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DETERMINANTS OF PARASITOID–HOST ASSOCIATIONS: INSIGHTS FROM A NATURAL TACHINID–LEPIDOPTERAN COMMUNITY

JOHN O. STIREMAN III[1,3] AND MICHAEL S. SINGER[2]

[1]*Department of Ecology and Evolutionary Biology, University of Arizona, Tucson, Arizona 85721 USA*
[2]*Interdisciplinary Program in Insect Science, University of Arizona, Tucson, Arizona 85721 USA*

Abstract. A major goal of insect community ecology is to understand how and why herbivorous insect species vary in the diversity of their parasitoid assemblages and the rates of parasitism that they experience. Most studies investigating these issues with Lepidoptera as hosts have relied on literature records of parasitoid–host associations that are often of limited quality and that do not necessarily reflect local interactions between hosts and parasitoids. We sampled externally feeding Lepidoptera in mesquite–oak savanna habitats of southeastern Arizona (USA) to assess the ecological and evolutionary determinants of parasitoid community structure. We focused on parasitoids in the family Tachinidae (Diptera) due to their dominance as larval parasitoids of macrolepidoptera at our site. Host abundance, morphology, coloration, gregariousness, and diet breadth of the host were all significantly correlated with tachinid species richness among hosts. Tachinid species richness also varied according to host taxonomy (family), but most of this variation appeared to be better explained by morphology and ecology than by phylogenetic position. Characteristics of host habitat and body size had no significant effect on tachinid species richness. Tachinid parasitism rates were higher for abundant, hairy, non-aposematic, and gregarious hosts. Hymenopteran parasitism rates were low and variable with only host family explaining a significant amount of variation. In general, we found that a substantial amount of the variation in tachinid species richness and parasitism rates among hosts can be explained by ecological attributes, and that interactions of host species with their host plants and predators may determine their suitability as hosts for parasitoids.

Key words: ecological specialization; enemy-free space; Lepidoptera; parasitism rate; parasitoid; parasitoid community ecology; species richness; Tachinidae.

INTRODUCTION

The study of insect parasitoids has shifted in recent years from a focus on the relationships between particular parasitoid species and their hosts, to the examination of the trophic interactions between communities of parasitoids and their hosts (Hawkins 1994, Hawkins and Sheehan 1994). This emerging field of parasitoid community ecology attempts to understand how these communities are assembled (Mills 1992, 1993, Price 1994, Hawkins and Mills 1996), how they function (Jones et al. 1994, Wilson et al. 1996), and ultimately how they contribute to the overall structure of ecological communities. Central to these interests is an understanding of how and why the diversity of parasitoid assemblages and parasitism rates vary among host species. That is, we seek to understand what historical and ecological factors determine the species richness of parasitoid assemblages on different hosts, and what ecological factors determine how rates of parasitism vary among host species.

Hawkins and colleagues' analyses of large host-parasitoid databases derived from the literature have provided considerable insight into these issues (Hawkins 1988, 1990, 1994, Hawkins and Lawton 1987, Hawkins et al. 1992), especially in demonstrating that host feeding niche and the size of host refuges strongly influences parasitoid species richness and parasitism rates (Hochberg and Hawkins 1992). More detailed analyses of parasitoid communities associated with hosts on particular plants (Lawton and Price 1979, Hawkins and Goeden 1984) or particular taxonomic groups of hosts, including oak-galling cynipid wasps (Askew 1961, Stone et al. 2002), tortricid moths (Mills 1992), tephritid flies (Hoffmeister and Vidal 1994), leafminers (Memmott et al. 1994, Rott and Godfray 2000), and aphids (Müller et al. 1999), have also revealed ecological characteristics of hosts that are correlated with parasitism rates and the richness of parasitoid assemblages which are helping to provide a general understanding of the processes that shape parasitoid communities.

The parasitoid community structure of exophytic Lepidoptera is of particular interest due to their dominance as herbivores in most forest ecosystems (Janzen 1988, Stamp and Casey 1993) and their prevalence as pests in agricultural systems (Stamp and Casey 1993). However, few studies have used comparative data to

[3] Present address: Department of Botany, Iowa State University, Ames, Iowa 50011 USA.

TABLE 1. The host characteristics examined in analyses of tachinid species richness (TSR), diversity (H'), and attack rates (PAR), with explanations of their form and possible values.

Host characteristic	Hypothesized relationship with TSR or H'	Values or levels
Sample size	strong positive relationship	total no. hosts sampled (PAR), total parasitized hosts (TSR, H')
Abundance	strong positive relationship	no. collections + no. sites where the host was observed but not collected
Family	greater on species-rich host families	Noctuidae, Saturniidae, Arctiidae, etc.
Plant type	herb < shrub < tree	herb, shrub, tree
Height above ground	positive relationship	1(0–1 m), 2(1–2 m), 3(>2 m)
Diet breadth	positive relationship	total no. plant families host observed feeding upon
Morphology	hairy, spiny > smooth	hairy, spiny, or smooth
Appearance	cryptic > aposematic†	brightly colored (aposematic)
	aposematic > cryptic†	cryptic (or not brightly colored)
Gregariousness	gregarious > solitary	gregarious (at least as young larvae), solitary
Body size	positive relationship	approximate length: small (0.5–3 cm), medium (3–5 cm), large (5–8 cm), very large (>8 cm)

† Both hypotheses may be expected.

examine how and why parasitoid assemblages and parasitism rates of these hosts vary (but see Sheehan 1994, Dyer and Gentry 1999, and Gentry and Dyer 2002).

