Pollinators as mediators of top-down effects on plants

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Abstract

This paper explores the idea that predators may disrupt plant–pollinator relationships and consequently inhibit reproduction in flowering plants. Amidst growing evidence that predators influence plant–pollinator interactions, I suggest that such pollinator-mediated indirect effects may be a common feature of terrestrial communities, with implications for research into top-down effects and pollination ecology. Experimental evidence of such an effect from a riparian system in northern California is provided, where crab spiders decreased seed production in inflorescences of the invasive plant *Leucanthemum vulgare* by reducing the frequency and duration of floral visits by pollinating insects.

Keywords

Crab spider, indirect effects, interaction web, *Leucanthemum vulgare*, *Misumenops schlingeri*, ox-eye daisy, pollen limitation, pollination, predation, risk effects.

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INTRODUCTION

Cascading impacts can be transmitted from a predator through its prey to primary producers. These top-down indirect effects can have important consequences for the structure and productivity of ecological communities, and ecologists have long sought to clarify their prevalence in nature. Top-down effects with community-wide bearing have been documented in intertidal (e.g. Paine 1966; Menge 1976), marine (e.g. Estes *et al*. 1978), lake (e.g. Carpenter *et al*. 1987) and river (e.g. Power 1990) systems. In terrestrial ecosystems, predation on herbivores has been shown to affect plant damage (e.g. Spiller & Schoener 1996), biomass (e.g. Schmitz & Suttle 2001), reproduction (e.g. Schemske 1980; Barton 1986) and diversity (Schmitz 2003), although the generality and community-scale importance of such interactions have been questioned (Strong 1992; Polis & Strong 1996; Polis 1999; *et al*. 2000; Shurin *et al*. 2002). In assessing the prevalence and importance of top-down effects in terrestrial communities, however, predation on a widespread, diverse, and invaluable guild of prey organisms has rarely been considered. The potential for top-down effects to transmit through pollinators warrants greater attention.

While top-down effects were originally proposed to explain patterns of terrestrial plant production (Leopold 1949; Hairston *et al*. 1960; Fretwell 1977), the concept was concretized with experimental demonstrations of trophic cascades in aquatic and marine systems (e.g. Estes *et al*. 1978; Carpenter *et al*. 1987; Power 1990). Following

suggestions that trophic cascades were restricted to these 'wet' environments (Strong 1992; Polis & Strong 1996), interest focused on whether analogous effects occur on land. This question has been the centre of work on top-down effects ever since (Polis 1999, Schmitz *et al*. 2000, Polis *et al*. 2000, Halaj & Wise 2001; Shurin *et al*. 2002) and has brought to light important differences in the structure and dynamics of aquatic, marine and terrestrial communities. It has also emphasized the importance of consumptive interactions, largely to the exclusion of important non- or quasi-trophic processes (*sensu* Polis & Strong 1996) that can similarly propagate through ecological communities. Thus, herbivory is rigorously incorporated into theory on top-down effects while pollination has received little consideration.

Just as pollinators have not factored heavily into studies of top-down effects on plants, so have predators been largely overlooked in pollination research. Apart from effects of ants, little is known about the influence of predators in plant–pollinator mutualisms, particularly when compared with other factors that can disrupt these mutualisms and indirectly inhibit plant reproduction (e.g. habitat fragmentation: Jennersten 1988; Aizen & Feinsinger 1994; extreme climatic events: Rathcke 2000; species invasions: Waring *et al*. 1993; pesticides: Kevan 1977; see Buchmann & Nabhan 1996; Allen-Wardell *et al*. 1998; Kearns *et al*. 1998; Wilcock & Neiland 2002 for reviews). Very few authors (Louda 1982; Wilkinson *et al*. 1991; Altshuler 1999) have examined consequences for plants of

predation on pollinators, and none to date have uncovered a net negative effect. One study even revealed a positive effect, wherein the presence of ants led to increased relocation of winged pollinators on flowers of the tropical shrub *Psychotria limonensis* (Rubiaceae), contributing to higher flower visitation and seed production (Altshuler 1999). Notwithstanding this beneficial role for ineffective predation, there are reasons to believe that predation can obstruct plant–pollinator mutualisms to the detriment of flowering plants.

