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What determines host range in parasitoids? An analysis of a tachinid parasitoid community

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Abstract Despite the vast diversity of parasitic insects and their importance in natural and agricultural communities, our knowledge of what determines their patterns of association with hosts remains sparse. Unlike most parasites that tend to be specialized, parasitoid flies in the family Tachinidae exhibit a broad spectrum of host-specificity, with many species attacking a wide range of hosts. This variability in host-specificity makes them a useful model for examining the ecological and historical factors that determine host associations. We analyzed data collected from a 5-year rearing program of Lepidoptera in southern Arizona to investigate the factors that influence tachinid-host associations. After controlling for a strong effect of sample size, a significant portion of the remaining variance in host range was explained by differences among phylogenetic groups of tachinids and/or their correlated reproductive strategies. Relatively specialized tachinids tended to be associated with monophagous or narrowly oligophagous hosts and attacked them at relatively high frequencies, a pattern we suggest is related to host location efficiency. Cluster analysis indicated that host abundance, gregariousness, food-plant type, and morphology are all important determinants of tachinid host use. Little concordance was found between how tachinid species cluster according to characteristics of their hosts and their estimated phylogenetic relationships. Together, the results of this study suggest that ecological factors are important determinants of host use in these parasitoids and although phylogenetic history may influence the range of hosts used, its power to explain the ecological or taxonomic character of hosts used appears limited.

Keywords Specialization · Polyphagy · Ecological determinant · Lepidoptera · Tachinidae

Introduction

Patterns of host use in parasitic insects have been the focus of an enormous amount of research by behavioral ecologists, evolutionary biologists, and community ecologists (Price 1980; Futuyma and Moreno 1988; Jaenicke 1990; Kawecki 1998). Much of this interest has centered around the goals of understanding how the diverse communities of these insects are maintained in ecological time and space and how they have diversified over evolutionary time (e.g., Ehrlich and Raven 1964; Labandeira et al. 1994). Although we have made great strides in identifying and understanding ecological patterns of food-plant associations in phytophagous insects (Strong et al. 1984; Singer and Parmesan 1993; Novotny et al. 2002) and their evolutionary development (Farrell and Mitter 1994; Futuyma and Mitter 1996; Nosil 2002), the patterns of host range of another diverse and ecologically important guild of parasitic insects, the parasitoids, remain much less well known. The number of studies exploring the evolutionary and ecological determinants of host use in parasitoids is growing (e.g., see Hawkins 1994; Hawkins and Sheehan 1994), but for most groups we have little idea of the relative importance of ecological habitat, processes of host location, physiological interactions with hosts, host defenses, or phylogenetic history in influencing parasitoid host ranges.

Although determining parasitoid host ranges is plagued with difficulties (Shaw 1994), it appears that most parasitoids attack only a narrow range of hosts (Herting 1971–1982; Memmott et al. 2000). The two principal

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factors that limit host ranges in parasitoids are thought to be host taxonomy and host ecology (Askew and Shaw 1986). The effect of host taxonomic affinity is believed to be related primarily to physiological (and morphological) defenses of hosts that may require specific adaptations of their parasitoids (Vinson and Iwantsch 1980; Godfray 1994; Kraaijeveld et. al 1998). The proposal that physiological defenses limit parasitoid host ranges is analogous to arguments concerning the importance of secondary chemicals in the specialization of phytophagous insects on food-plants (Dethier 1954; Ehrlich and Raven 1964). Ecological characteristics that influence host use by parasitoids include the plants on which a host feeds (Vinson 1981; Askew 1994), the microhabitat in which it feeds (Weseloh 1993), and the host's phenology (Clausen 1940; Askew 1961).

Flies in the family Tachinidae are unusual among parasitoids in the remarkably broad host ranges of many species despite their endoparasitic lifestyle (Eggleton and Gaston 1992; Belshaw 1994). Tachinids appear to avoid physiological defenses of hosts by forming respiratory funnels through which they maintain contact with outside air (Clausen 1940; Eggleton and Gaston 1992), and this trait appears to be associated with relatively broad host ranges (Belshaw 1994). This may obviate the need for biochemical adaptation to particular host species and permit polyphagy (Belshaw 1994). Tachinids may also be pre-adapted to tolerate defensive chemicals contained in hosts due to adaptations of their ancestors to other toxic environments (e.g., carrion; Gauld et al. 1992).

If tachinid host-use is not generally limited by host physiological defenses, and the range of potential hosts that can support development is quite large, what then determines which hosts are actually used by a particular species? Despite their relatively broad host ranges, most tachinids use only a tiny fraction of potentially available hosts (Stireman and Singer 2003). The difference between the potential host ranges and the much smaller realized host ranges in phytophagous insects and other parasitic insects has led several authors to suggest that ecological attributes of hosts may strongly influence host range for many species and the process of host location may play a significant role in determining patterns of host use (Bernays and Graham 1988; Feener and Brown 1997; Janz and Nylin 1997; Lill et al. 2002; Perlman and Jaenicke, in press).

In this study the determinants of tachinid-host associations are explored using data from a 5-year rearing program of Lepidoptera in southeastern Arizona. These data are used to address three primary questions:

1. How does the oviposition strategy and taxonomic affiliation of tachinid species influence the range of hosts they attack (i.e., what are the historical and/or physiological constraints on host range)?
2. Is there an association between the host specificity of tachinid species and the food-plant specificity of their host(s) due to selection for efficient host location and/or the necessity to tolerate host toxins?
3. Which ecological, behavioral, and physical characteristics of hosts are most important in determining the local patterns of host use?

