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### The natural history of the parasitic wasp *Trogus pennator* (Hymenoptera: Ichneumonidae): Host-finding behaviour and a possible host countermeasure

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# The natural history of the parasitic wasp *Trogus pennator* (Hymenoptera: Ichneumonidae): Host-finding behaviour and a possible host countermeasure

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## Abstract

The parasitic wasp *Trogus pennator* (Ichneumonidae) attacks the larvae of swallowtail butterflies (Papilionidae). Female *T. pennator* were followed in the field as they searched for larvae of the zebra swallowtail butterfly, *Eurytides marcellus* (Papilionidae), feeding on *Asimina* (Annonaceae) in central Florida, USA. Predictions of host-finding theory and interactions with the host were thus investigated in a natural setting. Wasps seldom flew to plants other than *Asimina* and apparently recognized the plants by visual cues. Plants were attractive regardless of host presence, as the wasps approached plants lacking *E. marcellus* feeding damage twice as often as they approached damaged plants. However, wasps approached damaged plants at a rate greater than their frequency in the *Asimina* population, indicating that they can detect host damage before they approach the plants. After approaching within 0.5 m of plants, wasps tended not to land on plants lacking feeding damage. A comparison of the plants they landed on, however, showed no consistent preferences for damaged plants. The weaker trends in the latter data indicate that the presence of feeding damage was not the sole criterion for landing, although it evidently influenced behaviour. After landing, wasps spent more time searching damaged plants than undamaged plants. Butterflies preferred to oviposit on plants shorter than those searched by *T. pennator*. Possible adaptive consequences of this phenomenon are discussed.

**Keywords:** Field observations, host-finding behaviour, Ichneumonidae, Papilionidae, parasitic wasp

## Introduction

Parasitoids that attack herbivorous insects must find small, sparsely distributed hosts in heterogeneous environments, a problem that can be lessened by limiting the search to the habitats and food plants associated with the hosts. The attraction of parasitoids to the food plants of their herbivorous hosts was initially inferred from observations of host range: some parasitoids specialize not on host taxa per se but on the insect fauna of particular plants or

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plant habitats, such as leaf miners or wood borers (Picard and Rabaud 1914; Cushman 1926). Starting in the 1930s, olfactometer experiments confirmed that female parasitoids are attracted to odours associated with their hosts (Laing 1937; Thorpe and Caudle 1938), and it has since been established that parasitoids of herbivorous insects rely largely on chemical cues to find both plants and hosts (Price 1981; Tumlinson et al. 1992). Plant volatiles, including those released from feeding damage, attract females in flight, while compounds derived from saliva, frass, cuticle, and silk are used to find and recognize larvae at close range (Weseloh 1981; Vinson 1984; Rutledge 1996). The host-searching process has been described as a hierarchical sequence of increasingly restricted steps, the three major stages being habitat (or plant, in the case of parasitoids of herbivores) finding, host finding, and host recognition and acceptance (Doutt 1959; Vinson 1976). More recently, "dynamic" models have attempted to account for the observed complexity in searching behaviour, including variation in the reliability and detectability of plant and host cues (Vet et al. 1990; Vet and Dicke 1992; Godfray 1994).

Work motivated by these ideas has provided a rich understanding of how parasitoids find their hosts. Yet there remain two significant shortcomings. Firstly, most systems studied (certainly all those studied in detail) are agricultural (Godfray 1994). Because these systems typically involve domesticated plant varieties, introduced insect and plant species, or artificial trophic associations, the evolutionary and ecological generalizations drawn from such studies are inherently limited. Secondly, parasitoids are seldom studied in the field, due to the small size of most species and the difficulty of obtaining adequate sample sizes (Casas 1989). The few field studies that exist focus on optimal foraging theory or reproductive strategy, not on the mechanistic aspects of plant and host location (Waage 1983; Thompson 1986; Connor and Cargain 1994; Heimpel and Rosenheim 1996). Almost all knowledge of host-finding mechanisms thus comes from experiments conducted in simplified arenas, such as flight chambers or wind tunnels, in which wasps are presented with just two, or a few, choices of plants or hosts. Although such experiments have provided detailed accounts of the nature and identity of cues used, and have been indispensable for studying learning, they cannot replicate field conditions. Consequently, little is known about the behaviour of wasps in natural habitats, amid a much more complicated array of plant species, some damaged (by a variety of herbivores), some not. Neither the degree of overlap in stages of host searching, nor wasps' responses to the reliability and detectability of cues have been examined in natural settings, where odours mix unpredictably and where wasps must orientate to plants across distances greater than the typical length of a flight chamber.

