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Contents lists available at ScienceDirect

Biological Control

journal homepage: www.elsevier.com/locate/ybcon

Conserving natural enemies with flowering plants: Estimating floral attractiveness to parasitic Hymenoptera and attraction's relationship to flower and plant morphology

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ARTICLE INFO

Article history:

Received 21 July 2010

Accepted 3 May 2011

Available online 10 May 2011

Keywords:

Attractants

Native plants

Malaise trap

Biological control

Landscape modification

Organic gardening

Conservation

ABSTRACT

Flowering plants in agricultural landscapes can provide ecological services, such as nectar-provision for adult parasitic Hymenoptera. Various flowering native, introduced/established and cultivated potted plants were used to bait interception traps along the wooded margins of fields planted seasonally with either feed-corn or rye. Depending on circumstances, controls consisted of traps baited with the same species of plant without flowers, a pot/area without plants, or both. In most cases pots were rotated among trap-sites. Of the 19 plant species tested, 10 captured significantly more summed ichneumonoids and chalcidoids, seven more Braconidae, two more Ichneumonidae and six more Chalcidoidea than controls. Among Braconidae, traps baited with certain plants captured significantly more individuals of specific subfamilies. “Attractive” and “unattractive” plant species tended to cluster in a principal components vector space constructed from plant morphological characteristics (flower width, flower depth, flower density and plant height). Flower width and plant floral-area (flower width² * flower density) were the variables that most often explained the variance in capture of the different parasitoid taxa. Our study identified particular plants that could be incorporated into regional conservation biological control programs to benefit parasitoid wasps. In addition, the results indicate that morphological characteristics might help identify further suitable plant candidates for agricultural landscape modification.

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1. Introduction

Insect predators and parasitoids are estimated to provide US agriculture with ~\$4.5 billion worth of pest control annually (Isaacs et al., 2008), and this value could be increased by manipulating the plant diversity of agricultural landscapes (e.g., Landis et al., 2000; Wilkinson and Landis, 2005). For example, the addition of plants that adult parasitoids require for shelter, food and alternative hosts may concentrate and increase parasitoid populations (Root, 1973) and help preserve a “library” of natural enemies that would be on hand to suppress new invasive pests (LaSalle, 1993; Cornell and Hawkins, 1993; Marino et al., 2006).

Flower-provided adult food for parasitoids is one of the principal benefits of the diversification of agricultural environments (Wäckers et al., 2005). Hymenopteran and dipteran parasitoids often feed on nectar, and occasionally pollen (Syme, 1975; Jervis et al., 1993; Landis et al., 2000). Nectar provides a valuable source

of carbohydrates, often the only source available (Wäckers et al., 1996), and is even consumed by those that host-feed (Jervis and Kidd, 1986). Floral feeding increases the longevity, fecundity and parasitism rates of certain wasps in the laboratory (Zhao et al., 1992; Idris and Grafius, 1995), in field cages (Dyer and Landis, 1996) and in the field (Zhao et al., 1992). While an experimental demonstration that sugars from flowers planted in agricultural settings contribute directly to pest suppression has proven to be a complex and difficult task (Lee and Heimpel, 2005), there is considerable circumstantial evidence that this is the case (Heimpel and Jervis, 2005).

However, not all parasitic Hymenoptera are able to exploit all the nutrients provided by specific flowers. Pollen feeding appears to be uncommon among parasitoids (Jervis et al., 1992), and in the case of nectar, the generally short mouthparts of most parasitic Hymenoptera restrict them to exploiting flowers with short corollas or with exposed nectaries (Patt et al., 1997). Some flower species also possess guard hairs which only allow access to certain parasitoids (Beattie, 1985; Jervis et al., 1992, 1993; Sivinski et al., 2006).

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Just as not all flower-resources are accessible, neither are all flowers attractive. For example, volatile compounds vary greatly among plant species (Dudareva et al., 2000), and insects presumably attracted to specific odor complexes also vary greatly at the level of species, family and even order (Pellmyr, 1986). Some plants such as *Ficus* sp. attract a single species of fig wasp (Agaonidae), while at the other end of the spectrum, species of the family Apiaceae often attract Hymenoptera from multiple families (e.g., Jervis et al., 1993). In addition to volatiles, flower color and the size of the floral display are important components of visual attractiveness (Kevan, 1972; Begum et al., 2004; Fielder and Landis, 2007a,b).

