby flowers and resumed feeding. The other encounters resulted in the bees' departure from the patch. The average (±SE) hourly prey delivery rate to the center of the bumble bee wolf aggregation was 199 ± 28 prey in 2003 and 850 ± 97 prey in 2004. Of the 87 victims I inspected closely, all but two were bumble bees.

DISCUSSION

Negative effects of beewolves on bees and plants

All lines of evidence indicate that the bumble bee wolf activity was associated with low bumble bee abundance and reduced fruit-set in the bumble bee–pollinated monkshood within an area of ~50 km^2 surrounding the single wasp aggregation. First, delivery rates to the wasp aggregation were as high as 1015 bumble bee prey/h. Second, I directly observed >250 wasp attacks at flowers near the aggregation and witnessed rapid declines in bumble bee densities directly linked to the commencement of beewolf predatory activity. Third, I recorded no differences in bumble bee abundance near and far from the aggregation before the start of wasp activity, but found large differences a few weeks later. Finally, there was no difference in flower phenology between the near and far areas. This is indicated by the nearly identical numbers of flowers on near and far monkshood plants (see Methods) and the fact that all patches of the three plant species observed were closely matched in phenology.

My observations at the bumble bee wolf aggregation indicate that the wasps captured from several hundred to a few thousand bumble bees per day. These high numbers are similar to Tinbergen's (1958) estimate for the hunting rate at an aggregation of the old-world honeybee wolf (Philanthus triangulum) and reports on honey bee wolves devastating the apiculture industry in several locations throughout Europe and Africa (Evans and O'Neill 1988). For example, Simonthomas and Simonthomas (1980) noted that a typical aggre-

gation of 3000 honey bee wolves in Europe could capture up to 30 000 honey bees per day.

Whereas honey bee and bumble bee wolves are the best-studied species of Philanthus, the genus consists of ~136 species, most of which prey on bees. Philanthus has a worldwide distribution, with the exception of tropical America and Australia. In tropical America, Philanthus is replaced by the closely related, derived genus, Trachypus, which also preys on bees. In Australia, a few species of the genus Bembix prey on bees (Evans and O'Neill 1988). Beewolves are among the most commonly encountered wasps in the field, and an individual can readily capture several bees per day (Evans and O'Neill 1988). Hence it is likely that bee densities and plant fitness are depressed in other localities where there are nest aggregations of either beewolves or the related genera that prey on bees.

The prevalence of beewolf aggregations of different sizes is unknown. Furthermore, the same aggregation studied over successive years may exhibit fluctuations in numbers. For example, an aggregation of P. sanbornii, which preys on solitary bees, contained between 50 and 200 nests per season over a 10-yr period (Stubblefield et al. 1993). Similarly, one of the only two other bumble bee wolf aggregations studied consisted of between 182 to 335 nests over three seasons (Gwynne 1981), whereas the other aggregation contained 20 nests of bumble bee wolf and 70 nests of three other beewolf species (O'Neill and Evans 1982). As the examples above illustrate, however, a variety of beewolf species create aggregations of between a few dozen to a few thousand nests (Evans and O'Neill 1988). In general, many ground-nesting bees and wasps nest in large aggregations, which most likely result from strong philopatry in localities with favorable soil and food conditions (Batra 1984, Michener 2000).

It is likely that the negative effects of beewolves on bees and plants are not limited to large wasp aggregations such as the one I studied. A beewolf aggregation of any size would impact its surroundings, with the negative effects extending farther with larger aggregations. This is because the wasps in an aggregation can maximize prey delivery rate by hunting as close as possible to the aggregation (Dukas and Edelstein-Keshet 1998). Thus even a small aggregation of a few dozen wasps, which can readily remove a few hundred bees per day from its immediate surroundings, can negatively impact local pollinators and plants. As predicted by theory (Dukas and Edelstein-Keshet 1998), the bumble bee wolves in the aggregation I studied started by hunting within a few hundred meters of their nests. As the season progressed, prey depletion caused the wasps to fly farther. For example, when the bumble bee wolf season started, I could most reliably locate hunting wasps at a coneflower patch 185 m from the aggregation. Toward the end of the season, I recorded most hunting wasps at a coneflower patch 3.7 km from the aggregation. In short, whereas the magnitude of neg-

ative effects by beewolves and related wasp predators may vary widely in time and space, there are probably numerous locations with beewolf aggregations that suffer some level of reduced pollinator density and possibly, low fruit-set in some plants.