The current study examines the ecological and evolutionary factors that influence the richness of parasitoid species and frequency of parasitism in a community of exophytic Lepidoptera associated with mesquite–oak savannas in the southwestern United States. Analyses of parasitoid species richness focus on flies in the family Tachinidae. Tachinids were emphasized because they dominate the parasitoid assemblages of externally feeding larval Lepidoptera in this and other ecological communities, in some regions achieving twice the rate of parasitism of all hymenopteran parasitoids combined (e.g., Schaffner and Griswold 1934, as cited in Sheehan 1994, Janzen 1995), and because tachinid–host associations are poorly known. We use these tachinid–Lepidoptera associations to evaluate the importance of a set of ecological and morphological factors that have been previously proposed as significant sources of variation in parasitoid species richness and parasitism rates among host species (Table 1). These factors are introduced in the next paragraphs with a brief explanation of their hypothesized effects. Although it is expected that parasitoid species richness should be correlated with parasitism rate (Hawkins and Gross 1992), the effects of ecological and morphological traits of hosts on these variables may differ in sign and magnitude.

Host abundance.—It is widely accepted that abundant host species should support more generalist and specialist parasitoid species than should rare hosts (Hawkins 1994). This measure, though often difficult to separate from sampling effort, may explain more of the variance in parasitoid species richness than any other single factor (e.g., Sheehan 1994).

Host family.—Host taxonomy, as it reflects phylogeny, may influence the number of parasitoid species of a host either through co-radiation of parasitoids with host taxa, or through an evolutionary affiliation of parasitoid taxa with diverse clades of hosts (Godfray 1994). In either case, it is predicted that host species belonging to more species-rich families will exhibit higher parasitoid species richness. Host taxonomy may also be correlated with physiological or developmental traits that may affect patterns of tachinid host use. However, for tachinids, which tend to be generalized and unconstrained by host physiology (Belshaw 1994), these factors may be of little importance.

Host plant growth form.—Several studies have indicated a pattern of increasing parasitoid species richness on hosts from herbs to shrubs to trees (Askew 1980, Hawkins 1988, 1994, Hawkins et al. 1990). This pattern is thought to be due to the richer complexes of hosts on trees, which results in an increased number of generalist parasitoids (Askew 1980), and possibly an increase in the abundance of hosts on trees versus shrubs or herbs (Askew and Shaw 1986).

Host defenses.—Morphological defenses of the host such as hairs or spines may require specific adaptations of parasitoids to overcome them. This may limit the number of generalist parasitoids that can attack these hosts and result in less diverse parasitoid assemblages (Sheehan 1994). Alternatively, if these defenses (and others such as the sequestration of toxins) reduce the susceptibility of hosts to predators, hosts bearing these defenses may indirectly be more suitable for parasitoids, resulting in higher parasitoid species richness and higher rates of parasitism (Gentry and Dyer 2002). Vulnerability of insect herbivores to predators and parasitoids were negatively associated in the few studies yet to examine this issue (Dyer and Gentry 1999, Memmott et al. 2000). The widespread use of hairy caterpillars by tachinids (Arnaud 1978) suggests that the latter scenario may be more important for these parasitoids.

Host diet breadth.—The host-plant range of the host may influence parasitoid species richness in at least two ways. First, polyphagous hosts may be utilized by more polyphagous parasitoids due to their relative lack

of plant-derived chemical defenses (Bernays and Graham 1988, see Feeny 1976 for an analogous argument concerning insect herbivores and plants). Second, polyphagous hosts are likely to occupy a wider diversity of microhabitats and thus be subject to attack from a variety of parasitoids that may be microhabitat specialists (Askew and Shaw 1986). In either case, it is predicted that hosts with broad host ranges should exhibit larger parasitoid assemblages. In contrast, frequencies of parasitism have been shown to be higher on specialist herbivores than on generalist herbivores (Dyer and Gentry 1999, Gentry and Dyer 2002). This may be a consequence of efficient location of these hosts by specialist parasitoids.

Host gregariousness.—Gregarious hosts may be more easily located by parasitoids (Sheehan 1994), and may also experience higher rates of parasitism due to the ease of parasitizing multiple individual hosts once a group is located (e.g., Gentry and Dyer 2002). Thus, gregarious hosts should be characterized by both diverse parasitoid assemblages and high levels of parasitism.