Given the known variance in the attractiveness of flowers, and presumably in their ability to hold insects in their vicinity because of differences in nectar-accessibility, we used interception traps to evaluate the differences in the parasitic Hymenoptera associated with a variety of Florida-native, introduced/established and cultivated flowering plants. We emphasized native and successfully established plants, postulating they would require less care under local conditions. In some cases we had observed unusual degrees of insect activity on their blossom and others were believed to be well suited to agricultural environments; i.e., they flourished in open, disturbed habitats along field margins. In the following we have identified the captured Ichneumonidae to genus and often species, Braconidae to subfamily and Chalcidoidea to family, and related their capture to flower density, width, depth and height above ground. Such information will serve as a foundation for a predictive model to help growers choose plants to enhance parasitoid-based biological control within their crops (Fielder and Landis, 2007a,b).

2. Materials and methods

2.1. Plants examined

Plants were purchased from commercial nurseries, principally Micanopy Wildflowers (Micanopy, FL), a specialist in growing native plants. All potted plants were grown in 4 l plastic containers. Depending on the weather, plants were either maintained on the grounds of the USDA, Center for Medical, Agricultural and Veterinary Entomology (CMAVE), Gainesville, Florida or in a greenhouse at the same site. In the absence of rain, all plants were watered daily at CMAVE or every other day when in the field. Fertilizer (slow release 19N-6P-12K) was applied as needed to plants obtained be-

fore flowering. Some plant species were growing *in situ* (see Section 2.6 below) and received no maintenance. The plants used to bait traps are listed in Table 1.

2.2. Malaise traps

The numbers and kinds of natural enemies, ichneumonoid or chalcidoid, attracted to various plants and their controls were compared by placing flowering plant-baited traps along a field margin. Insects were collected in Malaise traps (BioQuip Products Inc. Rancho Dominguez, CA, model 2875D) based on the Townes pattern and designed to be particularly effective in the capture of parasitic Hymenoptera (Entomological News 83:239–247, 1962). Traps were constructed of a dark green fine mesh (10 threads/cm) (Townes, 1962) and measured 1.8 m long by 1.2 m wide. Collecting heads were located at the top of a 1.8 m aluminum pole on one end of the trap and this end was oriented to the southwest. These heads (BioQuip Products Inc., model 2875 WDH) were opaque and measured 140 mm wide by 215 mm tall with a 19 mm diameter opening for insect egress. Ethanol (95%) was added to a depth of 2–3 cm in order to preserve the trapped insects.

2.3. Insect curation

All Ichneumonoid and chalcidoid parasitoids were mounted on points and labeled with location information, including GPS coordinates and the associated flower (or control). All insects have been retained in the authors' collections at CMAVE and AEI.

2.4. Floral measurements

The width and depth of ten randomly chosen flowers, completely open, were measured under a binocular microscope with a stage micrometer (5 mm wide with divisions of 0.1 mm). Depth was considered the distance from the margin of the flower's petals to the underside of the calyx. Width in radially symmetrical flowers was simple corolla diameter. In bilaterally symmetrical flowers, width was the shorter of the two axes. Flower density was estimated using an open plastic quadrat with inner measurements of 15 × 15 cm. The quadrat was randomly tossed five times onto a patch of plants and all the flowers counted within its boundaries regardless of where they occurred along the height of the plant.

Table 1

The species, common name and family of the tested plants, as well as the Julian date of the start of tests.

Species	Common name	Family	Julian date
Agastache hybrid	Blue fortune anise hyssop	Lamiaceae	177
<i>Ageratina aromatica</i> (L.) Spach	Lesser snakeroot	Asteraceae	319
<i>Aloysia virgata</i> (H.R. Lopez & J.A.Pavón.) A.L. de Jussieu	Almond bush	Verbenaceae	212
<i>Buddleja davidii</i> Franch.	Orange eye butterflybush	Buddlejaceae	212
<i>Calamintha nepeta</i> (L.) Savi	Lesser calamint	Lamiaceae	150
<i>Conoclinium coelestinum</i> (L.) DC.	Blue mist flower	Asteraceae	266
<i>Daucus carota</i> L.	Queen anne's lace	Apiaceae	142
<i>Galium aparine</i> L.	Stickywilly	Rubiaceae	83
<i>Geranium carolinianum</i> L.	Crane's bill	Geraniaceae	79
<i>Lobularia maritima</i> L.	Alyssum	Brassicaceae	102
<i>Monarda punctata</i> L.	Dotted horsemint	Lamiaceae	251
<i>Pityopsis graminifolia</i> (Michx.) Nutt.	Narrowleaf silkgrass	Asteraceae	272
<i>Phyla nodiflora</i> (L.)	Greene turkey tangle fogfruit	Verbenaceae	242
<i>Raphanus raphanistrum</i> L.	Wild radish	Brassicaceae	74
<i>Sisyrinchium angustifolium</i> P. Mill	Narrow leaf blueeyedgrass	Iridaceae	91
<i>Solidago fistulosa</i> P. Mill	Pinebarren goldenrod	Asteraceae	247
<i>Spermacoce verticillata</i> L.	Shrubby false buttonweed	Rubiaceae	120
<i>Stachys floridana</i> Shuttleworth	Hedge nettle	Lamiaceae	98
<i>Stellaria media</i> (L.)	Villars chickweed	Caryophyllaceae	43