By exploring these questions we hope to expand our understanding of the determinants of host range in the relatively poorly known tachinid parasitoids, which may in turn provide insight into the forces that shape host associations in other parasitic insects.

Tachinid biology

Female tachinids possess a wide variety of oviposition strategies and morphological specializations involved in host attack that may influence the range of hosts they attack. Some genera deposit unincubated eggs on the host that must develop for several days before hatching (Clausen 1940). However, most species that deposit eggs on hosts possess uterine incubation such that the eggs hatch quickly after oviposition. The necessity of expelling these developing offspring may lower thresholds for selecting hosts and lead to broad host ranges. Approximately 40% of species either deposit larvae on substrates frequented by hosts (e.g., leaves of food plants) or deposit "microtype" eggs upon the food plant of the host that are inadvertently ingested by the host (O'Hara 1985; Wood 1987). In either case the adult fly does not contact the host and such "indirect" oviposition strategies may result in a large number of offspring dying before they encounter hosts. For this reason, these taxa may be more likely to attack hosts that feed gregariously where encounter probabilities may be much higher. They may also be expected to possess broader host ranges due to opportunistic attack of any host encountered due to the low probability of such encounters (Belshaw 1994). These hypotheses are also evaluated in this study.

Materials and methods

Sampling methods

Larval macrolepidoptera were sampled from 1996 to 2000 in southeastern Arizona within an area of approximately 9,000 km^2. Sampling was generally restricted to mesquite-oak savannas as well as associated riparian areas at elevations between ca. 1,000 and 1,600 m. Sampling was conducted by walking haphazardly through the appropriate habitats and visually inspecting herbs, shrubs, and trees up to a height of approximately 3 m. Ultimate and penultimate instar caterpillars were preferentially sampled to allow maximum exposure to parasitoids in nature. Either all of the individual caterpillars observed (of the appropriate size/age classes), or at least 20 individuals per species per sampling site were collected. If a particular species was abundant, it was sampled from a variety of individual food-plants.

Caterpillars were collected in plastic vials with their food plant and transported to the University of Arizona. As they were collected they were assigned an identification code, and their identity, food plant, size, habitat, gregariousness, and morphology were recorded. They were then reared in plastic cups or containers in a laboratory growth chamber (28°C, light:dark16:8 h) on their natural food plants collected from the field. Frass and unused plant

Table 1 The host characteristics used in cluster analyses of tachinid species reared from two or more hosts. Each of the levels of each host characteristic was assigned a rank for analysis. Host size is measured as the approximate length of the final instar larva

Host characteristic	Levels
Abundance	Number of collections+observations without collection
Size	1=1-3 cm 2=3-5 cm 3=5-8 cm 4=8+cm
Morphology	1=Smooth 2=Hairy 3=Spiny
Food-plant type	1=Herb 2=Shrub 3=Tree
Gregariousness	1=Solitary 2=Gregarious

material were removed and new plant material added every other day. When caterpillars ceased feeding, all plant material was removed and the caterpillar was allowed to pupate. Lepidoptera were identified by comparison of reared adults to specimens in the University of Arizona Insect Collection (UAIC) and through determinations made by R. Nagle, B. Walsh, and J. Tuttle. Voucher specimens are deposited in the UAIC.

All parasitoids that emerged from hosts were collected, given a code relating them to the host, and mounted on pins for identification. Tachinids were identified by J. O. Stireman using Wood (1987), and by comparison with specimens in the UAIC and Canadian National Collection of Insects (CNC). In addition, determinations of certain species were made by N. E. Woodley (USDA, Systematic Entomology Laboratory), J. E. O'Hara (CNC) and D. M. Wood (formerly of the CNC). Voucher specimens of all tachinid species reared have been retained by the authors for use in identifying further reared specimens and, when possible, deposited in the UAIC.

Analysis

To assess the extent of tachinid polyphagy at a local scale, we first conducted a log-log regression of host range against the number of host collections from which a tachinid species was reared. A regression of host range against the number of individual hosts explained less variance (see results) and may violate assumptions of independence of records. A nested analysis of covariance (ANCOVA) was used to examine the effects of tachinid oviposition strategy and tribal affinity on host range with the number of host collections (>1) included as a covariate. Oviposition strategy consisted of four levels: unincubated (on host), incubated (on host), indirect macro (off host), and microtype (off host). We used tribal placement (or subfamily; Herting 1984) of each species (nested within oviposition strategy) as a rough indication of phylogenetic relationships to assess the importance of phylogenetic history and closely associated traits on host range. A more explicit phylogenetic control was not possible due to the lack of phylogenetic analyses of Tachinidae and uncertainties in their classification (Wood 1987; but see below). To test whether tachinids with indirect oviposition strategies are associated with gregarious hosts, we compared the number of tachinid species with direct and indirect oviposition that attacked at least one gregarious host species. Hosts were classified as gregarious if individuals feed in a group during any part of the larval stage based upon field observations.

To test for an association between tachinid polyphagy and food plant range of their hosts, tachinid species were classified as either oligophagous (one host family) or polyphagous (more than one host family) based on the current data set as well as Arnaud's (1978) catalog of tachinid-host associations. We compared the mean food-plant range of the hosts of these two groups of tachinids using a Kruskal-Wallis test. Food-plant ranges were derived from the number of plant species on which we observed hosts feeding within our study area. An ANOVA was used to assess whether the maximum parasitism rate inflicted by a tachinid species on any of its hosts differed between oligophagous and polyphagous tachinid taxa. To minimize artifacts of sampling, only tachinids that were reared from at least ten host individuals were included in this analysis. All statistical analyses were performed using the JMP 3.2.1 (SAS Institute 1996), unless otherwise noted.