The aim of the work reported here was to observe parasitic wasps searching for hosts in a natural, non-agricultural setting, and thus to test whether current ideas about host-finding behaviour, which are based largely on studies of captive wasps, describe what parasitic wasps actually do in the field. The ichneumonid *Trogus pennator* (Fabricius) is unusual among parasitic Hymenoptera in that it is easily observed in the wild: it is large, with a wingspan of up to 2 cm, and strikingly coloured, with a bright orange body and iridescent purple wings. Like that of other *Trogus* species, the host range of *T. pennator* is restricted to swallowtail butterflies (Lepidoptera: Papilionidae) (Sime and Wahl 2002). Females lay a single egg in caterpillars of any age. The host develops normally through the pupal moult, after which the wasp larva begins to feed. The adult emerges from the remains of the host pupa (Mitchell 1981). *Trogus pennator* is widespread in the USA, though most common in the south-eastern states, and attacks nearly all of the papilionids in its range, including *Eurytides marcellus* (Cramer) and several *Papilio* species (Heinrich 1962; Mitchell 1983;

Sime 2001). These hosts feed on a variety of plants but each species tends to specialize within plant families (Feeny 1991).

The present study exploited a population of *T. pennator* in central Florida pine forests, where the usual host is the zebra swallowtail, *E. marcellus*, which feeds on pawpaw (Annonaceae: *Asimina* spp.). The ecology and behaviour of *E. marcellus* has been much studied in this habitat and *T. pennator* is common, routinely parasitizing a substantial proportion of the spring brood (Damman 1986a, 1986b). It is the only swallowtail specialist present; species of Tachinidae (from the pupae) and *Trichogramma* (from eggs) are occasionally reared as well.

Experimental work with *T. pennator* (Sime 2001, 2002) has demonstrated that food-plant odours are attractive in flight, while frass and feeding-damage odours act as arrestants, and that the frass and feeding-damage odours of papilionid larvae are distinguished from those of other Lepidoptera. Plant cues are learned whereas cues derived from the host are innately attractive. These findings are consistent with the predictions of the reliability-detectability model of host-finding for a wasp that specializes on host taxa but must contend with diverse food plants (Vet and Dicke 1992; DeMoraes and Mescher 1999). In the current study, two predictions of this model were tested in the field. The first emerges from attributes of the population studied: although *T. pennator* attacks a variety of hosts over its geographic range, it is largely or entirely restricted to *E. marcellus* in central Florida. Because this host is restricted to *Asimina*, *Asimina* plants are expected to provide reliable information about the location of *E. marcellus* larvae, and female *T. pennator* are expected to seek them out systematically. The second prediction is that host-derived cues become more useful (because more easily detectable) as the distance to the host decreases (Vet and Dicke 1992). This study therefore included an investigation of the wasps' responses to feeding damage prior to close approach, after approach and after alighting on the plant. This information also tests a prediction of the hierarchical model of host finding, that plant-derived cues are used to find plants from a distance while host-derived cues are used to find hosts after alighting (Doutt 1959; Vinson 1976).

An additional inquiry was prompted by observations of the butterflies' oviposition behaviour (Damman 1986b; Haribal and Feeny 1998). Although the *Asimina* species in question commonly reach about a metre in height, female *E. marcellus* prefer tiny plants, at least during the early part of the season—which is also the only time of year that *T. pennator* are observed in this area. The butterflies expend considerable effort pushing through the leaf litter in order to place their eggs on plants just a few centimetres tall. This behaviour is puzzling: because the caterpillars cannot complete their development on the scant foliage of smaller plants, they must eventually wander away in search of other plants, thus risking predation and starvation (Damman 1986a). Damman and Feeny (1988) investigated various plant attributes linking female choice with larval survivorship in *E. marcellus*. The female butterflies favour plants with the young, soft leaves that are most suitable for the development of the larvae. In early spring, however, both large and small plants bear fresh leaves, so something else must underlie the preference for smaller plants. Damman and Feeny found no correlation of female choice with overall larval mortality due to predation, but did not consider the possibility that the caterpillars on smaller plants are protected from some subset of the natural enemy fauna. To test this hypothesis, the work reported here included an investigation of whether *T. pennator* females tend to search plants larger than those preferred by female *E. marcellus*.

