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A meta-analysis of physiological and behavioral responses of parasitoid wasps to flowers of individual plant species

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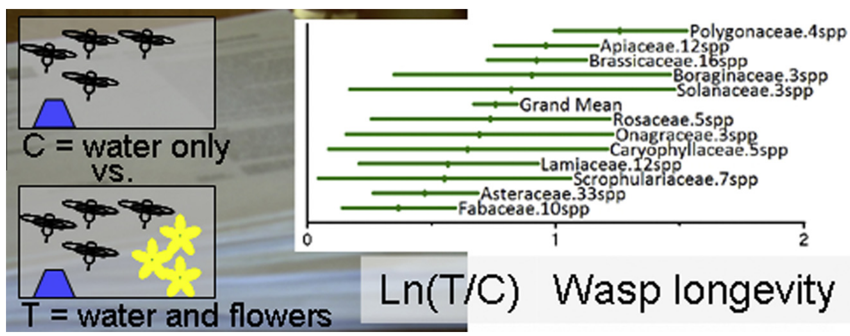
HIGHLIGHTS

- Wasp longevity trials have measured physiological responses to 120 plant species.
- Attraction studies have tested for wasp behavioral responses to 104 plant species.
- Species in Brassicaceae and Apiaceae plant families tended to increase wasp longevity.
- Some species of Asteraceae and Lamiaceae increased wasp longevity but others did not.
- Plant species in the Chenopodiaceae and Amaranthaceae did not increase wasp longevity.

GRAPHICAL ABSTRACT



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ABSTRACT

This meta-analysis summarizes published information on the use of various plant species by parasitoid wasps. Trials measured either a physiological response such as wasp longevity when supplied with flowers from a single plant species, or a behavioral response like attraction of wasps to field plantings. The log response ratio was the effect size used to standardize estimates and meta-analyses were conducted to make overall estimates for plant species included in multiple trials. Physiological response trials have been conducted on 126 different plant species and behavioral response trials tested 104 plant species. The log response ratio of different plant species ranged from 0 to 2.7 for longevity, and up to 4.1 for attraction. The longevity response ratio estimate is equivalent to a nearly 15-fold increase in the ratio of days longevity with the flower to days longevity in the starvation control. Wasp longevity increased the most with plants in the Polygonaceae, Apiaceae, Brassicaceae, Boraginaceae, Solanaceae, and Rosaceae. Plant species in the Onagraceae, Caryophyllaceae, Lamiaceae, Scrophulariaceae, Asteraceae, and Fabaceae tended to slightly increase wasp life spans, but their effect was lower and less consistent among species. There were a number of families which did not increase wasp longevity over the controls at all such as Chenopodiaceae. This review can help identify plant species which have been proven to supply nectar for parasitoids for potential use in a conservation biological control program, but plant selection should not be limited to the small list of species that were included in these studies.

1. Introduction

Parasitoid wasps occur worldwide and can be a significant mortality factor in pest populations (Wearing et al., 2012; Keasar and Steinberg, 2008). Most parasitoid species depend on floral nectar to complete part of their lifecycle (Syme, 1975; Idris and Grafius, 1995). Parasitoid wasps need to eat frequently to avoid starvation, and many species have increased longevity and fecundity when provided with floral resources (Baggen and Gurr, 1998; Siekmann et al., 2001). A variety of crops, weeds, and wild plants can occur

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on agricultural landscapes, but not all of these species provide resources for parasitoid wasps. Some of the plant species do not produce nectar, while others may have long or complicated corollas that can limit nectar availability for small wasps and other short mouthed insects (Baggen et al., 1999; Arévalo and Frank, 2005; Vattala et al., 2006). Even plant species with accessible nectar may vary in the quantity and nutritional characteristics of the floral resource such as the sucrose to hexose ratio of the nectar (Koptur, 2005).

Agricultural plant communities can be assessed for whether there are plant species that produce nectar available to foraging parasitoid wasp adults. Plants that do not produce any nectar or species which produce nectar inside flowers that hinder access for wasp sized insects generally would not provide available floral resources for parasitoid wasps. Species that produce flowers with accessible nectaries would be the most likely source of nourishment for adult wasps on the landscape. There is a growing body of literature that reports direct tests of the suitability of specific floral resources for parasitoid wasps. The literature is diverse and scattered, making it difficult to use it to comprehensively evaluate the suitable floral resources available in agricultural landscapes. The goal of this study was to synthesize the body of literature and to provide estimates of the relative parasitoid resource suitability for a range of floral types. I met that goal by answering two main questions with a meta-analysis of the available literature. First, I estimated the effect of flowers from different plant species on parasitoid longevity relative to a starvation control. Second, I estimated the relative attractiveness to parasitoid wasps of flowers from different plant species. I also answered both questions with respect to different plant families.