The few studies that have examined patterns of parasitoid richness or parasitism rates in Lepidoptera have tended to rely on records of parasitoid–host associations derived from the literature (e.g., Hawkins 1994, Sheehan 1994, Dyer and Gentry 1999; though see Gentry and Dyer 2002), which is known to be fraught with misidentifications of both hosts and parasitoids (Shaw 1994). In addition, these studies most often use data derived from a variety of ecological communities and ecosystem types, which obscures the local determinants of parasitoid–host associations within an ecological community. Local differences in such determinants may be an important, overlooked source of variation. The relatively restricted geographic area and ecosystem surveyed in this study allows an analysis of patterns of parasitism and parasitoid species richness within an ecological community in which nearly all members of the community have at least the potential to interact. Furthermore, the focus on tachinid flies allows us to examine how these important yet poorly understood parasitoids respond to, and potentially shape, the ecology of exophytic Lepidoptera.

PLATE 1. *Schizura biedermani* (Barnes & McDunnough) (Notodontidae), one of the many oak-feeding caterpillars reared in the current study. Note the white oval tachinid egg on the second abdominal segment. Photograph by Michael S. Singer.

METHODS

Geographic location and habitat

Immature Lepidoptera were sampled in southeastern Arizona (USA) within an area of ~9000 km^2, centered on the Santa Rita Mountains and roughly bounded by the city of Tucson to the north and the United States–Mexico border to the south. Sampling was focused on mesquite–oak savanna as well as associated riparian areas between ~1060 m and 1580 m in elevation. The majority of sampling sites were located either in or in the vicinity of the Atascosa, Santa Rita, Patagonia, Huachuca, Santa Catalina, and Rincon mountain ranges. This region is characterized by two primary growing seasons: the spring, lasting from early March through May, and the summer, occurring from July to September. Sampling was conducted in both of these seasons, though the vast majority (~80%) of records are derived from the latter. The lepidopteran fauna of southeastern Arizona is exceptionally species rich relative to most other areas of the United States and is heavily influenced by its proximity to the diverse fauna of Mexico and the neotropics (Bailowitz and Brock 1991).

Study organisms

The host taxa sampled generally belong to the macrolepidoptera (or ''higher Ditrysia'') as defined by Scoble (1992) (see Plate 1). Certain microlepidoptera (or ''lower Ditrysia'') were included due to their large size, including Psychidae, Megalopygidae, Limacodidae, Pyralidae, and at least one tortricid. Although sampling was focused on taxa that feed in exposed situations, some leaf rollers (Pyralidae), case bearers (Psychidae), and tent makers (Lasiocampidae, Arctiidae) were sam-

pled as well. The small number of hosts from these feeding niches restrict testing of whether these feeding modes affect the parasitoid communities of these hosts. The taxa collected represent a heterogeneous sample of the much larger assemblage of potential host Lepidoptera present in the habitats surveyed.

As stated previously, analyses of parasitoid species richness in this study focus entirely on tachinid parasitoids. Tachinids are a diverse family of Diptera (over 8500 described species; Cantrell and Crosskey 1989) in which all known species are parasitoids. In contrast to hymenopteran parasitoids, many, if not most, tachinid species exhibit broad host ranges (Eggleton and Gaston 1992, Belshaw 1994), no tachinid species are known to attack egg or pupal stages of hosts, and they generally cannot oviposit into concealed hosts. However, ~40% of species oviposit away from the host and it is the juvenile stage (eggs or larvae) that in some way contacts the host (Belshaw 1994). These differences are likely to influence how tachinids respond to ecological, behavioral, and morphological characteristics of their hosts.

Sampling methods

Caterpillars were sampled over a 4-yr period from 1996 to 2000. Sampling was conducted by walking haphazardly through the sampling areas (usually several hectares) and visually inspecting herbs, shrubs, and trees up to a height of ~3 m. In general, tree-feeding species were much more likely to be found on low branches than higher up in the trees. Often we used leaf damage and caterpillar feces as cues to examine plants more closely for the presence of caterpillars. Ultimate and penultimate instar caterpillars were sampled to allow maximum exposure to parasitoids in nature. For some collections, we returned to sites where we had observed young larvae to collect them once they had grown. We generally attempted to collect either all the individual caterpillars we observed (of the appropriate size/age classes), or at least 20 individuals per species per sampling site. If a particular species was abundant, we attempted to sample it from a variety of individual host plants. In some collections that occurred later in the sampling period, we focused on caterpillar species for which we had small sample sizes. Gregarious tent-making species were often collected in groups. Some chrysomelid larvae were included in the sampling due to their ecological similarity to caterpillars and their susceptibility to attack by several tachinid species that also use Lepidoptera (Arnaud 1978).