Countless arthropods and birds prey extensively on pollinating insects (Dukas 2001b and included references), and human predation threatens populations of pollinating mammals and birds throughout the world (Allen-Wardell *et al.* 1998). At least 67% of flowering plants depend on insect pollinators (Tepedino 1979), and perhaps 90% use animals (Buchmann & Nabhan 1996). Several studies have demonstrated top-down components to interactions between flowering plants and their animal pollinators: both ants (Willmer & Stone 1997; Altshuler 1999) and spiders (Louda 1982; Dukas & Morse 2003), can interfere with pollinator visitation to flowers, and certain pollinators display pronounced anti-predator adaptations (Wasserthal 1993) and behaviours (Lima 1991). When one further considers the high incidence of pollen limitation of fruit and seed production in nature (Burd 1994), the potential for predation on pollinators to affect plant reproduction is easy to conceptualize.

Indeed, because many pollinators respond to predation risk (Cartar 1991; Lima 1991; Craig 1994; Dukas 2001a; Dukas & Morse 2003), direct lethal effects of predators on pollinators should not even be necessary for indirect effects on plants to manifest. Numerous arthropod predators hunt directly from flowers (Gertsch 1939; Caron 1990); predator avoidance by pollinators could trigger or exacerbate pollen-limitation even where direct predation is infrequent. Analogous behavioural changes in herbivores facing predation risk have been shown to produce dramatic effects on plants (Power & Mathews 1983; Turner & Mittelbach 1990; Beckerman *et al.* 1997; Schmitz *et al.* 1997; Rudgers *et al.* 2003).

Whether indirect effects on plants are brought about through direct influences on pollinator behaviour, population abundance or a combination of the two will probably vary with predator species (see Schmitz & Suttle 2001). Crab spiders and other floral predators may have more local impacts by altering pollinator behaviour and host choice, while highly mobile and roaming predators such as birds and other flying animals may have broader impacts by reducing pollinator population abundance.

While theories of top-down effects and plant–pollinator interactions have yet to coalesce, this cannot be far off. Even when focused on debate over trophic cascades, Polis

& Strong (1996) cautioned against the assumption that feeding links are the major factor structuring ecosystems, citing the general and profound importance of pollination in terrestrial ecosystems. Many ecologists now espouse an 'interaction web' approach to community studies that allows for the inclusion of important non-trophic interactions precluded by a strict 'food web' perspective (Menge 1995; Price 2002). Likewise, researchers in pollination ecology are advocating a broader, community-wide focus for the study of plant–pollinator mutualisms (Kearns *et al.* 1998). Lima (1991), Dukas (2001a,b), and Dukas & Morse (2003) have called specifically for consideration of predators in studies of plant–pollinator relationships.

EMPIRICAL SUPPORT

In support of this broadened perspective, I draw from empirical work in a riparian system in northern California, where pollinating insects mediate an indirect interaction between crab spiders and an invasive plant. At the Angelo Coast Range Reserve in Mendocino County, California (39°43′45″ N, 123°38′40″ W), the crab spider *Misumenops schlingeri* (Thomisidae) is a common sit-and-wait predator in the flowers of riparian vegetation adjacent to the South Fork Eel River. This system has been invaded by the ox-eye daisy, *Leucanthemum vulgare* (Asteraceae), a short-lived perennial forb native to Europe and a common hunting site for these spiders. *M. schlingeri* preys on the many species of butterflies (Lepidoptera), flies (Diptera) and bees (Hymenoptera) that visit these inflorescences seeking nectar.

Several characteristics of this system make pronounced and detectable effects of spiders on the ox-eye daisy plausible.

