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Author: Sivinski, John

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THE ATTRACTION OF LEPIDOPTERA TO FLOWERING PLANTS ALSO ATTRACTIVE TO PARASITOIDS (DIPTERA, HYMENOPTERA)

JOHN SIVINSKI[1,*]
[1]USDA, ARS, Center for Medical, Agricultural and Veterinary Entomology, 1600 SW 23rd Dr., Gainesville, Florida 32608, USA

*Corresponding author: john.sivinski@ars.usda.gov

ABSTRACT

Flowering plants added to agricultural environments can provide food, shelter and alternative hosts for natural enemies and so increase crop yields. However, these same resources might be exploited by certain pests. Twelve species of plants known to attract parasitic Hymenoptera and Tachinidae and candidates for conservation biological control were examined for their attractiveness to Lepidoptera, a largely herbivorous order. Interception traps (Malaise traps) were erected along the wooded margin of an agricultural field. Under these traps were placed plants with flowers and controls consisting of plants without flowers and/or no plants. Trapped Lepidoptera were counted, their wing lengths (size) measured and when possible identified to family and species. Five of the 12 plant species in flower attracted greater numbers of Lepidoptera than their control(s), and the attracted moths tended to be relatively large species. Flower depth, but not width, was correlated to attractiveness as was floral area, but not plant height. Finally the relative capacity of plants to attract both natural enemies and selected herbivores was compared. Such comparisons are useful in choosing non-crop plants for inclusion in agro-landscape modifications.

Key Words: conservation biological control, Crambidae, Geometridae, Tachinidae, Braconidae, Chalcidoidea

RESUMEN

Plantas que florecen que son añadidas a campos agrícolas pueden proporcionar alimento, refugio y hospederos alternos a enemigos naturales y por lo tanto pueden aumentar el rendimiento de los cultivos. Sin embargo, algunas plagas pueden utilizar estas mismas plantas. Doce especies de plantas, la mayoría de ellas nativas de Florida o establecidas, que son atractivas a himenópteros y taquínidos parasíticos, y que son candidatos para la protección de elementos de control biológico fueron examinadas en cuanto a su atracción para Lepidóptera, un orden de insectos en gran mayoría herbívoro. Trampas de intercepción ("Malaise traps") se instalaron a lo largo de márgenes de campos. Se colocaron debajo de estas trampas macetas con plantas en flor o, para control, con plantas sin flores o sin plantas. Las macetas se rotaron de posición entre las varias trampas. Se contaron los lepidópteros colectados; se les midieron las alas (para representar su tamaño), y cuando fué posible, se identificaron a familia y especie. Cinco de las 12 plantas en flor atrajeron un mayor número de Lepidóptera que los controles y éstas eran polillas relativamente grandes. La profundidad de las flores, pero no su ancho, correlacionó a su atracción, al igual que el área floral, pero no la altura de las plantas. Y por último, se comparó la capacidad relativa de las plantas para atraer a los enemigos naturales y a herbívoros representativos y se sugiere que estas comparaciones pueden ser útiles en la elección de plantas no cosechables para ser incluidas en modificaciones de agro-paisajes.

Palabras Clave: conservation biological control, Crambidae, Geometridae, Tachinidae, Braconidae, Chalcidoidea

Pararasitic wasps alone save U.S. agriculture an estimated $20 billion annually through their suppression of crop pests (Pennisi 2010). If non-crop plants that provided these and other natural enemies with food, shelter or alternative hosts were integrated into agricultural ecosystems this biocontrol benefit might be increased (e.g., Landis et al. 2000; Wilkinson & Landis 2005). On the other hand, certain pest insects are also attracted to and sustained by the same resources (Chaplin-Kramer 2013). Nectars, for example, can be made available by diversifying the flora of agricultural environments (Wäckers 2005), and both dipteran and hymenopteran parasitoids exploit this valuable source of carbohydrates (Jervis et al. 1993; Landis et al. 2000; Syme 1975; Wäckers et al. 1996). However, nectars are also among the principal adult foods of taxa containing major pests such as the Lepidoptera (e.g. Bentley & Elias 1983; Dudareva & Pichersky 2006). In a study

of Michigan-native flowering plants and their associated insects, herbivores and natural enemies responded similarly to various plant characteristics, albeit the relationships were weaker among herbivores (Fiedler & Landis 2007a).

Given this potential duality, the choice of plants to be incorporated into landscape modifications in support of biological control should be chosen not only by their effects on predators and parasitoids but their influence on the numbers and condition of the herbivores that infest a specific crop. For example, buckwheat, *Fagopyrum esculentum* Moench, bordering cabbage, *Brassica oleracea* L., plots increased parasitism of several pest Lepidoptera in the crop but had no effect on pest egg densities (Lee & Heimpel 2005). However, interplanted *Agastache foeniculum* (Pursh) raised egg densities of one of the same pests (Zhao et al. 1992). While *Iberis umbellata* L. grown with the cabbage cultivar broccoli had no effect on egg numbers of still another one of the pest species it did influence their distribution (Bigger & Chaney 1998).

