

Predator Effects on Plant-Pollinator Interactions, Plant Reproduction, Mating Systems, and Evolution

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indirect interactions, natural selection, plant mating systems, plant-pollinator interactions, predators, mutualism disruption

Abstract

Plants are the foundation of the food web and therefore interact directly and indirectly with myriad organisms at higher trophic levels. They directly provide nourishment to mutualistic and antagonistic primary consumers (e.g., pollinators and herbivores), which in turn are consumed by predators. These interactions produce cascading indirect effects on plants (either trait-mediated or density-mediated). We review how predators affect plant-pollinator interactions and thus how predators indirectly affect plant reproduction, fitness, mating systems, and trait evolution. Predators can influence pollinator abundance and foraging behavior. In many cases, predators cause pollinators to visit plants less frequently and for shorter durations. This decline in visitation can lead to pollen limitation and decreased seed set. However, alternative outcomes can result due to differences in predator, pollinator, and plant functional traits as well as due to altered interaction networks with plant enemies. Furthermore, predators may indirectly affect the evolution of plant traits and mating systems.

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Indirect effect: the effect of one species on another through an intermediary species

Density-mediated indirect interaction (DMII): a type of indirect interaction where one species affects another by altering the density and/or abundance of an intermediary species

Risk effect: the cost of the behavioral response of a prey species to a predator

Trait-mediated indirect interaction (TMII): a type of indirect interaction where one species affects another by altering a trait, such as a behavior, of an intermediary species

1. INTRODUCTION

All organisms are embedded within food webs and interact directly and indirectly with other species. Plants convert sunlight and atmospheric CO₂ into carbon compounds that nourish a diverse community of primary consumers ranging from plant enemies (e.g., herbivores or pathogens) to mutualists (e.g., pollinators, fungi, ants). When these primary consumers are preyed upon by secondary consumers (i.e., predators), trophic cascades can be generated with indirect positive, neutral, or negative effects on plant fitness (Ripple et al. 2016). Predation on plant enemies generates diverse indirect ecological effects that typically improve plant growth and reproduction (Hairston et al. 1960, Schmitz et al. 2000). The indirect effects generated by predation on mutualistic primary consumers are less well studied but are expected to negatively affect plant reproduction and population growth (Knight et al. 2006). Further, by altering plant fitness and plant-animal interactions, predators are expected to indirectly affect the evolution of plant traits, particularly floral traits and plant mating systems (Estes et al. 2013, Walsh 2013, McPeck 2017, terHorst et al. 2018).

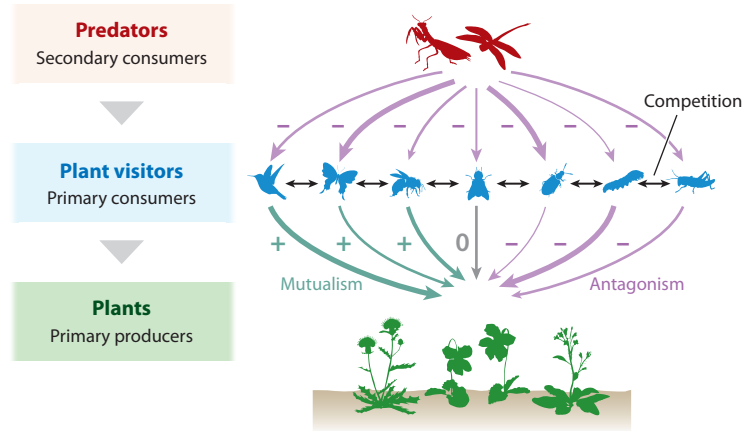
In this review we focus on the keystone mutualism between plants and their pollinators, a reciprocal relationship vital for the integrity of natural ecosystems, agricultural systems, and human economies. Because plants are stationary, they have evolved elaborate strategies to achieve outcrossed sexual reproduction, often engaging animal pollinators to carry pollen between plants. In exchange, plants offer nectar, pollen, scent, or other valuable resources to reward their pollinators. Pollinators are thought to be the key drivers of the evolution of floral forms. Pollinators exert natural selection on their plant partners, and shifts in pollinators explain ~25% of the shifts in floral diversity across angiosperms (van der Niet & Johnson 2012). Thus, information about additional unmeasured factors, or those not previously considered, is needed to understand the process of floral evolution.

While plant evolution and pollination mutualisms have long been a central focus of biology [Sprengel 1793, Darwin 2018 (1859)], they are typically studied as pairwise interactions without considering the indirect effects generated by multispecies interactions and higher trophic levels (Strauss & Irwin 2004, Strauss & Whittall 2006). To understand the forces that shape plant ecology and evolution, we need to integrate the study of plants and pollination with community ecology and consider the direct and indirect effects of predators (terHorst et al. 2018). In this review, we begin to fill this gap by providing evidence for the varied effects of predators on plants via pollinators. We highlight the evidence for indirect effects of predators on plant reproduction, mating systems, and the evolution of floral traits. We end with future avenues of research and approaches to test the role of pollinator predators in shaping the evolution of plant reproductive strategies.

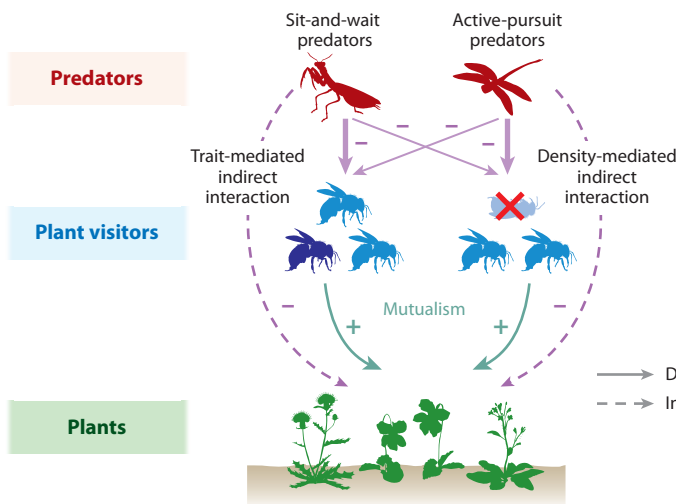
Predators of pollinators exploit and disrupt plant-pollinator mutualisms by consuming pollinators and altering their behavior, with myriad potential consequences for plants. By decreasing pollinator abundance, predators create density-mediated indirect interactions (DMII) (Abrams 1995) (**Figure 1**). Furthermore, the presence of predators can alter aspects of pollinator foraging behavior through risk effects (Preisser et al. 2005, Creel & Christianson 2008) and affect plants via trait-mediated indirect interactions (TMII) (Werner & Peacor 2003) (**Figure 1**).