## Methods

### Field site

This study was conducted in the Ocala National Forest, in central Florida, near the Lake Delancy Recreation Area (29°25'N, 81°47'W). All observations took place in the Riverside Pine Island, an extensive stand of longleaf pine woods (*Pinus palustris* Miller) with an open understorey dominated by wiregrass (*Aristida stricta* Michx.) and scattered low shrubs, mostly oaks (*Quercus incana* Bartr. and *Q. laevis* Walt.) and pawpaw. This plant community is particularly favourable for observing insects: the openness allows unobstructed views and the grasses provide a bland background against which the wasps may be spotted at distances of up to some 20 m. The food plants of *E. marcellus* here are two pawpaw species, *Asimina speciosa* Nash and *A. obovata* Willd., and hybrids between them (Damman 1989). Additional information concerning this field site was given by Damman (1986a) and Kalisz and Stone (1984).

The parasitic wasp overwinters within the hardened remains of its host's pupa. Adults of *T. pennator* and *E. marcellus* begin to emerge from winter dormancy at the onset of warm spring weather, usually in mid-March. Both species are conspicuous for about a month thereafter, with populations peaking about 2 weeks after the first sightings. In each of the 5 years in which the author worked at this field site, the wasp flight peaked 1–2 weeks after the butterfly peak. The peak of *E. marcellus* flight activity coincides with the *Asimina* bud burst, the first butterflies emerging before any leaves are present (Damman and Feeny 1988). Few *T. pennator* were seen searching plants during this period. Although *E. marcellus* has a second brood in the summer, *T. pennator* is only observed in the spring (Damman 1986a). Data for the present study were collected in March and April 1997 and 1998.

### Pursuit of wasps

The wasps are easily recognized, even from a distance of a few metres, by their colouring and by the distinctive blocky shape of their abdominal segments. When a female *T. pennator* was spotted, the investigator drew to within 1–2 m and followed the wasp for as long as possible. The wasps gave no sign of being disturbed by human proximity. As each wasp was followed, the species of each plant it approached, whether or not it landed on the plant, and the length of time it spent searching the plants after landing were recorded. An "approach" was recorded if the wasp flew to within  $\approx 0.5$  m of a plant and interrupted its flight, either to land or to pause and circle for a few seconds above or next to the plant. Searching time included the time a wasp spent tapping the plant surface with its antennae while walking about the plant, not time spent grooming or standing still. After a wasp departed from a plant, the plant was marked with coloured flagging tape. Later, the heights of the plants were recorded and they were examined to see whether *E. marcellus* larvae or their feeding damage were present.

The larvae of *E. marcellus* are cryptic in colouring and habits, sometimes resting in the leaf litter or on adjacent herbs, but their feeding damage is easily identified. The damage of younger larvae is characterized by small holes in young leaves or irregular bites along the leaf margin, while the older larvae typically remove distal slices of leaf perpendicular to the midvein. Few other insects feed on *Asimina* in the Ocala National Forest (Damman 1986a). One other herbivore, *Omphalocera munroei* Martin (Pyrilidae), becomes common as spring progresses, but the gregarious larvae are invariably found in their rolled leaf

shelters (Damman 1989) and thus not confused with *E. marcellus*. A case-bearer (*Thyridopteryx ephemeraeformis* (Haworth) (Psychidae)) and a chrysomelid beetle (*Cryptocephalus* sp.) feeding on *Asimina* were also occasionally observed during this study. Neither produced damage patterns similar to that of *E. marcellus*.

### *Plant survey*

If female *T. pennator* use *Asimina* plants to narrow the search for hosts, they should fly to *Asimina* plants more often than if they simply approached plants at random. If not, the proportion of *Asimina* among the plants they approached would be the same as that in the local flora. A vegetation survey was conducted to establish the frequency of *Asimina* plants among the flora of the observation area. A grid was mapped out along the dirt path along which most of the field observations were made, with seven  $50 \times 50$  m squares marked off on each side of the path. Within each square,  $5 \times 5$  m plots located at the centre, 10 m from the edge of the path, or offset from the centre by 10 m and located 20 m from the path were surveyed. These plots were sampled in random order until the *Asimina* distributions stabilized (at 16 plots). At this site, *Asimina* and other small understorey shrubs and herbs occur in a matrix of dry grass; for this survey the number of individuals of each broad-leaved species was counted and the grasses, which the wasps were not observed to search, were ignored. A chi-square test was used to compare the fraction of the flora represented by *Asimina* with the proportion of *Asimina* among plants approached by the wasps.