Once located, caterpillars were placed in small plastic vials, plastic tubs, or plastic bags with a small quantity of food plant and stored in a cooler chilled with cold packs for transport to the University of Arizona. As they were collected they were assigned an identification code, and we recorded their identity, food plant, height off the ground, size, and plant growth form. Caterpillars were further categorized according to morphology (Table 1) at this time. Once caterpillars were transported to a rearing facility at the University of Arizona, they were transferred to rearing cups and/or plastic tubs with food plants collected from the field. A few species (*Grammia geneura*, *Estigmene acrea*: Arctiidae) were reared on a wheat-germ-based artificial diet (Yamamoto 1969). The rearing facility was kept at 28°C with a 16 h light:8 h dark photoperiod. Feces and old plants were removed and new host plant added every day or every other day depending on the rate of caterpillar feeding and condition of the rearing chambers. Host plants were collected from the field and stored in plastic bags kept refrigerated at 4°C. Repeated collections of host plants from the field were often necessary to complete caterpillar rearing. When caterpillars ceased feeding, all host plants were removed and the caterpillar was allowed to pupate. Species were identified by comparing adult voucher specimens to specimens in the University of Arizona Insect Collection (UAIC) and through determinations made by R. Nagle, B. Walsh, and J. Tuttle. Some species for which adults were not reared or that we could not identify were assigned temporary designations reflecting their family, morphology, or ecology. Voucher specimens for all species for which adults were reared are retained in the authors' private collections as vouchers for an ongoing host–parasitoid database. Additional vouchers are deposited in the UAIC.

We recorded all parasitoids that emerged from hosts either as larvae or adults. Adult parasitoids were killed by freezing, given an identification code relating them to the host, and mounted for identification. Tachinids were identified by J. Stireman using published keys (most notably Wood 1987), comparisons with specimens in the UAIC, and comparisons with specimens in the Canadian National Collection (CNC) of insects. In addition, identifications of certain species were determined by N. E. Woodley (USDA, Systematic Entomology Laboratory), J. E. O'Hara (CNC), and D. M. Wood (formerly of the CNC). As with the Lepidoptera, voucher specimens of all tachinid species reared are retained by the authors for use in identifying further reared specimens. For species in which many individuals were reared, additional vouchers were placed in the UAIC. Voucher specimens of all hymenopteran parasitoids were also retained, but several species have yet to be identified.

Analysis

Each caterpillar species sampled was assigned values or levels for each of 10 ecological, taxonomic, or morphological variables: sample size, abundance, family, plant growth form, host-plant range, height, morphology, appearance, gregariousness, and size (Table 1). We used two measures of sample size in analyses: 1) the total number of hosts from which parasitoids were reared, for analyses of parasitoid species richness and diversity, and 2) the total number of hosts sampled

(corrected to exclude caterpillars that experienced mortality during the larval stage due to factors other than parasitoids), for analyses of parasitism rates. We treated each caterpillar as an independent sample despite the gregarious habits of some species due to problems with equating solitary hosts with groups of hosts in analyses and the arbitrariness and difficulty of any other definition of an independent sample. Although there may be cases in which parasitism of hosts in groups was not independent, there are likely many others where it was independent (e.g., many caterpillars are gregarious for only part of their larval development and others such as *Hemihyalea* sp. only when resting). Because sample sizes spanned multiple orders of magnitude, these variables were log-transformed in all analyses.

In addition to the total number sampled, the abundance of host species at a larger scale was estimated by the total number of sampling sites and dates in which the species was observed. This provided a somewhat independent measure that could be used to examine effects of host abundance once the effect of sample size was removed. The mean height of the caterpillar above the ground was used as an additional habitat variable due to the variability in size of shrubs and trees, though it is not independent of plant growth form. The measure of host-plant range was based on the number of host-plant families on which we observed the caterpillar species feeding over the region sampled. This focus on the local pattern of host-plant use was deemed more appropriate than global host range in analyzing its effect at the local community level. Sample sizes of hosts ranged from 1 to 800, though hosts for which fewer than four individuals were reared were excluded from analyses of tachinid species richness. Although we attempted to avoid biases in our sampling, we were unable to sample caterpillars in a completely random manner. Systematic biases large enough to effect our results are unlikely to be present with respect to across-species comparisons of parasitoid diversity and attack rates, however we acknowledge that this possibility exists and results should be interpreted with this caution in mind. Statistical analyses were performed using the program JMP IN 3.2.1 (SAS Institute 1996).