Thus it seems reasonable that a first step in the addition of natural enemy-supporting plants to a particular agricultural landscape is to identify both the potential advantages and disadvantages of the various local flower-candidates. The following describes the Lepidoptera, as a representative group of herbivorous insects, captured in interception traps erected over any one of 12 species of flowering plants and their simultaneous controls consisting of traps over plants-without-flowers and/or no plants at all. These 12 plant species were chosen from a larger group of 19 because they were significantly attractive to at least one of the following parasitoid taxa, Braconidae, Chalcidoidea, Ichneumonidae (Rohrig et al. 2008a; Sivinski et al. 2011) and Tachinidae (Al -Dobai et al. 2012) in the same series of experiments.

It was then determined if: 1) adult Lepidoptera in general were associated with particular plants; 2) if species representative of various common lepidopteran families were attracted to certain plants; 3) whether Lepidoptera size was associated with attraction to flowering plants; and 4) if physical characteristics of the flowers (depth and width) or the plants (height and floral area) were related to attractiveness. Finally the capacities of the plants to attract both parasitoids and Lepidoptera were compared, providing some initial insight into the suitability of these flowers for northern Florida agricultural landscape modifications.

Materials and Methods

Plants Examined

The 12 flowering plants included in the present analysis had simultaneously attracted hymenopteran and/or dipteran parasitoids (Table 1; Al-Dobai et al. 2012; Sivinski et al. 2011) and

TABLE 1. THE SPECIES, COMMON NAME AND FAMILY OF THE TESTED PLANTS, THE JULIAN DATE OF THE START OF TEST, THEIR ORIGINS (C = CULTIVATED, E = ESTABLISHED, N = NATIVE) AND THE TYPE(S) OF NATURAL ENEMY ATTRACTED (AL-DOBAI ET AL. 2012; SIVINSKI ET AL. 2011).

Species	Common Name	Family	Julian date	Origin	Natural Enemy Attracted
Agastache hybrid	Blue fortune anise hyssop	Lamiaceae	177	C	Tachinidae
Ageratina aromatica (L.) Spach	Lesser snakeroot	Asteraceae	319	N	Braconidae, Chalcidoidea, Ichneumonidae, Tachinidae
Aloysia virgata (H.R. Lopez & J.A. Pavón.) A.L. de Jussieu	Almond bush	Verbenaceae	212	C	Chalcidoidea, Tachinidae
Buddleja davidii Franch.	Orange eye butterflybush	Buddlejaceae	212	C	Chalcidoidea, Tachinidae
Calamintha nepeta (L.) Savi	Lesser Calamint	Lamiaceae	150	C	Braconidae
Conoclinium coelestinum (L.) DC.	Blue Mist Flower	Asteraceae	266	N	Chalcidoidea
Daucus carota L.	Queen Anne's lace	Apiaceae	142	E	Braconidae, Chalcidoidea, Tachinidae
Galium aparine L.	stickywilly	Rubiaceae	83	N	Ichneumonidae, Tachinidae
Monarda punctata L.	Dotted horsemint	Lamiaceae	251	N	Chalcidoidea
Pityopsis graminifolia (Michx.) Nutt.	narrowleaf silkgrass	Asteraceae	272	N	Braconidae
Phyla nodiflora (L.) Greene	turkey tangle fogfruit	Verbenaceae	242	N	Braconidae
Stellaria media (L.) Villars	chickweed	Caryophylla-ceae	43	E	Braconidae, Tachinidae

included native, established and cultivated species. Among these there were a disproportionate number of plants native-to or established-in northern Florida, USA. Such species had the advantage of being suited to local environments and presumably would be relatively easy to maintain in agricultural landscapes. Flower and plant morphologies represented a range of flowers depths and widths and plant heights and floral areas. Details on plant origin and care are available in Al-Dobai et al. (2012) and Sivinski et al. (2011). All potted plants were individually established in 4- l plastic containers. Two plant species were growing *in situ* (see section on "Sampling Designs") and received no maintenance.

Since flower/floret width and depth of flowers might influence access to nectar these were measured in ten randomly chosen blossoms, one from each of ten randomly chosen plants of each species (details in Al-Dobai et al. 2012; Sivinski et al. 2011). Depth was the distance from the margin of the flower's petals to the underside of the calyx. Width, in radially symmetrical flowers was the corolla diameter and in bilaterally symmetrical flowers, the shorter of the 2 axes; i.e., the axis most likely to control access. Flower density was estimated by randomly tossing an open 30 cm × 30 cm plastic frame onto the plants under a Malaise trap and counting all the flowers within its boundaries. "Floral area" was the mean area of a flower/floret multiplied by flower density (for details see Al-Dobai et al. 2012; Sivinski et al. 2011). In the case of Asteraceae floral area included the additional width provided by the ray flowers (the apparent "petals"). Plant height was randomly sampled, by blind pointing, 10 times and in the case of potted plants the height of the pot was included in total height. Detailed measurements are available in Sivinski et al. (2011).