We used cluster analysis of principal components to identify host characteristics that were important in determining patterns of tachinid host use. For this analysis, we classified all hosts according to their abundance, size, morphology, habitat, and gregariousness. Each of the levels of these variables was ranked (Table 1), and the average rank of all hosts of a particular tachinid (reared from at least two hosts) was entered into a principal components analysis. The values of the first three principal components (explaining a cumulative variance of 92.9%) were then used in a hierarchical cluster analysis using Ward's distances to produce a dendrogram, which could then be used to assess how tachinid taxa aggregate in relation to characteristics of their hosts. In addition, the phylogenetic mixed model option of COMPARE 4.1 (Martins 2001) was used to calculate the "phylogenetic heritability" (H^2; Lynch 1991) of each of the host-associated characters based upon a provisional phylogeny with all branch lengths assumed to be equal. This conservative phylogenetic hypothesis for the subset of taxa included in this analysis was based on recent analyses of the subfamily Exoristinae (Stireman 2002) along with inferences from classification and morphology (Herting 1984; Wood 1987).

Results

Our collections yielded 64 species of tachinids reared from 75 species of Lepidoptera (Appendix 1). The number of host species per tachinid species ranged from one to 19, with 59% of tachinid species being reared from only a single host species (Fig. 1a). The regression of host range against the total number of collections from which a tachinid species was reared was highly significant [adjusted (adj.) r^2=0.747; $F_{1,62}$=99.7, P<0.001; Fig. 1b], suggesting that many of the narrow host ranges may be due to inadequate sampling. A parallel regression using the number of individual hosts explained considerably less variance in host range (adj. r^2=0.397; $F_{1,62}$=42.4, P<0.001). Fourteen of the 26 tachinid species reared from more than one host species were also reared from more than one host family, demonstrating a lack of conservatism with respect to host taxonomy.

Taxonomic group (tribe) of the tachinid species had a significant effect on host range after controlling for effects of sample size (ANCOVA: Collections, $F_{1,38}$=55.2, P<0.001; Oviposit, $F_{1,38}$=1.0, P=0.418; Tribe (Oviposit), $F_{1,38}$=4.2, P=0.020). This appears to be due to the wide host ranges of the Exoristiini and relatively narrow ranges of Winthemiini and Tachininae (Fig. 2a). Contrary to expectation, oviposition strategy (Oviposit) did not significantly affect host range. However, tachinids that deposit unincubated eggs on hosts tended to possess

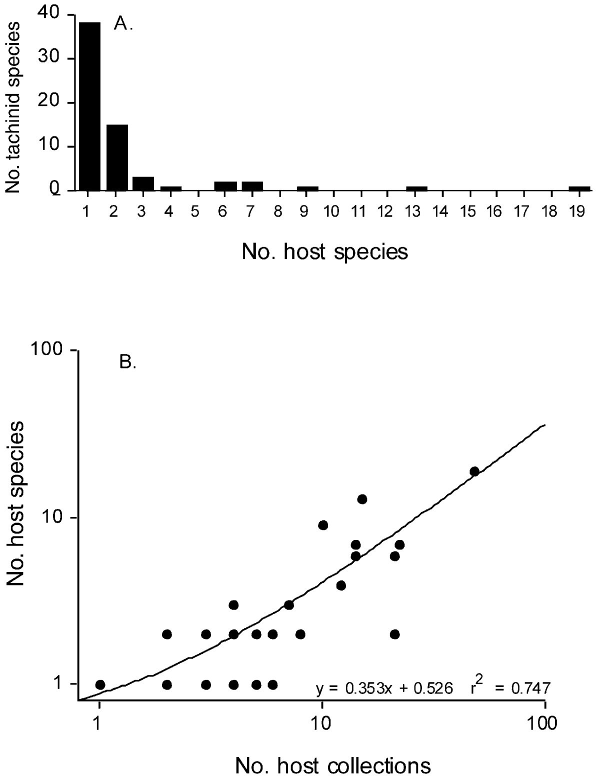


Fig. 1 **A** The distribution of the number of host species from which each tachinid species was reared in this study. **B** A linear regression of the log number of host species from which tachinid species were reared against the log number of host collections they were reared from

