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Tachinidae (Diptera) associated with flowering plants: Estimating floral attractiveness

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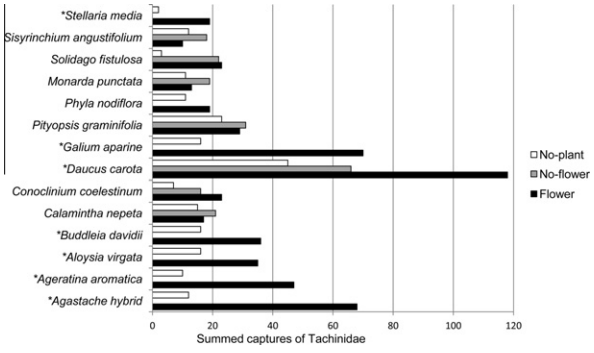
HIGHLIGHTS

- Of 14 flowering plant species seven captured significantly more Tachinidae than controls.
- Species of Dexiinae, Exoristinae and Tachininae, but not Phasiinae, were collected.
- The magnitude of attraction was not related to flower width, depth or density.
- Specific plants may be means of concentrating Tachinidae for biocontrol.

GRAPHICAL ABSTRACT



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ABSTRACT

Non-agricultural flowering plants in agricultural settings provide ecological services, such as nectar-food for adult parasitic flies. In order to determine the attractiveness of flowers to Tachinidae, 12 species of cultivated, introduced/established and native potted plants-in-flower were individually placed beneath interception traps erected along the wooded margins of fields planted seasonally with either feed-corn or rye. Simultaneous controls consisted of traps associated with the same species of plant without flowers, a pot without plants or both. In two additional instances where flowering-plants grew *in situ* it was necessary to compare initial trap captures to those following the removal of the plants. Of the 14 plant species tested five captured more Tachinidae at the family level than controls (*Agastache* hybrid, *Ageratina aromatica* (L.), *Aloysia virgata* (Lopez & Pavon), *Daucus carota* L. and *Stelleria media* (L.)). At the tachinid subfamily and genera/species levels traps associated with *Buddleia davidii* Franch., *Galium aparine* L., *Agastache* hybrid, *A. aromatica*, *A. virgata* and *D. carota* caught significantly more flies than controls. Over all taxonomic levels, half (7) of the plant species-in-flower were associated with trap-catches greater than those associated with plants out-of-flower and/or without plants. There was no relationship between the ratios of flies captured in flowering plant-baited traps relative to those captured in controls and flower widths, flower depths, flower densities, numbers of flowers or floral areas (flower area * number of flowers). However particular plants were identified that might be incorporated into regional conservation biological control programs.

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1. Introduction

Insect predators and parasitoids annually provide US agriculture with an estimated $4.5 billion worth of pest control (Isaacs et al., 2008), and this amount might be increased by changing the species composition and densities of non-crop plants in agricultural landscapes. For example, many adult parasitoids and predators benefit from or require shelter, food and alternative hosts obtained from flowering plants (Root, 1973; Hickman and Wratten, 1996; Harmon et al., 2000). Thus additions of appropriate non-crop plants could serve to enhance the numbers and efficacy of natural enemies in the vicinities of crops (e.g., Landis et al., 2000; Wilkinson and Landis, 2005). Maintaining natural enemy diversity with non-crop plants might also increase the possibility that any novel pest to the area would come under immediate attack by already present predators or parasitoids (LaSalle, 1993; Cornell and Hawkins, 1993; Marino et al., 2006).

Floral and extrafloral nectars are one of the beneficial products that can be increased in diverse agricultural environments (Wäckers et al., 2005), and substantial research has focused on the hymenopteran parasitoids that exploit nectar as a valuable and often the principal, source of carbohydrates (Jervis et al., 1993; Landis et al., 2000; Syme, 1975; Wäckers et al., 1996). Nectars enhance longevity, fecundity and parasitism rates of some wasps in the laboratory (Idris and Grafius, 1995; Zhao et al., 1992), in field cages (Dyer and Landis, 1996) and in the field (Zhao et al., 1992). While experimental proof that floral sugars from agricultural environments contribute directly to pest suppression is neither simple nor easy to obtain (Lee and Heimpel, 2005; Lavandero et al., 2006), there is a large body of circumstantial evidence that flowering plants do benefit biological control (Heimpel and Jervis, 2005).

In contrast to parasitic Hymenoptera and beetle and dipteran predators (Harmon et al., 2000; Colley and Luna, 2000), there have been fewer studies of the nutritional ecology of adult Tachinidae, although these parasitic flies are important sources of insect mortality and substantially influence the population dynamics of various pests, particularly Lepidoptera and Coleoptera (Stireman et al., 2006). In general, tachinids have been divided in terms of adult-feeding into two groups, short and long-tongued species. The majority of species are "short-tongued", with the proboscis length less than or equal to the height of the head and the labellum broadened for sponging liquids (Wood, 1987). These species primarily feed on hemipteran honeydew and exposed nectaries. The less numerous "long-tongued" species are specialized floral-nectar feeders (Gilbert and Jervis, 1998). Their proboscis length is greater than the height of the head, and the labellum is reduced or slender and elongate (Wood, 1987). However, these distinctions in morphology do not lead to exclusive feeding habits. For example, in a 30+ year Mississippi field survey Allen (1929) collected 13 of 18 "long-tongued" species exclusively from flowers but the other five were seen at both flowers and extrafloral nectaries or honeydew. Of the 24 "short-tongued" species, only one was found exclusively on flowers, though seven were recorded at extrafloral nectaries and flowers, and 16 were restricted to nectaries or honeydew only. In an intermediate group of nine species with the proboscis as long as the vertical diameter of the head, six visited flowers to one degree or another. Thus nearly two-thirds of the local tachinid species were associated with flowers either consistently or occasionally.