Lepidoptera Curation

All Lepidoptera from a specific sample were removed from 95% ethanol, used as preservative in the traps described below, and immediately placed between two 15 cm × 15 cm Plexiglas sheets held together with binder clips. Smaller microlepidoptera were compressed whole while larger micro- and macrolepidoptera had one fore and hind wing removed for preservation. The Plexiglas cassettes were labeled with location information, the associated flower and treatment (flowers present or control). Each specimen was given a unique number and the length of the forewing was measured under magnification with a micrometer. Larger Noctuidae, were identified by Julieta Brambila (USDA-APHIS-PPQ). Otherwise, several easily distinguished species served as representative of common families and were identified by JS with the guides of Kimbal (1965, butterflies and moths), Covell (1984, moths), Kaufman (2003, butterflies) and Beadle & Leckie (2012, moths). These species were: Arctiidae- *Halysidota tesselaris* (Smith); Crambidae- *Desmia funeralis* (Hbn.)*, Diaphania* spp.*, Hymenia perspectalis* (Huber)*, Pyrausta tyralis* (Guenée)*, Samea* sp.*, Syngamia florella* (Stoll); Gellichiidae- *Anacampsis coverdalella* Kearfott; Geometridae- *Disclisioprocta stellata* (Guenée); Hesperidae- *Epargyreus clarus* Cramer *, Lerema accius* (Smith); Noctuidae- *Ctenoplusia oxygramma* (Geyer)*, Chrysodeixis includens* Walker*, Marimatha nigrofimbria* (Gn.), *Spodoptera* spp.; Zygaenidae- *Harrisina americana* (Guerin-Meneville).

Specimens have been retained in the author's collections at CMAVE.

Malaise Traps

The numbers and kinds of Lepidoptera attracted to various flowering plants and their flowerless controls were compared by placing plants or no-plant controls underneath interception traps, i.e., Malaise traps (BioQuip Products Inc. Rancho Dominguez, California, model 2875D) based on the Townes design [Entomol. News 83: 239-247, 1972]; see Al-Dobai et al. 2012; Sivinski et al. 2011 for details). When erect with their long axis oriented to the southwest, traps were 1.8 m long by 1.2 m wide and had an opaque plastic collecting jar located at the top of one pole filled with 2-3 cm of 95% ethanol.

Traps were erected in set locations at the University of Florida Dairy Research Unit in Hague, Florida, Alachua County (in the vicinity of N 29° 47.332' W 082° 25.012'). These sites were along the edge of a field planted with corn or rye (*Zea mays* L. and *Secale cereale* M. Bleb) depending on season. Bordering the field was a forest dominated by water oak (*Quercus nigra* L.) and slash pine (*Pinus elliottii* Englem.) and with an understory rich in pokeberry (*Phytolacca americana* L.) and green briar (*Smilax* sp.). Traps were placed in the center of a 5m × 5m black plastic weed-cloth that prevented other plants from growing nearby (although see exceptions in trapping design #1 in section "Sampling Designs"). Wild plants were continuously removed for 3 m around the weed-cloths (Rohrig et al. 2008a). For trapping designs #2 and #3 (see section "Sampling Designs") the 2 or 3 traps sites were chosen on the basis of similar environments and separated by 30-50 m. Fifty individually potted plants or pots-without-plant controls were rotated among the sites (see section "Sampling Designs"). Pots were placed in 6 tightly-packed rows directly underneath the canopy of the Malaise traps, i.e., 3 rows on each side of the central barrier-wall.

Sampling Designs

Depending on the availability and location of flowers, 3 different trapping designs were used, all of which had different capacities to provide unambiguous results (Sivinski et al. 2011). These are described below in order of increasing confidence.

1. Trapping with Flowers in Situ, Followed by their Removal

Wild *Galium aparine* L. (Gentianales: Rubiaceae)and *Stellaria media* (L.) grew along the forest/field edge in homogeneous stands large enough (~ 5 m x 5 m) to place a Malaise traps in their center. The 3 sites used for each species were within ~50 m of each other. No potted plants were used. A transect through the plots determined flowering plant homogeneity within sites and details are available in Al-Dobai et al. (2012) and Sivinski et al. (2011).

As in all experimental designs, random samples of flower width, depth and density, and plant height were taken prior to Malaise trap placement (see details in Al-Dobai et al. 2012; Sivinski et al. 2011). In one of the 3 sites the flowering plants were mowed down and the ground covered with a 5m × 5m sheet of plastic weed cloth. Simultaneous collections in the single mowed and the 2 plant-containing sites continued as long as practical (at least 1 week, generally time was limited by projected declines in target-plant flowering). Following this collection, one of the 2 flower patches was mowed down and covered by a 5m × 5m sheet of weed cloth. Collections then continued on all 3 sites for the same length of time as the pre-flower-removal collections (see Al-Dobai et al. 2012; Sivinski et al. 2011). Lepidoptera captured in the site that had flowers during the first collection period but which had its plants removed prior to the second could then be compared to: i) numbers captured in the site that never had flowers. If Lepidoptera capture numbers changed in the site where flowers were mowed down prior to the second collection period to a greater degree than captures in the site where there had never been flowers then it could be inferred that the flowering-plants had influenced the rate of insect capture; ii) numbers of insects trapped in the site left in bloom after the manipulated site was mowed down. This comparison of changes in insect capture could reflect any changes due to floral abundance/attractiveness. Data analysis was by contingency χ^2 test, with site (continuous flowering plants available, plants removed half way through collecting period and no flowering plans ever present) and collection period (pre-flowering plant removal in the modified site and post-plant removal in the modified site) defining the contingency table (Zar 1974 for further details see Al-Dobai et al. 2012 and Sivinski et al. 2011). Because plants with and without flowers were not examined separately, significant differences in captures did not demonstrate floral attraction in the strictest sense. Other plant parts and plant-induced micro-environments, e.g., shade, wind-shelter and oviposition opportunities, could also be responsible for higher trap catches relative to sites without plants.

