Spiders do not affect fruit set in *Byrsonima intermedia* (Malpighiaceae)

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Considering the theoretical background of trait-mediated interactions, this investigation used artificial spiders to test for indirect effects of predator presence on fruit set in *Byrsonima intermedia* shrubs. The presence of models simulating a predation risk for insect visitors did not affect fruit set. Characteristics of the plant’s reproductive system, such as self-compatibility, local availability of visitors, and visitor behavior regulate the outcome of these interactions, potentially explaining the results obtained. For instance, regardless of the number of cross-pollination events – which are influenced by the presence of model spiders – the number of fruits remains unchanged because of self-pollination events. Moreover, this type of interaction requires the availability of a particular group of species in the community (i.e., a specific plant and its pollinators, which in turn have specific predators) – a combination of elements expected to render this occurrence uncommon. Trophic cascade effects caused by the presence of carnivores may therefore end up being overestimated due the lack of reports that describe the absence of this effect, which could bias our expectations about the generality of this kind of effect in nature.

**Introduction**

Because indirect interactions further understanding on the complexity of ecological systems, knowledge of these interactions is crucial in designing conservation plans and environmental management strategies (Wootton 2002). A common example is that of terrestrial habitats where predators trigger trophic cascades that have repercussions on plant reproductive success (Schmitz 1997).

Such trophic cascades are reported for a number of ecosystems and their strength varies not only with the predator and prey species involved, but also with the environment itself and the methodologies adopted. Most studies on terrestrial trophic cascades focus their positive effect on plant success consequential to the elimination of herbivores by predators, but over the past decade greater emphasis has been placed on understanding the effect of trophic cascades on the reproductive success of plants that depend on insect pollination (Romero & Koricheva 2011).

Foraging sit-and-wait insectivores tend to be found on entomophilous flowers, as these have evolved to attract pollinators, which are potential prey for these predators (Dukas & Morse 2003). Mantids, phymatids, and spiders are among the several sit-and-wait predators often found on these flowers (Halaj & Wise 2001), and many of
these predator species have developed remarkable similarities with the flowers they forage (Chittka 2001, Thery & Casas 2002). Noteworthy among spiders is the Thomisidae family, known to ambush insects on flowers (Morse 2007). Members of this family are commonly found on *Byrsonima intermedia* shrubs in the geographic area covered by the present study (Ribas et al. 2011).

The outcome of this type of trophic cascade for a given plant depends on the interaction between predators and floral visitors. Plant reproductive success can be enhanced by eliminating herbivores (Romero & Vasconcellos-Neto 2004) or altered, either positively or negatively, by the impact of predators on the mutualistic relationship between plant and pollinators (Suttle 2003, Dukas 2005). Among floral visitors, avoiding flowers with predators constitutes an adaptive behavior (Stoks et al. 2003) that may be related to recognition of predator morphological traits (Freitas & Oliveira 1996), aggressiveness (Ness 2006), or odor (Dicke & Grostal 2001).

Despite a number of studies on the mechanisms governing these interactions (e.g., Higginson et al. 2010), few have evaluated the net effect of trophic cascades on terrestrial plants, making it difficult to ascertain the extent of these cascades among ecosystems (Romero & Koricheva 2011). In the present study, spider models were experimentally used to evaluate the occurrence of indirect interactions capable of affecting fruit set in *B. intermedia*. Spider models allowed predation risk to be simulated on the flowers of this shrub in a Cerrado area undergoing forest regeneration.

**Methods**

An experiment was conducted in an area of Cerrado (*stricto sensu*) in Campo Grande, Mato Grosso do Sul, Brazil (20°26′36.6″S, 54°43′30.6″W), from 15 Nov. to 15 Dec. 2009. The area, now undergoing regeneration, harbors a large number of *B. intermedia* specimens ranging in height from 0.9 to 1.6 m (mean ± SD = 1.24 ± 0.25 m). The species has entomophilous self-compatible flowers that last for one day on average and develop into a drupe. Buttons in pre-anthesis and flowers produce oil and pollen that serve as resources for visitors (Oliveira et al. 2007).

For the experiment, spider models were constructed with copper wire and epoxy resin, similar to those used by Gonçalves-Souza et al. (2008). Each model was composed of two pairs of copper wire segments (approximately 50 mm long) twisted into a cross shape to simulate the eight legs of a spider. Two resin spheres (each approximately 5 mm in diameter) were attached to the center of the cross to simulate the head and abdomen (Fig. 1a). Yellow acrylic paint (Acrilex, São Bernardo do Campo, São Paulo, Brazil) was applied to the models to simulate a pattern of cryptic color on flowers.

In order to assess the effect of these model materials on fruit set, a model control was employed, which consisted of a resin sphere attached to a piece of copper wire, both coated with the same yellow paint but not resembling a spider’s body (Fig. 1b).

Each of 14 experimental blocks consisted of three inflorescences containing only green buttons developing on the same *B. intermedia* specimen. Each inflorescence within a single experimental block was given a different treatment—namely, spider model, model control, or control (i.e., no object attached to inflorescence). The models were placed next to the basal button of the inflorescence to simulate a foraging spider, but ensuring that visitor access to the inflorescence was not blocked.

For statistical analysis, fruit set (the response variable) was calculated as the number of fruits yielded on the inflorescence one month after the experiment was started, divided by the number of buttons found on each inflorescence at the beginning of the experiment. This ratio was arcsine square-root transformed to avoid circularity effects on analysis of variance (Sokal & Rohlf 1995).