### *The roles of leaf damage*

The responses of wasps to feeding damage were examined at three stages: before approaching the plant (i.e. prior to pausing within  $\approx 0.5$  m), after approaching but before alighting, and after alighting on the plant.

If feeding damage attracted the wasps before they approached the plants, they would be expected to approach damaged *Asimina* plants more often than predicted by chance. Otherwise, they would be expected to approach damaged plants at the same rate as damaged plants occurred in the local *Asimina* population. The proportion of the plants with *E. marcellus* feeding damage was determined using a vegetation survey designed like the floral survey described above. Plots lacking *Asimina* were omitted from the analysis; in the end 13  $5 \times 5$  m plots containing *Asimina* were sampled. A chi-square test was used to compare the fraction of the *Asimina* population damaged by *E. marcellus* to the proportion of damaged *Asimina* among all plants approached by the wasps.

In order to determine whether the presence of feeding damage influenced the decision to land, the behaviour of those wasps that both rejected (i.e. flew away without alighting) and landed on some plants after approach was examined. Rejections and landings were analysed separately, using sign tests to compare the numbers of wasps that more often rejected plants with feeding damage and those that more often landed on plants with feeding damage.

Finally, the effect of feeding damage on the time spent searching the plants after alighting was examined. For those wasps that searched both damaged and undamaged plants, the average times spent searching on damaged and undamaged plants were compared using a paired *t* test.

*Comparison of butterfly and parasitoid behaviour*

The average size of plants searched by *T. pennator* was compared with the average size of plants chosen by female *E. marcellus* for oviposition. As discussed above, the heights of *Asimina* plants approached and searched by the wasps were recorded. Following the methods described by Damman and Feeny (1988), female *E. marcellus* were tracked as they inspected and oviposited on plants. The identity and height of each plant approached, and whether the butterfly ultimately laid an egg on the plant before departing, were recorded. The butterfly and wasp data were collected in the same spring (1997), within a 4-week period. Some of the butterfly data were collected up to 10 days before the wasp data were collected, but it is unlikely that the data set was biased as a result: *Asimina* plants grow very slowly and they were not observed to change in height over the course of data collection.

## Results

### *General observations*

A total of 82 female *T. pennator* were followed, 57 in 1997 and 25 in 1998. On average a wasp was followed to  $5.2 \pm 0.6$  plants (range 1–17) before it was lost to sight. The female wasps flew slowly, 1–1.5 m above the ground, just above the level of most understorey vegetation. They often appeared to fly directly from one *Asimina* plant to the next, and seldom approached other small shrubs. They usually landed on the plants, but sometimes circled at close range, within  $\approx 0.5$  m, then flew away. The wasps almost always landed on the top surfaces of leaves. Upon alighting, they tapped the plant surface with the distal third of their antennae. Sometimes they stayed for just a few seconds, but at other times they searched the plant very thoroughly, examining nearly every leaf and stem, often walking off the base of the plant to investigate the surrounding leaf litter. Searching bouts as long as 4.5 min were observed. Usually the wasps found nothing, but about 20 attacks in the field were witnessed. If its antennae touched an *E. marcellus* larva, a wasp would immediately try to sting it. No *E. marcellus* larvae were rejected if contacted by the antennae. Moreover, the wasps did not seem to recognize hosts if the antennae missed them, and some even stepped on small *E. marcellus* caterpillars without detecting them. The wasps searched plants with larvae of any age: eight plants with first-instars were searched, three of which were stung, and 29 plants with second instars were searched (the largest category), four of which were stung. A few older larvae were found and attacked as well. The numbers of each instar that were attacked probably simply reflected their proportions within the field population, though this supposition was not tested in this study.