2. Rotation of Flowering Plants and No-Plant Controls between 2 Trap Sites

Fifty individually-potted flowering plants of a particular species were rotated among Malaise traps erected on 2 weed-cloth prepared sites 3 to 6 times (6-12 48-hour long collection replicates per species). Sites were distinct from experimental design #1. No-plant controls consisted of 50 pots+soil and were initially placed in rotation under the alternate Malaise trap. The 5 plant species examined in this manner were: *Agastache* hybrid, *A. virgata, B. davidii, C. nepeta* and *P. nodiflora.* Plants-in-flowers were not examined separately from the plants-without-flowers so that significant differences in captures were best interpreted as flowering-plant, not floral, attraction. The mean numbers of Lepidoptera collected in traps with and without plants were compared by t-tests, using the Satterthwaite method in cases of unequal variances (SAS Inst. 2004).

3. Rotation of Flowering Plants, Non-Flowering Plants and No-Plant Controls among 3 Trap Sites

This design provided the best estimation of floral attraction by simultaneously comparing a blank (no plant) control with plants both in and out of flower. The 5 species so examined were: *A. aromatica*, *C. coelestinum, D. carota, M. punctata* and *P. graminifolia.* As above, 50 potted plants of a particular species were rotated among sites. There were 6-9 replications per species (2-3 complete rotations), each typically 48 h long. When it was necessary to remove flowers from plants serving as "no-flower" controls, a comparable amount of tissue was cut from those that retained their flowers. Lepidoptera captures for each plant-condition (a particular species of plant in flower, out of flower and pot with no plant) were compared by ANOVAs followed by Waller's mean separation test (Proc ANOVA; SAS Inst. 2004).

Additional Analyses

Large enough numbers of the representative species of common families were captured at certain flowers to analyze floral attractiveness at the species/family level (at least 20 individuals

and a capture ratio (n[captured in flower-traps]: n[captured in no-flower controls] of at least 1.5). These smaller numbers of more sporadically captured individuals were summed by treatment (flowering plant, no-plant and when available plants without flowers) and compared by chi-square analysis (Zar 1974).

The mean sizes (fore-wing length) of moths captured in traps with and without flowers were compared by t-tests, using the Satterthwaite method in cases of unequal variances (SAS Inst. 2004). The following analysis was used to determine if difference in mean size was due to a greater proportion of smaller moths captured in the treatment with the smaller mean or a greater proportion of larger moths were captured in the treatment with the larger mean. The numbers of moths in each treatment whose wings that fell above or below 1 standard deviation of the overall mean length were used to create a contingency table and compared by chi-square test (Zar 1974). The relationship between capture ratio (n[captured in flower-traps]: n[captured in no-flower controls] and relative wing length (mean[captured in flower-traps]: n[captured in no-flower controls]) was determined by Spearman rank correlation (Zar 1974).

Relationships between floral characteristics (width and depth) and plant characteristics (height and floral area) with capture ratio (n[captured in flower-traps]: n[captured in no-flower controls] were determined by correlation (Zar 1974).

Results

The following items were determined from the trapping data: 1) which plant species were significantly associated with adult Lepidoptera; 2) which plant species were associated with representative species of various common families of Lepidoptera; 3) whether Lepidopteran size was related to flowering-plant association; and 4) if physical characteristics of the flowers (depth and width) or the plants (height and floral area) were related to associations with Lepidoptera.

Attractiveness to Lepidoptera and their Relative Size

Five of the 12 flowering plants attractive to parasitoids also significantly attracted Lepidoptera (Tables 2 and 3). The attracted moths and occasional butterflies were often relatively large (Table 4). All the attractive plants cluster at the upper end of captured insect size ratios as determined by a comparison of the mean wing lengths in traps containing flowering plants and controls without plants (Fig. 1). A comparison of the numbers of large (mean + 1 SD) and small moths (mean -1 SD) shows these ratios were due to a greater representation of larger Lepidoptera associated with flowers as opposed to a relative absence of small moths (Table 5).

Table 2. The capture ratios (n[captured in flower-traps]: n[captured in no-flower controls]) of the various flowers with numbers captured in parentheses. *Refers to a significant difference.

Flower	Summed captures flower: control	Significance
Calamintha	1.2 (241:201)	NS
Aloysia	2.2 (308:140)	*
Buddleja	5.3 (743:140)	*
Phyla	0.95 (357:375)	NS
Ageratina	5.4 (304:56)	*
Agastache	2.2 (824:379)	*
Pityopsis	1.1 (222:206)	NS
Daucus	1.1 (346:321)	NS
Conoclinium	1.4 (214:149)	NS
Monardia	1.5 (406:268)	*
Gallium	0.8 (33:41)	NS
Stellaria	1.2 (24:20)	NS

Table 3. The capture ratios (n[captured in flower-traps]: n[captured in no-flower controls]) of individuals of lepidopteran families (see text) at the various flowers with numbers captured in parentheses. *Refers to a significant difference.