The following describes the tachinids captured in interception traps erected over any one of 14 species of flowering plants and the simultaneous controls that consisted of traps over plants-without-flowers and/or no plants at all. By this means we first determined if tachinid adults were associated with particular plants and then assessed if any characteristics of the flowers (depth and width), plants (height and floral area) or tachinids (sex and tongue length) accounted for any such plant-associations.

2. Materials and methods

2.1. Plants examined

Plants used included native, established and cultivated species. Those native to northern Florida, USA were emphasized on the assumption that sympatric flies might have evolved responses to familiar nectar sources. Both native and established-exotic species had the additional advantage of being suited to local environments and so were unlikely to require costly human inputs to maintain in agricultural environments. On occasion plants were tested that occurred locally only under cultivation (i.e., did not self-perpetuate in nature), but seemed in preliminary observations to be particularly attractive to a variety of insects. In addition, there was an attempt to present a range of flower and plant morphologies, i.e., flowers of different depths and widths and plants of different heights and floral areas.

Plants were purchased from commercial nurseries, principally Micanopy Wildflowers (Micanopy, Florida; micanopywildflowers@yahoo.com), a specialist in growing native plants. All potted plants were individually established 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, FL, USA 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 was applied as needed to plants obtained before flowering. Two plant species were growing *in situ* (see section on trapping protocols below) and received no maintenance. All plants placed under the traps are described in Table 1.

2.2. Tachinidae curation

All tachinids were pinned and labeled with location information, including GPS coordinates and the associated flower (or control). Insects were identified by SR, using the generic key of Wood (1987) with taxonomic status updated from O'Hara and Wood (2004). Species were identified with available keys. Specimens have been retained in the authors' collections at CMAVE.

2.3. Malaise traps

The numbers and kinds of Tachinidae attracted to various plants and their flowerless controls were compared by placing flowering-plants underneath interception traps. Insects were collected in Malaise traps (BioQuip Products Inc., Rancho Dominguez, CA, model 2875D) based on the Townes design (Ent. News 83:239-247, 1972) ((BioQuip Products Inc., Rancho Dominguez, CA, model 2875 WDH); see Sivinski et al., 2011 for details). These consisted of a horizontal mesh barrier "wall" held in place by two aluminum poles and with shorter mesh perpendicular-extensions at both ends. There was also a mesh sloping roof that ran along both sides of the central-wall. 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. Ethanol (95%) was added to a depth of 2–3 cm in order to preserve the trapped insects.

2.4. 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

Table 1
The species, common name and family of the tested plants, as well as the Julian date of the start of tests and the nature of their occurrence in north Florida.

Species	Common name	Family	Julian date	Native	Introduced	Cultivated
Agastache hybrid	Blue fortune anise hyssop	Lamiaceae	177			X
Ageratina aromatica (L.) Spach	Lesser snakeroot	Asteraceae	319	X		
Aloysia virgata (H.R. Lopez & J.A. Pavón.)	Almond bush	Verbenaceae	212			X
Buddleia davidii Franch.	Orange eye butterflybush	Buddlejaceae	212			X
Calamintha nepeta (L.) Savi	Lesser Calamint	Lamiaceae	150			X
Conoclinium coelestinum (L.) DC.	Blue Mist Flower	Asteraceae	266	X		
Daucus carota L.	Queen Anne's lace	Apiaceae	142		X	
Galium aparine L.	Stickywilly	Rubiaceae	83	X		
Monarda punctata L.	Dotted horsemint	Lamiaceae	251	X		
Pityopsis graminifolia (Michx.) Nutt.	Narrowleaf silkgrass	Asteraceae	272	X		
Phyla nodiflora (L.) Greene	Turkey tangle fogfruit	Verbenaceae	242	X		
Sisyrinchium angustifolium P. Mill	Narrow Leaf Blue-eyed Grass	Iridaceae	91	X		
Solidago fistulosa P. Mill	Pinebarren goldenrod	Asteraceae	247	X		
Stellaria media (L.) Villars	Chickweed	Caryophyllaceae	43		X	

County. Traps were placed along the interface of a diverse forest dominated by water oak (*Quercus nigra* L.) and slash pine (*Pinus elliottii* Englem.) and an understory rich in pokeberry (*Phytolacca americana* L.) and green briar (*Smilax* sp.) and agricultural fields used to grow corn or rye (*Zea mays* L. and *Secale cereale* M. Bleb) depending on season (in the vicinity of 29° 47.332 N, 082° 25.012 W). Traps were erected in the center of a 5 × 5 m piece of black plastic weed-cloth that prevented other plants from growing in the immediate vicinity of the traps (although see exceptions in tapping design 1 in Section 2.5). Wild plants were regularly mowed or cut down within 3 m of the weed-cloth margins (Rohrig et al., 2008). For trapping designs 2 and 3 (Section 2.5) Malaise traps were erected in 2 or 3 sites separated by distances of 30–50 m and chosen on the basis of similar environments. These two experimental designs relied on the rotation of 50 individually potted plants or pot-without-plant controls among the sites (Section 2.5). These were placed in six tightly-packed rows directly underneath the canopy of the Malaise traps, i.e., three rows on each side of the central barrier-wall.