Several observations of the behaviour of *E. marcellus* larvae that were relevant to the behaviour of *T. pennator* were made. The larvae almost invariably feed with their bodies on the underside of leaves, and rest either under leaves or away from the site of feeding damage, such as on the stem or off the plant entirely, on a nearby plant or in the leaf litter. The wasps, however, landed on and initially examined the top surfaces of leaves. They were never observed to land first on the stems or in nearby litter, although during longer searches they often inspected these areas. The larvae also responded actively to the presence of the wasps. They dropped from their leaves when wasps landed on their leaves or on a nearby part of the plant; the wasps did not immediately notice the decampment but continued to search the upper reaches of the plants. The larvae also usually deployed their osmeterial glands (eversible sacs coated with butyric acid that are stowed behind the head capsule) when touched by wasps, though with mixed effectiveness. If the osmeteria met any part of a

wasp's body other than the antennae, the wasp continued the attack. If the osmeteria touched an antenna, the wasp would react immediately and dramatically, discarding the caterpillar and quickly flying away, usually to a nearby plant to groom its antennae for several minutes.

In both 1997 and 1998, some *E. marcellus* larvae were collected in the field and reared to pupation to determine the extent of parasitism by *T. pennator*. In 1997, of 49 pupae obtained, 11 produced *T. pennator* (22%), 32 produced butterflies and six produced species of Tachinidae. In 1998, 10 pupae survived; three produced *T. pennator*, three produced butterflies and four produced tachinids. For comparison, H. Damman (personal communication) reported parasitism by *T. pennator* at the same field site at 15% (6 of 39 pupae).

#### Identification of *Asimina* by *T. pennator*

The vegetation survey indicated that *Asimina* plants comprised 7.5% of the broad-leaved plants in the Lake Delancy habitat (Figure 1). In contrast, of 270 plants approached by 57 wasps, 93% were *Asimina*. The significant difference between these distributions indicates that the wasps do not approach plants at random but orient specifically to *Asimina*.

The mistakes in plant identification provide some clues to the nature of the cues involved. The few non-*Asimina* plants approached by the wasps resembled *Asimina* in height, colour and leaf shape, presenting a similar visual profile against the background of dry grass. The commonest of these included small oaks (saplings or low shrubs) and vines (*Smilax*, *Vitis*). These observations suggest that the wasps rely at least in part on visual cues to locate and identify *Asimina* from a distance.

#### The roles of leaf damage

Of the *Asimina* plants surveyed in 1998, 16.4% (of 566 plants examined) bore evidence of *E. marcellus* feeding damage (Figure 2). Of 175 plants approached by female *T. pennator*, 36% were damaged. The few (five) plants approached that bore only the damage of other

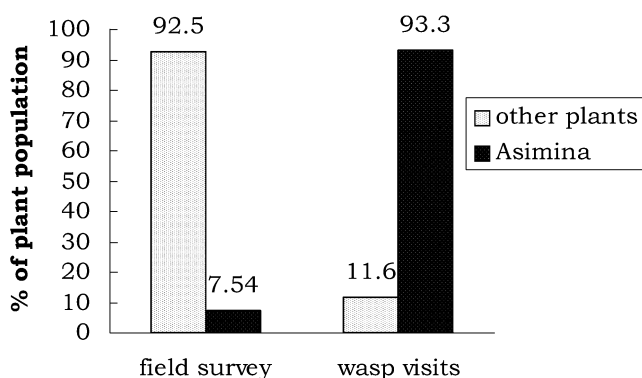


Figure 1. A vegetation survey was conducted in spring 1997 to establish the frequency of *Asimina* among the broad-leaved plants in the understorey. The mean percentage *Asimina* was determined at 7.5% by counting stems in 5 m × 5 m plots. Plants counted as "other" most commonly included *Quercus incana*, *Q. laevis*, *Vitis rotundifolia* Michaux, *V. aestivalis* Michaux, *Mimosa*, sp., *Smilax* spp., and several unidentified Compositae. In contrast, 93.3% of plants visited by the wasps were *Asimina* ( $P < 0.001$ , chi-square test).