	Crambidae	Hesperidae	Geometridae	Noctuidae	Zygaenidae
Calamintha			38:20 (1.9)*		
Aloysia	54:4 (14)*	26:3 (8.7)*	25:1 (25)*		
Buddleja	55:2 (28)*	25:2 (13)*		60:5 (12)*	
Phyla					
Ageratina	15:7 (2.4)		77:8 (9.6)*		
Agastache	32:12 (2.3)*	49:2 (>24)*	441:61 (7.2)*		
Pityopsis	10:17 (0.6)				
Daucus			41:28 (1.5)		
Conoclinium					
Monardia	63:11 (5.8)*		19:11 (1.7)		22:0 (>22)*

TABLE 4. THE RATIOS OF MEAN WING LENGTHS OF LEPIDOPTERA CAPTURED IN FLOWER-BAITED TRAPS RELATIVE TO THE MEANS OF THOSE CAPTURED IN CONTROLS. MEANS ARE IN PARENTHESES AND *REFERS TO STATISTICAL SIGNIFICANCE.

Flower	Mean wing length flower : control	Significance
Calamintha	1.0 (6.8:6.8)	NS
Aloysia	1.5 (7.9:5.4)	*
Buddleja	1.7 (9.1:5.4)	*
Phyla	1.0 (7.3:7.6)	NS
Ageratina	1.1 (10.2:9.1)	*
Agastache	1.5 (11.5:7.7)	*
Pityopsis	1.0 (7.8:7.7)	NS
Daucus	1.0 (7.4:7.2)	NS
Conoclinium	0.9 (7.9:9.0)	NS
Monardia	1.3 (8.3:6.6)	*
Gallium	.80 (6.5:7.9)	NS
Stellaria	1.0 (7.4:7.3)	NS

Characteristics of Attractive Flowers and Flowering Plants

Of the flower characteristics, i.e., width and depth, only depth was significantly correlated to the ratio of the number of captured Lepidoptera in traps with and without flowering plants (Fig 2). Of the plant characteristics height, i.e., flower-density and floral area, only floral area was related to capture ratios (Fig. 3).

DISCUSSION

The flowers examined differed substantially in their attractiveness to Lepidoptera, well over 90% of which were moths. Among the Rhopalocera, only Hesperidae were occasionally abundant. Malaise traps can produce biased samples, some species being more prone toward upward flight when encountering a barrier and the absence of a species among the captured does not guarantee its absence at the sampling site (Miller et al. 2013). On the other hand, their ability to capture insects night and day over long periods of time lets them accurately sample the variance in the abundances and activity-periods of vulnerable species.

The capacities of flowering plants to attract both herbivores and their natural enemies dictates that the choice of non-agricultural plants to be added to agricultural landscapes be made on the basis of greatest good and least harm. In Fig. 4 and 5 those plants in the upper left quadrant ranked high in parasitoid and low in moth attraction,while those in the lower right were the opposite. For example, *B. davidii*, the aptly named butterfly bush, is a source of synthesized lepidopteran attractants (Guédot et al. 2008; Landolt et al. 2012) and served as a positive control. As expected it occupied the "less desirable" lower far-right portion of the distribution. On the other hand, wild carrot (*D. carota*), in the most desirable upper-left quadrant, has been previously considered for use in conservation biological control outside of Florida (Fiedler et al. 2008) and appears to be a good local candidate as well. Of course, this information only provides some guidance in the case of Lepidoptera, and then only to the moths of north central Florida. Even among the captured moths only *Spodoptera* spp., (armyworms), *D. funeralis* (grape leaf folder), *H. perspectalis* (spotted beet webworm), *Diaphania* spp. (pickle and melonworms), *H. americana* (grapeleaf skeletonizer) and *C. includens* (soybean looper) are pests of any note. Of these, *H. perspectalis* was the most frequently recovered in significant numbers from flower-baited traps (*Agastache* hybrid [capture ratio = n[captured in flower-traps]: n[captured in no-flower controls] = 6.8], *A. virgata* [capture ratio = 16.5], *B. davidii* [capture ratio = 35], *M. punctata* [capture ratio = 11.3]. Significant numbers of *D. funeralis* [capture ratio = 8.0] and *H. americana* [capture ratio = 12.5] were also caught in traps with

TABLE 5. THE NUMBERS OF MOTHS CAPTURED AT PARTICULAR FLOWERS OR THEIR CONTROLS WHOSE WING LENGTHS WERE EITHER 1 STANDARD DEVIATION LONGER OR SHORTER THAN THE OVERALL MEAN.

Flower	n (mean + 1 std dev)	n (mean – 1 std dev)	χ^2	p
Aloysia (Flower)	58	48	15.3	< 0.001
Aloysia (Control)	10	40		
Ageratina (Flower)	90	62	3.5	< 0.10
Ageratina (Control)	13	20		
Agastache (Flower)	206	152	91.1	< 0.001
Agastache (Control)	26	157		
Monardia (Flower)	79	28	26.6	< 0.001
Monardia (Control)	41	67		
Buddleja (Flower)	139	88	1834	< 0.001
Buddleja (Control)	6	72		