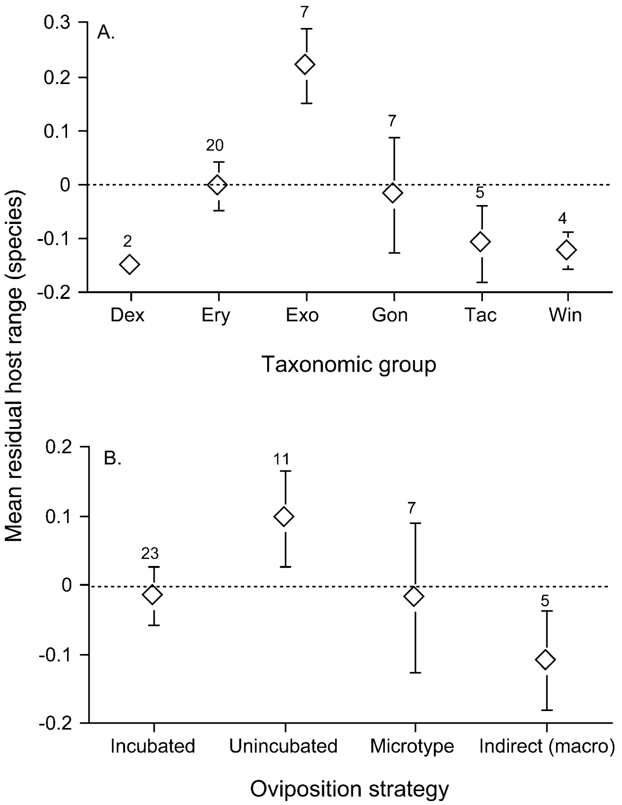


Fig. 2 **A** The average (±SE) residual host range after the removal of effects of number of collections for tachinids belonging to six tribes/subfamilies of tachinids [Dexiinae (*Dex*), Eryciini (*Ery*), Exoristini (Exo), Goniini (Gon), Tachininae (Tac), Winthemiini (Win)]. *Numbers above the error bars* indicate the number of tachinid species belonging to each taxonomic group. **B** The same measures plotted for four different oviposition strategies: *Incubated* eggs laid on the host after uterine incubation, *Unincubated* eggs laid on the host without uterine incubation, *Microtype* eggs deposited on the host's food and ingested by hosts, *Indirect (macro)* eggs deposited on a substrate and the larva contacts the host; see text for statistics

Table 2 A comparison of the average (±SE) food-plant range (no. of species) of the hosts of oligophagous (one host family) and polyphagous (more than one host family) tachinid species with classification into diet breadth categories based on data from the current study and based on literature records from Arnaud (1978). See text for statistics

Tachinid classification	Food-plant range of host	
This study	Mean	SE
Polyphagous	5.33	0.83
Oligophagous	2.27	0.51
Literature		
Polyphagous	5.92	1.10
Oligophagous	2.93	0.49

broad host ranges and those that oviposit macrotype eggs or larvae indirectly tended to exhibit relatively narrow host ranges (Fig. 2b). Indirect oviposition was significantly associated with the attack of gregarious host species (Fisher's exact test: P=0.012; Fig. 3).

The hosts of polyphagous tachinids exhibited significantly broader (average) food-plant ranges than those attacked by oligophagous species (Table 2) whether tachinids were classified as oligophagous or polyphagous according to the current data or literature records (Current, χ^2=5.95, df=1,63, P=0.015; Arnaud 1978, χ^2=10.07, df=1,59, P<0.002). Maximum parasitism rates inflicted by oligophagous tachinids were higher than those due to polyphagous species (mean±SE: oligo, 51.4±5.1%; poly, 27.3±7.6%; $F_{1,20}$=5.72, P=0.027).

The dendrogram resulting from the hierarchical cluster analysis grouped tachinid taxa into five primary clusters (Fig. 4). These clusters are largely defined by whether the hosts attacked by the tachinids are gregarious or solitary, their morphology (smooth or hairy), body size, and abundance. Several groups within these clusters tend to be defined by the habitat of their hosts (herbs, shrubs, or trees), and one small cluster of taxa can be defined by shared use of Sphingidae. A comparison of this dendrogram with the provisional phylogeny of the tachinids suggests little correlation between ecological-morphological patterns of host use and the phylogenetic relationships among tachinid species (Fig. 4). Various alternate rootings of the dendrogram did not affect this result.

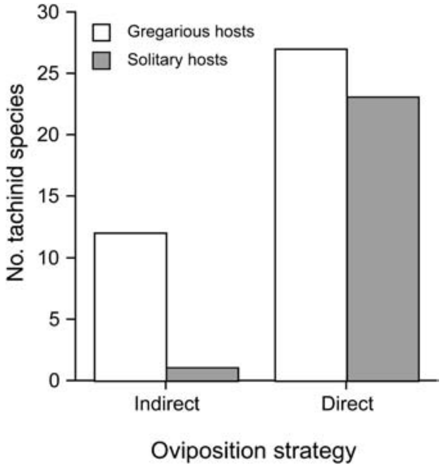


Fig. 3 The number of tachinid species with indirect (both microtype and indirect macro) and direct oviposition strategies (see text) that were reared from at least one gregarious host species (*white bars*), and the number reared from only solitary host species (*gray bars*). See Fig. 2 for terms and text for statistics

Phylogenetic H^2 values of the host traits examined based upon the hypothesized phylogeny were quite low, ranging from 0.015 to 0.104, supporting a limited influence of phylogeny on patterns of host use.