Predation on pollinators is widespread and common both geographically and taxonomically. We searched the literature on predators of pollinators for natural history sightings, scientific studies, and other reports of predators. We found examples of pollinator predators in diverse ecosystems around the globe. Predators of pollinators include insects such as wasps (Hymenoptera), dragonflies (Odonata), true bugs (Hemiptera), flies (Diptera), and mantids (Mantidae), as well as spiders (Araneae), various birds (Aves), lizards (Squamata), and frogs (Ranidae) (**Figure 2**).

a Tri-trophic food web: direct interactions



b Mutualists



c Antagonists

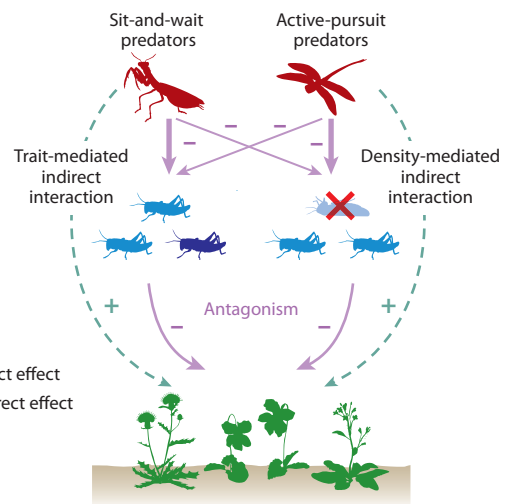


Figure 1

(a) A tri-trophic food web among plants, primary consumers, and predators. The direct effects of each trophic level on the organisms it consumes are shown by solid arrows; the strength of these effects is shown by the arrow width. Positive effects are indicated by green arrows and a plus symbol, and negative effects are shown as purple arrows with a minus symbol. The predator community (represented by red) negatively affects the community of primary consumers (blue); however, it is important to note that not all primary consumers are equally affected. The effect strength is context and taxon dependent. Further, primary consumers compete with and affect one another. The primary consumers range from having positive (mutualistic, +), to neutral (0), to negative (antagonistic, -) effects on plants. Again, the strength of these effects depends on context and taxon. Panels *b* and *c* depict the mechanisms by which predators can indirectly affect plants via (b) mutualists and (c) antagonists. Indirect effects are represented by dashed arrows. Predators indirectly affect plants both by altering the density of primary consumers [density-mediated indirect interaction (DMII)] and/or by affecting the traits of primary consumers (represented by darker blue icons), especially foraging behavior [trait-mediated indirect interaction (TMII)]. The hunting mode of the predator (sit-and-wait versus active-pursuit) is expected to impact the relative strength of DMII and TMII. Many predators are generalists and will indirectly affect plants via both mutualists and antagonists.

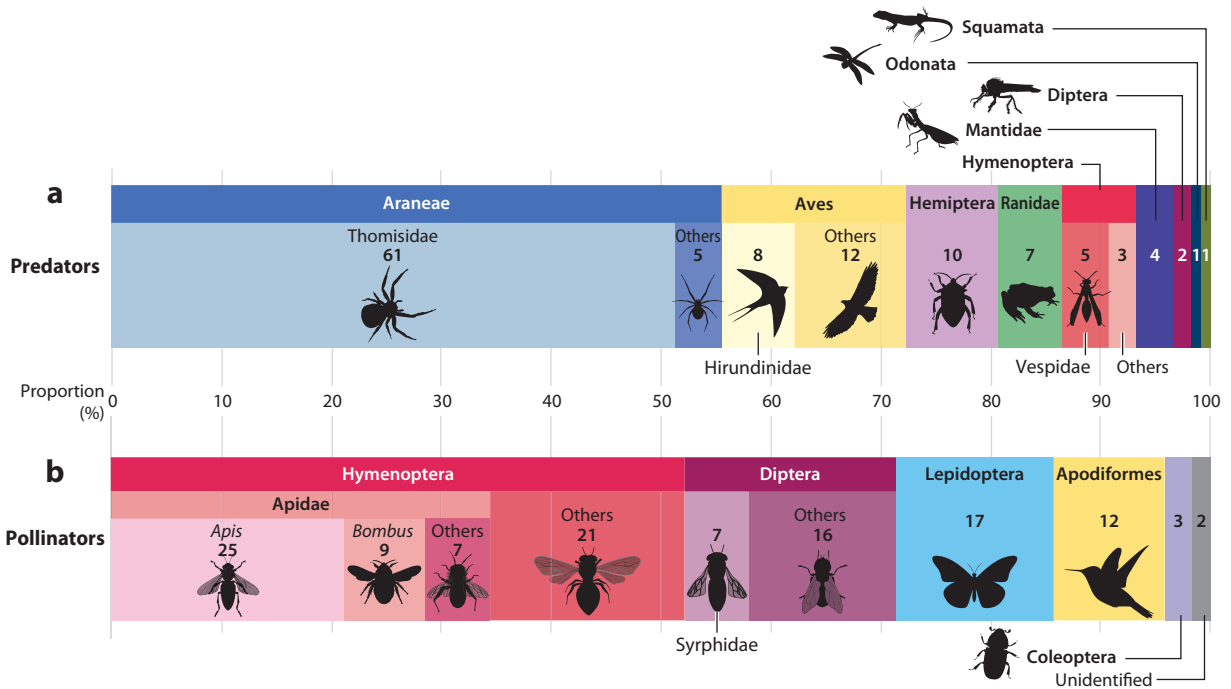


Figure 2

Web of Science and Google Scholar searches yielded 62 relevant articles describing 114 predator-pollinator taxonomic pairings (e.g., Thomisidae consuming *Bombus*). These articles are listed in the **Supplemental Appendix**. The taxa described as predators of pollinators are shown in panel *a*. The taxa of pollinators described as prey in these articles are shown in panel *b*. The size of each rectangle is proportional to the number of times each taxa was described in these predator-prey pairings; sample size is indicated within. This is a snapshot of currently available studies with biases regarding which taxonomic groups have more available data; popular study systems (e.g., Thomisidae and Apidae) may be overrepresented while other ecologically relevant predator-prey relationships may be underrepresented.

Supplemental Material >

Pollinator predators are ubiquitous and diverse and have the potential to commonly affect plant-pollinator interactions, plant fitness, and reproduction across ecosystems.

2. HISTORICAL CONTEXT AND CURRENT UNDERSTANDING OF PREDATION ON POLLINATORS

One of the earliest written descriptions of predation on pollinators affecting plant communities comes, unsurprisingly, from the keen observations of Darwin. In *On the Origin of Species*, Darwin [2018 (1859)] notes that domestic cats control populations of mice, thereby limiting the amount of honeycomb that mice eat, in turn affecting honey-bee populations and the abundance of red clover. Darwin [2018 (1859), p. 51] concludes, “Hence it is quite credible that the presence of a feline animal in large numbers in a district might determine, through the intervention first of mice and then of bees, the frequency of certain flowers in that district!”

Despite Darwin’s description of pollinator predators causally shaping plant populations, the misconception that predation on pollinators was rare and insignificant took hold, and the effects of pollinator predators on plants were rarely considered until recently. Two main assumptions led to this misconception: Hymenoptera, the most common pollinators on Earth, were assumed to be protected from predation by their defensive sting, and pollinator predators were assumed to be

too rare and have too low a prey-capture rate to impact pollinators (Morse 1986, Dukas 2001b, Schmalhofer 2001). Further, workers from pollinating social insect taxa were viewed as numerous and expendable. Therefore, it was assumed that selective pressure for predator-avoidance behaviors would be negligible, or negated by stronger selection to maximize resource acquisition (Morse 1986). Because few studies directly addressed these ideas, nearly two decades ago Dukas (2001b) called for studies to fill the knowledge gap. Since then, research focused on predator-pollinator interactions has demonstrated that predators can significantly affect pollinator abundance and behavior. We review evidence regarding the effects of predators on pollinator abundance and behavior published since the review by Dukas (2001b) and discuss the implications for plant reproduction, fitness, and the evolution of floral traits and plant mating systems.