2.5. Sampling designs

Three different trapping designs were used depending on the availability and location of flowers, and these differed in their capacity to provide unambiguous results (Sivinski et al., 2011). In order of increasing experimental confidence these were:

2.5.1. Trapping with flowers in situ, followed by their removal

In two instances, *Galium aparine* and *Stelleria media*, we found three sites within ~50 m of each other where wild plants growing along the previously described forest/field interface occurred in homogeneous clumps large enough in our estimation (~5 × 5 m) to erect Malaise traps in their midst's. No potted plants were used in these cases and plants were not rotated among sites. In order to estimate the initial homogeneity of each patch, all the vegetation in a 1 m long × 30 cm wide center transect was collected, sorted to species and weighed (wet weight) to estimate proportion of ground covered. 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 designs (see below), random samples of flower width, depth and density, and plant heights were taken in each patch prior to Malaise trap placement (see Section 2.6). In one of the three sites the flowering plants were mowed down and replaced with a 5 × 5 m sheet of plastic weed cloth. Simultaneous collections in the single mowed and the two 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 flower patch was mowed down and replaced by a 5 × 5 m sheet of weed cloth, and collections then continued on all three sites for the same length of time as the pre-flower-removal collections (Table 2). In this way, tachinids captured in the site that originally had flowers but which were subsequently removed could be compared to (1) the numbers captured in the site that never had flowers; i.e., if insect captures changed in the site where flowers had been mowed down half way through the collection period to a greater degree relative 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 and (2) the numbers of insects trapped in a site left in bloom after the treated 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). As described above, this compared the ratio of insects trapped at a modified site during time 1 (pre-plant removal) and 2 (post-plant removal) to sites where no plants were present at either time or to sites where plants were always present. While this method tested for capture differences with different flowering plant-conditions and for differences in different time periods and location, the interactions of time and space could not be addressed. Because plants with and without flowers were not examined separately, significant differences in the ratios could not demonstrate floral attraction. Other plant parts and plant-induced micro-environments, e.g., extra-floral nectar, shade and wind-shelter, could also be responsible for higher trap catches.

2.5.2. Rotation between two trap sites of flowering plants and no-plant controls between sites

Fifty individually-potted flowering plants of a particular species were rotated among Malaise traps erected on two weed-cloth prepared sites 3 to 6 times (6–12 48-h long collection replicates per species; sites distinct from experimental design #1 and described

Table 2
A diagram of the experimental design used to test the attractiveness of flowering *Galium aparine* and *Stellaria media*, two species occurring *in situ*.

	Site 1	Site 2	Site 3
Trapping period 1	Flowering plants	Flowering plants	Plants removed
Trapping period 2	Flowering plants	Plants removed	Plants removed

in Section 2.3). No-plant controls, consisted of 50 pots + soil and were initially placed in rotation under an alternate Malaise trap. The six plant species examined in this manner were: *Agastache* hybrid, *Aloysia virgata*, *Buddleia davidii*, *Calamintha nepeta*, *Phyla nodiflora* and *Sisyrinchium angustifolium*. As in the previous design, the flowers were not examined separately from the plants themselves so that significant differences in captures between were best interpreted as flowering-plant, not floral, attraction. The mean numbers of tachinids collected in traps with and without plants were compared by *t*-tests, using the Satterthwaite method in cases of unequal variances (SAS Inst., 2004).

2.5.3. Rotation among three trap sites of flowering plants, non-flowering plants and no-plant control

The design that provided the best estimation of floral attraction simultaneously compared a blank (no plant) control with plants both in and out of flower. The six species examined in this manner were: *Ageratina aromatica*, *Conoclinium coelestinum, Daucus carota, Monarda punctata, Pityopsis graminifolia* and *Solidago fistulosa*. As above, 50 potted plants of a particular species were rotated among set sites, in this case three sites that included those used in trapping protocol 2 (see Section 2.3), for 6–9 replications, each typically 48 h long. It was sometimes necessary to remove flowers from some of another 50 plants so they could serve as "no-flower" controls. In order that any volatiles that might be emitted by damaged foliage would be as similar as possible in plants in and out of flower, a comparable amount of tissue was cut from those plants that retained their flowers. Tachinid 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).

2.6. Comparisons of captures at the subfamily and genus/species levels and additional analyses

Sufficient numbers of some tachinid subfamilies, genera and species were captured at certain flowers to analyze floral attractiveness at these finer taxonomic levels; e.g., a particular species could be attracted to a certain flowering plant, but at the family level their numbers would be veiled by still larger numbers of multiple species that did not display a preference. The subfamilies, genera and species so examined were: subfamilies = Dexiinae, Exoristinae and Tachininae; the genera/species *Archytas* spp., *Campylocheta townsendi, Paradidyma* spp. and *Prosenoides flavipes* (see results Section 3.1). 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 tachinid captures in plants-in-flower traps from all experimental designs were compared to captures in traps without plants and traps with plants-without-flowers by *t*-test (Zar, 1974). Also including data from all experimental designs, χ^2-tests were used to compare the summed males and females captured in: (1) all flower-containing-traps and their no-plant-controls (i.e., a contingency table format with columns representing males and females and rows no-plant-controls and flower-containing-traps); (2) as above in flowering plants that were significantly more attractive than controls; and (3) as above in flowering plants that were not more attractive than controls.

2.7. Floral and plant measurements

Because the width and depth of flowers or florets (as in the Asteraceae) might influence access to nectar these dimensions were measured in ten randomly chosen blossoms from 10 randomly chosen plants of each species. Measurements were made 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 the corolla diameter and in bilaterally symmetrical flowers, the shorter of the two axes; i.e., the axis most likely to control access. Flower density was estimated using an open plastic frame with inner dimensions of 15×15 cm. The square was randomly tossed five times onto the plants arrayed under a Malaise trap and all the flowers within its boundaries were counted regardless of where they occurred along the height of the plant. "Floral area" was then calculated as the area of a flower/floret multiplied by flower density. In the case of Asteraceae a second form of floral area was also calculated, one that 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. There was no effort made to measure the different variables the same plants. Measurements are available in Sivinski et al. (2011). Separate regressions were used to examine relationships among tachinid capture ratios (ratio of tachinids captured in association with a particular flowering plant to those captured in controls and (1) flower characteristics (width and depth) and (2) plant characteristics (height and floral area [with and without the effect of asteraceous ray flowers]) (SAS Inst., 2004).