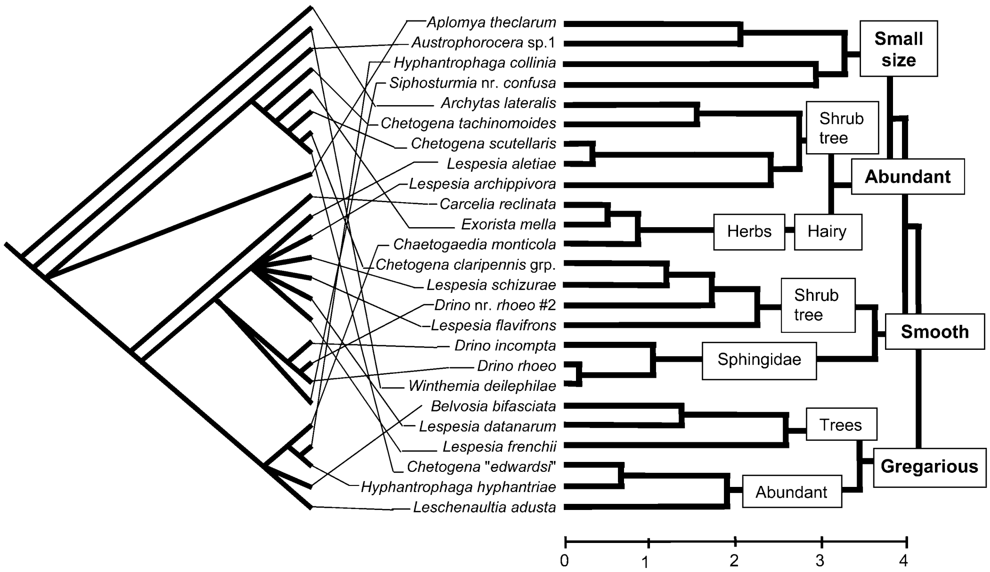
Discussion

A number of patterns emerged from these analyses that provide clues to the determinants of host use in tachinids. However, we caution that without well resolved phylogenetic hypotheses, the influence of shared history and phylogenetically correlated variables on the ecological patterns we uncover is difficult to ascertain. For many Tachinidae, which exhibit great evolutionary plasticity in host-associations (Wood 1987), these issues may not seriously affect conclusions, but for other groups in which host-associations are much more conserved, issues of phylogenetic independence become more prominent (e.g., Futuyma and Mitter 1996).

The positive relationship between the number of host collections from which a tachinid was reared and tachinid host range is consistent with the conclusions of Eggleton and Gaston (1992) and Belshaw (1994) that tachinids are polyphagous as a whole. However, much of the variance in host range explained by the regression is likely due to a small subset of highly polyphagous species. Tachinids with narrow host ranges are unlikely to be reared often, and contribute little to the regression in relation to their species richness. For example, as of 1990, over half of European species of tachinids had no known hosts (Mellini 1990), probably because the majority of these species are relatively specialized. The difficulty of identifying tachinid species (Crosskey 1976) and the poor quality of host records derived from the literature (Shaw 1994) may also contribute to the correlation between sample size and host range, though these problems are minimized when using data from a cohesive rearing program as was done here. These issues are likely to distort the perceived host ranges of other parasitic taxa as well.

The effects of oviposition strategy and tribal placement on host range are confounded, with members of a tribe almost always sharing the same oviposition strategy, and thus it is difficult to separate the effects of these two variables. Even with a reliable phylogenetic estimate of relationships, the low number of potentially independent contrasts may severely limit the power of such an analysis to resolve effects of oviposition strategy. In the current analysis, tribal affinity (phylogeny), or some trait associated with phylogenetic relationship appears to be a better predictor of host range. The degree of developmental synchrony with hosts, which Belshaw (1994) found to have a significant effect on host range in

Fig. 4 On the *right*, a dendrogram of tachinid species (reared from two or more host species) resulting from a hierarchical cluster analysis based on a series of five classes of host characteristics (see Table 1). The primary host characteristics responsible for the major clusters are indicated at the *base of the clusters*. *Sphingidae* indicates that all hosts are sphingids. Distance (Ward's) is indicated on the *scale below the dendrogram*. On the *left* is a provisional phylogenetic tree based on taxonomic classification and molecular phylogenetic analysis (see text)



tachinids (high synchrony=more specialized), may be such a trait.

Contrary to conventional wisdom (Clausen 1940), tachinids with indirect oviposition strategies exhibited the lowest average host range of the four groups examined, and those possessing microtype eggs had host ranges no larger than expected given sample sizes. Belshaw's (1994) analysis of literature-derived data from the Palaearctic region also failed to find elevated host ranges in tachinids with indirect reproductive strategies. This may be a consequence of depositing offspring on specific substrates (e.g., particular food-plant species), and high specificity in the cues used to locate hosts (Roland et al. 1995, Mondor and Roland 1997, 1998). The association between indirect oviposition strategies and attack of gregarious hosts may partially explain the finding that host ranges of these taxa are no greater than those of direct ovipositors. By attacking hosts that feed in groups, these species can increase the probability that their larvae or eggs will be encountered by hosts, and the opportunities for encountering other host species will be reduced. It has been suggested that indirect oviposition strategies evolved in Tachinidae as adaptations to attack concealed hosts that are otherwise inaccessible (e.g., leaf tiers, stem borers; Belshaw 1994). While this may have originally contributed to the evolution of this habit, only three of this study's 14 species with indirect (and microtype) oviposition attacked concealed hosts. The data presented here suggest that an increased efficiency in attacking gregarious hosts contributes to the maintenance of this trait.

Specialists versus generalists

Two hypotheses may explain the relationship we identified between parasitoid host-specificity and the food-plant specificity of their hosts. First, hosts that are specialized with regard to their food plants may gain defensive benefits from these plants (e.g., Bernays and Graham 1988), which limit their physiological suitability for non-adapted parasites. Alternatively, the pattern may be related to selection for more refined host location cues to locate specialized hosts, which should lead to narrowing of parasitoid host ranges. Examination of the data indicates that the latter explanation is more likely. Generalist tachinid species such as *Lespesia aletiae* and *Chetogena tachinomoides* attack and successfully develop in specialist as well as generalist hosts, although the majority of records are from abundant generalist host species (e.g., *Grammia geneura*, *Estigmene acrea*, *Spodoptera* sp.). Furthermore, literature records of tachinid-host associations suggest that tachinid host ranges are not generally constrained by chemical defenses of hosts (Arnaud 1978). Oligophagous tachinid taxa, however, tend to be more restricted to food-plant specialized hosts. Over 70% of the 47 tachinids classified as oligophagous attack only specialized hosts (two or fewer observed food plants).