3. PREDATOR EFFECTS ON POLLINATOR ABUNDANCE AND BEHAVIOR

3.1. Effects on Abundance

Predators can be a major source of mortality for pollinators and can significantly decrease pollinator population size. Predators can reduce the abundance of pollinators through direct consumption and increased mortality via risk effects (Preisser et al. 2005, Creel & Christianson 2008). For example, wasps are aggressive bee predators. An aggregation of North American bumblebeewolves (*Philanthus bicolor*) was estimated to kill more than 850 bumblebees per hour within a 4-km radius (Dukas 2005). Likewise, novel predation by invasive wasps (*Vespa* spp.) can be a major source of mortality for native bees (e.g., genus *Hylaeus* in Hawaii) as well as domestic and naturalized honey bees (*Apis mellifera*) (Hanna & Eason 2013, Monceau et al. 2013). Numerous other predator taxa also affect pollinators. Dragonflies reduce the number of pollinating sweat bees (Halictidae) near ponds (Knight et al. 2005a). True bugs, such as ambush bugs (*Phymata* spp.) and assassin bugs (Reduviidae), and other insects such as robber flies (Asilidae) and mantids (Mantodea) prey upon pollinators at flowers or while in flight (e.g., Dukas 2001b, Shankar 2015). Birds, such as swallows (Hirundinidae) (Meehan et al. 2005) and bee-eaters (Meropidae) (Łangowska et al. 2018), are voracious predators of pollinators, especially bees. Spiders are also significant predators; crab spiders (Thomisidae), the best-studied pollinator predators, attack pollinators as they visit flowers (Morse 2007). Orb-weaving spiders exploit foraging pollinators by luring them to their webs with UV reflectance (Llandres et al. 2011). Many of the existing studies describe predation on pollinating insects, in particular economically important social bees (i.e., *Apis* and *Bombus*). Predators are likely to have similar effects on other pollinator taxa; there are simply fewer data currently available (Figure 2).

Importantly, even relatively rare predators with low prey-capture rates can significantly affect pollinator populations. Morse (1986) found that only 2 of 531 bumblebees visiting inflorescences harboring crab spiders were captured and killed. This low prey-capture rate is often cited as evidence that spider predation is not an important source of bee mortality; however, Cresswell (2017) found that when this magnitude of spider-caused mortality is included in a demographic matrix projection model, it has a significant effect on colony growth and reproduction. Using Morse's (1986) data, Cresswell estimated that bumblebees have a 3.4×10^{-3} chance of mortality when encountering a spider and that there are 4.7×10^{-3} spiders per inflorescence. Given that bumblebees visit an estimated 527 inflorescences per day, there is a 1% daily chance that a forager will be killed by a spider. Using this predation rate, over the course of a season, Cresswell's (2017) matrix model projects that 47% of workers will be killed by spiders. Further, if spider abundance doubles, a density common in field observations, 60% of workers would be killed, new queen production would decrease by 11%, and male production would decline by 1%. Cresswell (2017) was

able to model colony growth only within a season because data on queen hibernation survival are lacking. These results strongly suggest that even at low density and with low prey-capture rates, sit-and-wait predators can be a major source of bee forager mortality. Therefore, strong selection on foragers to avoid these predators is expected (Cresswell 2017).

Predators will not affect all pollinator taxa equally. Differences in pollinator taxa, body size, and sociality are expected to mediate the effects of predators on pollinator populations. To examine how ambush predators are expected to impact populations of solitary bee species that differ in body size and resource requirements, Rodríguez-Gironés (2012) developed a mathematical model. Similar to the findings of Cresswell (2017), this model suggests that low abundances of sit-and-wait predators (1–2% of flowers harboring predators) can exert strong top-down control on solitary bee populations. The model results demonstrate that key factors driving pollinator declines included bee resource requirements, predator encounter rates, and foraging and defensive behaviors. Specifically, these critical factors are the number of flowers bees must visit to provision their offspring (the more flowers that are visited, the more likely a bee is to encounter a predator), the bee's ability to avoid landing on flowers that harbor predators (i.e., inspection and avoidance behavior), and the bee's susceptibility to attack if it does land on a predator-harboring flower (i.e., chance of escape) (Rodríguez-Gironés 2012). The model results suggest that medium-sized solitary bees are most vulnerable to population decline, even when ambush predators are relatively rare. Small-bodied bees are less vulnerable because they are able to provision their offspring with fewer flower visits, while large-bodied bees are less vulnerable because they are better able to survive attempted predator attacks (Rodríguez-Gironés 2012).

The work of Cresswell (2017) and Rodríguez-Gironés (2012) exemplifies how demographic and mathematical models can improve our understanding of how predators impact pollinator populations. Unfortunately, such studies are rare. While there are many examples of predation on pollinators (**Figure 2**), the impact of these predators on pollinator population dynamics is poorly understood. Many pollinators, and insects in general, are declining globally, largely due to anthropogenic factors (Potts et al. 2010, Regan et al. 2015, Hallmann et al. 2017). The role of native and introduced predators in these declines is unclear; further, it is unclear how anthropogenic activities affect the populations of these predators. We expect that the effects of predators on pollinator populations will depend on pollinator taxa, body size, sociality, and behavior, but more data are needed to fully appreciate the effects of predators on pollinator population dynamics.

3.2. Effects on Behavior

Many pollinator taxa alter their behavior in response to predators. Pollinators can inspect flowers and detect cryptic ambush predators before landing (Chittka 2001, Théry & Casas 2002). While inspection behavior decreases foraging speed, the ability to evaluate risk at each flower is an important behavioral adaptation to mitigate predation (Chittka et al. 2003, Higginson & Houston 2015). Using predator models on flowers, Ings & Chittka (2008) found that naive bees landed on flowers with or without model predators as often as expected by chance. However, after experiencing simulated predator attacks while visiting flowers with predator models, bees increased inspection time and learned to avoid the predator models. In the same study, bees were equally good at detecting and avoiding cryptic and more conspicuous predator models. However, when the models were cryptic, bees slowed their foraging and inspected flowers 1.7 times longer, indicating a trade-off between foraging speed and accuracy of predator detection (Ings & Chittka 2008). Interestingly, the reward level of flowers may mediate the behavioral response of bees to predation. Bees that experienced a simulated predator attack at highly rewarding flowers responded by shifting to foraging on less rewarding flowers, while bees experiencing attacks at low-reward flowers reduced their overall foraging activity (Jones & Dornhaus 2011). Building on these results, Wang

et al. (2013) investigated whether bees can make simultaneous foraging decisions based on predator presence and the level of floral reward. Bees exposed to conspicuous predator models learned to avoid them and were able to simultaneously choose higher-reward flowers. In contrast, bees exposed to cryptic predator models also successfully learned to avoid them, but did not discriminate among flower reward levels. Together, these studies, among others (Dukas 2001a, Chittka et al. 2003, Dukas & Morse 2003, Robertson & Maguire 2005, Jones 2010, Jones & Dornhaus 2011, Antiqueira & Romero 2016), demonstrate that predator avoidance can be learned and that bees prioritize predator avoidance over foraging speed and efficiency. However, it is important to note that learning seems to require multiple failed predator attacks (Ings & Chittka 2008); therefore, learning is likely more important to pollinators with low predator susceptibility (e.g., pollinators with large bodies), because pollinators that are more susceptible to predators may be killed before they are able to learn.