2.8. Tachinidae tongue measurements

The length of the tongue (=proboscis) was estimated by first taking images of the entire visible proboscis of each fly with a digital camera (Nikon Digital Sight DS-Fi1, Nikon Inc., Melville, NY) mounted on a Nikon SMZ800 stereoscopic zoom microscope connected to a computer with NIS-Elements F imaging software (Nikon Inc., Melville, NY). Haustella (median section of proboscis, composed of labrum–epipharynx and the labium) were then measured with image measurement software (SigmaScan Pro; SigmaScan Inc., San Jose, CA). The haustellum was chosen as an estimator of relative proboscis length because it was typically visible even when flexure during drying obscured the basal rostrum or distorted the distiproboscis ("oral sucker"). An assumption in comparing heterospecific proboscis lengths via haustella lengths is that the haustellum makes up a similar proportion of the proboscis in all the species examined. In very long tachinid tongues in particular, rostrums may make up a greater or lesser percentage of the total proboscis length than they typically do in those with shorter proboscises. However, long-tongued tachinids were rare in our collections (Fig. 1). A regression examined the relationship between the tongue lengths of tachinids captured in association with a particular flowering plant to flower characteristics (width and depth) (SAS Inst., 2004). Mean tongue lengths of tachinids captured in flower-associated traps were compared to controls with either ANOVAs (controls consisting of both plants-without-flowers and pots-without-plants) or *t*-tests (control consisting of pots-without-plants) (SAS Inst., 2004).

3. Results

3.1. Capture of Tachinidae in traps erected over various flowers

Overall, significantly more Tachinidae were captured in traps baited with flowering plants than in traps that contained no plants ($t = 2.2$; df = 26; $p < 0.05$). However, there was no difference between traps baited with plants in flower and plants without flowers ($t = 0.74$; df = 19; $p > 0.46$). For five individual flower species, *Agastache* hybrid ($p < 0.05$), *A. aromatica* ($p < 0.05$), *D. carota* ($p < 0.05$), *A. virgata* ($p < 0.05$) and *S. media* ($p < 0.05$), traps baited

with flowering plants caught more total tachinids than their respective no plant controls (Fig. 2).

A regression that addressed the relationship between capture ratios (numbers caught in flower baited trap/numbers caught in control) and the flower-morphology variables width and depth was insignificant ($F = 1.03$; df = 5, 7; $p > 0.46$). The model that related capture ratios to plant-morphology variables, floral area and height, was insignificant ($F = 2.5$; df = 5,7; $p = 0.13$), although the variable height was independently significant with a weak negative relationship ($F = 6.5$; df = 1; $p < 0.04$) as was the interaction between floral area and height ($F = 5.6$; df = 1; $p = 0.05$). When the floral area measurements were modified to take into account the increase visual cue due the expanded ray flowers (petals) in the four species of Asteraceae the model was again not significant ($F = 2.5$; df = 5, 7; $p = 0.13$), but height was again independently significant ($F = 6.0$; df = 1; $p < 0.05$) and the interaction between height and floral area bordered on significance ($F = 2.1$; df = 1; $p = 0.08$).

At the subfamily level, over 99% of the flies captured were Dexiinae, Exoristinae and Tachininae (Table 3). Only three Phasiinae were collected. Of the 14 instances with sufficient sample sizes (20 or more insects) to compare flower-associated trap captures at the subfamily level with a control(s), seven found significantly higher numbers of flies captured in flower-baited traps.

Overall, females were significantly more abundant than males (proportion female = 0.60; $\chi^2 = 16.2$, df = 1, $p < 0.001$). However, the proportions of females were similar in no-plant controls and flower-baited traps across all tested plants (0.63 female in baited traps vs. 0.59 female in control traps; $\chi^2 = 2.1$, df = 1, $p > 0.10$), and this female biased sex ratio was the case when flowering plants were significantly more attractive than controls (0.60 female vs. 0.64; $\chi^2 = 0.33$, df = 1, $p < 0.90$) or when flowering plants were not more attractive than controls (0.71 female vs. 0.67; $\chi^2 = 0.34$, df = 1, $p < 0.50$).

At the levels of genus and species, the numbers of individuals were often too low for analysis (Table 4; <20 specimens associated with a plant species). However, there were notable exceptions (Table 5).

(1) Seventy-five *Archytas* spp. were captured, principally on *A. aromatica* (n[no-plant] = 0; n[flower] = 21) and *D. carota* (n[no plant] = 2, n[no-flower] = 3; n[flower] = 22; $\chi^2 = 34.8$, df = 1, $p < 0.001$).

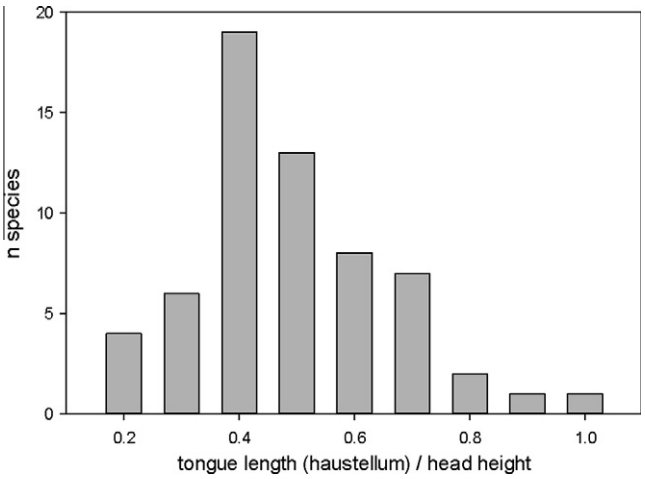

Fig. 1. A frequency histogram of the ratios of haustella length to head height for all Tachinidae species collected in Malaise traps erected over flowering plants, over plants-without flowers and pot-without-plants. Tachinids with elongated, flower-feeding specialized mouthparts were relatively rare in the collections.