Tachinid species richness

The tachinid species richness (TSR) of hosts was used as a measure of diversity to facilitate comparisons with previous studies which have tended to focus on species richness (e.g., Hawkins and Lawton 1987, Hawkins 1994, Sheehan 1994), however Shannon-Weiner diversity indices (H') were also calculated and used as a response variable in parallel analyses due to the uncertainty in true TSR of host species. These analyses were conducted by first performing a stepwise regression to identify which measured variables were important explanators of TSR. This was done by initially including all variables and factors in the model and subsequently removing them one by one (with replacement) while noting changes in the variance explained by the model. We retained factors that caused significant reductions in the explanatory power of the model when removed, using a P-to-remove of 0.1. All retained variables were subsequently included in an ANCOVA model with continuous variables as covariates. TSR was square-root transformed for these analyses to improve the distribution of residuals. Many higher order interactions could not be properly examined due to the loss of degrees of freedom in the models including them, but all two-way interactions between variables were examined in the ANCOVA and nonsignificant interaction terms were removed. A similar ANCOVA analysis using residuals from a regression of tachinid species against log sample size as a normally distributed response variable was also performed. This analysis revealed the same significant effects and resulting mean residual TSRs are used to illustrate effects of factors after sample size is controlled. However, specific results of this analysis are not included due to recent criticisms of the method (García-Berthou 2001). Post hoc Tukey tests were conducted between levels of the factor ''morphology'' employing Bonferroni corrected α values. Separate post hoc linear regressions of TSR against abundance (for aposematic and nonaposematic hosts and gregarious and solitary hosts) and host plant families were performed to illustrate effects of these factors. Because these analyses treat each species as an independent sample, despite the lack of true phylogenetic independence, the results must be treated with caution. Possible effects of phylogenetic history in determining patterns of TSR and parasitism rates are discussed throughout this paper.

As stated in the introduction, there are two potential effects of phylogeny on parasitoid species richness independent of shared morphology, behavior, ecology, or other factors: co-cladogenesis of hosts and parasitoids and accumulation of parasitoid taxa on diverse clades of hosts. An examination of published host associations (Arnaud 1978) with respect to phylogenetic relationships within Tachinidae (Stireman 2002*a*), indicates that tachinids generally exhibit a high degree of evolutionary plasticity in host use. This, together with the broad host ranges of many species, suggests that most tachinids have not extensively co-radiated with their hosts. Thus, the importance of this potential effect of host phylogeny is probably minimal. To assess the relationship between the species richness of host families and tachinid species richness, we performed linear regressions of TSR (from this study) on the local, regional, and global diversity of species in each of the families of Lepidoptera represented. Local diversity was measured by the number of species per family represented in southeastern Arizona (B. Walsh, *personal communication*). Regional and global diversity estimates were taken from Heppner (1991) and Scoble (1992).

Parasitism rates

The relationship between tachinid parasitism rate and the ecological and morphological characteristics of hosts was examined with a series of multiple regressions using two measures of parasitism frequency as a response variable: the mean parasitism rate over all collections and the maximum parasitism rate for any collection, where a collection is defined as all individuals of species collected on a particular sampling date at a single geographic site. It has been suggested that maximum parasitism rate may be an especially informative measure for comparing ecological risks of parasitism among host taxa because it provides an inverse measure of the size of the host's refuge from parasitism (Hochberg and Hawkins 1994, Mills 2000). Only hosts with sample sizes of at least 10 were included in the analyses and some caterpillars collected by individuals other than the authors, for which rates of parasitism were unreliable, were excluded. The analyses were performed as described in *Methods: Analysis*, but due to difficulties with correlated variables, potentially important factors were identified in two iterative stepwise regressions (in which each term was evaluated with respect to the full model, as above); the first employed an *F*-to-remove of 1.0 and retained variables were then examined in another smaller model with a *P*-to-remove of 0.10. An ANCOVA was used to evaluate the significance of retained variables (at $\alpha = 0.05$). Parallel analyses of parasitism rates due to hymenopteran parasitoids were conducted to evaluate if and how tachinids and parasitic wasps differed in their response to the host characteristics measured. For all analyses, parasitism frequencies were arcsine transformed.

Results

Over the entire study, a total of 169 species of Lepidoptera in 21 families were reared, though many were reared in only small numbers (see the Appendix). Over 8500 individuals were collected, of which 7269 were reared to pupation. Seventy-four of the caterpillar species yielded ~2000 individual tachinid parasitoids belonging to 60 species (Fig. 1). Most of these tachinid–host associations have not been previously recorded. Pooling hosts over all species, the total frequency of tachinid parasitism was 14.7% (Fig. 2). The frequency of hymenopteran parasitism was 3.7%. The mean parasitism frequency by tachinids per host species was somewhat lower (11.5%). The distribution of the number of tachinid species per host for hosts where total $N > 4$ suggests that most host species are attacked by only one species of tachinid or none at all (Fig. 3). However, when hosts with sample sizes <20 are excluded, a more normal distribution results, with a mean TSR of 2.3 species.

Species richness

No significant relationship was found between any of the measures of host-family species richness (local, regional, world) and the residual tachinid species richness of hosts (all $R^2 < 0.01$; $F_{1,15} = 0.061, 0.123, 0.136$; $P = 0.808, 0.730, 0.718$, respectively).