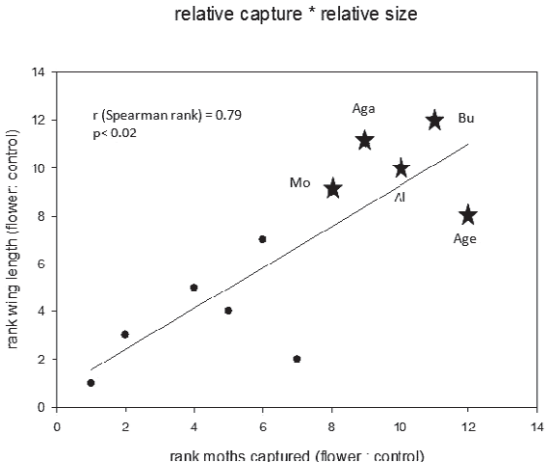

Fig. 1. The rank relationship between capture ratio (n[captured in flower-traps]: n[captured in no-flower controls] and relative wing length (mean[captured in flower-traps]: n[captured in no-flower controls]). Stars represent species whose flowers were significantly attractive to Lepidoptera and the abbreviations refer to: Aga = *Agastache* hybrid; Age = *Ageratina aromatica*; Al = *Aloysia virgata*; Bu = *Buddleja davidii*; Mo = *Monardia punctata.*

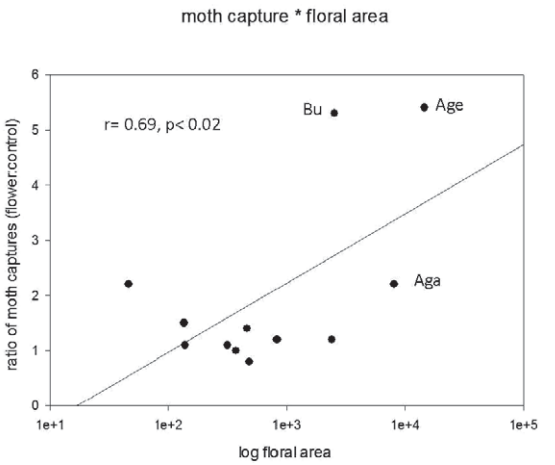

Fig. 3. The relationships between capture ratio (n[captured in flower-traps]: n[captured in no-flower controls]) and log floral area. Abbreviations refer to plants important to the slope of the correlation: Aga= *Agastache* hybrid; Age = *Ageratina aromatica*;; Bu = *Buddleja davidii*.

blooming *M. punctata.* Other pests, including non-Lepidoptera, and their natural enemies in other areas would require their own cost-benefit analyses.

An apparent regional difference in the attractiveness of *M. punctata* to natural enemies is an illustrative instance of inconsistent local benefits. In Florida, of the flowers that were significantly associated with parasitoids, *M. punctata* was the least attractive (Sivinski et al. 2011), but in Michigan it was one of the more attractive late-flowering plants to a broad range of natural enemies (Fiedler & Landis, 2007b). The insects associated with *A. aromatica* represent a case were the details of precisely which pests and biological control agents are attracted would be invaluable in agricultural planning. The flower is highly attractive to a wide range of parasitoids but is also highly attractive to Lepidoptera. Details would reveal if a subset of individually beneficial species outweighs the costs of subsidizing particular detrimental species.

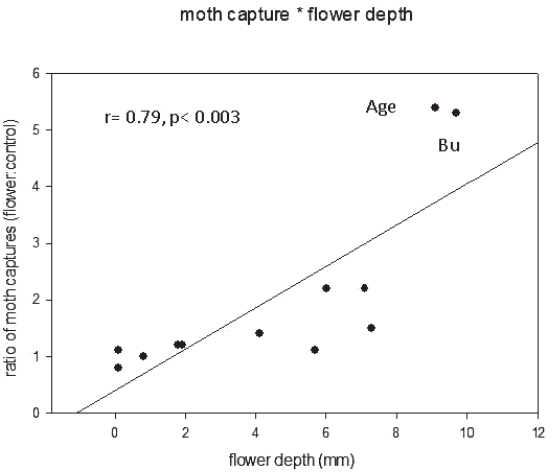

Fig. 2. The relationships between capture ratio (n[captured in flower-traps]: n[captured in no-flower controls]) and flower depth. Abbreviations refer to plants important to the slope of the correlation: Aga = *Agastache* hybrid; Age = *Ageratina aromatica*; Bu = *Buddleja davidii*.

There were plant/flower characteristics correlated to attractiveness to Lepidoptera and which might allow extrapolation to identify problematic flowers. Plants with greater floral areas tended to be more attractive. This was also the case for hymenopteran, but not dipteran, parasitoids (Sivinski et al. 2011; Al-Dobai et al. 2012) and greater floral area, as opposed to flower density, may represent a more conspicuous signal directed to generalist pollinators. Flower depth was also significantly related to attractiveness, and flowers pollinated by moths often have long corolla tubes (Knudsen & Tollsten 1993).