(2) *C. townsendi* (Smith), was represented by 309 specimens, 32% of total captures. Examples of substantial trapping include: *Agastache* hybrid (n[flower] = 28; n[no-plant] = 2; $\chi^2 = 22.5$, df = 1, $p < 0.001$); *A. virgata* (n[flower] = 21; n[no-plant] = 5; $\chi^2 = 9.8$, df = 1, $p < 0.005$); *C. nepeta* (n[flower] = 12; n[no-flower] = 5; n[no-plant] = 6; $\chi^2 = 3.8$, df = 2, $p < 0.10$); *D. carota* (n[flower] = 21; n[no-plant] = 9; n[no-flower] = 13; $\chi^2 = 5.3$, df = 2, $p < 0.10$); *M. punctata* (n[flower] = 10; n[no-plant] = 3; n[no-flower] = 15; $\chi^2 = 6.6$, df = 2, $p < 0.05$); *P. graminifolia* (n[flower] = 15; n[no-plant] = 16; n[no-flower] = 19; $\chi^2 = 0.6$, df = 2, $p < 0.75$) and *S. fistulosa* (n[flower] = 11; n[no-flower] = 16; n[no-plant] = 0; $\chi^2 = 9.2$, df = 2, $p < 0.005$).

(3) Seventy-seven individuals of the Tachininae genus *Paradidyma*, were captured. The sole plant with substantial representation was *D. carota* (n[flower] = 14; n[no-flower] = 12; n[no-plant] = 2; $\chi^2 = 8.9$, df = 2, $p < 0.03$).

(4) *P. flavipes* (Coquillett) was likewise numerous only on *D. carota* (n[flower] = 17; n[no-flower] = 5; n[no-plant] = 7; $\chi^2 = 7.9$, df = 2, $p < 0.03$).

3.2. Relation of haustella length to flower morphology

There were few flies collected with elongated-flower-specialist mouthparts. Most could be characterized as "short" or "intermediate-tongued" species (as defined by Allen, 1929; Fig. 1). Overall, the haustella of flies captured in flower-baited traps were longer than those collected in traps without plants (mean[flower] = 1.05(0.04) mm vs. mean[control] = 0.88(0.05) mm, $t = -2.45$, df = 410, $p < 0.02$). There were only three individual plants with significant differences, two in which the flower-trapped flies had significantly longer haustella than those captured at controls: *A. aromatica* (mean[flower] = 1.47(0.13) mm vs. mean[control] = 0.72(0.21) mm, $t = -2.28$, df = 52, $p < 0.03$); *B. davidii* (mean[flower] = 1.29(0.21) mm vs. mean[control] = 0.78(0.14) mm, $t = -2.03$, df = 49.8, $p < 0.05$); and one plant, *P. nodiflora* in which the haustella of flies caught at flower traps were significantly shorter than those caught at the controls (mean[flower] = 0.50(0.03) mm vs. mean[control] = 0.71(0.06) mm, $t = 3.4$, df = 23, $p < 0.003$). There was no relationship between haustellum length and the flower morphology variables depth and width, the quadratics of width and depth or the interaction between width and depth ($F = 1.41$, df = 5, 7, 12, $p > 0.32$).

4. Discussion

Nine-hundred and forty six tachinids were captured and identified to genus, and often species. Their sex was determined and the lengths of their mouthparts estimated. We then compared the numbers, sexes and tongue-lengths of flies collected in flower-baited and control traps. These controls were either associated with plants-without-flowers or pots-without-plants or both. The ratios of flies captured in the flower-baited to control traps were subsequently related to flower density, width, and depth, and plant height in order to test the hypothesis that flower and plant morphology influenced their attractiveness and/or accessibility to Tachinidae (Fiedler and Landis, 2007a,b; Sivinski et al., 2011).

Half of the plant species tested was attractive to tachinids at one taxonomic level or another (Table 6). However two caveats must be offered at the outset: (1) Although Malaise traps readily collect Diptera (Brown 2005), including Tachinidae (Belshaw, 1992), they are not equally effective at capturing all insect taxa so that negative results are not necessarily evidence of non-attraction. For example, Phasiinae were almost nonexistent in our samples although they commonly feed on flowers (Tooker et al.,