Pollinators can utilize indirect cues as indicators of risk when choosing flowers. The use of some indirect cues may be linked to pollinator sociality. For example, bumblebees avoid flowers with dead conspecifics or the scent of dead conspecifics; however, solitary bees do not (Abbott 2006, Llandres et al. 2013). Honey bees that encounter dead conspecifics perform fewer waggle runs, thereby recruiting fewer hive mates to potentially dangerous resource patches (Abbott & Dukas 2009). Scent may be an important factor in indirect cues. Bees avoid the scent of crab spiders and the silk they leave behind on flowers (Reader et al. 2006). Furthermore, social bees use alarm pheromones to warn conspecifics of danger; heterospecific social bees, but not solitary bees, can eavesdrop on these alarm pheromones to make more adaptive foraging decisions (Goodale & Nieh 2012; Wang et al. 2016a,b; Wen et al. 2017; McClenaghan et al. 2019; Romero-Gonzalez et al. 2019). Social bees may also use direct social information; for example, in environments known to be risky, social bees are more likely to land on a flower that is already occupied by a foraging conspecific (Dawson & Chittka 2014, Lihoreau et al. 2016). The use of indirect cues and social-information sharing allows pollinators to assess and avoid risk while foraging. In this respect, social pollinators that can share information have an advantage over solitary pollinators.

Much of the work discussed so far pertains to how insect pollinators detect and avoid sit-and-wait ambush predators on flowers. Thus, there are two important gaps: Not all pollinators are insects, and not all predators are ambush hunters. Information on the behavioral responses of noninsect pollinators to predation is limited. There is some evidence that hummingbirds engage in risk-reducing behaviors such as avoiding flowers close to the ground and increasing vigilance at the expense of efficiency (Lima 1991). Hummingbirds may also engage in antipredator mobbing behavior (Zenzal et al. 2013, and references therein). While there are many examples of active-pursuit predators preying upon pollinators, the effect of these predators on pollinator behavior is less clear. Studies of active-pursuit predators often measure pollinator floral visitation rates as a response variable; however, the mechanistic cause for reduced pollinator visitation is unclear. Active-pursuit predators may be causing reduced visitation by decreasing pollinator abundance and/or by altering pollinator foraging behavior.

4. EFFECT OF POLLINATOR PREDATORS ON PLANT-POLLINATOR INTERACTIONS

As discussed in Section 3, predators cause pollinator abundance to decline via mortality, and predators alter the behavior of pollinators, causing decreased foraging activity and speed. As a result, we expect predators to reduce interactions between plants and pollinators. Consequentially, both pollinators and plants will receive fewer benefits from this mutualism: Pollinators will collect fewer resources, and plants will export and receive less pollen. A meta-analysis (Romero et al. 2011) shows that, on average, predators decrease pollinator visits by 36% and

visit duration by 51%. This response can result from two mechanisms: decreased pollinator abundance (i.e., a density-mediated effect of predators) or decreased pollinator foraging activity and/or speed (i.e., a trait-mediated effect of predators) (**Figure 1**). Both mechanisms lead to weakened plant-pollinator interactions. However, while the mean effect is that predators reduce both the frequency and duration of pollinator visits to flowers, the outcome of each specific case is context dependent and variable. The effect of a predator on plant-pollinator interactions depends on predator traits, pollinator traits, and plant traits.

In some contexts, predators increase pollinator visitation to flowers. This is attributed to predator traits that serve as deceptions or lures. Orchid mantises exemplify deception. The bodies of these mantids mimic a flower's physical and chemical structure, and when deceived pollinators attempt to visit the apparent flower they are attacked by the mantid (Mizuno et al. 2014, O'Hanlon et al. 2014). A well-studied and complex example of lures is found in the Australian crab spider, *Thomisus spectabilis*. These spiders lure bees by reflecting UV light to create contrast between their bodies and flowers (Heiling et al. 2003, 2005a,b). Honey-bee visitation to *Chrysanthemum frutescens* increases twofold when an anesthetized, UV-reflecting crab spider is present (Heiling et al. 2003). However, anesthetization of spiders may falsely inflate the increase in visitation. Llandres & Rodríguez-Gironés (2011) found that large, nonanesthetized, UV-reflecting crab spiders increased honey-bee attraction but did not increase visitation compared to spider-free flowers. Honey bees were attracted only to large UV-reflecting spiders; when small spiders reflected UV, honey bees avoided them. Interestingly, Llandres & Rodríguez-Gironés (2011) found that color matching between crab spiders and flowers did not affect honey-bee visitation, but rather, the most important determinants were crab-spider size, movement, and UV reflectance. The evolution of UV reflectance in crab spiders occurred in Australia and has not been found in other regions (Herberstein et al. 2009, Gawryszewski et al. 2017). Interestingly, while both honey bees and native Australian bees were attracted to UV-reflecting spiders, only introduced European honey bees increased visitation (Heiling & Herberstein 2004, Llandres et al. 2011), suggesting that pollinator species have different responses to predator traits. It is unclear whether the difference in response is due to a longer coevolutionary history between native bees and Australian crab spiders or if novel selection for UV reflectance to exploit a sensory bias of honey bees occurred after European honey bees were introduced to Australia (Llandres & Rodríguez-Gironés 2011). While the strongest evidence that predators can increase pollinator attraction comes from Australian crab spiders, another intriguing case has been observed. Welte et al. (2016) found increased pollinator visitation to flowers harboring crab spiders in a North American prairie; however, they did not find support for crab spider use of UV reflectance as a lure. Their result suggests that crab spiders may use lures other than UV reflectance.

In some contexts, predators have little to no effect on pollinator visitation rates (Dukas et al. 2005, Schwantes et al. 2018, Rodríguez-Gironés & Jiménez 2019). A possible explanation is that effective predator crypsis may prevent some pollinators from perceiving and responding to danger (Chittka 2001, Cheng et al. 2006, Anderson & Dodson 2015, Rodríguez-Morales et al. 2018). This is especially likely if pollinators forage quickly and do not inspect flowers before landing or if foragers lack experience (Dukas et al. 2005). Furthermore, not all pollinators are equally susceptible to predation (Morse 2007, Rodríguez-Gironés 2012). Pollinator taxa with very low susceptibility to predator attack may be less likely to alter their foraging behavior in response to predators (Dukas & Morse 2005, Romero & Koricheva 2011, Gavini et al. 2020). Similarly, predators can have prey preferences that modify the level of threat they pose to different taxa (Morris & Reader 2016). As a result, some pollinator taxa may experience fewer failed attacks and therefore may not learn to avoid predators. Or, more generally, even if a pollinator taxon is both susceptible to attack and a preferred prey, if the majority of foragers in a population are naïve and

have not learned to avoid predators, then avoidance behavior may not be observed. In addition, finding no change in plant-pollinator interactions in response to predators may result from the experimental methods. For example, pollinators may not respond to model predators or to dead predators in the same manner that they would respond to live ones (e.g., Brechbühl et al. 2010).