Plant height was sampled 10 times and in the case of potted plants the height of the pot was included in total height.

2.5. Trap sites and flower placement

Trapping was done at various locations on the grounds of the University of Florida Dairy Research Unit in Hague, Florida, Alachua County. Traps were placed along the interface of deciduous trees/associated undergrowth and fields used to grow corn or rye (*Zea mays* L. and *Secale cereale* M. Bleb) in rotation (in the vicinity of 29° 47.332 N, 082° 25.012 W). Unless traps were placed in patches of wild, *in situ* plants (see below), they were erected in the center of a 5 m × 5 m piece of black plastic weed-cloth that prevented other plants from growing in the immediate vicinity of the traps. Wild plants were regularly mowed or cut down within 3 m of the weed-cloth trap sites. All sites were cleared simultaneously prior to flower inclusion in order to minimize any effect of wounded-plant volatiles on insect captures.

2.6. Trapping protocols

Several different trapping protocols were used depending on the availability of flowers and their occurrence either as growing *in situ* in the field or growing in pots. Three experimental designs were used and, as explained below, they varied in their capacity to provide unambiguous evidence of the attractiveness of flowers alone as opposed to entire flowering plants. In order of increasing confidence, these were:

(1) *Trapping with flowers in situ, followed by their removal*: We occasionally found limited numbers of sites where plants in the field occurred in homogeneous clumps large enough in our estimation (~5 m × 5 m) to erect traps in their midst's. In order to estimate the homogeneity of a patch, all the vegetation in a 1 m long × 30 cm wide transect was collected, sorted to species and weighed (wet weight). All of the patches used in the experiment were >90% monospecific by weight and none had plants in bloom other than the focal species. As in other protocols, random samples of flower density, height, width and depth were taken by the means described previously. To estimate parasitoid attraction in these situations, we initially compared insects trapped in the flower-patch with a control that consisted of a Malaise trap set in the center of a 5 m × 5 m sheet of plastic weed-proof cloth placed where the flowers had occurred before being mowed down. Collections continued as long as practical, at least 1 week, where time was limited by decline in target-plant flowering or the invasion of another plant into the patch that could compromise results. Following this series of collections, the flower patch was mowed and replaced by a 5 m × 5 m sheet of weed cloth, and collections continued from the former flower site and original control site. In this way, parasitoids captured in contemporary sites with and without a particular flower could be compared to the parasitoids captured in the same two sites with flowers in neither. In two instances, *Galium aparine* and *Stellaria media*, an additional site was added to the experiment, one that was left in bloom after the treated site was mowed. This allowed us to compare changes in insect capture to any change in floral abundance/attractiveness. Data analysis was by contingency χ^2 Test with site and collection period defining the contingency table (Zar, 1974). In essence this compared the ratio of insects trapped in time 1 and 2 at sites where there were plants under the traps at time 1, but not time 2, to sites where no plants were present at either time (or in the specific cases addressed above, sites where plants were always present). While this tested for capture differences with different flower baits and for differences in different time periods and locations, the interactions of time and space could not be addressed. Because plants with and without flowers were not examined separately, significant differ-

ences in the ratios could not demonstrate floral attraction. Other plant parts and plant-induced micro-environments, e.g., shade and wind-shelter, could also be responsible for higher trap catches. None of the plant genera we tested are described as having extrafloral nectaries (Keeler, 2008), and we inspected plants during trap rotations and took care to remove any of the rarely found honey-dew producing insects.