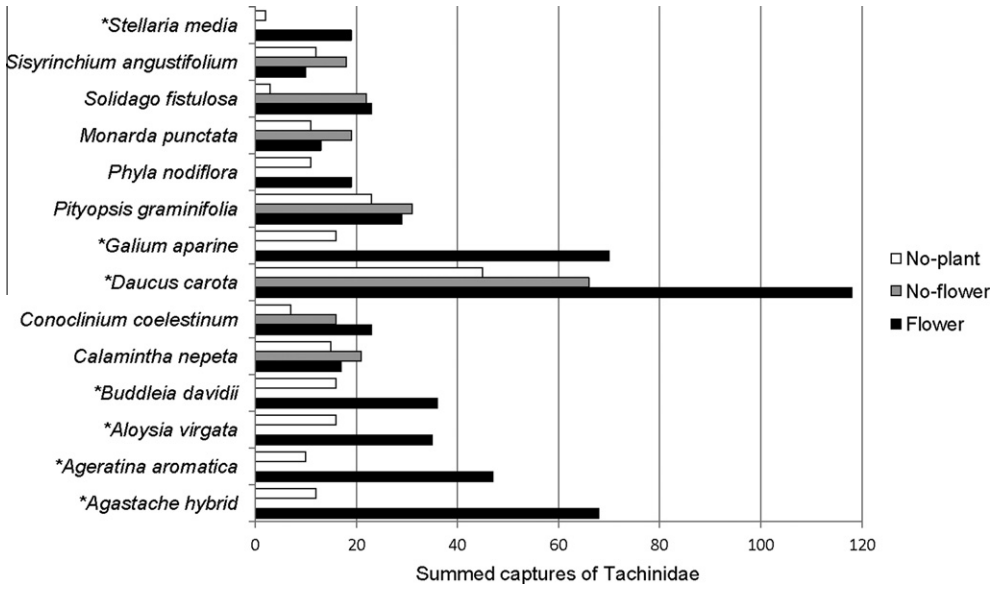

Fig. 2. The total numbers of Tachinidae caught in traps baited with flowering plants, plants-without-flowers and pots-without-plants. In seven of the 14 examined plant species there were significantly greater captures of Tachinidae in flower-associated-traps than in controls at the family, subfamily or genus/species level. There were no instances of significantly fewer tachinids captured in flower-associated-traps. Asterisks (*) denote significant differences.

Table 3
The numbers of various tachinid subfamilies captured in significant numbers in association with various different flowering plants: flower = flowering plant-baited trap, no-flower = plant without flowers-baited trap and no-plant = no plants used to bait trap.

	Flower	No-flower	No-plant	p
Agastache hybr				
Dexiinae	36	*	6	$\chi^2 = 21.4$, df = 1, $p < 0.001$
Exoristinae	19	*	5	$\chi^2 = 8.2$, df = 1, $p < 0.005$
Daucus carota				
Dexiinae	40	21	17	$\chi^2 = 6.6$, df = 1, $p < 0.03$
Tachininae	40	16	8	$\chi^2 = 8.3$, df = 1, $p < 0.005$
Ageratina aromatica				
Tachininae	29	*	2	$\chi^2 = 23.5$, df = 1, $p < 0.001$
Alloysia virgata				
Dexiinae	20	0	0	$\chi^2 = 20.0$, df = 1, $p < 0.001$
Buddleia davidi				
Dexiinae	21	*	5	$\chi^2 = 9.8$, df = 1, $p < 0.001$

* Refers to the absence of a particular treatment.

2006; Stireman et al., 2006). In a data set of 909 records of tachinids feeding on flowering plants, obtained from the literature (provided by JS on request), 28% were Phasiinae. Thus they either avoided capture or were locally rare. (2) Significant comparisons were sometimes between flower-baited and no-plant traps. When this was the case it was possible that foliage or unnoticed extrafloral nectaries rather than flowers were attractive. This presents a particular difficulty in interpreting tachinid captures since they initially forage for hosts using habitat-derived chemical cues rather than host-derived (Stireman et al., 2006) and so may be attracted to plants in the absence of hosts. Indeed, there were instances when flower-associated and no-flower captures were similar though both were greater than those from no-plant traps: e.g., Dexiinae at *M. punctata* and *S. fistulosa* and Exoristinae at *P. graminifolia*. However, from the perspective of natural enemy concentration, attraction to either flowers or foliage might lead to greater pest suppression, although flowers could provide the additional benefit of adult parasitoid food.

The sex ratios of flies captured in the various types of traps might clarify the nature of responses to plants. If host-searching was the motivation for entering flower-baited traps, greater absolute and relative abundances of females might be expected in the flower and no-flower traps compared with the no-plant traps. In contrast, a sexually independent motive (perhaps such as floral feeding?) would leave sex ratios the same in all traps. Overall, sex ratios were female biased but there were no differences in the proportions of males and females taken in the flower-baited and control traps, in either significantly attractive or unattractive plants.

If attracted insects were not searching for hosts on foliage, they might have been seeking extrafloral nectaries or honeydew, potentially present in both flower and no-flower baits. However, none of the plant genera we tested are known to have extrafloral nectaries (Keeler, 2008). We inspected plants during trap rotations and took care to remove any of the rarely found honeydew producing insects.

At the very least we can conclude that certain plants, in flower or not, were more frequented than others. Two plants deserve special consideration because they exceeded or failed to meet expectations. (1) *D. carota* in-flower attracted more Dexiinae and Tachininae than no-flower and no-plant controls, suggesting there is floral attraction to this plant species. At the genus level, traps with flowering *D. carota* collected significantly more *Archytas*, *Paradidyma* and *Prosenoides*, genera that include both short and longer tongued species. It was arguably the most attractive of our tested plants. *D. carota* exceeded expectation since none of the 185 feeding associations between tachinids and Apiaceae species in our literature compilation were from *D. carota*. Apiaceae in general were less frequently represented than were Asteraceae and Rosaceae in the long term field surveys of tachinid-flower associations analyzed by Tooker et al. (2006). However, while Apiaceae comprised only 7% of the species monitored in those surveys, this family accounted for seven out of the 10 flowering plants associated with the greatest tachinid diversity. (2) The genus *Solidago* (Asteraceae) had 29 feeding records in our literature compilation, but *S. fistulosa* was not as effective as predicted. It was certainly attractive to some Diptera since thousands of Bibionidae were captured in flower-associated traps while next to none were found in

Table 4
Tachinid genera and the plants associated with their capture: F = flower-bated trap, NF = plant without flower-baited trap, NP = no plant used to bait trap.