Most commonly, pollinators decrease the frequency and duration of floral visits in response to the presence of predators (reviewed in Romero et al. 2011). The above cases are intriguing exceptions to this pattern. Clearly, the effect of predators on plant-pollinator interactions depends on context. Ecological factors and experimental design may affect whether predators decrease, increase, or have no effect on plant-pollinator interactions. Because pollinators do not need to move far to be safe from sit-and-wait predators, the spatial scale of a study could influence the strength and detectability of the effect of predators on plant-pollinator interactions (Huey & Neih 2017). Visitation has been studied on a scale ranging from a single flower or inflorescence (e.g., Suttle 2003) up to an entire patch of flowering individuals (e.g., Dukas & Morse 2003, 2005). Too large a scale may lead to finding no effect of predators on visitation. Alternatively, a very small scale will increase the likelihood of finding an effect on visitation, but the results may not be ecologically relevant. For example, decreased visitation to a single flower may not have a significant impact on plants with many flowers but may be significant for plant species that produce few flowers. If predators affect plants through TMII, then a small scale (e.g., individual flowers or plants) may be appropriate because pollinators can detect and avoid predators at the flower/inflorescence level (e.g., Ings & Chittka 2008). Alternatively, if predators affect plant-pollinator interactions through DMII, then a larger spatial scale may be more appropriate. For example, one could compare visitation to plants near and far from an aggregation of bees (Dukas 2005). Similar to spatial scale, plant traits such as size, morphology, and inflorescence structure may mediate how predators affect visitation. The hunting success of predators varies across plant species with differing flower morphologies (e.g., Morse 2007). Plants with large inflorescences may not experience declines in visitations because visitors can land on a part of the inflorescence a safe distance from the predator and leave if the predator approaches (Morse 1986, Greco & Kevan 1994). A clearer understanding of how the environment and functional traits mediate the effect of predators on plant-pollinator interactions will aid in predicting the effects of predators on plant reproduction.

5. POLLINATOR PREDATOR EFFECTS ON PLANT REPRODUCTION

Given that predators can affect pollinator abundance, behavior, and the frequency and duration of floral visitation, it follows that predators will affect plant reproduction. Predators can affect plant fitness along four major axes. First, if predators decrease pollinator visitation frequency and duration, and thus reduce the amount of pollen imported, then there may not be sufficient pollen to fertilize all ovules within flowers, and consequently, seed set will be reduced. Second, if predators decrease pollinator visitation frequency and duration, and thus reduce the amount of pollen exported, then the number of seeds that the plant can sire will be limited, and plant male fitness will decline. Third, in self-compatible plants, changes in pollinator visitation, and thus the amount of pollen imported and exported, may affect the proportion of ovules fertilized by self versus outcross pollen, which could then impact the expression of inbreeding depression (Jain 1976, Husband & Schemske 1996). Fourth, predators can alter interaction networks between plants and primary consumers. For example, generalist predators often suppress plant antagonists in addition to pollinators and can thereby reduce the number of seeds, flowers, and leaves damaged by plant enemies. Whether and how predators affect plant reproduction are expected to depend on predator traits, pollinator traits, and plant traits, as well as the presence and abundance of other community members such as herbivores, nectar/pollen thieves (Hargreaves et al. 2009), and other plant antagonists.

5.1. Pollen Import and Export

By reducing plant-pollinator interactions, predators reduce the amount of pollen imported to flowers. Consequently, predators can cause pollen limitation of plant reproduction (i.e., when individual plants do not receive sufficient pollen to fertilize all ovules) (Knight et al. 2005b). For example, Knight et al. (2005a) found that *Hypericum fasciculatum* was significantly more pollen limited when it grew near ponds without fish than near ponds with fish. This is because immature dragonflies are more likely to survive to become adults in fishless ponds, and dragonfly adults are predators of the Halictidae bees that pollinate *H. fasciculatum*. The dragonflies reduce pollinator visitation, increase the magnitude of pollen limitation, and thereby decrease seed set (Knight et al. 2005a). Pollen limitation can be quantified by comparing the seed set of naturally pollinated plants to the seed set of plants in a pollen supplementation treatment (Knight et al. 2005b). While pollen limitation is easily quantified, few studies examining the impact of predators on seed set have done so. Despite the lack of direct measurement, pollen limitation can be inferred to be the mechanism behind decline in seed set caused by reduced pollinator visitation. For example, Suttle (2003) found that flowers of the invasive oxeye daisy *Leucanthemum vulgare* (Asteraceae), a self-incompatible, insect-pollinated, perennial herb, produced 17% fewer seeds when occupied by a crab spider. Crab spiders reduced both visitation frequency and duration, presumably leading to pollen limitation (Suttle 2003). Similarly, seed production of *Chuquiraga oppositifolia* (Asteraceae), a South American self-incompatible, insect-pollinated shrub, declined twofold when lizards on rocks adjacent to shrubs reduced insect visitation frequency and duration (Muñoz & Arroyo 2004). Seed set of sweet clover, *Melilotus officinalis*, an introduced self-compatible herb, was significantly affected by proximity to nesting cliff swallows (*Hirundo pyrrhonota*) (Meehan et al. 2005). The diet of cliff swallows overlapped with insect taxa that visited *M. officinalis*, leading to a 50% decline in fruit set of plants growing near nesting cliff swallows before fledging (Meehan et al. 2005). Western monkshood (*Aconitum columbianum*), a self-incompatible, bumblebee-pollinated wildflower, also showed decreased seed set as a function of proximity to an active bumblebeewolf (*Philanthus bicinctus*) aggregation—individuals near the aggregation produced half as many fruits as those far from the aggregation (Dukas 2005). The plants in these studies have several traits in common: They are all insect pollinated and either they are wholly dependent on pollinators (i.e., self-incompatible) or, if they are self-compatible, they have low reproductive success when pollinators are excluded (e.g., *M. officinalis*). Plants that are self-incompatible, prone to pollen limitation, or reliant on specialized pollinators are predicted to be more negatively affected by pollinator predators. Further, plants that depend on pollinators that are more susceptible to attack (i.e., smaller-bodied pollinators and/or taxa that are less able to detect and avoid predators) are also predicted to be more negatively affected by pollinator predators.

Pollen limitation is a measure of how pollen receipt impacts plant reproductive output. Similarly, declines in pollen export can also reduce plant fitness. Most plant species are hermaphroditic. Seed set represents only the female component of plant fitness. Plants also export pollen and thus sire seeds. This male component of plant fitness is much more difficult to quantify than the female fitness component; therefore, little is known about how pollinator predators affect plant male fitness. We expect that as pollinator visitation declines, pollen export, and therefore male fitness, will also decline.

5.2. Plant Mating System and Inbreeding Depression

Declining pollinator visitation could change the relative amount of outcross pollen versus self-pollen that fertilizes ovules. This is rarely quantified in the context of pollinator predators.

However, data regarding how other factors that disrupt plant-pollinator interactions, such as disturbance (Eckert et al. 2010) or habitat fragmentation (Aguilar et al. 2008), affect plant mating systems can be used to make predictions. We expect that decline in outcross pollen receipt in the presence of predators could affect mating systems by increasing the selfing rate of a population. Indeed, if a plant species is self-compatible and has no physical barriers to self-fertilization, ovules fertilized in the presence of predators could be primarily selfed. Chronic or unpredictable outcross pollen limitation can be a potent force in shaping reproductive traits of plants. Results may include the evolution of plant floral traits that are less attractive to pollinators (i.e., selfing-syndrome traits) (reviewed in Sicard & Lenhard 2011), changes in the mating systems of local populations (shifts along the spectrum of outcrossing, mixed, and selfing mating systems) (Stebbins 1974, Jain 1976, Wyatt 1983, Barrett et al. 1996, Fishman & Wyatt 1999), and ultimately declines in population-level fitness via inbreeding depression.