The difference between the maximum parasitism rates achieved by oligophagous and polyphagous tachinid species is largely a consequence of the absence of parasitism rates >50% by generalists. This pattern may be related to the greater host-finding efficiency of more specialized parasitoids and their concentrated attack on one or a few host species. This would be consistent with Dyer and Gentry's (1999) finding that specialist caterpillars in the northeastern United States exhibit significantly higher parasitism rates than generalist species. However, Dean and Ricklefs (1980) found the opposite pattern for hymenopteran parasitoids (i.e., parasitism frequency increased with the number of hosts attacked), suggesting differences in the ways these two groups interact with hosts.

Determinants of host use patterns

The influence of morphological and ecological characteristics of a host on whether it is used by a particular tachinid species appears complex. The well-defined clustering relative to the use of solitary and gregarious hosts indicates that this characteristic has a strong influence in determining whether a caterpillar species is attacked by a particular tachinid species. Host morphology serves to unite at least two groups of tachinids. In some cases these groupings may represent the use of particular host families (e.g., Sphingidae=smooth), but it is likely that the morphological features themselves are important given the apparent adaptations for utilizing hairy hosts in some tachinids (e.g., projectile oviposition of *Carcelia* species).

The observation that the food-plant type on which hosts feed appears to unite a number of small groups within the main clusters suggests that habitat use may be less constraining than host morphology, gregariousness, or abundance. The clustering effect of food-plant architecture is likely a reflection of the searching strategies used by tachinids to locate hosts. More specific effects of microhabitat may also occur at the level of food-plant species, but the data were not sufficient to explore the role of microhabitat at this fine scale.

Attack of abundant hosts defines two clusters and may contribute to several others (e.g., the "gregarious" cluster). For *L. aletiae*, *Chetogena scutellaris*, and other highly polyphagous tachinids, host abundance may be the primary factor determining which hosts are attacked. However, the large role of host abundance in clustering taxa may be biased due to the exclusion in this analysis of many relatively specialized tachinid species.

The lack of correspondence between the tachinid phylogeny and the cluster analysis dendrogram and the low estimates of phylogenetic heritability suggest that the host characteristics that govern patterns of tachinid host use are not historically conserved, at least at large phylogenetic scales. Although certain tachinid taxa were restricted to particular taxonomic groups of hosts, over half of tachinid species that were reared from more than one host species were also reared from more than one host family.

Together, the results of this study suggest that tachinid-host associations are strongly influenced by ecological traits of hosts (e.g., food-plant specificity, gregariousness, abundance), but the importance of these traits appears to be highly plastic among tachinid taxa. Although the breadth of hosts used appears to be influenced by phylogenetic relationships and developmental synchrony with hosts (Belshaw 1994), the identity of hosts in terms of morphology, phylogeny, and ecology is not closely related to tachinid phylogeny. We suspect that several of these ecological factors may also influence patterns of host use in other parasitic groups that may not be heavily constrained by physiological interactions with hosts such as idiobiont parasitoid wasps (Askew and Shaw 1986). If ecological or other attributes of hosts that are not highly conserved over evolution are the primary determinants of patterns of host use by many tachinids, then coevolutionary interactions between these parasites and their hosts are expected to be weak and their effects on communities relatively diffuse. Functionally, they are more predators than parasites. Several results of this study suggest that the process of host-finding is instrumental in determining both the range and character of hosts used by tachinid species. As more natural history, physiological, and phylogenetic data become available, these hypotheses can be more fully evaluated and the determinants of host use in parasitoids better understood, providing valuable insight into the evolutionary and ecological implications of diet breadth and the structure of parasite-host communities.

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Appendix 1

Tachinids and their hosts reared over the course of the sampling program of macrolepidoptera in mesquite-oak savannas of south-eastern Arizona. Taxonomic affiliations are given for tachinids and their hosts, as well as the number of host collections (*NC*) from which each tachinid species was reared. Host species producing tachinids that were collected from elevations or geographic areas that neighbor the focal habitat are indicated by an *asterisk*