Subfamily	Genus	*Agastache*	*Argeritina*	*Aloysia*	*Buddleja*	*Calamintha*	*Conoclinium*	*Daucus*	*Galium*	*Monarda*	*Phyla*	*Pitopsis*	*Sisyrinchium*	*Solidago*	*Stellaria*
Dexiinae	*Billaea*					3NF, 4NP									
Dexiinae	*Campylocheata*	28F, 2NP	5F, 3NP	21F, 5NP	15F, 5NP	12F, 5NF, 6NP	2F, 3NF, 1NP	21F, 16NF, 9NP	5F, 2NP, 1F	10F, 15NF, 3F	3F, 4NP	15F, 19NF, 16 NP	1NF	11F, 16NF	5F, 3NF
Dexiinae	*Metaplagia*														
Dexiinae	*Prosenoides*	7F, 4NP	3F	8F	8F	1F	1F	17F, 5NF, 7NP	4F, 3NP				1F		6F, 1NP
Dexiinae	*Spaethedexia*											1NF			
Dexiinae	*Uramya*						1NF								
Dexiinae	*Voria*							1F							
Dexiinae	*Wagneria*								2F, 1NP						
Dexiinae	*Zelia*						1F					1F, 1NP		1F	
Exoristinae	*Admontia*	4F		1F		2NP	1NF	2F, 4NF, 4NP	4F, 5NP				2NF, 1NP		1F
Exoristinae	*Allophorocera*			1F			1F, 1NP				2F, 1NP	3F		2F	
Exoristinae	*Ametadoria*									1F		1NF		1NF	
Exoristinae	*Anoxynops*							2F							
Exoristinae	*Austrophorocera*						2NF	1NF	1F						
Exoristinae	*Belvosia*		1F												
Exoristinae	*Blepharipa*											1NF, 1NP			
Exoristinae	*Calolydella*								1F						
Exoristinae	*Carcelia*				1NP		1NP	1F, 1NP	1F, 1NP			1F	1NP		
Exoristinae	*Chaetonodexodes*				1NP		1F	5F				1F, 1NF			
Exoristinae	*Chetogena*	2F, 2NP						2F, 7NF, 4NP							
Exoristinae	*Distichona*		1F		2NP			1F, 1NP	1F						
Exoristinae	*Drino*	2NP		2F	2NP	1F, 1NF	3F, 1NP	1F, 3 NF, 3NP		2NP	2NP			1F, 1NF, 1NP	
Exoristinae	*Eucelatoria*	1F			1F, 2NP		2F, 1NF	4F, 2NF, 1F	4F	2NP	4F, 1NP	1F	1F, 2NF, 1NP	1F	
Exoristinae	*Exorista*											1F			
Exoristinae	*Frontiniella*												1NP		
Exoristinae	*Gaediopsis*							1NF			2F				
Exoristinae	*Gonia*		1F, 1NP				1F, 1NP								
Exoristinae	*Gueriniopsis*	1NP						3F, 1NF							
Exoristinae	*Hemisturmia*										1F				
Exoristinae	*Houghia*	1F						1NF	2NP	1F, 1NF, 1NP	1F	1F, 2NF			
Exoristinae	*Leschnaultia*							2F, 1NF, 1NP							
Exoristinae	*Lespesia*	1F	2NP	1F		1F, 3NP	1NF	2NF	1F	1NF	1F, 1NP	1NF	1NF		
Exoristinae	*Medina*							1NF				1F			
Exoristinae	*Nilea*							1F							
Exoristinae	*Patelloa*		1F		1NP						1NF				
Exoristinae	*Phasmophaga*								1NP						
Exoristinae	*Phorocera*													1F	
Exoristinae	*Phytoyptera*								1F						
Exoristinae	*Prospherysa*								2F						
Exoristinae	*Pseudochaeta*	1F		3F, 1NP				2NF, 1NP							
Exoristinae	*Siphosturmia*		1F		1NP					1NP					
Exoristinae	*Tachinomyia*						1NF						1NP		
Exoristinae	*Thelairodoria*	8F	3F, 3NP	2F, 3NP	1NP			3F	2F	2F	2F, 2NF, 2NP	3F	1F, 2NF	1F, 1NP	
Exoristinae	*Vibrissina*		1NP						1NP						
Exoristinae	*Winthemia*						1F, 2NF	1F, 3NP	3F, 1NP			2F, 1NP	1F, 1NP		

(*continued on next page*)

Table 4 (*continued*)

Subfamily	Genus	*Agastache*	*Argeritina*	*Aloysia*	*Buddleja*	*Calamintha*	*Conoclinium*	*Daucus*	*Galium*	*Monarda*	*Phyla*	*Pitopsis*	*Sisyrinchium*	*Solidago*	*Stellaria*
Exoristinae	*Zaira*						1F, 2NF						1F, 1NP		
Phasiinae	*Clairvillia*													1NF	
Phasiinae	*Cylindromyia*		2F												
Tachininae	*Archytas*	11F	21F		5F	2F, 1NF, 1NP		23F, 3NF, 2NP	2F, 1NP						2F
Tachininae	*Ceracia*	1F, 1NP			1F			4NP	1NP		1NP			1F	
Tachininae	*Deopalpus*	1F	2F			1NP		2NF	2F				1F		1F
Tachininae	*Jurinia*				1F										
Tachininae	*Leskia*				1NP			1F						2F, 1NF	
Tachininae	*Lypha*		2F, 2NP						4F						
Tachininae	*Nearea*								1F						
Tachininae	*Neomintho*	1F			1NP		2F	1F		1NF					
Tachininae	*Paradidyma*	1NP	4F	2F		1F. 3NP	1F, 1NP	14F, 12NF, 2NP	1F, 2NP	1NP	2F	1F, 5NF, 3NP	3F, 9NF, 4NP	2F, 1NF	
Tachininae	*Peletaria*		1F		1NP										
Tachininae	*Tachina*			1F	1F	1F								1F	

no-flower and no-plant traps. Perhaps there is an unrevealed variance in attractants/nectar within the genus. Over a multi-year survey of Illinois Tachinidae-flower associations, *Solidago canadensis* L. was fed upon by a high diversity of flies while *Solidago gigantea* Aiton was not (Tooker et al., 2006).