Analysis of variance was performed on randomized blocks, considering each plant as one block. Each block was subjected to three treatments (spider model, model control, or control), which together represented the predation risk factor. R software (R Development Core Team 2010) was used for statistical analysis.
Results

Inflorescences bore 32 buttons on average (SD = 9), with a mean number of four fruits (SD = 4) per inflorescence. Mean fruit set was 0.19 (SD = 0.16) for spider models, 0.12 (SD = 0.12) for model controls, and 0.15 (SD = 0.12) for controls (Fig. 2). In statistical terms, the differences were non-significant (Table 1).

Published data on mean fruit biomass (n = 23 plants; Gonçalves-Souza et al. 2008) and seed yield (n = 10 branches; Louda 1982) in treatments with vs. without spiders have revealed that even samples as small as that employed in the present study (n = 14) can have sufficient statistical inference power to demonstrate the occurrence or otherwise of this indirect (plant–insect–spider) interaction. However, based on the power of the test (Crawley 2007) of our study, results indicated an absence of indirect effect of predation risk on fruit set in *B. intermedia* (β = 28%).

Discussion

In the geographic study area, spiders of families Thomisidae and Anyphaenidae are commonly associated with flowers of *B. intermedia* throughout the flowering period (Ribas et al. 2011), but the use of spider models revealed no trophic cascade effects derived from non-consumptive influence of predators on prey behaviors, known as trait-mediated interactions (Gonçalves-Souza et al. 2008). No differences were detected in
predation risk factor levels, in contrast with most published data (Romero & Koricheva 2011). For instance, the presence of spiders on *Haplopappus venetus* Blake (Asteraceae) decreased seed and fruit set (Louda 1982), while *Phox roemeriana* Scheele (Polemoniaceae) produced 38% fewer seeds in the presence of *Misumenops celer* (Thomisidae) (Ott *et al.* 1998). The use of models to represent the risk of predation by spiders also proved an effective method for testing the presence of trophic cascades that affect plant success, confirming a 42% reduction in the production of seeds in *Rubus rosifolius* (Rosaceae) (Gonçalves-Souza *et al.* 2008).

Several factors can mitigate the effects of trophic cascades on the reproductive success of *B. intermedia*. In this species, the decrease in visits by pollinators caused by the presence of spiders can be offset by self-compatibility, which permits fruit production by self-crossing, thus maintaining a steady level of fruit production per inflorescence. In the genus *Byrsonima*, however, spontaneous self-pollination does not usually lead to high fruit production (Sigrist & Sazima 2004).

A number of mechanisms operate to prevent self-fertilization in *B. intermedia*, including the spatial separation between anthers and stigmas and the presence of a stigmatic cuticle that prevents pollen adhesion — common features in Malpighiaceae (Sigrist & Sazima 2004). Nonetheless, decreased fruit set caused by pollen shortage — a result of self-compatibility — reduces the possibility of spider presence having a negative effect on fruit set through trophic cascades, as demonstrated by the model proposed by Higginson *et al.* (2010).

Flowering asynchrony in *B. intermedia* (Rocha Filho & Lomônaco 2006) can also affect fruit set. In the experiment, individuals bearing numerous fruits in inflorescences unselected for treatment might abort pollinated flowers located in inflorescences undergoing treatment, thus increasing variability in fruit set across individuals (Wise & Cummins 2008).

A further relevant aspect to be taken into account in interpreting the current results is visitors’ sensitivity to danger, important in predicting the end effect of this type of indirect (plant-insect-spider) interaction (Higginson *et al.* 2010), which varies across orders of insect visitors (Gonçalves-Souza *et al.* 2008) and even across species belonging to the same guild of visitors, as with bees (Dukas & Morse 2003). This sensitivity is particularly important in Malpighiaceae, given their well-known strong co-evolution with oil-collecting bees such as Apidae (formerly Anthophoridae). Bees of this family, having specialized on oil-producing flowers, are now the most efficient pollinators of the majority of Malpighiaceae species (Bunchmann 1987).

The behavior of *B. intermedia* pollinators — usually *Epicharis* sp. (Centridini) bees — includes a high frequency of visits and adoption of a trapline strategy. Although under natural conditions this behavior may contribute to an overall high fruit set and similar yields across inflorescences (Sigrist & Sazima 2004), quantification of its effect would require experiments involving different treatments for each plant. However, experiment designs not based on blocks also have drawbacks, such as differences in fruit set results stemming from differences across individuals.

Achieving the evolutionary benefits of this type of interaction requires availability of a particular set of species in the community, which is probably a rare occurrence in most biological communities. Variability in environmental conditions and in strategies adopted by the species involved in the interaction leads to fluctuation in the effect that trophic cascades have on pollination (Romero & Koricheva 2011). Based on

| Table 1. Analysis of variance of fruit set relative to predation risk factor (levels: spider model, model control, and control) and plants (blocks). |
|----------------|----------------|----------------|---|---|
| Degrees of freedom | Sum of squares | Mean of squares | F | P |
| Treatment | 2 | 0.106 | 0.053 | 1.205 | 0.316 |
| Plant | 13 | 0.750 | 0.058 | 1.312 | 0.268 |
| Residual | 26 | 1.143 | 0.044 | | |
simulations, Gomulkiewicz et al. (2003) demonstrated that the relationship between species may change from mutualism to antagonism in a stochastic manner when a natural variability of strategies is available to generate both mutualism and antagonism.

Further studies that include variations both in sites and plant species are needed to broaden the current understanding of indirect interactions. Conservatism of floral morphology among Malpighiaceae (Bunchmann 1987) may be a feature warranting investigation. The presence of these plants in a range of habits (e.g., lianas, shrubs, or trees) in different ecosystems makes this group a promising model for experimentation and for determining the extent of trophic cascades in terrestrial ecosystems.

References