We felt this was the weakest of our protocols, and because of this we attempted to duplicate results obtained in an earlier and more rigorously controlled experiment with our new design. Rohrig et al. (2008a) using rotations of species of potted plants and a blank control (see below), found that *Lobularia maritima* attracted significant numbers of small ichneumonoids, particularly opiine braconids. Potted *L. maritima* remained at one site and another was used continuously as a control. Following five 48 h long collections, the plants were removed, and five more collections were made with both sites. After obtaining a significant difference in the ratios of braconids captured over the two time periods at the two sites (see Section 3), we proceeded to adapt this experimental design to other, *in situ* flowers (Table 1). These included: *G. aparine* (no-flower control and flower-control), *Raphanus raphanistrum* (no-flower control), *Stachys floridana* (no-flower control), *Geranium carolinianum* (no-flower control), and *S. media* (flower-control and no-flower control).

(2) *Rotation of flowering plants and no-plant controls between sites*. Fifty flowering plants were rotated between two weed-cloth prepared sites 3–6 times (6–12 collection replicates). Plants examined in this manner were: *Sisyrinchium angustifolium*, *Aloysia virgata*, *Buddleja davidii*, *Calamintha nepeta*, and *Phyla nodiflora*. In the case of *S. angustifolium*, an additional site was added to the rotation in order to compare a blank control with a control that consisted of a pot with soil but no plant. In another instance, *A. virgata* and *B. davidii* were simultaneously compared to a blank control. As in the previous design, the flowers were not examined separately from the plants themselves so that significant differences in captures were interpreted as flowering-plant, not floral, attraction. Data analysis was by t-test (SAS Inst., 2009), except in the cases of *S. angustifolium* and *A. virgata*/*B. davidii* where mean captures were compared by Analysis of Variance (ANOVA) followed by Waller's mean separation test (SAS Inst., 2009).

(3) *Rotation of flowering plants, non-flowering plants and no-plant control*: The design that provided the best estimation of floral attraction compared a control with plants both in and out of flower. Species examined in this manner were: *Ageratina aromatica*, *Conoclinium coelestinum*, *Daucus carota*, *Pityopsis graminifolia*, *Monarda punctata*, and *Solidago fistulosa*. As above, potted plants were rotated among set sites for at least 6–9 replications, each typically 48 h long unless inclement weather prolonged a particular replication. It was sometimes necessary to remove flowers from certain plants. In order to make volatiles that might be emitted by damaged foliage as similar as possible in the different treatments, a comparable amount of tissue was cut from those plants that retained their flowers. Mean captures of ichneumonoids and all chalcidoids were compared by ANOVAs followed by Waller's mean separation test (SAS Inst., 1992).

(4) *Additional analyses*: Sufficient numbers of the braconid sub-families, Alysiinae, Braconinae, Microgastrinae and Opiinae were captured at some flowers to attempt analysis of floral attractiveness at this finer taxonomic level. These smaller numbers of more sporadically captured individuals were summed by treatment and compared by χ^2 test (Zar, 1974). The same analysis was applied to specimens of the chalcidoid family Eulophidae captured in *C. coelestinum*-baited traps.

Table 2

Summary table of the flowers tested: the numbers of parasitoids captured, plant status as a native, introduced and established or exotic and present only under cultivation, and morphological features of the flower (width, depth and density [#/15 cm²] and plant (ht.).

Flower	Total	Ichneumonid	Braconid	Chalcid	Native	Introduce	Cultivated	Width	Depth	Density	ht.
<i>Agastache hyb</i>	139	55	56	28			X	4.6	7.1	486	76.3
<i>Ageritina aromatica</i>	156	23	48	86	X			2.1	9.1	1404	86.8
<i>Alloysia virgata</i>	92	43	26	22		X	X	2.8	6	7.4	52.8
<i>Buddlja davidii</i>	92	43	26	22			X	8.2	9.7	48	68.5
<i>Calamintha nepeta</i>	316	130	102	84			X	4.7	1.9	138.8	52.5
<i>Conoclinium coelestinum</i>	383	69	102	212	X			0.5	4.1	791	52.3
<i>Daucus carota</i>	263	112	88	63		X		2.2	0.1	84.4	69.3
<i>Galium asperine</i>	205	124	68	13	X			2.4	0.1	108	32
<i>Geranium carolin</i>	183	106	77	0	X			4.6	3.3	9.3	43
<i>Lobularia maritima</i>	354	198	151	5			X	6.7	1.4	316	31.8
<i>Monardia punctata</i>	165	53	93	19	X			4.1	7.3	10.4	120.2
<i>Phyla nodiflora</i>	136	25	89	22	X			2.6	0.8	70.8	29.5
<i>Pityopsis graminifolia</i>	189	66	86	37	X			0.5	5.7	235.6	79.1
<i>Raphanus raph</i>	151	.	.	.		X		7.4	17.2	24.3	48
<i>Sisyrinchium angustifolium</i>	367	181	139	47	X			19.4	2	3	32.3
<i>Solidago fistulosa</i>	176	61	97	18	X			0.5	4.8	928	140.2
<i>Spermacoce verticillata</i>	798	514	284	0			X	1.3	1.1	186	59.1
<i>Stachys floridana</i>	112	.	.	.	X			9.3	7.7	28.6	40.3
<i>Stellaria media</i>	343	98	203	42		X		4.6	1.8	50	25