In the ANCOVA with all factors included, the following factors were found to have a significant effect on TSR: sample size, abundance, diet breadth, morphology, and the interactions between appearance (coloration) and abundance, and gregariousness and abundance (Table 2). The same factors were found to significantly affect tachinid species diversity, except that diet breadth was not significant and gregariousness was (H'; Table 2). The resulting model explained almost 90% of the total variance (adjusted $R^2 = 0.887$). Parallel analyses indicated that these results were relatively insensitive to the exclusion of hosts with sample sizes of <10 and <20, with the main factors sample size, abundance, morphology, host plant range, and interactions involving coloration and gregariousness having significant effects. The sample size of parasitized hosts had by far the largest effect on TSR, with an R^2 of 0.768 when used as the sole explanatory variable in a regression (Fig. 4), though it is highly correlated with abundance, which also has a large effect when considered alone in a regression ($R^2 = 0.515$). Hosts that fed on shrubs tended to have higher TSR than those on herbs or trees when covariates were included in the model, but this effect was not significant. Tachinid species richness was significantly positively correlated with the number of host plant families on which a caterpillar species fed after effects of sample size were removed ($R^2 = 0.183$; $F_{1,96} = 21.55$, $P < 0.001$; Fig. 5). Caterpillars defended by hairs had more rich (TSR) and more diverse (H') tachinid assemblages than those with smooth integuments ($F_{89,3} = 4.255$, $P < 0.01$; $F_{89,3} = 5.066$, $P < 0.005$, respectively; Fig. 6); though hairy and spiny, and spiny and smooth hosts did not differ significantly (all $P > 0.5$). Aposematic or brightly colored hosts tended to be attacked by fewer tachinid species than were hosts that were cryptic or otherwise inconspicuous; however, this pattern was only apparent relative to abundance for TSR. In contrast to nonaposematic hosts, aposematic hosts exhibited no (trending toward slightly negative) relationship between abundance and TSR (Table 2; Fig. 7). The greater diversity (H') of tachinid species attacking gregarious hosts (mean ± 1 SE: 0.429 ± 0.087) than solitary hosts (0.165 ± 0.057) was significant ($P = 0.036$), but explained only a small amount of variance in the regression model when included with other factors. However, the interaction of gregariousness and abundance had strong effects on both measures of tachinid diversity, with gregarious species being more abundant and exhibiting a steeper relationship between abundance and tachinid diversity (Fig. 8). The abundance of gregarious hosts may have been relatively overestimated due to their greater apparency, however this is unlikely to affect the slope of the regression line. Although host families differed widely in their mean tachinid species