Flower/plant-morphological patterns in our tachinid captures were largely absent; this is in contrast to the parasitic Hymenoptera also captured in the present experiment (Sivinski et al., 2011). Among wasps, larger floral areas were more attractive and this was a characteristic similar to one positively associated with predator and parasitoid abundance on a variety of native and introduced plants in Michigan (Fielder and Landis, 2007a,b). Floral area could increase flowering plant conspicuousness and advertise the presence of denser and more abundant resources. In New Zealand, the tachinid *Protohystricia huttoni* (Malloch) makes more visits per hour to individual *Myosotis colensoi* (Kirk) (Boraginaceae) plants with larger floral displays (Robertson and MacNair, 1995).

Overall, trapping data suggests two generalizations concerning floral feeding by northern Florida tachinids compared to the parasitic Hymenoptera at the same sites. (1) There were similar proportions of significantly tachinid-attractive flowering plants in the present sample relative to parasitic Hymenoptera captured in the same experiment (50% vs. 53% [10 of 19 species]), and a moderate amount of overlap in which species were attractive (Sivinski et al., 2011). *A. aromatica*, *A. virgata*, *D. carota* and *S. media* were associated with both significantly greater numbers of parasitic Hymenoptera and Tachinidae. However, the coarser level of parasitic Hymenoptera identification (at most, and then occasionally, to subfamily) could have led us to overlook the unusual abundance of a particular species in one type of trap or another. (2) Those tachinids that did seek floral foods were not as strongly influenced by plant/flower morphology as were the simultaneously captured parasitic Hymenoptera, particularly in terms of floral area. Although flies collected in flower-baited traps overall had longer mouthparts than those taken in controls, the absence of such tongue/flower patterns argues that tachinids were not seeking flowers to which their mouths were particularly adapted; i.e., longer-tongued flies did not predominate at deeper-flowers. Long tongues of course need not preclude feeding on shallow flowers (Allen 1929), but the inclusion of more species of plants with deep flowers in our study may have produced a stronger association with long tongued tachinids. That and the likelihood that even shorter tongues wielded by large and burly flies could gain access to many of the experimental flowers would have tended to homogenize the mean tongue lengths among flower-baited traps.

What remain unknown are the attractive qualities/cues possessed by those plants that did lure tachinids into the traps. If not the measured components of floral morphology, it is possible that differences in floral volatile components underlie the variance in attraction and these are presently under investigation.

There is a substantial body of evidence that increasing the floral diversity of agroecosystems enhances natural enemy diversity and abundance and ultimately the biological control of pest insects. Certainly some of the abundantly collected tachinids in the present

Table 5
Significant captures of tachinid species/genera in traps with flowers compared to control(s) without flowers (see text).

	Agastache	*Ageratina*	*Aloysia*	*Daucus*	*Galium*
Archytas spp.		X		X	
Camplyocheta townsendi	X		X		X
Paradidyma spp.				X	
Prosenoides flavipes				X	

Table 6
A summary of significant captures of Tachinidae relative to control(s) at various taxonomic levels. Dark squares represent no significant differences compared to control(s).

	Family	Subfamily	Genus/species
Agastache hybrid	X	Dexiinae; Exoristinae	*Campylocheta townsendi*
Ageritina aromatica	X	Tachininae	*Archytas* spp.
Aloysia virgata	X	Dexiinae	*Campylocheta townsendi*
Buddleia davidii		Dexiinae	
Calamintha nepeta			
Conoclinium coelestinum			
Daucus carota	X	Dexiinae; Tachininae	*Archytas* spp. *Paradidyma* spp. *Prosenoides flavipes*
Galium aparine			*Campylocheta townsendi*
Monarda punctata			
Phyla nodiflora			
Pityopsis graminifolia			
Sisyrinchium augustifolium			
Solidago fistulosa			
Stellaria media	X		

study might contribute to pest suppression. For example, species of the tachinine genus *Archytas* attack a wide variety of Lepidoptera larvae (Arnaud, 1978) and some are of considerable agricultural importance, even being mass-reared for augmentative release (e.g., Mannion et al., 1995). Although the hosts of *C. townsendi*, which made up 32% of the captured Tachinidae, have not been identified, species of *Campylocheta* have been recovered from larvae of the pest-containing families Geometridae, Notodontidae, Noctuidae and Tortricidae (as *Chaetophlepis* in Arnaud, 1978).

Adjacent-crop pollination is another potential advantage to increasing tachinid numbers with non-crop flowers. In some pollinator guilds, Tachinidae are relatively common flower-visitors (e.g., Medan et al., 2002). But this is not universally the case (e.g., Campbell, 1985; Herrera, 1989), nor are tachinids always relatively efficient at pollen transfer following their visits (e.g., Herrera, 1987).

While the relationship between some tachinids and some flowers has been illuminated, the lack of pattern between flower/plant morphology and tachinid-attractiveness makes it difficult to predict from the present study which other flowers might be profitably added to agricultural landscapes. However, regional field surveys, such as this, can offer empirically-based guidance for plant selection (Allen, 1929; Tooker et al., 2006).

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