3. Results

3.1. Estimates of attraction

In total, 4528 ichneumonoids and chalcidoids were captured, with the numbers per flower included in Table 2. In 10 of the 19 plant species tested, the combined ichneumonoids and chalcidoids were significantly more abundant in traps baited with flowers than in controls (Fig. 1). Because of incomplete early curating, three plant species, *G. carolinianum*, *R. raphanistrum*, and *S. floridana*, were removed from analyses of lower taxonomic levels (Fig. 2). Only two of the 16 remaining plants attracted Ichneumonidae, but seven were associated with greater numbers of Braconidae. In another three plants, numbers of chalcidoids were too small to analyze (zero, zero and five insects captured, respectively). Of the remaining 13 species, six had significantly more parasitoids associated with flowers than with controls. In no instance, at any taxonomic level, did controls capture significantly more parasitoids than flower-baited traps.

Among the Braconidae there were instances of greater flower-baited capture in all four of the most commonly collected subfamilies. The summed Braconinae taken at flowering *M. punctata* were significantly more abundant than those captured at non-flowering plants ($\chi^2 = 11.4$, $df = 1$, $p < 0.005$), and flowering *D. carota*-baited

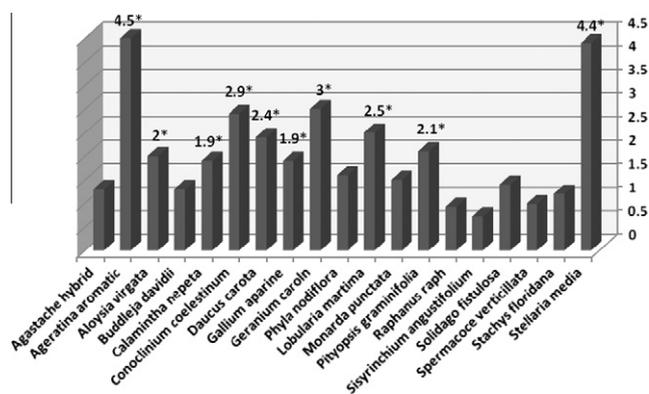


Fig. 1. The ratios of the summed hymenopteran parasitoids captured over flowering plants divided by the most conservative control. An * represents a significant difference between or among treatments.

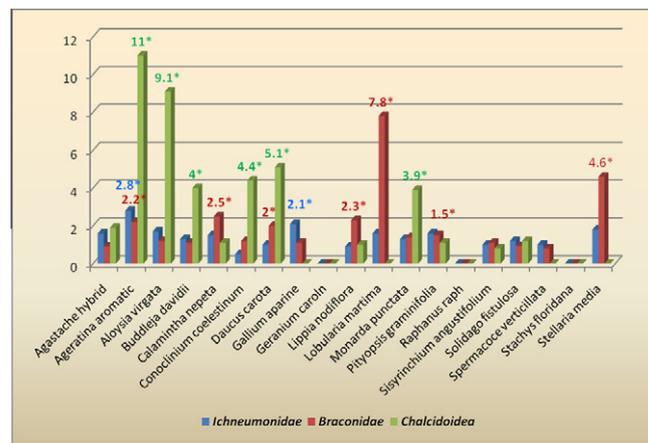


Fig. 2. The ratios of various parasitoids (see color codes in figure) captured over flowering plants divided by the most conservative of the control. An * represents a significant difference between or among the treatments.

traps caught substantially more braconines than did non-flowering traps ($\chi^2 = 3.3$, $df = 1$, $p < 0.10$). *L. maritima*- baited traps captured significantly more Opiinae ($\chi^2 = 58.0$, $df = 1$, $p < 0.001$) and Alysiiinae ($\chi^2 = 8.6$, $df = 1$, $p < 0.005$). Significant numbers of Microgastriinae were collected in traps baited with *P. nodiflora* ($\chi^2 = 10.2$, $df = 1$, $p < 0.005$), *A. aromatica* ($\chi^2 = 5.7$, $df = 1$, $p < 0.01$) and *D. carota* ($\chi^2 = 10.3$, $df = 1$, $p < 0.005$). Lack of significant captures sometimes reflected small sample sizes. The sole chalcidoid sample large and homogeneous enough for analysis, Eulophidae on *C. coelestinum*, contained significantly more insects from flower-baited traps than in either traps containing plants without flowers or pots without flowers ($\chi^2 = 115$, $df = 1$, $p < 0.001$).