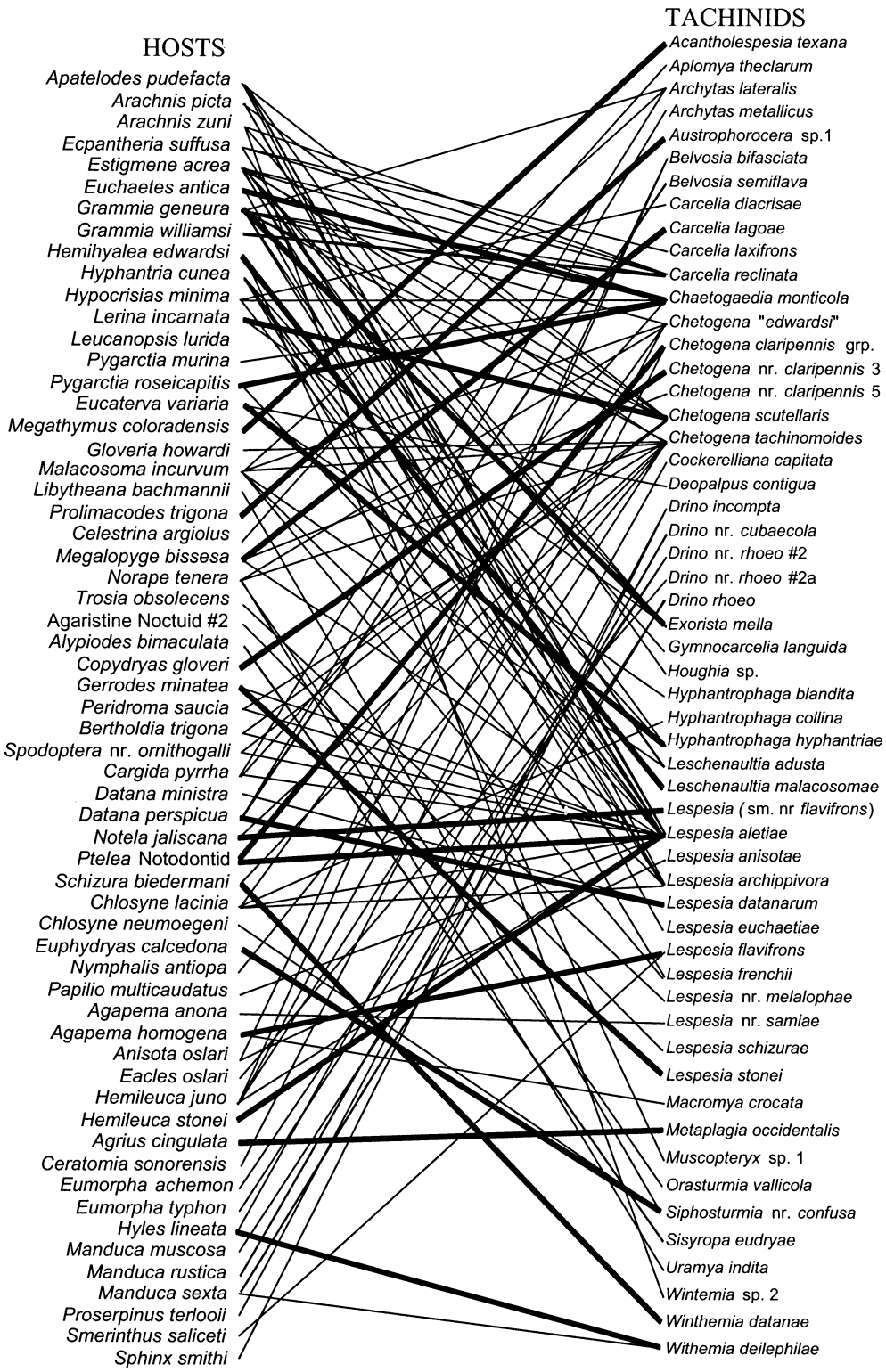

FIG. 1. A summary of tachinid–host associations from the current study in the form of a semiquantitative parasitoid food web. The thickness of the lines connecting tachinid and caterpillar species indicate general parasitism frequencies (thin, <10%; thick, >10%).

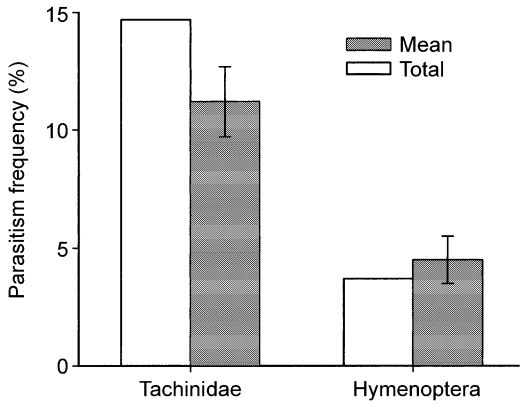

FIG. 2. The pooled parasitism frequency over all hosts and the mean parasitism frequency per host species (±1 SE) by tachinid and hymenopteran parasitoids (N = 99 host species, with sample size of ≥4).

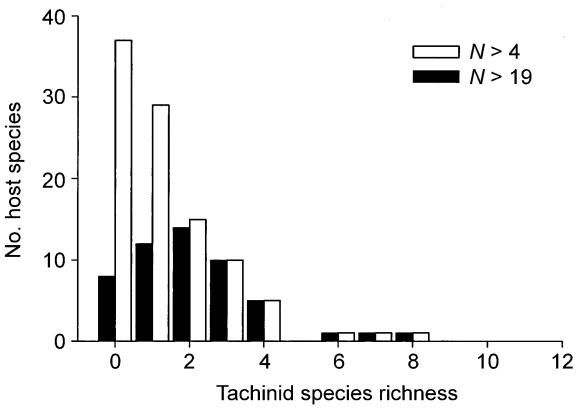

FIG. 3. The distribution of the number of tachinid species per host species excluding hosts with sample sizes <4 (N = 99) and <20 (N = 52).

richness (e.g., Arctiidae, N = 16, mean ± 1 SE = 2.75 ± 0.528; Saturniidae, N = 13, mean ± 1 SE = 1.0 ± 0.338), host family contributed very little to the regression models, suggesting that these differences are primarily due to ecological and morphological characteristics of hosts.

Parasitism frequency

In general, parasitism frequencies were extremely variable for both tachinids and hymenopteran parasitoids across hosts and collections and we identified few factors that significantly affected either measure of parasitism frequency (Table 3). Variables that significantly affected parasitoid attack rates by tachinids included abundance, sample size, morphology, gregariousness, and coloration. Maximum and mean parasitism rates were both positively correlated with at least some measure of host abundance (e.g., abundance explained 32.5% (adjusted R^2) of the variance in maximum parasitism rates when examined independently of other variables, Fig. 9). Hairy hosts suffered marginally significantly higher maximum and mean parasitism by tachinid flies than spiny hosts (Tukey test: $F_{51,3} = 4.16$, $F_{50,3} = 3.833$, respectively; $0.01 < P < 0.025$; Fig. 10), but no differences were observed between hairy and smooth or smooth and spiny hosts (all $P > 0.1$). Mean parasitism by tachinids was lower for brightly colored than cryptic hosts (mean ± 1 SE: 14.44 ± 2.96% vs. 18.36 ± 2.03%) and maximum parasitism was lower for solitary than gregarious hosts (mean ± 1 SE: 23.74 ± 3.47% vs. 30.24 ± 4.26%).