Additionally, it is possible that sit-and-wait predators directly affect seed set of self-compatible plants by facilitating the transfer of self pollen from anther to stigma while they hunt within a flower. If pollen adheres to the bodies of predators, it could be deposited onto a receptive stigma. Supporting this idea, we found that self-compatible *Calochortus luteus* flowers that harbored crab spiders produce more seeds than spider-free flowers, despite decreased pollinator visitation frequency and duration (A.D. Benoit & S. Kalisz, unpublished manuscript).

5.3. Altered Visitor Networks: Net Effects of Antagonists, Commensalists, and Mutualists

Many pollinator predators are generalist hunters who prey upon plant antagonists and commensalists in addition to pollinators and other mutualists. Therefore, the net effect of a predator's impact on plant fitness will depend on the relative strength of the predator's negative effect via suppression of plant mutualists and the predator's positive effect on plant fitness via suppression of plant antagonists. Predators positively impact plant fitness when their effect via antagonists is stronger than their effect via mutualists (Romero & Vasconcellos-Neto 2004, Romero & Koricheva 2011). For example, green lynx spiders hunt from the inflorescences of *Haplopappus venetus* (Asteraceae) and reduce both visitation and seed set; however, the spiders also decrease seed damage by antagonistic insects. Thus, plants harboring spiders produced more viable seeds than plants without spiders, despite reduced fertilization (Louda 1982). Similarly, a net neutral effect on plant fitness results when a predator's negative effect on plant fitness via suppression of pollinators is balanced by an equivalent positive effect via suppression of antagonists. For example, predatory frogs simultaneously suppressed herbivores and pollinators, leading to a net neutral effect and therefore no change in seed set of the Tibetan lotus *Nelumbo nucifera* (Zhao et al. 2016).

Importantly, usually only a small proportion of taxa that visit flowers are effective pollinators; other visitors consist of commensalists or antagonists that take floral resources while providing little to no pollination service to the plant in return. Predators may reduce foraging by visitors that are ineffective pollinators more than foraging by effective pollinators, thereby decreasing total visitation with little to no change in effective pollination service or seed set (Quintero et al. 2015, Telles et al. 2018). How predators affect visitation of effective pollinators versus other floral visitors is predicted to depend on taxonomic differences, including behavior, susceptibility, and sociality, as well as body size (Romero et al. 2011, Rusch et al. 2015).

Further, it is possible that predators increase plant seed set by increasing pollinator visitation of effective pollinators via lures and deception. This effect could potentially increase pollination and seed set; however, to our knowledge this has not been tested. This hypothesis would apply only to predators that hunt from flowers.

5.4. Integration of Predator Effects on Plant Reproduction

Pollinator predators exploit and disrupt plant-pollinator mutualisms. Predators can reduce the abundance of pollinators and alter their behavior, leading to fewer interactions between pollinators and plants. This affects plant reproduction in several ways. Plants export and receive less pollen, affecting female and male components of plant fitness. The proportion of plant ovules fertilized by self versus outcross pollen may be altered, which in turn could affect seed viability and offspring fitness through inbreeding depression as well as the amount of standing genetic variation within populations. Furthermore, predators may alter the network of interactions among plants and their mutualists, commensalists, and antagonists, thereby affecting both pollination services and plant and seed damage. Through these nonmutually exclusive mechanisms, pollinator predators can cause plant seed set to increase, decrease, or stay the same. However, an important caveat is that predator effects on seed set are not the complete story: We lack data on male fitness and on the proportion of seeds produced via self pollen versus outcross pollen and the consequent seed viability, offspring fitness, and genetic variation within populations. Much remains to be learned about the impact of predators on plant reproduction. For example, new insight into the evolution of selfing syndrome and outcross mating systems could be gained by incorporating pollinator predators into the theoretical framework of plant mating system evolution. Further, the study of plant demography and plant conservation could be advanced by incorporating predator effects, especially those of nonnative predators, on plant reproduction and population vital rates, such as seed production, recruitment, and survival.

6. THE EFFECT OF PREDATOR HUNTING MODE ON PLANT-POLLINATOR INTERACTIONS AND CONSEQUENCES FOR SELECTION ON PLANT TRAITS

Pollinator predators are a diverse group of animals. Differences among predators mediate their indirect effects on plants. We expect that predator hunting mode significantly affects the type of indirect interaction predators generate (Rinehart et al. 2017; A.D. Benoit & C.M. Caruso, unpublished manuscript). Predators vary in hunting mode along a continuum from sit and wait to active pursuit (Pianka 1966, Schoener 1971, Huey & Pianka 1981). Additionally, a predator's hunting location is predicted to impact how predators indirectly affect plants. Predators can attack pollinators at flowers, while in flight, or at the pollinator's nest or colony (**Figure 3**).

Active-pursuit predators are generally more mobile, are more conspicuous, and have higher prey-capture rates than sit-and-wait predators (Pianka 1966, Schoener 1971, Huey & Pianka 1981). Therefore, pursuit predators are expected to have larger effects on prey abundance and, consequently, to generate stronger DMII than sit-and-wait predators (**Figure 1**). In contrast, sit-and-wait predators are more cryptic, are largely stationary, and have low prey-capture rates (Pianka 1966, Schoener 1971, Huey & Pianka 1981). They are therefore expected to have a smaller effect on prey abundance than active-pursuit predators. However, because pollinators can learn to detect and avoid sit-and-wait predators (e.g., Ings & Chittka 2008), they are expected to generate stronger TMII (**Figure 1**). Similarly, predator hunting location is expected to affect the relative strengths of TMII and DMII. Predators that consume pollinators at their nests or colonies or consume queens are expected to have larger effects on pollinator abundance and generate DMII, while predators that prey upon pollinators while they visit plants are predicted to have a larger effect on pollinator foraging behavior and to generate TMII (**Figure 3**).

Sit-and-wait predators choose hunting sites with reliable prey availability, such as flowers (Yong 2005, Morse 2007, O'Hanlon et al. 2014), whereas active-pursuit predators generally capture prey in flight or at nests or colonies (Calvert et al. 1979, Dukas 2005, Meehan et al. 2005). When