Unlike Braconidae, examination at the finer taxonomic scales of ichneumonid subfamilies ($n = 24$) and species revealed no patterns of capture. That is, those plants that attracted significantly more Ichneumonidae attracted species across a range of subfamilies and not any in particular.

3.2. Morphological correlates of "attraction"

Ratios of insects captured in flower-baited traps relative to the control were calculated in the most conservative manner possible

within the diverse experimental procedures. When possible, traps baited with flowering plants were compared to traps containing plants without flowers; when this was not possible, pots without plants were used and finally blanks, such as the weed cloth covered sites used in *in situ* designs. When mean flower width, depth, density and plant height of plants attractive and unattractive to summed parasitoids were examined by Principal Component Analyses, separations between significant and insignificant mean capture ratios revealed a pattern with 10% misclassification; i.e., the percent of trap-ratio points associated with the opposite data cluster (Fig. 3). The two of 19 summed-parasitoid points misclassified were both “unattractive” plants located in the largely “attractive” plant-vectorspace.

Linear models of capture ratios to flower variables, (flower width, depth, width and depth quadratics, and width and depth interaction) found that flower width, the quadratic of width (with intermediate widths having greater captures in both instances) and the interaction of width and depth were of significance to Ichneumonidae and Braconidae (Table 3). Only in the Ichneumonidae was the quadratic of depth significant (shallower and deeper flowers having greater capture ratios), and none of the variables were significant for the Chalcidoidea.

Linear models of capture ratios to plant variables, (plant height, floral area [flower width² * density of flowers/15 cm²], height and area quadratics, and the interaction of height and depth) found that floral area was of positive significance to Braconidae and Chalcidoidea, as were the interactions of height and area (Table 4). There appeared to be a tendency for shorter plants with larger floral areas to have higher capture ratios.

4. Discussion

Traps baited with certain flowering-plants captured more parasitoids than controls. Ten species captured significantly more summed ichneumonoids and chalcidoids, seven more Braconidae, two more Ichneumonidae and six more Chalcidoidea. Among Braconidae, traps baited with certain plants captured significantly more of specific subfamilies. In some cases the experimental design allowed us to be confident that the flowers themselves played a role in the higher captures, while in others we can only state that more insects were captured in the presence of plants in flower and

that other aspects of the plants, e.g., foliage, could have been responsible for any differences. Even when flowers were demonstrated to have a role in relatively greater trap captures, the baited-Malaise trap experiment did not demonstrate that the Hymenoptera captured were feeding on flowers. Although nectar feeding, and to a much lesser extent pollen consumption, appears to be common in the parasitic Hymenoptera (Jervis et al., 1993), direct observations of feeding were not recorded.

However, there are at least two plausible explanations for the differences in insect numbers captured in the flower-baited traps: (1) there were differences in floral attractiveness and (2) there were differences in floral food quality/availability so that particular insects spent more time in the vicinity of more nutritious/available flowers and thus were more likely to be captured. In the only similar flower-baited Malaise trap comparison to date, floral volatiles of experimental plants were identified. The synthetic equivalent of a major component unique to a bait-flower associated with Opiine braconid capture was tested in a flight tunnel and it was indeed found to be attractive to an exotic opiine species in culture (Rohrig et al., 2008b).

Attraction does not necessarily imply species-level co-evolution between signaler and receiver. In general parasitic Hymenoptera are not adapted to be pollinators. They seldom feed on pollen and are not setaceous enough to transport substantial amounts of pollen (Jervis et al., 1993; Jervis, 1998). In some instances, it may benefit a plant to attract parasitoids with a nectar reward, particularly those natural enemies that destroy herbivores early in their development and thus prevent foliage damage (Wäckers et al., 2005). In other cases, parasitic Hymenoptera may provide no service and practice “flower larceny” (in the sense of Irwin et al., 2001). In still other instances wasps are attracted to plants whose nectar is inaccessible and attraction is apparently coincidental (Wäckers, 2004).