Tachinid species	NC	Host species	Host family
Dexiinae			
Cockerelliana capitata Twnsd	1	*Hyles lineata* Fabricius	Sphingidae
Eulasiona comstocki Twnsd	1	*Epinotia* sp.*	Tortricidae
Metaplagia occidentalis Coq.	3	*Agrius cingulata* Fabricius	Sphingidae
Muscopteryx sp. 1	1	*Hemihyalea edwardsi* Packard	Arctiidae
Uramya indita (Walker)	3	*Norape tenera* Druce	Megalopygidae
Exoristinae			
Blondeliini			
Eucelatoria armigera *(Coquillett)*	1	*Peridroma saucia* (Hübner)	Noctuidae
Eryciini			
Acantholespesia texana (Ald. & Webb.)	1	*Megathymus coloradensis* Riley	Hesperiidae
Aplomya theclarum (Scudder)	3	*Celastrina argiolus* L.	Lycaenidae
		*Incisalia mossii** Edwards	Lycaenidae
Carcelia diacrisae Sellers	1	*Hypocrisias minima* Neumoegen	Arctiidae
Carcelia Formosa (Ald. & Webb.)	1	*Turuptiana permaculata** (Pack.)	Arctiidae
Carcelia lagoae (Twnsd)	3	*Megalopyge bissesa* Dyar	Megalopygidae
Carcelia laxifrons Vill.	1	*Ecpantheria suffusa* (B. & M.)	Arctiidae
Carcelia reclinata (Ald. & Webb.)	21	*Arachnis zuni** Neumoegen	Arctiidae
		Ecpantheria suffusa (B. & M.)	Arctiidae
		Estigmene acrea (Drury)	Arctiidae
		Grammia geneura (Strecker)	Arctiidae
		Arachnis picta Packard	Arctiidae
		*Grammia williamsi** Dodge	Arctiidae
Drino incompta (Wulp)	4	*Sphinx asella* (Roth. & Jord.)	Sphingidae
		Proserpinus terlooii Edwards	Sphingidae
		Sphinx smithi	Sphingidae
Drino nr. *cubaecola* (Jaennicke)	2	*Manduca rustica* (Fabricius)	Sphingidae
Drino nr. *rhoeo* #2	4	*Eumorpha achemon* Drury	Sphingidae
		Eumorpha typhon Klug	Sphingidae
Drino nr. *rhoeo* #2a	1	*Eacles oslari* Rothschild	Sphingidae
Drino rhoeo (Walker)	6	*Manduca muscosa* (Roth. & Jord.)	Sphingidae
		Manduca sexta (L.)	Sphingidae
Gymnocarcelia languida (Walker)	6	*Estigmene acrea* (Drury)	Arctiidae

Tachinid species	NC	Host species	Host family
Lespesia aletiae (Riley)	48	*Apatalodes pudefacta* Dyar	Apatalodidae
		Arachnis picta Packard	Arctiidae
		Cargida pyrrha Druce	Notodontidae
		Chlosyne lacinia (Geyer)	Nymphalidae
		Ecpantheria suffusa (B. & M.)	Arctiidae
		Estigmene acrea (Drury)	Arctiidae
		Gerrodes minatea Dyar	Noctuidae
		Grammia geneura (Strecker)	Arctiidae
		Hemileuca juno Packard	Saturniidae
		Hemileuca stonei Lemaire	Saturniidae
		Hyphantria cunea (Drury)	Arctiidae
		Hypocrisias minima Neumoegen	Arctiidae
		Megalopyge bissesa Dyar	Megalopygidae
		Papilio multicaudatus Kirby	Papilionidae
		Peridroma saucia (Hübner)	Noctuidae
		Bertholdia trigona Grote	Arctiidae
		Pygarctia roseicapitis (N. & D.)	Arctiidae
		Spodoptera nr. *ornithogalli*	Noctuidae
		Notodontid (*Telea* feeder)	Notodontidae
Lespesia anisotae (Webb.)	3	*Anisota oslari* Rothschild	Saturniidae
Lespesia archippivora (Riley)	14	*Apatalodes pudefacta* Dyar	Apatalodidae
		Estigmene acrea (Drury)	Arctiidae
		Grammia geneura (Strecker)	Arctiidae
		Pygarctia roseicapitis (N. & D.)	Arctiidae
		Hyphantria cunea (Drury)	Arctiidae
		Malacosoma incurvum (Edwards)	Lasiocampidae
		Chlosyne lacinia (Geyer)	Nymphalidae
Lespesia datanarum (Twnsd)	8	*Datana perspicua* Grote & Rob.	Notodontidae
		Datana integerrima Grote & Rob.	Notodontidae
Lespesia euchaetiae (Webb.)	3	*Euchaetes antica* Walker	Arctiidae
Lespesia flavifrons Beneway	2	*Agapema homogena* Dyar	Saturniidae
		Smerinthus saliceti Boisduval	Sphingidae
Lespesia frenchii (Williston)	3	*Hyphantria cunea* (Drury)	Arctiidae
		Malacosoma incurvum (Edwards)	Lasiocampidae
Lespesia nr. *melalophae* (Allen)	1	*Trosia obsolecens* Dyar	Megalopygidae
Lespesia nr. *samiae* (Webb.)	1	*Agapema anona* (Ottolengui)	Saturniidae
Lespesia nr. *cuculliae* (Webb.)	1	*Furcula* sp.	Notodontidae
Lespesia schizurae (Twnsd.)	4	Agaristine Noctuid #2	Noctuidae
		Schizura biedermani Brns & McD.	Notodontidae
		Maple Notodontid #1*	Notodontidae
Lespesia sp. nr. *flavifrons*	3	*Notela jaliscana* Schaus	Notodontidae
Lespesia stonei Sabrosky	6	*Gerrodes minatea* Dyar	Noctuidae
Madremyia saundersii (Williston)	2	Vanessa cardui *L.*	Nymphalidae
Phryxe vulgaris (Fallén)	1	Pine Noctuid # 2	Noctuidae
Siphosturmia nr. *confusa* Rnhd.	3	*Chlosyne neumogenia* Skinner	Nymphalidae
		*Euphydryas calcedona** Dblday.	Nymphalidae
Sisyropa eudryae (Twnsd.)	3	*Alypiodes bimaculata* (Her.-Schf.)	Noctuidae
Exoristini			
Austrophorocera sp. 1	2	*Parassa chloris* (Her.-Schf.)	Limacodidae
		Prolimacodes trigona (Edwards)	Limacodidae
Chetogena "*edwardsi*" (Williston)	14	*Chlosyne lacinia* (Geyer)	Nymphalidae
		Grammia geneura (Strecker)	Arctiidae
		Hemileuca juno Packard	Saturniidae
		Malacosoma incurvum (Edwards)	Lasiocampidae
		Vanessa cardui *L.*	Nymphalidae
		Norape tenera Druce	Megalopygidae
Chetogena claripennis grp. (Macquart)	2	*Ceratomia sonorensis* Hodges	Sphingidae
		Notodontid (*Telea* feeder)	Notodontidae
Chetogena scutellaris (Wulp)	10	*Alypiodes bimaculata* (Her.-Schf.)	Noctuidae
		Apatalodes pudefacta Dyar	Apatalodidae
		Arachnis picta Packard	Arctiidae
		Estigmene acrea (Drury)	Arctiidae
		Grammia geneura (Strecker)	Arctiidae
		Catocaline Noctuid #2	Noctuidae
		Lerina incarnata Walker	Arctiidae
		*Datana integerrima*Grote & Rob.	Notodontidae
		Spodoptera nr. *ornithogalli*	Noctuidae
Chetogena nr. *claripennis* 3	1	*Euscirrhopterus gloveri* Grote & Rob.	Noctuidae
Chetogena nr. *claripennis* 5	2	*Megalopyge bissesa* Dyar	Megalopygidae