Lepidopteran size was related to capture at flowering plants. All of the attractive plants were also the ones that captured significantly larger Lepidoptera than their controls. This would suggest that nectar-feeding moths tend to be larger than those that either do not feed as adults or

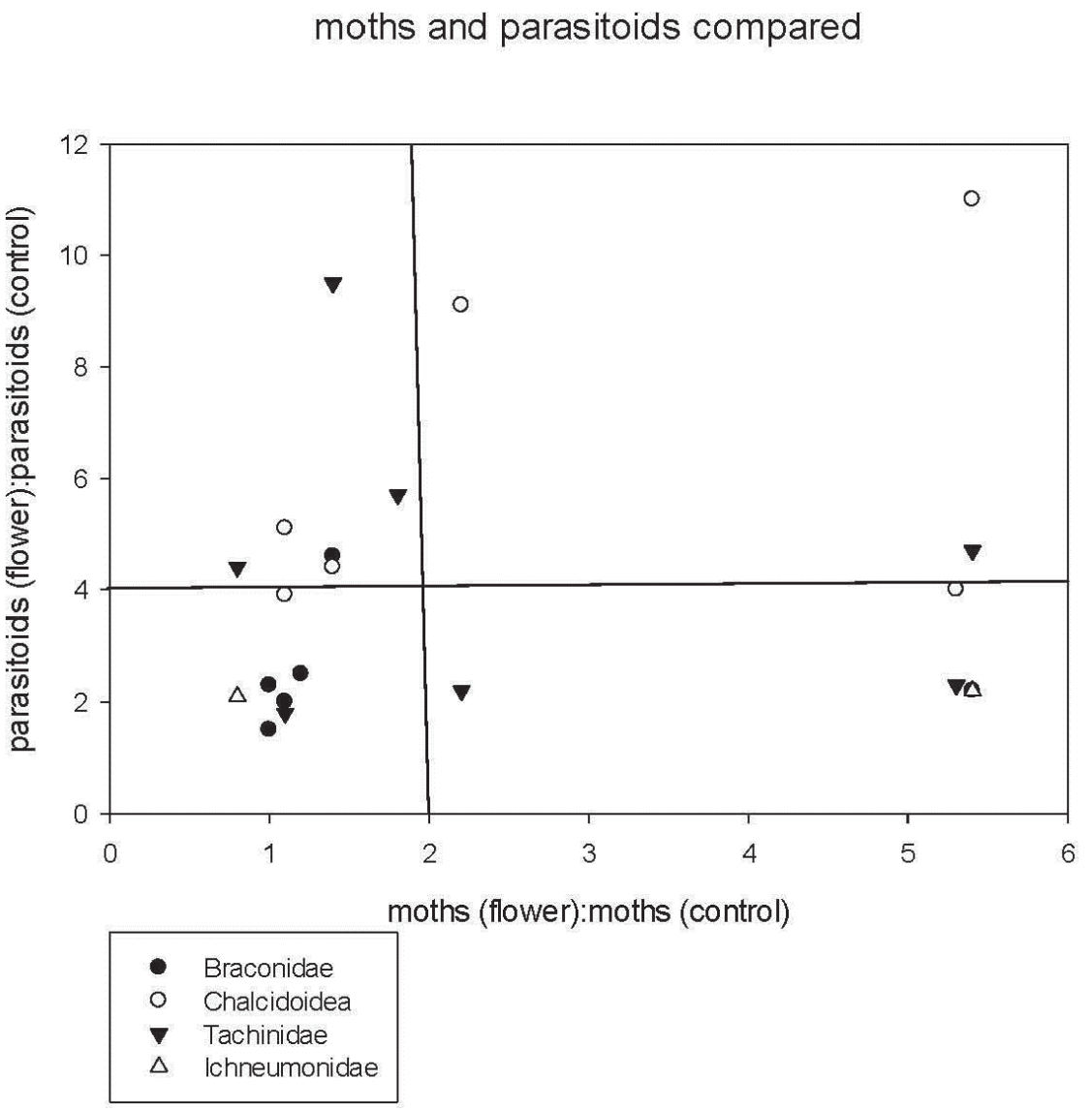

Fig. 4. Plants compared by their capture ratios (n[captured in flower-traps]: n[captured in no-flower controls]) of both parasitoids and Lepidoptera. The lines bisecting graph "a" represent the mean values for the axes and in "b" the median ranks. Abbreviations refer to plant species: Aga = *Agastache* hybrid; Age = *Ageratina aromatica*; Al = *Aloysia virgata*; Bu = *Buddleja davidii*; Ca = *Calamintha nepeta*; Co = *Conoclinium coelestinum*; Da = *Daucus carota*; Ga = *Galium aparine*; *Monardia punctata*; Pi = *Pityopsis graminifolia*; Ph = *Phyla nodiflora*; St = *Stellaria media.*

consume other foods. If true, it would be a generalization with many exceptions. Giant silk moths (Saturniidae), for example have non-functional mouthparts (Krenn 2010). Many butterflies, large Lepidoptera, feed at flowers, but papilionoids were infrequently captured. One of the most commonly taken, and larger species, was the geometrid *D. stellata.* While species of Geometridae have a variety of proboscis morphologies, some capable of obtaining nectar, at a family level they are not considered to be among those that are either frequently associated with flowers (Norris 1936) or have a high adult feeding capacity (Miller 1996).