Negative effects of other predators on bees and plants

There are currently very few reports suggesting negative effects of predators on local pollinator densities and plant fruit-set. This probably reflects the fact that little research effort has been devoted to the topic until recently (Dukas 2001b). Experiments with crab spiders (*Misumena vatia*) revealed that significantly fewer bumble bees of a small species (*Bombus ternarius*) visited experimental milkweed (*Asclepias syriaca*) plots harboring crab spiders than matched plots with no crab spiders, although two large bumble bee species (*B. vagans* and *B. terricola*) showed no response to the spiders (Dukas and Morse 2003). Suttle (2003) also reported that fewer insects visited inflorescences of ox-eye daisy (*Leucanthemum vulgare*) harboring crab spiders (*M. schlingeri*) than inflorescences with no spiders, and his observations also suggested lower seed set in ox-eye daisy inflorescences harboring crab spiders compared to spider-free inflorescences. 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* in the Chilean Andes Mountains. Furthermore, plants exposed to lizards had lower seed set compared to lizard-excluded plants (Muñoz and Arroyo 2004).

In addition to the quantitative studies mentioned above, various reports suggest that a variety of predators negatively impact flower-visiting insects. First, many of the old-world bee eaters (*Merops* spp.) feed predominantly on hymenopterans such as bumble bees and honey bees (Fry 1983). Second, social wasps, most notably hornets (*Vespa* spp.) are notorious bee predators that cause damage to honey bee operations (De Jong 1990).

The effect of predation on bumble bee behavior and population dynamics

The reported high predation rates by bumble bee wolves raise two obvious questions. First, did bumble bees show behavioral avoidance of bumble bee wolves and, if not, why? Whereas direct effects of the predators were clearly dominant, I have no evidence for indirect effects caused by bumble bees permanently fleeing the high-predation area. First, ~60% of the bees experiencing failed wasp attacks resumed foraging within the same patch. A few times I watched a bee continuing to forage after a failed wasp attack and instantly being attacked again by the same wasp. Second, in many cases, bumble bees struggling with beewolves released large amounts of alarm pheromone, which I could readily smell. This, however, did not result in fleeing of the other bumble bees from the patch. Bumble bees typically encounter a variety of sphecid wasps feeding on nectar at flowers. Perhaps bumble bees do not distinguish between such harmless encounters with nectar-feeding wasps and predation attempts by bumble bee wolves.

A theoretical model specifically addressing predator avoidance by social bees concluded that workers should exhibit antipredatory behavior in order to maximize their lifetime fitness contribution to their colony (Clark and Dukas 1994). Indeed, controlled experiments with honey bees indicated strong avoidance of flowers associated with danger (Dukas 2001a), and field experiments evaluating bumble bee response to cues indicating predation risk are currently underway. It appears that, although social bees are able to respond to clear cues indicating danger as predicted by theory, the bees cannot readily associate predatory activity with danger under complex field settings.

The second inevitable question is, how are local bumble bee densities maintained over years in the face of high predation rates by the bumble bee wolves? Two factors probably contribute to the yearly renewal of bumble bees near the beewolf aggregation. First, the wasps begin activity relatively late in the bumble bee colony cycle, which allows some level of queen production. I have observed numerous male bumble bees during peak activity of the wasps at flowers near the aggregation and as prey delivered to the wasps' nests, which suggests relatively high levels of queen production near the aggregation. Second, queen bumble bees flying from locations far from the wasp aggregation may recolonize the area near the aggregation every spring.

Finally, the broad question raised by this study is the generality of my finding. In other words, what proportion of plant communities are affected by predation on pollinators, and how strong are the effects? Whereas it is premature to answer this question given the limited data available, it is relevant to note that tradition, the convenience of focusing on only two trophic levels, and practical difficulties of observing predation events may have caused pollination biologists to underestimate the importance of predation on pollinators.

In sum, intense predatory activity by bumble bee wolves resulted in low numbers of bumble bees and low fruit-set in the bumble bee–pollinated monkshood at the vicinity of the wasp aggregation. The ubiquity of beewolves and other pollinators' predators suggests that the threat of predation is sometimes an important selective force affecting pollination systems.

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Literature Cited

Adler, L. S., and J. L. Bronstein. 2004. Attracting antagonists: does floral nectar increase leaf herbivory? Ecology **85**: 1519–1526.