Among the attractive plants, several were of special interest. (1) *D. carota*: 49% of the 156 published records of parasitic Hymenoptera recorded visiting/feeding on *D. carota* were chalcidoids (literature compilation available from JS, John.Sivinski@ARS.USDA.GOV). Of the 746 parasitic Hymenoptera flower feeding/visitation records not associated with *D. carota*, chalcidoids made up only 25%. While these figures were not derived from random sampling they do provide additional, if circumstantial, evidence for *D. carota*'s attractiveness to chalcidoids. *D. carota* has long been established in the area and insects in the vicinity may have had an opportunity to associatively learn that it represented a food source. This in turn might have contributed to its unusual degree of attractiveness relative to the controls. (2) *Lobularia maritima*: The present trapping of significant numbers of Braconidae in *L. maritima*-baited traps was consistent with earlier Malaise trapping by Rohrig et al. (2008a). As in previous floral attraction-experiments, Opiinae were significantly over represented, and in the present collections, Alysiinae, a closely related subfamily, were also significantly more abundant in the presence of flowering *L. maritima*. Both subfamilies are parasitoids of immature Diptera (Wharton et al., 1997). Females, but not males, of the exotic opiine *Diachasmimorpha longicaudata* (Ashmead) taken from colony are attracted to acetophenone, a major component of *L. maritima* volatiles (Rohrig et al., 2008b). This particular attraction is unlikely to be a coevolved response as *L. maritima* is not native to Florida or to *D. longicaudata*'s Australasian region of origin. It is possible that acetophenone, or some other compound, is similar to a cue emitted by the shared dipteran hosts of Opiinae and Alysiinae. (3) *A. aromatica*: This was the only bait-plant significantly associated with captures of all the higher taxa, Ichneumonidae, Braconidae and Chalcidoidea.

There were patterns in the ratios of parasitoids captured in flower-bated traps/controls, even with the ambiguities associated with comparing the results of different experimental procedures,

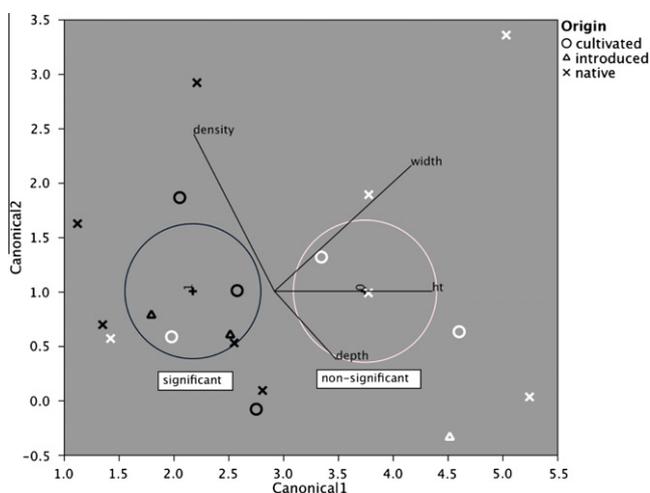


Fig. 3. Principal component analyses of the distribution of the summed Ichneumonidae and Chalcidoidea capture ratios (flower-baited trap/control) of significantly attractive and unattractive flowers across a vector space created from flower width, height and density and plant height: number misclassified = 2, percent misclassified = 10.

Table 3

Floral characteristics and their relationship to family/superfamily capture ratios; i.e., the numbers captured in flower-baited traps/controls. Only significant relationships ($p < 0.05$), or those bordering on significance ($p < 0.10$), are included. Degrees of Freedom (df) are model, error. NS = not significant.

Flower characteristic	Ichneumonidae	Braconidae	Chalcidoidea	Summed parasitoids
Flower width	$F = 9.6$; $df = 5, 10$; $p = 0.01$	$F = 18.1$; $df = 5, 10$; $p = 0.0025$	NS	$F = 4.4$; $df = 5, 13$; $p = 0.06$
Flower width (quadratic)	$F = 6.0$; $df = 5, 10$; $p = 0.03$	$F = 17.8$; $df = 5, 10$; $p = 0.002$	NS	$F = 4.2$; $df = 5, 13$; $p = 0.06$
Flower depth	NS	NS	NS	NS
Flower depth (quadratic)	$F = 9.5$; $df = 5, 10$; $p = 0.01$	NS	NS	NS
Flower width * depth (interaction)	$F = 14.8$; $df = 5, 10$; $p = 0.003$	$F = 7.3$; $df = 5, 10$; $p = 0.02$	NS	$F = 6.4$; $df = 5, 13$; $p = 0.03$

Table 4

Plant characteristics and their relationship to family/superfamily capture ratios: i.e., numbers captured in flower-baited traps/control. Only significant relationships ($p < 0.05$), or those bordering on significance ($p < 0.10$), are included. Degrees of Freedom (df) are model, error. NS = not significant.