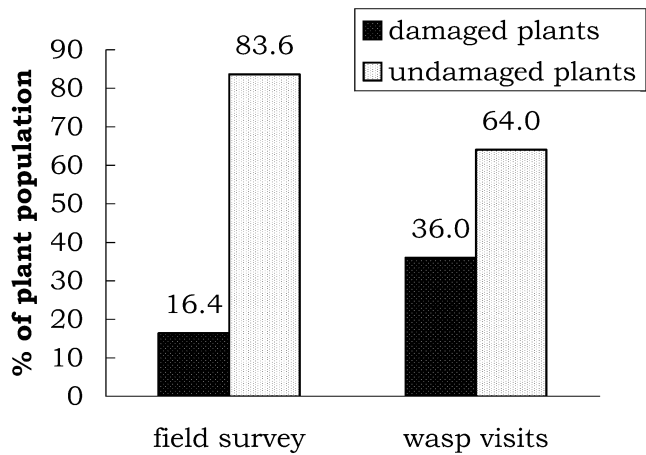


Figure 2. The frequency of plants damaged by *Eurytides marcellus* in the population was estimated at 16.4%. In contrast, 36% of the plants visited by the wasps were damaged ( $P<0.001$ , chi-square test).

herbivores were excluded from this analysis. The significant difference between these distributions indicates that the wasps are attracted to *E. marcellus* damage from a distance. It should not go unremarked, however, that *undamaged* plants were nonetheless approached about twice as often as were damaged plants. This observation confirms that the presence of *E. marcellus* damage is not the sole criterion of plant identification, and that visual or olfactory cues unrelated to the presence of hosts are important.

Some wasps both landed on and rejected (i.e. flew away without landing on) some of the plants that they approached within  $\approx 0.5$  m (Table I). Their behaviour provides some support for the idea that feeding damage positively influences the decision to land. Leaving without landing is strongly associated with the absence of damage, though landing was not consistently associated with damage. This mixed result indicates that the decision to land is influenced by but partly independent of the presence of damage.

After alighting, the wasps spent significantly more time searching those plants with *E. marcellus* feeding damage than those plants lacking damage (Figure 3). (No wasp searched on non-*Asimina* plants for  $>5$  s.) This result indicates that feeding damage acts as an

Table I. The feeding damage of *Eurytides marcellus* was investigated as a basis of selectivity for those wasps that both rejected and landed on some plants after approaching within 0.5 m.

Damaged	Number of wasps that more often rejected plants that were:		
	Clean	No preference	
0	13	3	$P<0.01$ (1997)
0	12	3	$P<0.01$ (1998)
Damaged	Number of wasps that more often landed on plants that were:		
	Clean	No preference	
10	3	3	$P<0.05$ (1997)
10	6	0	NS (1998)

Sign tests were used for all comparisons. “No preference” indicates that the wasp rejected (or landed on, in the second data set) equal numbers of damaged and clean plants. In both 1997 and 1998, no wasp rejected damaged plants. In 1997 but not in 1998, a significant number of wasps tended to land on damaged, rather than clean plants.

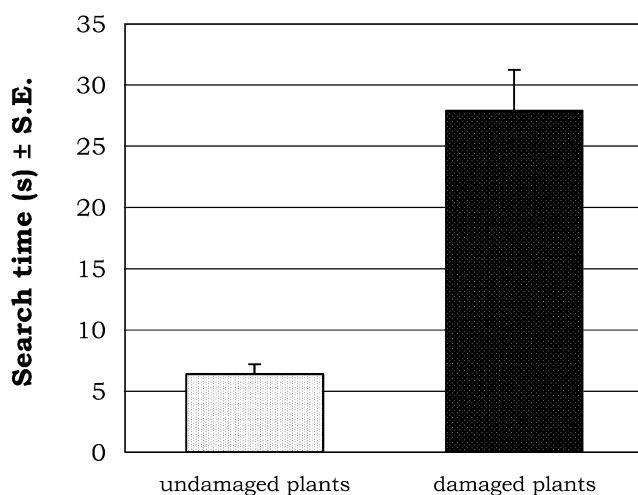


Figure 3. For those wasps ( $n=33$ ) that landed on and searched both undamaged *Asimina* plants and plants that were damaged by *Eurytides marcellus*, average searching times were significantly longer on damaged plants ( $P=0.0016$ , two-tailed paired  $t$  test).

arrestant. The wasps were often observed to pause at the chewed edges of leaves, stroking the leaf margins repeatedly with rapidly vibrating antennae.

#### Comparison of butterfly and wasp

Forty-one *E. marcellus* females were observed laying eggs. The average height of the plants they chose for oviposition (22 cm) was significantly lower than the average height of plants searched by *T. pennator* in the same season (51 cm) (Figure 4). The butterfly data are similar to those reported by Damman (1986a) in spring 1982 (19 cm) and 1983 (12 cm).