Leucanthemum vulgare flowers in this system are self-infertile and depend on insects as pollen vectors. Indirect effects of predation should manifest more often in plants with an obligate plant–pollinator mutualism than in those in which the relationship is facultative. Automatic self-pollination in the absence of insects has been reported for a *L. vulgare* population in England (Knuth 1908), but pollination tests in this study system indicate that neither automatic self-pollination nor self-fertility exists in this population. In June 2002, 24 new inflorescences were enclosed in mesh to prevent insect visitation. The disc florets of 12 of these were gently brushed with separate cotton swabs every 3 days to encourage pollen exchange within each inflorescence, while leaving the other 12 enclosed but otherwise unmanipulated. No seeds were produced in either group.

As *L. vulgare* plants produce few inflorescences, impacts within an individual inflorescence may translate to considerable plant-level effects. Plants in this riparian system produce between one and nine inflorescences, with most

plants producing three and with a population average of 3.4 inflorescences per plant. In plants producing multiple inflorescences, the pollination tests described above yielded no evidence of compensation for decreased seed production in one inflorescence with increases in the others. Seed production in unmanipulated inflorescences on plants with a covered (pollinator excluded) inflorescence was similar to that in the general population, at 205.4 ± 26.0 and 219.5 ± 28.2 seeds, respectively (mean $\pm$ standard error; $t_{35} = -0.37$, $P = 0.71$).

Finally, the arrangement of florets in daisy inflorescences limits the possibility of concealment for these ambush predators. When hunting on *L. vulgare,* crab spiders sit motionless on the ray florets with their enlarged raptorial forelimbs spread around the central disc florets (Fig. 1). Conversely, spiders that hunt pollinating insects from umbel-bearing plants tend to conceal themselves within the umbels. This does not preclude influences on pollinators (see Louda 1982; Dukas & Morse 2003), but renders such effects more dependent on actual attacks or approaches by predators, and subsequent association of patch and risk by pollinators. *Misumenops schlingeri* may represent a more overt threat when hunting on daisies, prompting avoidance by pollinators.

Figure 1 The crab spider *Misumenops schlingeri* hunting on the ox-eye daisy *Leucanthemum vulgare.*

Experimental Design

Paired-flower observations were conducted to determine whether *M. schlingeri* influences the behaviour or host choice of pollinating insects. Indirect effects of spider predators on the ox-eye daisy were then explored with an experiment comparing achene (i.e. small, dry seed-like fruit, hereafter 'seed') production in flowers on which spiders were present with those from which spiders were removed.

Direct effects of spiders on pollinators

Two observers simultaneously recorded data on individual, unmolested inflorescences, similar in height, size and appearance. One inflorescence contained a crab spider and the other was a paired control from a nearby plant. I selected inflorescences on which crab spiders naturally occurred or were absent to avoid introducing observer bias of inflorescence quality and altering the hunting behaviour of spiders. As a result of natural variation in inflorescence quality, a comparison of plants with spiders and those from which spiders were removed may have provided a more rigorous test, but it is unlikely that spiders would preferentially choose low quality inflorescences and bias results for pollinator visitation. Indeed, crab spiders are known to assess flower quality and select high quality inflorescences as hunting sites (Morse & Fritz 1982; Morse 1988, 1993).

Inflorescences were observed through binoculars from a minimum distance of four meters to avoid influencing insect or spider behaviour. The number and duration of all floral visits by insects were recorded over a continuous twenty-minute span between 10:00 AM and 2:00 PM, the hours of maximum insect activity. Sixty such observations were conducted during June 2000 and June 2001. Visit frequency data were compared between inflorescences with a spider and those without using a paired sample *t*-test, and visit duration data with a *t*-test. Paired sample tests were not appropriate for duration data because of 'missing' data for inflorescences receiving zero visitors. Duration data were log-transformed to meet assumptions of normality.