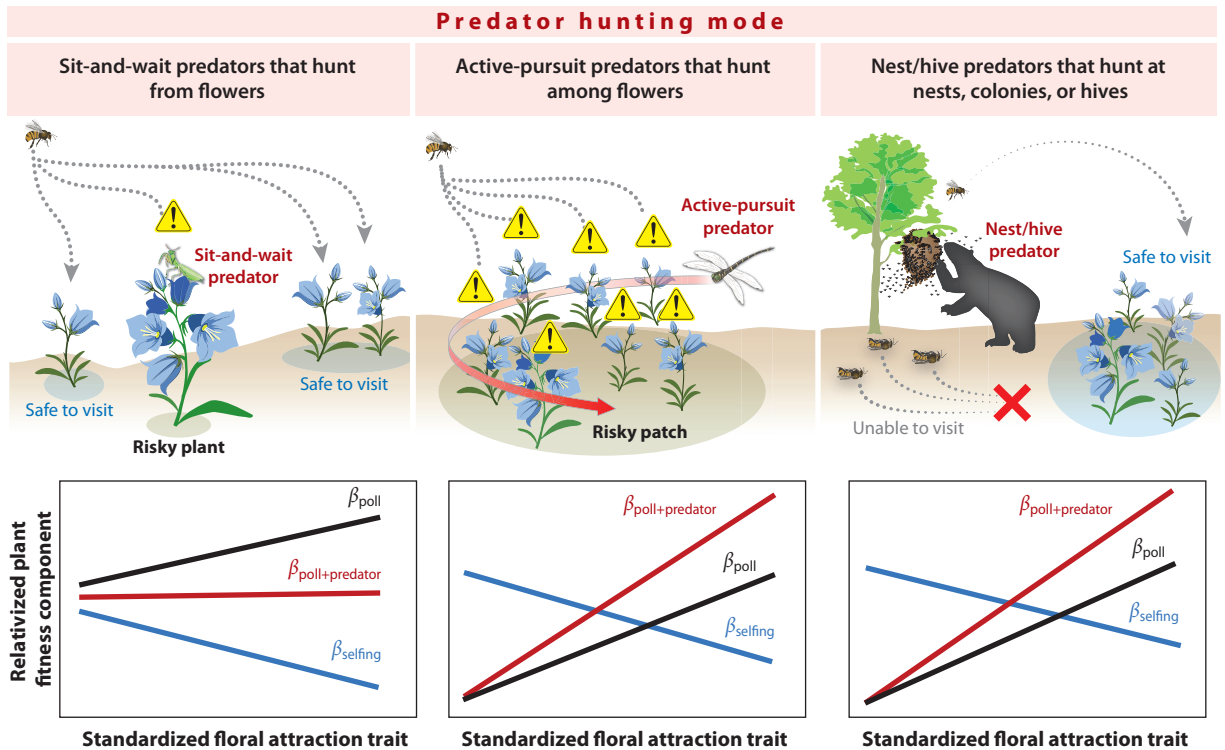


Figure 3

Predictions regarding how predator hunting mode and location affect pollinator behavior and abundance and how these interaction modifications affect the strength and direction of phenotypic selection on plant traits. Sit-and-wait predators are expected to hunt from plants with phenotypes that are highly attractive to pollinators, thereby making plants with highly attractive phenotypes risky for pollinators (risk indicated by *yellow warning signs*), while neighboring, less attractive plants will remain safe to visit. Sit-and-wait predators are expected to alter pollinator behavior more than pollinator abundance. Active-pursuit predators are highly mobile and hunt at the patch level; therefore, they are expected to make an entire patch of plants risky regardless of plant phenotype. Consequently, patches with active-pursuit predators are expected to have lower densities of pollinators. Note, this decrease in density may be caused by mortality or by altered foraging behavior, such as pollinators decreasing the amount of time they forage or choosing to forage elsewhere; in either case, from the plant's perspective, the abundance of pollinators in the patch will decline. Nest/hive predators do not make any plants risky to visit but will locally reduce pollinator abundance through mortality. In the absence of predators, pollinators generate selection for attractive and rewarding plant traits (β_{poll} ; *black line*). If outcross pollination is unreliable or costly and plants are self-compatible, there can be selection for self-pollination, which will favor smaller, less costly flowers (β_{selfing} ; *blue line*). Predators are expected to alter pollinator-mediated selection ($\beta_{\text{poll+predator}}$; *red line*). Sit-and-wait predators are expected to weaken selection for traits that attract pollinators, because these predators hunt from plants with attractive phenotypes and decrease their relative fitness. Conversely, active-pursuit predators will create competition among plants to attract scarce pollinators, thereby increasing the strength of selection on attraction traits.

sit-and-wait predators hunt from plants, pollinators can modify their behavior to avoid risky plants and visit safe plants instead (e.g., Jones & Dornhaus 2011). In contrast, active-pursuit predators patrol larger areas and are expected to decrease visitation both by consuming pollinators and by deterring pollinators from foraging in risky patches. Therefore, sit-and-wait predators are expected to decrease visitation to plants that harbor them and to increase visitation to neighboring safe plants, while active-pursuit predators are expected to decrease visitation more uniformly across plant patches (**Figure 3**). Similarly, predators that hunt at nests or colonies are expected to have a larger impact on pollinator abundance and a much smaller effect on foraging behavior and,

Interaction strength:
the per capita effect of
one species on the
fitness of individuals of
another species
combined with the
population size of each
species

therefore, are expected to cause a more uniform decrease in visitation to all nearby plants via a density-mediated effect (Preisser et al. 2007) (**Figure 3**).

Because sit-and-wait predators do not pursue their prey, they experience strong selection to choose profitable hunting sites where prey will come to them (e.g., Olive 1982). Hence, many sit-and-wait predators hunt from flowers that pollinators and other insects reliably visit. Visitation rates can vary greatly among flowers based on species, phenotype, phenology, and surrounding community. The clearest cue a predator can use to find a profitable hunting site is direct observation of prey (Morse 1988, Greco & Kevan 1995). In the absence of an observable, highly visited site, it is possible predators use indirect cues such as flower shape, color, and scent (Greco & Kevan 1994, Heiling et al. 2004, 2005a, Wignall et al. 2006, Peixoto et al. 2012, Dodson et al. 2013). However, it is debatable whether pollinator predators use associative learning (e.g., Defrize et al. 2014). It is perhaps more likely that sit-and-wait predators choose hunting sites by direct observation of prey when possible and randomly when direct cues are unavailable (Morse 1988; Greco & Kevan 1994, 1995; Defrize et al. 2014). Once a hunting site is selected, predators remain if prey availability is high but leave after a giving-up time if prey availability is unreliable (Morse 2007). Via direct cues and trial and error, predators locate hunting sites with high prey availability. Therefore, sit-and-wait predators are not expected to be randomly distributed across plant phenotypes. Instead, sit-and-wait predators are expected to be more common on plants with phenotypes that attract many pollinators and other visitors (i.e., plants with attractive phenotypes) (Jones 2010). For example, ambush bugs (*Phymata* spp.) hunt from *Lobelia siphilitica* plants with larger than average daily display sizes (A.D. Benoit & C.M. Caruso, unpublished manuscript), and crab spiders hunt from *C. luteus* with wider than average floral diameter (A.D. Benoit & S. Kalisz, unpublished manuscript). Since plants with more and/or larger flowers are well known to attract more visitors (Cohen & Shmida 1993), it is likely that pollinators and their predators use a common set of cues to choose flowers.

By hunting from plants with phenotypes that attract many visitors, sit-and-wait predators can affect the strength of pollinator-mediated selection on floral traits. Plants with traits that are attractive and/or rewarding to pollinators receive more visits, resulting in better pollination and higher fitness; thus, pollinators generate selection for increased attraction and reward. Sit-and-wait predators exploit the attractiveness of flowers to capture prey, and in the process, they decrease visitation to highly rewarding and/or attractive plants and increase visitation to safe, albeit less rewarding and/or attractive, neighboring plants (Jones 2010, Jones & Dornhaus 2011) (**Figure 3**). Therefore, we expect that sit-and-wait predators will weaken the strength of pollinator-mediated selection on plant traits that attract and/or reward pollinators. Supporting this hypothesis, A.D. Benoit & C.M. Caruso (manuscript in preparation) found that in the absence of predators, *L. siphilitica* experiences pollinator-mediated selection for larger daily floral displays; however, when ambush bugs are present the direction of pollinator-mediated selection reverses, and there is selection for smaller daily floral displays. Similarly, crab spiders were found to significantly alter the strength of selection on the width of *C. luteus* flowers (A.D. Benoit & S. Kalisz, manuscript in preparation).