Tachinid species	NC	Host species	Host family
Chetogena tachinomoides (Twnsd.)	15	*Gloveria howardi* (Dyar)	Lasiocampidae
		Grammia geneura (Strecker)	Arctiidae
		Hemileuca juno Packard	Saturniidae
		Malacosoma incurvum (Edwards)	Lasiocampidae
		Norape tenera Druce	Megalopygidae
		Noctuid (*Erodium* feeder)	Noctuidae
		Notela jaliscana Schaus	Notodontidae
		Peridroma saucia(Hübner)	Noctuidae
		Lepipolys perscripta Guenee	Noctuidae
		Nymphalis antiopa (L.)	Nymphalidae
		Eryinnis obscura (Fab.)	Sphingidae
		Schizura biedermani Brns & McD.	Notodontidae
		Estigmene acrea (Drury)	Arctiidae
Exorista mella (Walker)	12	*Arachnis zuni** Neumoegen	Arctiidae
		Estigmene acrea (Drury)	Arctiidae
		Grammia geneura (Strecker)	Arctiidae
		Lerina incarnata Walker	Arctiidae
Goniini			
Belvosia bifasciata (Fabricius)	2	*Anisota oslari* Rothschild	Saturniidae
		Hemileuca juno Packard	Saturniidae
Belvosia semiflava Aldrich	5	*Datana perspicua* Grote & Rob.	Notodontidae
Chaetogaedia monticola Bigot	22	*Cargida pyrrha* Druce	Notodontidae
		Estigmene acrea (Drury)	Arctiidae
		Euchaetes antica Walker	Arctiidae
		Grammia geneura (Strecker)	Arctiidae
		Hypocrisias minima (Neumoegen)	Arctiidae
		Pygarctia murina (Stretch)	Arctiidae
		Pygarctia roseicapitis (N. & D.)	Arctiidae
Houghia sp.	1	*Apatalodes pudefacta* Dyar	Arctiidae
Hyphantrophaga blandita (Coq.)	1	*Eucaterva variaria* Grote	Geometridae
Hyphantrophaga collina (Rnhd.)	5	*Chlosyne lacinia* (Geyer)	Nymphalidae
		Eucaterva variaria Grote	Geometridae
Hyphantrophaga hyphantriae (Twnsd.)	2	*Estigmene acrea* (Drury)	Arctiidae
		Hyphantria cunea (Drury)	Arctiidae
Hyphantrophaga virilis (Ald. & Webb.)	2	Pierid chrysalis	Pieridae
		Pine Noctuid #3*	Noctuidae
Leschenaultia adusta (Loew)	21	*Estigmene acrea* (Drury)	Arctiidae
		Malacosoma incurvum (Edwards)	Lasiocampidae
Leschenaultia nr. *malacosomae*	1	*Hemihyalea edwardsi* Packard	Arctiidae
Winthemiini			
Orasturmia vallicola Rnhd.	3	*Norape tenera* Druce	Megalopygidae
Winthemia datanae (Twnsd.)	3	*Schizura biedermani* Brns & McD.	Notodontidae
Winthemia deilephilae (Ost. Sack.)	8	*Hyles lineata* Fabricius	Sphingidae
		Manduca sexta (L.)	Sphingidae
Winthemia rufonotata (Bigot)	2	*Peridroma saucia* (Hübner)	Noctuidae
Tachininae			
Archytas apicifer (Walker)	2	*Peridroma saucia* (Hübner)	Noctuidae
Archytas lateralis (Macquart)	7	*Cargida pyrrha* Druce	Notodontidae
		Grammia geneura (Strecker)	Arctiidae
		Malacosoma incurvum (Edwards)	Lasiocampidae
Archytas metallicus (Rob.-Des.)	5	*Datana perspicua* Grote & Rob.	Notodontidae
Campylochaeta semiothisae (Brooks)	1	*Semiothisa* sp.*	Geometridae
Deopalpus contiguus (Rnhd.)	4	*Eucaterva variaria* Grote	Geometridae
Macromya crocata Rnhd.	3	*Agapema homogena* Dyar	Saturniidae

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