### Discussion

Females of *T. pennator* are striking to observe in the field as they focus persistently on the food plants of *E. marcellus*. They seldom stray from *Asimina*, and then only briefly, despite variation in the shapes and sizes of plants and in the plants' surroundings, and despite the presence of many other plant species of comparable stature. The finding that they are highly attracted to the food plants of their hosts (Figure 1) underscores the usefulness of information about the food plant to narrow the search (Vinson 1976). Whether or not the ability to identify *Asimina* is learned cannot be determined in a field study; it must be assumed that all wasps observed had experience with *E. marcellus*. Laboratory evidence indicates that learning of plant odours plays a role (Sime 2002).

The systematic seeking out of *Asimina* plants contrasts with the evidently more haphazard pursuit of hosts, a difference that most likely reflects the greater detectability of plants compared with larvae. As would be expected if detectability of host-derived cues decreased with distance, this haphazardness was most apparent prior to approaching within 0.5 m. Although the wasps could detect feeding damage from a distance, they nonetheless approached clean plants twice as often as they approached damaged plants (Figure 2). After close approach, the wasps tended to reject clean plants without further examination, which

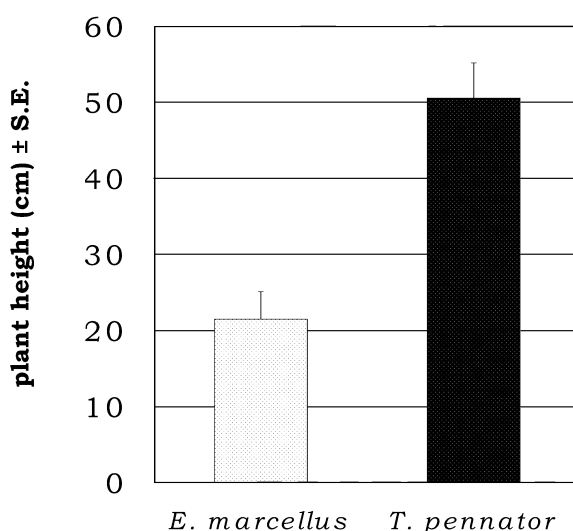


Figure 4. The average height of plants searched by *Trogus pennator* ( $n=57$  wasps, range=8–145 cm) and selected for oviposition by *Eurytides marcellus* ( $n=41$  butterflies, range=2–95 cm) was compared in spring 1997. The wasps searched plants significantly taller than those preferred by the female butterflies ( $P<0.0001$ , two-tailed  $t$  test).

indicates that detectability increased at close range (Table I). Even so, their landing preferences were incompletely correlated with the presence of damage. Most females landed on and searched briefly at least some plants that lacked damage. These observations indicate that the host-derived cues are not always detected before landing, and that the wasps may land on a suitable plant regardless of whether host odours are detected.

When the wasps simply fly to plants (regardless of whether damage is present) and then search them for hosts, their behaviour is consistent with the simple hierarchical model of searching behaviour. However, when they orient directly to damaged plants (the “plant–host complex” (Vet et al. 1995), the behaviour of the wasps departs from this model. The hierarchical model thus describes a subset of the wasps’ behavioural patterns, which must be adjusted for the relative strength of cues from the plant or from feeding damage. The observations reported here for *T. pennator* are consistent with experimental reports indicating that the “steps” in the searching hierarchy are defined arbitrarily and may overlap (Vinson 1981, 1984). While some parasitoids search the food plant of the host regardless of host presence (Vinson 1981), others are led to the host via odours given off by plants damaged by herbivores (Tumlinson et al. 1992). If such odours are specific to the herbivore species, the plant- and host-location and host-recognition steps collapse into one.

The occasional approach of the wasps to plants of colour and stature similar to *Asimina* indicates that visual cues are used to identify plants from a distance. Confusion of plant odours is another possibility, although less likely if it is assumed that plants vary more in their chemistry than in their stature and in the gross outline and colour of their leaves. Although the finding that damaged plants are approached more often than random (Figure 2) indicates that odours associated with the presence of the hosts are detectable at a distance, the observation that uninfested plants are also searched (and more often than are infested plants) indicates that a mixture of host-derived and plant-derived cues are used at a distance, with plant cues predominant. The host-derived cues would include volatiles released from host-damaged plants and odours from the host or its frass (Sime 2002),

though it is also possible that feeding damage is identified visually (Wäckers and Lewis 1999). The reliance on the antennae after landing indicates that arrestant cues are olfactory.