Plant characteristic	Ichneumonidae	Braconidae	Chalcidoidea	Summed parasitoids
Plant height	NS	NS	NS	NS
Plant height (quadratic)	NS	NS	NS	NS
Floral area	NS	$F = 3.4$; $df = 5, 10$; $p = 0.10$	$F = 6.4$; $df = 5, 6$; $p = 0.05$	NS
Floral area (quadratic)	NS	NS	NS	NS
Plant height * floral area (interaction)	NS	$F = 5.4$; $df = 5, 10$; $p = 0.04$	$F = 9.1$; $df = 5, 6$; $p = 0.02$	NS

which allowed us to propose that plants with larger floral areas were more likely to support parasitoid populations. The equivalent of our “floral area” was found by Fielder and Landis (2007a,b) to be positively associated with predator and parasitoid abundance on a variety of native and introduced plants in Michigan. Floral area could increase flowering plant conspicuousness and advertise the presence of denser and more abundant resources. We did not address the role of color in flower apparency, largely because of the possibility of undetected ultra-violet components (although all of the three noteworthy flowers mentioned above are white to the human eye). In addition and as discussed by Wäckers (2005), insects detect achromatic contrasts at a greater distance than chromatic (Giurfa et al., 1996), and contrasting floral surface area is a major component of achromatic apparency (Ne'eman and Kevan, 2001).

Flower morphology influences insect access to nectar and pollen (Patt et al., 1997; Wäckers, 2004), and the characters most likely to effect access are corolla width and corolla depth (Stang et al., 2006). A narrow corollar diameter might block the entrance of an insects head and a deep corolla might make nectar unavailable to parasitic Hymenoptera with their typically short tongues (Jervis, 1998). Small wasps might be better suited to feeding on shallow flowers (or parenthetically on large flowers that would seem cavernous to a small parasitoid). While flower width, in one form or another, was frequently significantly involved with the variance in capture ratios, depth rarely was. Perhaps relatively small parasitic Hymenoptera can simply enter corollas and not be concerned with reaching nectar from outside.

Negative trapping results present a particular difficulty in the present study. Not all parasitoid taxa are equally vulnerable to capture by Malaise traps (Sunderland et al., 2005). Thus, there may be attracted insects missing in the trap catches. More difficult to account for are taxa that were expected to be attracted, were captured in large numbers, but were not more likely to be taken in flower-baited traps. Ichneumonidae were commonly trapped, are known to be associated with flowers (48% of the Hymenoptera in the feeding-literature compilation dataset), but were significantly more abundant in traps baited with only two species of flower. It may be that our choice of plants was not compatible with whatever species were present, but this hypothesis must wait additional testing. Similarly, microgasterine braconids were not significantly attracted to *L. maritima*, although in the laboratory some species thrive on its flowers (Johanowicz and Mitchell, 2000). Since

microgasterines were captured in traps baited with other flowers it may be that confined parasitoids were able to exploit *L. maritima* in their cage, but were unable to locate it in the field. If this were the case, it would emphasize the need for further field studies where parasitoids are confronted with complex environments not available in the laboratory.

As to bases of attraction outside of morphology, in subsequent papers we will attempt to correlate floral volatile constituents to the capture of various parasitoids and consider sex ratios in floral-baited traps and controls. In addition, we will address the attractiveness of the flowers used in the present study to dipteran parasitoids, particularly Tachinidae, and potential lepidopteran pests. The capacity of a plant to attract herbivorous insects, as well as natural enemies, should influence its suitability for agro-landscape modification (George et al., 2010). Beyond simple attractiveness, the consequences of parasitoids visiting flowering plants also need to be determined. For example, Wäckers (2004) found a relatively small proportion of the flowers he provided parasitic Hymenoptera were both attractive and had accessible nectar. Thus concentrating and nurturing natural enemies could often be disconnected. While there are pest control schemes that rely on attracting natural enemies but do not provide additional rewards (e.g., the application of chemicals that mediate “induced plant defenses”; Turlings and Wäckers, 2004), these would likely have different effects on parasitoid fecundity and longevity than attractants directly associated with adult food.

Acknowledgments

We are indebted to the staff at the University of Florida Dairy research Unit at Hague, Florida for allowing us to erect our traps at their facility. Drs. Howard Frank and Rob Meagher made many useful comments on earlier version of the manuscript, as did two anonymous reviewers. Dr. Robert Wharton, Texas A&M University, had previously assisted in the identification of local braconid sub-families which made the present sorting possible.

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