2. Methods

2.1. Literature selection

The objective of the literature search was to compile the results of direct tests on the use of specific plant species by parasitoid wasps. There were two major types of investigations frequently conducted to answer that question, physiological response trials and behavioral response trials. Longevity trials are the most common physiological response trial and involve enclosing individuals or groups of parasitoids with flowers from a single species of plant and measuring the duration of survival of the wasps. In some of the longevity trials the mean number of eggs produced by each female wasp was also measured, providing a more in depth look at the nutritional benefit of the nectar. However, the number of plant species tested in fecundity trials is limited and so this review focuses on the more commonly conducted longevity trials. Behavioral response trials include both observations of wild parasitoids being attracted to plantings of different species in a common garden and studies of insect response to flowers in the lab.

The review of parasitoid physiological responses was limited to trials that estimated the ability of flowers of a plant species to increase the longevity of parasitoid wasps. The trials used a water only control to determine how long the species could live without food and compared that with the survival of insects with access to flowers of a single plant species. In many studies, a sugar water or honey water positive control was also included, but that data was not used in this analysis. The experiments used either excised flowers, or they enclosed the insects with just the flowers of a rooted plant. Previous research suggests that results from either type of study are comparable, so both types of studies were included in this review (Wade and Wratten, 2007).

The goal of the review of parasitoid behavioral response studies was to compare how well flowers of a plant species can attract parasitoid wasps in relation to other plant species. Behavioral response studies provide less conclusive evidence than tests of physiological performance because insects may also respond to colors or smells of the flower that do not necessarily indicate that there is available nectar (Slater and Calder, 1988). The attraction studies included in this review reported the number of parasitoids attracted to plants in the field, or they compared the response of insects to flowers in the lab. This review focuses on the responses of parasitoids to whole flowers, so it did not include olfactometer studies.

Initial searching for longevity or attraction studies involved using online databases (i.e., Web of Science, Agricola, Google Scholar) to find articles using search terms including but not limited to "parasitoids and longevity", "parasitoids and attraction", or "parasitoids and flowers". Substituting a variety of synonyms and different phrasings maximized the number of articles identified. The works cited sections of articles found in the original searches provided additional candidate articles. I also received recommendations of articles I did not identify on my own from scientific colleagues.

Many of the articles reported results from multiple trials. Within articles, each plant species tested was considered a single trial. If multiple wasp species were tested, each plant species – wasp species combination was also considered a separate trial. Some articles included more than one round of experimentation so there were multiple tests of the same plant – wasp combination. In this meta-analysis, each test was considered an independent trial. There were a number of plant species that were tested in more than one article, with more than one wasp species, or multiple times in one article. These species were included in multiple independent trials so I was able to conduct a meta-analysis to estimate the mean effect size across studies for the plant species. The meta-analysis did not include plant species tested in a single trial, but I report the standardized effect size that was calculated for that trial. For genera that included more than one species which was represented in only one study, the unreplicated species were grouped and a meta-analysis was done on those species in the genus. The species used to calculate the genus groups do not include any species of the genus that had sufficient replication to be meta-analyzed separately.

2.2. Data collection and analysis

2.2.1. Effect size selection

I chose the log response ratio [ln(treatment mean/control mean)] as the effect size to use in the meta-analysis (Hedges et al., 1999). The log response ratio is scaled to the value of the control for each wasp species so it takes into account differences in the life histories of the wasp species that are being tested. When there was no difference in response between the flower treatment and the control, the effect size is zero. Positive effect sizes indicate an increase in the treatment response with respect to the control.

This review compares numerous plant species tested in studies with a variety of experimental designs. Many of the longevity studies had nested replication (multiple wasps in each replicated experimental unit). This resulted in inconsistencies in how the sample size was calculated between studies. The log response ratio was chosen because it is a measure of the actual difference in responses scaled to the control mean. Other effect sizes are scaled to the pooled variance, which is important when trying to determine the statistical significance of a result. However in this review the goal was to make comparisons between species, which is much more straightforward with an effect size scaled to the control mean. Another advantage of the log response ratio is that it is not adjusted by sample size, which could be misleading due to the nested replication and different meaning of reported sample