Damman (1986a, 1986b) reported that *E. marcellus* larvae have three defences against natural enemies: everting their osmeterial glands, dropping off leaves and resting away from the site of damage. Although Damman (1986a) found that the use of osmeteria was correlated with lowered predation rates overall, he stated that they were ineffective in deterring *T. pennator*. Evidently he did not witness a successful deployment; the observations reported here show that the osmeteria can be effective against *T. pennator*. The other two behaviours would also be useful in evading the wasps, reducing the risk of encounter by removing the larvae from areas most likely to be searched by wasps. None of these defences are particular to *T. pennator*: the osmeteria are effective against a variety of invertebrates (Damman 1986a) and the dropping and resting behaviours can help elude birds (Heinrich 1979, 1993).

The question of whether the butterflies' preference for oviposition on small plants represents an evasive action against *T. pennator* is similarly complicated, for it is not entirely obvious that parasitism by *T. pennator* is an important selective force. Damman (1986a, 1986b) considered *T. pennator* a minor contributor to mortality in *E. marcellus* because mortality is concentrated in the earliest stages due to predation by various spiders and ants. It may be argued, however, that by parasitizing 15% and more of *E. marcellus* larvae, *T. pennator* is not insignificant and may represent the *single* most important natural enemy species. As the only specialist on *E. marcellus*, *T. pennator* is the only source of mortality that appears to be a consistent threat over time, given its recurrence over many years of collecting at the Ocala field site.

Damman and Feeny (1988) examined the criteria used by *E. marcellus* to select plants for oviposition, and concluded that the butterflies chose plants most suitable in leaf texture and nutrition content for larval growth. They found no significant correlation between plants chosen and overall larval mortality caused by natural enemies. As evidence for the improbability of the butterflies being able to identify plants on which their progeny would be relatively free from predators, they cited the mobility of most natural enemies and the random distribution of spiders and ants. Their approach was incomplete, however. First, Damman and Feeny only measured female discrimination between the approach and oviposition phases; they did not include in their data set any measure of the plants *not* approached by female *E. marcellus*. Second, the use of general correlations obscures patterns attributable to a single natural enemy. Butterflies would not be expected to adapt to avoid a predator that is either seldom important or that is truly random in its searching habits. They might, however, evolve to avoid a persistent enemy that prefers certain plant traits. The differences reported here in the sizes of plants favoured by butterflies and wasps are suggestive, though they would be more conclusive if parasitism rates on large and small plants had been evaluated as well. It would also be useful to determine whether other natural enemies of *E. marcellus* favour larger plants.

In a different environment (rural New York meadows), Feeny et al. (1985) noted that parasitism rates of the black swallowtail (*Papilio polyxenes* Fabricius) by *T. pennator* were highest on poison hemlock (*Conium maculatum* L.), which was the tallest, most conspicuous plant used by this host in that study. This and examples from other systems indicate that microhabitat can provide possibilities for escape, although female choice in herbivorous insects is not usually linked explicitly with the susceptibility of the offspring to parasitoids. Shahjahan and Streams (1973) reported that the braconid *Leiophron*

*pseudopallipes* Loan was most able to find its hemipteran hosts (*Lygus* species) on large plants and in dense, more visually apparent stands of plants. Ohsaki and Sato (1990, 1994) reported that *Pieris napi* (L.) (Pieridae) eludes the braconid *Cotesia glomerata* (L.), to which it is otherwise entirely susceptible, through its preferential use of *Arabis* over other crucifers as its food plant. Although *Arabis* is nutritionally inferior to other available crucifers, it is advantageous to *P. napi* in that it is seldom searched by *C. glomerata*. The *Arabis* plants are small and typically obscured by other herbs, whereas the wasps tend to search the upper portions of taller plants.

The finding that *T. pennator* and *E. marcellus* favour different sizes of plants underscores the importance of field studies of the host-finding behaviour of parasitic wasps. The responses of wasps to the variability (in size, odour, presence of hosts and other herbivores, etc.) that occurs across an entire plant population simply cannot be examined in experimental arenas. The role of vision in plant identification is also underemphasized in experimental work—and indeed is difficult to study, because of the impossibility of adequately re-creating the context of a plant with its neighbours in a complex environment. Finally, the relative distances at which visual and olfactory cues are reliable and detectable can probably only be realistically studied in the field.

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