Armitage, K. B. 1965. Notes on the biology of *Philanthus bicinctus* (Hymenoptera: Sphecidae). Journal of the Kansas Entomological Society **38**:89–100.

Batra, S. W. T. 1984. Solitary bees. Scientific American **250**(2):86–93.

Bosch, M., and N. M. Waser. 1999. Effects of local density on pollination and reproduction in *Delphinium nuttallianum* and *Aconitum columbianum* (Ranunculaceae). American Journal of Botany **86**:871–879.

Brown, K. 2002. A compromise on floral traits. Science **298**: 45–46.

Chittka, L., and J. Thomson. 2001. Cognitive ecology of pollination. Cambridge University Press, Cambridge, UK.

Clark, C. W., and R. Dukas. 1994. Balancing foraging and antipredator demands: an advantage of sociality. American Naturalist **144**:542–548.

De Jong, D. 1990. Insects: Hymenoptera (ants, wasps, and bees). Pages 135–155 *in* R. A. Morse and R. Nowogrodzki, editors. Honey bee pests, predators, and diseases. Cornell University Press, Ithaca, New York, USA.

Dukas, R. 2001*a*. Effects of perceived danger on flower choice by bees. Ecology Letters **4**:327–333.

Dukas, R. 2001*b*. Effects of predation risk on pollinators and plants. Pages 214–236 *in* L. Chittka and J. Thomson, editors. Cognitive ecology of pollination. Cambridge University Press, Cambridge, UK.

Dukas, R., and L. Edelstein-Keshet. 1998. The spatial distribution of colonial food provisioners. Journal of Theoretical Biology **190**:121–134.

Dukas, R., and D. H. Morse. 2003. Crab spiders affect patch visitation by bees. Oikos **101**:157–163.

Evans, E. E., and K. M. O'Neill. 1988. The natural history and behavior of North American beewolves. Cornell University Press, Ithaca, New York, USA.

Fry, C. H. 1983. Honeybee predation by bee-eaters, with economic considerations. Bee World **64**:65–78.

Galen, C., and J. Cuba. 2001. Down the tube: pollinators, predators, and the evolution of flower shape in the alpine skypilot, *Polemonium viscosum*. Evolution **55**:1963–1971.

Gwynne, D. T. 1981. Nesting biology of the bumblebee wolf *Philanthus bicinctus* Mickel (Hymenoptera: Sphecidae). American Midland Naturalist **105**:130–138.

Irwin, R. E., L. S. Adler, and A. K. Brody. 2004. The dual role of floral traits: pollinator attraction and plant defense. Ecology **85**:1503–1511.

Laverty, T. M. 1980. The flower visiting behaviour of bumble bees: floral complexity and learning. Canadian Journal of Zoology **58**:1324–1335.

Michener, C. D. 2000. The bees of the world. Johns Hopkins University Press, Baltimore, Maryland, USA.

Muñoz, A. A., and M. T. K. Arroyo. 2004. Negative impacts of a vertebrate predator on insect pollinator visitation and seed output in *Chuquiraga oppositifolia*, a high Andean shrub. Oecologia **138**:66–73.

O'Neill, K. M., and B. E. Evans. 1982. Patterns of prey use in four sympatric species of *Philanthus* (Hymenoptera: Sphecidae) with a review of prey selection in the genus. Journal of Natural History **16**:791–801.

Pyke, G. H. 1979. Optimal foraging in bumblebees: rule of movement between flowers within inflorescences. Animal Behaviour **27**:1167–1181.

Real, L. 1983. Pollination biology. Academic Press, Orlando, Florida, USA.

Simonthomas, R. T., and A. M. J. Simonthomas. 1980. *Philanthus triangulum* and its recent eruption as a predator of honeybees in an Egyptian oasis. Bee World **61**:97–107.

Stubblefield, J. W., J. Seger, J. W. Wenzel, and M. M. Heisler. 1993. Temporal, spatial, sex-ratio and body-size heterogeneity of prey species taken by the beewolf *Philanthus sanbornii* (Hymenoptera: Sphecidae). Philosophical Transactions of the Royal Society of London B **339**:397–423.

Suttle, K. B. 2003. Pollinators as mediators of top-down effects on plants. Ecology Letters **6**:688–694.

Tinbergen, N. 1958. Curious naturalists. Basic Books, New York, New York, USA.

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