In summary, some plants that attract parasitoids, especially those with expansive floral areas, also attracted relatively large moths. It was not always clear what the bases of these attractions were (Rohrig et al. 2008b) but nectar-food

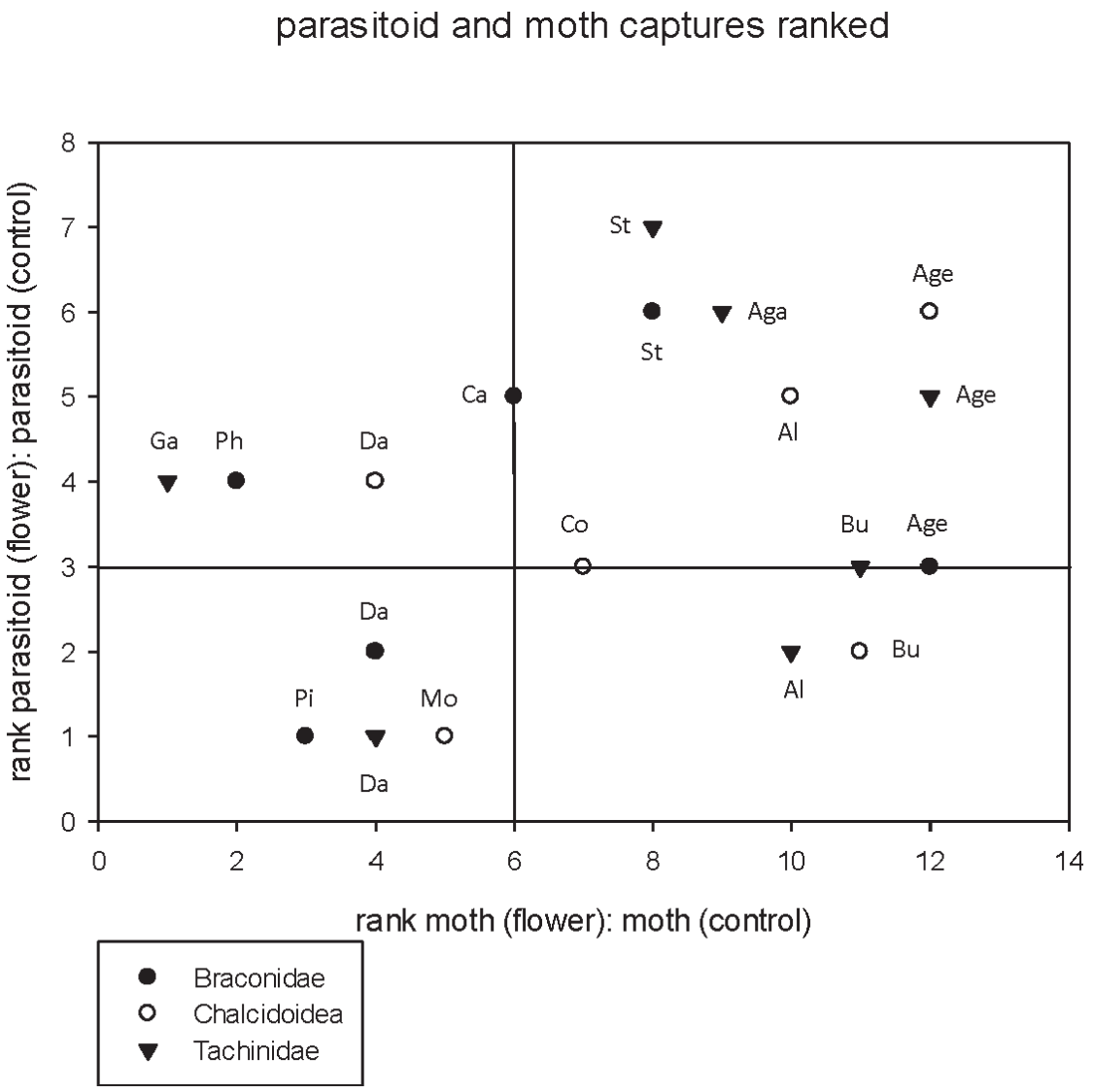

Fig. 5. Plants compared by their ranked capture ratios (n[captured in flower-traps]: n[captured in no-flower controls]) of both parasitoids and Lepidoptera. Ranks were employed to space points and allow a more easily viewed set of relationships. Ichneumonidae are not included because the small number of plants with significant captures did not lend themselves to rank relationships. The lines bisecting graph "a" represent the mean values for the axes and in "b" the median ranks. Abbreviations refer to plant species: Aga = *Agastache* hybrid; Age = *Ageratina aromatica*; Al = *Aloysia virgata*; Bu = *Buddleja davidii*; Ca = *Calamintha nepeta*; Co = *Conoclinium coelestinum*; Da = *Daucus carota*; Ga = *Galium aparine*; *Monardia punctata*; Pi = *Pityopsis graminifolia*; Ph = *Phyla nodiflora*; St = *Stellaria media.*

is a leading hypothesis, particularly since moth-attractive flowers had relatively greater corollar depth and such morphologies are characteristic of moth-pollination syndromes. That said there are important caveats. The first is that general attractiveness to a broad range of moth species may have little to do with a particular pest problem. If there is concern about a flowering plant concentrating and supporting a specific herbivore, then it and its natural enemies should be the subjects of a focused experiment. In fact, not only herbivores should be considered. Even predators supported by increased environmental complexity, such as spiders, can consume pollinators and reduce yield (Romero & Koricheva 2011). The second is that future experiments would do well to identify both how and where added-plants are to be integrated and what are

the subsequent consequences for attracted insects (Letourneau et al. 2011). Even if a plant is attractive it need not necessarily have a significant effect on pest survival and fecundity.

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