Indirect effects of spiders on plants

On 12 June 2002, 25 pairs of inflorescences were established, with each inflorescence in a pair occurring on a different plant. One in each pair was randomly assigned as 'Spider Present' and the other as 'Spider Absent'. Inflorescences that were just beginning to open were selected, and the size and height were matched for each pair to minimize *a priori* biases in pollinator preference. The following morning, a female crab spider was placed on each 'Spider Present' inflorescence and any spiders found on 'Spider Absent' inflorescences were removed. Female crab spiders showed high site fidelity, remaining on individual daisies for up to 2 weeks, or nearly the entire flowering duration for a

given plant. Nonetheless, some movement occurred, so every morning until flowers senesced (from 15 to 22 days) each experimental inflorescence was examined for spider presence/absence. Any crab spider found on a 'Spider Absent' flower was removed and any spider missing from a 'Spider Present' flower was replaced.

Eight inflorescences did not retain spiders through the first week of the experiment despite repeated restocking. Stocked spiders may have responded to risk cues such as silk lines already present on these inflorescences or to some cue regarding flower quality. Each of these inflorescences and its 'Spider Absent' complement were eliminated from the study. One additional matched pair was eliminated after the spider wove the ray florets into a chamber around the disc florets, presenting a physical barrier to insect visitation (see Ott *et al.* 1998). Analysis is therefore based on 16 pairs of inflorescences.

As flowers senesced, all seeds produced were collected and counted. Seed production data were analysed with analysis of covariance, including as a covariate the diameter of each composite flower's central disc, which was measured as a proxy for the relative number of florets, or maximum possible seed output, of each inflorescence.

Experimental Results and Discussion

Crab spiders had a significant effect on insect visitation to *L. vulgare* inflorescences. Both the frequency and duration of floral visits by insects were reduced in the presence of *M. schlingeri* (Fig. 2a,b), so that fewer insects probably transferred pollen to inflorescences occupied by crab spiders, and those that did visited far fewer florets on those inflorescences. This direct effect of *M. schlingeri* on pollinator visitation cascaded to a significant indirect effect on *L. vulgare*. Seed production was higher in inflorescences from which crab spiders were excluded than in those on which spiders hunted ($F = 6.12$, $P < 0.02$). By repelling pollinating insects, crab spiders reduced inflorescence seed production from 214.2 ± 10.2 seeds to 178.2 ± 10.2 seeds (least square mean $\pm$ SE) (Fig. 3).

The 36 seed difference amounts to a 17% mean reduction in fecundity for spider-occupied inflorescences. Given the observed range in plant inflorescence production, this translates to single-year, individual plant fecundity losses between 2 and 17% for plants occupied by a single crab spider. Population-wide fecundity effects will depend in part on the overall commonness of spiders on inflorescences, which ranged through the years of this study from $12.5\% \pm 0.8\%$ (mean $\pm$ SE) of flowers occupied in June 2000 to $6.8\% \pm 1.4\%$ (mean $\pm$ SE) in June 2002. Crab spider abundances in this riparian habitat are sufficiently low so as to make population-level effects minimal (<2% overall reduction in seed production in a given year).
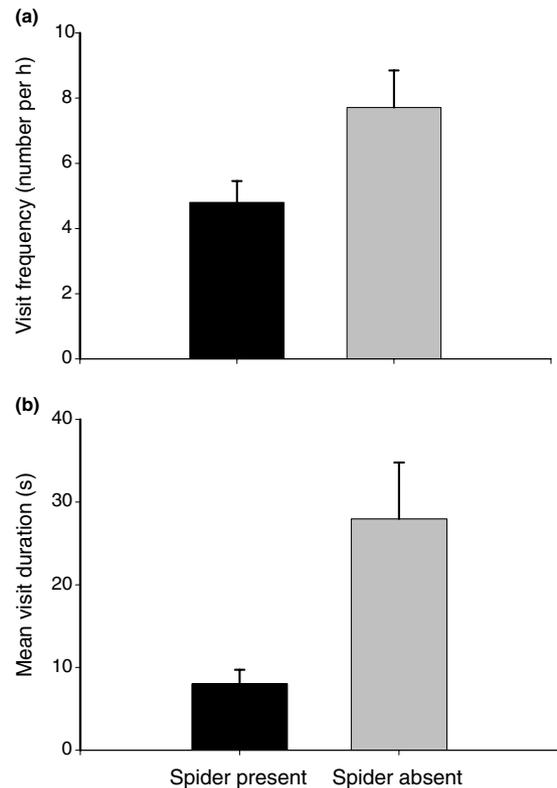