Unlike sit-and-wait predators, active-pursuit predators are expected to decrease pollinator visitation more uniformly across their hunting range (**Figure 3**). Thus, we predict that active-pursuit predators will alter pollinator-mediated selection via a different mechanism than sit-and-wait predators. Active-pursuit predators are expected to decrease plant-pollinator interactions, leading to pollen limitation and reduced seed production. By weakening the interaction strength between plants and their mutualists and by decreasing mean plant fitness, active-pursuit predators are expected to increase the opportunity for selection and the maximum strength of selection (Benkman

2013). Therefore, we predict that selection on plant traits that attract and/or reward pollinators will increase in strength when active-pursuit predators are present (**Figure 3**).

Predators that consume pollinator's nests, colonies, or queens are expected to have little to no effect on pollinator foraging behavior but a large effect on pollinator density. Therefore, these predators are expected to affect plants via DMII similarly to active-pursuit predators. Furthermore, these predators could alter pollinator community composition, decreasing social pollinators that aggregate or store resources such as honey—an attractive target for predators—while having a negligible effect on solitary pollinators (for a review of nest predators of Asian bees and bee responses to nest predation, see Fuchs & Tautz 2011). Shifts in the pollinator community could affect pollen limitation and pollinator-mediated selection on plant traits.

Predators may also cause selection on plant traits that have functions other than attraction or reward. For example, predators may affect selection on flowering phenology. Dukas (2005) found that before bumblebeewolves (*P. bicinctus*) became active, bumblebee densities were equal near and far from the beewolf aggregation. However, after beewolves became active in July, the density of bumblebees near the aggregation was halved, and consequently, the fruit set of monkshood near the beewolf aggregation was also halved. While Dukas (2005) did not measure phenotypic selection on the plants, we predict that bumblebeewolves generate selection for earlier flowering phenology in monkshood populations near beewolf aggregations. To our knowledge, no field data exist regarding how predator phenology indirectly affects selection of plant phenology. Kagawa & Takimoto (2013) explored coevolutionary diversification among predators, pollinators, and plants in a simulation and found that predators promote divergence of plant-pollinator mutualisms. Further, Abbott (2010) suggested that flower color may evolve to better match sit-and-wait predator color in order to reduce the ability of pollinators to detect predators and thereby prevent decreased pollinator visitation when predators are present. Whether floral traits like petal color reflect a coevolutionary arms race between plants and the pollinator predators that hide in them is unknown. Indirect interactions have the potential to significantly shape phenotypic selection, but data on their effect on selection are rarely collected (Estes et al. 2013, Walsh 2013).

A further possibility is that predators may indirectly affect selection on plant mating systems. Selfing-syndrome plant species have evolved repeatedly from outcrossing taxa (reviewed in Sicard & Lenhard 2011). One hypothesis is that scarce and/or unreliable pollinators cause selection for autonomous self-pollination as a reproductive assurance (Sicard & Lenhard 2011). Predators that reduce pollinator abundance and foraging activity could lead to the type of unreliable pollination environment that may favor the evolution of selfing-syndrome traits. If predators make pollinators scarce, plants that can self-pollinate, and are therefore less reliant on pollinators, may have higher relative fitness. Thus, the advantage of costly pollinator attraction traits would diminish, and smaller, less costly flowers adapted for self-pollination would be favored (i.e., selfing syndrome) (**Figure 3**). The inclusion of indirect effects of predators on phenotypic selection could help us to understand patterns of mating-system evolution.

7. CONCLUSION

Plants are the foundation of food webs and thus interact with myriad other organisms at higher trophic levels. Primary consumers range from plant mutualists, such as pollinators, to plant antagonists, such as florivores. Primary consumers are nourished by plants and in turn provide nourishment to secondary consumers (i.e., predators). Since the 1960s, ecologists have recognized that predators can have profound indirect effects on plant populations and communities via plant antagonists; yet, understanding of how predators affect plant populations and communities via plant mutualists has lagged. Our goal in this review is to synthesize current knowledge regarding the effects of predators on pollinators and plants to spur interest and further investigation.

By better understanding the indirect effects generated by predation on pollinators, we will gain insight into the ecology and evolution of flowering plants. Plant-pollinator interactions form a vitally important keystone mutualism. These interactions drive diversification, provide much of the food humans rely on, and aid in maintaining genetic diversity within plant populations. We have learned much by studying pairwise interactions between plants and pollinators. Now, by understanding the role of predators in shaping these interactions, we can gain a more nuanced view.

We find ourselves at a critical juncture in history: We live in an unprecedented period of rapid extinction and global change caused by aggressive human exploitation of natural resources. Through the introduction of nonnative species, extinctions, and climate-driven range shifts, we have profoundly altered the composition of communities. Now as we scramble to conserve threatened native pollinators and plants, it is important to consider how higher trophic levels shape the behavior, abundance, reproduction, and demography of plants and their pollinators.

FUTURE ISSUES

1. We need a clearer understanding of how predator traits (e.g., hunting mode, hunting site, and prey preferences) and pollinator traits (e.g., sociality, cognitive ability, body size, and taxon) mediate the effects of predators on pollinator demography and, further, how pollinator demography impacts plant demography. The inclusion of pollinator and predator effect data as covariates in demographic models will provide insights into the magnitude of these effects.
2. Pollinator predators can significantly decrease pollinator visitation rates; however, the extent to which this indicates altered foraging behavior versus declining pollinator population size needs further investigation.
3. The presence of pollinator predators has been linked to decreased pollinator visitation and seed set, likely through pollen limitation, but the full impact of predators on plant reproduction needs further study to determine (a) if predators affect the male component of plant fitness, (b) if predators affect the proportion of self-pollinated versus outcross-pollinated seeds in self-compatible plant species, and (c) if predators affect the expression of inbreeding depression in plant populations. Manipulative experimental studies controlling indirect and direct effects of predators on plants are needed to answer these questions.
4. By altering the reliability of pollinators and the availability of outcross pollen, predators may be affecting the evolution of plant mating systems, potentially contributing to the maintenance of mixed mating systems or the transition from outcross mating systems to selfing mating systems. Manipulative experiments and studies across gradients of predator pressure will provide new insights.
5. If predators increase rates of self-pollination, they could affect the expression of inbreeding depression and decrease the amount of genetic variation within populations. Currently, we have no data to address these hypotheses.
6. Observational studies and manipulative experiments that measure the strength and direction of pollinator-mediated selection on plant traits under different levels of predator pressure will provide insights into how predators indirectly shape selection on plant traits.

7. The extent to which floral traits that both attract pollinators and attract and/or camouflage predators trigger an arms race is unknown.
8. Range shift due to climate change, introduction of non-native species, and expatriations and/or extinctions could affect predator-pollinator-plant interactions. Studies using areas with and without introduced predators and introduced pollinators can provide unique opportunities for quantifying how changes in community composition and species interactions alter plant fitness and trait evolution.
9. Humans pose the greatest threat to pollinators, and global pollinator decline is a major economic and environmental concern. Understanding how anthropogenic activities have altered predator-pollinator-plant interactions, as well as pollinator and plant demography, is an essential step in understanding how to manage conservation efforts effectively.
10. Studies that address how predators affect the network of primary consumer-plant interactions are needed to determine the net effect of predators on plant fitness, reproduction, and selection on plant traits.

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