Figure 2 Flower visitation by nectarivorous insects (mean $\pm$ SE). (a) The presence of a spider caused a significant reduction in visit frequency, from 7.7 ± 1.1 visits per hour (mean $\pm$ SE) on unoccupied inflorescences to 4.8 ± 0.7 visits per hour on those with a crab spider (one-tailed paired sample *t*-test, $t_{29}=2.8$, $P < 0.01$). (b) Visit duration fell from 28.0 ± 6.8 s (mean $\pm$ SE) to only 8.0 ± 1.7 s (mean $\pm$ SE) in the presence of a crab spider (one-tailed *t*-test, $t_{50} = 2.6$, $P < 0.001$).

The crab spider population is kept sparse by seasonal inundation of the study site from winter flooding of the South Fork Eel River, so that most crab spiders in the riparian habitat are not members of a resident population but colonists each year from surrounding meadows. The opposite is the case for these meadow environments, where *M. schlingeri* is abundant and *L. vulgare* is very rare. Although the ox-eye daisy has intermittently occurred in low numbers in these meadows in past years (Patterson 1977; K. B. Suttle, personal observation), it is absent at present. Plants invading systems with intact and abundant predator assemblages may be most susceptible to pronounced population-wide effects, as predator–plant and predator–pollinator ratios may be highest under these circumstances.

CONSTRAINTS ON IMPORTANCE

High population turnover for *L. vulgare* in this riparian system, attributable to periodic flooding and accompanying
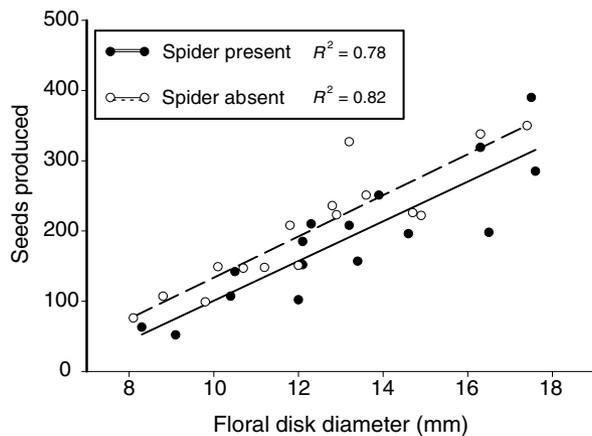
Figure 3 Seed production. Results of an experimental manipulation of crab spider occurrence on daisy inflorescences. Accounting for differences in the size of the composite flowers ($F = 112.9$, $P < 0.0001$), ANCOVA revealed a significant influence of crab spiders on seed production ($F = 6.12$, $P < 0.02$; non-significant interaction term $P > 0.85$).

physical disturbances, lends added importance to seed production for this plant population. In general, consequences for plants of pollinator-mediated effects on seed production will depend on the role of seeds in population dynamics. Specifically, impacts will hinge on the degree to which plant population abundance and biomass depend on seed production. Seed-limitation varies with plant life form, habitat type, and the successional characteristics of the plant species and habitat (Turnbull *et al.* 2000), but should be particularly common and consequential in populations of invasive plants (Parker 1997). Not just the presence or absence, but the degree, of seed-limitation in a plant population needs to be understood in order to evaluate whether predation on pollinators will have meaningful consequences at the population level.

IMPLICATIONS FOR COMMUNITY ECOLOGY

Pollinators interact within terrestrial food webs, deriving their energy from primary producers and providing energy to higher consumers. Yet the focal interaction of this plant–pollinator association is not consumption, but mutualism via pollen service, so the effects described cannot be considered as trophic cascades. Pollination is a directly positive non-food-web effect (Schoener 1993). While herbivores generally have a deleterious impact on primary producers, pollinators are beneficial, if not essential, to most flowering plants. The implications of this discrepancy for community ecology are considerable.

According to classic food chain theory, a predator's effect on primary producers depends on the number of trophic levels through which that effect transmits (Fretwell 1977;

Oksanen *et al.* 1981). In a food chain with three trophic levels, the top predator exerts a positive effect on plants by suppressing herbivores. Alternately, in a four-level food chain, the top predator exerts a negative effect on plants by reducing predators of herbivores and allowing herbivores to flourish and suppress plants. There may exist a whole class of unstudied top-down effects that propagate down interaction webs in a manner similar to those cascading through herbivores, but with opposite consequences for primary producers. Interestingly, both types of effect could arise from a single predator, if it interacts with both pollinators and herbivores. Predators that remain on inflorescences after pollination, for example, may dampen or offset negative effects by repelling seed predators. Net effects on plant fitness will then depend on the balance between loss of pollinator services and reduction of plant damage or seed predation. Louda (1982) observed such counteracting top-down effects from the green lynx spider, *Peucetia viridans,* hunting in umbels of *Haplopappus venetus* (Asteraceae). As crab spiders, which often depart senescing inflorescences prior to seed maturation, are much more likely to interact with pollinators than with seed predators, negative effects on pollination are unlikely to be mitigated by reduced seed predation.

While the relative influence of top-down effects transmitted through herbivores and those transmitted through pollinators is obviously unclear, the lack of experimental demonstrations of pollinator-mediated effects need not imply that effects cascading through herbivores are necessarily stronger or more important. As Polis *et al.* (2000) point out, most experimental demonstrations of terrestrial trophic cascades involve a subset of the community and affect only one or a few plant species, carrying little biological significance from a population or community perspective (but see Schmitz 2003). As with the pollinator-mediated effect I report, plant responses are usually measured as some decrement in plant performance that rarely translates clearly to meaningful population-level impacts on plant abundance (Polis *et al.* 2000; Schmitz *et al.* 2000). Community-level pollinator-mediated effects are conceivable, and perhaps likely, in ecosystems where predation leads to local extinction of the pollinator guild. For example, we can expect such effects on many South Pacific islands from which human predation has eradicated entire populations of flying foxes (Fujita & Tuttle 1991; Nabhan 1996), keystone pollinators of most flowering plants (Cox *et al.* 1991).

SUMMARY

Plant-pollinator relationships are often at the center of research into pollen-limitation in flowering plants. I suggest that this focus excludes an important interactor; clearly

predators have a greater role in pollination ecology than is currently appreciated. Likewise, should we broaden our thinking on the influence of predators in terrestrial communities to include pollinators as potential prey animals. The role of predators in natural systems was underestimated until Leopold (1949), Hairston *et al.* (1960), and Paine (1966) emphasized the community-wide importance of top-down effects. We now recognize strong, indirect impacts of predation and predation risk in aquatic, marine, intertidal, and terrestrial environments, and we are learning that the interactions mediating these impacts are not limited to herbivory. Primary producers can be affected when competition for space (Paine 1966; Menge 1976), nutrient translocation (E. Danner & J. Estes, personal communication), seed dispersal (Rainey *et al.* 1995), and, as demonstrated here, pollination are disrupted by predators.

Predation on pollinators is widespread, as is pollen limitation of fruit and seed production in flowering plants. We may begin to discern the extent to which the former influences the latter by bridging gaps in our thinking on top-down effects and pollination ecology.

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