Host family was the only factor identified to have a significant effect on maximum parasitism rates due to Hymenoptera and no factor was demonstrated to significantly affect mean parasitism rates by these parasitoids (Table 3). The effect of host family on the Hymenoptera is likely due to the low mean parasitism frequencies of Notodontidae (0%), Sphingidae (2.1%), Noctuidae (2.5%), and Papilionoidea (all butterflies: 3.1%) relative to groups such as the Arctiidae (17%) and Saturniidae (12.5%). Parasitism by tachinids also

TABLE 2. Results of the stepwise regression and ANCOVA analysis of factors listed in Table 1 on tachinid species richness (TSR) and tachinid species diversity (H').

Factor	TSR			H'		
	df	F	P	df	F	P
Log N (sample size)	1, 88	103.5	**0.000**	1, 89	27.011	**0.000**
Log abundance	1, 88	9.807	**0.002**	1, 89	13.582	**0.000**
Host family	6, 75	(0.716)	0.638	6, 75	(0.666)	0.677
Plant type	2, 75	(0.950)	0.675	2, 75	(0.438)	0.647
Height above ground	2, 75	(1.598)	0.210	2, 75	(0.988)	0.323
Diet breadth	1, 88	31.186	**0.000**	1, 89	(0.293)	0.590
Morphology	2, 88	3.522	**0.034**	2, 89	5.293	**0.007**
Appearance	1, 88	1.091	0.299	1, 89	2.240	**0.025**
Appearance × Abundance	1, 88	8.908	**0.004**	1, 89	6.880	**0.010**
Gregariousness	1, 88	0.322	0.572	1, 89	4.518	**0.036**
Gregariousness × Abundance	1, 88	4.680	**0.033**	1, 89	17.179	**0.000**
Body size	3, 75	(0.085)	0.772	3, 75	(0.183)	0.670

Notes: Factors with F ratios in parentheses were not included in the final ANCOVA model. P values are reported for two-tailed F tests. Those in bold indicate significant effects. Total adjusted R^2 for final models are 0.887 (TSR) and 0.728 (H').

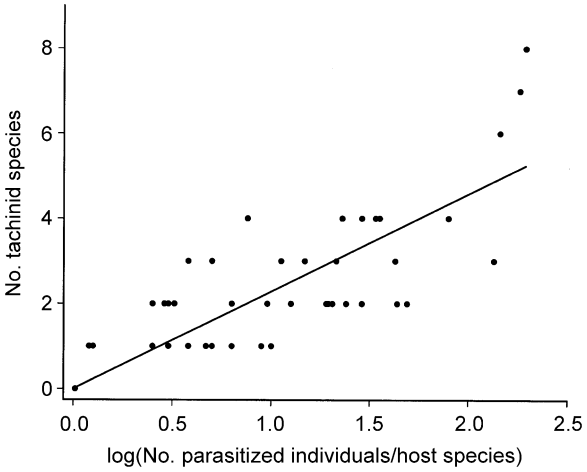

FIG. 4. A least-squares regression of tachinid species richness against log(sample size per host species).

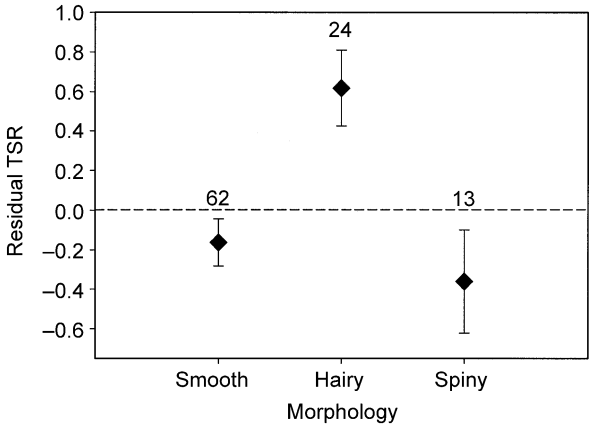

FIG. 6. The mean (±1 SE) residual tachinid species richness (TSR) of hosts according to morphological defense type. Numbers of host species are indicated above error bars. See Table 2 for statistics.

varied widely among host families, but this did not explain a significant amount of variance in parasitism rates when included with other host variables. It is difficult to separate effects of ecological traits of hosts from effects related to phylogenetic history in the absence of phylogenetic hypotheses for host and parasitoids. Each of these regression models explains considerably less than half of the variance in parasitism rates and it is likely that phylogenetic history or traits that are closely associated with phylogeny may be responsible for a considerable portion of the remainder. Both maximum and mean rates of parasitism by tachinids were correlated with tachinid species richness (after effects of abundance are controlled for: adjusted $R^2 = 0.177$, $F_{1,97} = 21.24$, $P < 0.001$ and adjusted $R^2 = 0.156$; $F_{1,97} = 18.135$, $P < 0.001$, respectively).

DISCUSSION

The parasitoid community of the Lepidoptera sampled in this study was dominated by a diverse assemblage of tachinids. This agrees well with other studies of temperate communities of exophytic Lepidoptera (e.g., deciduous forest, northeastern USA) in which ~39% of collections yielded tachinid parasitoids vs. 17.5% that yielded hymenopteran parasitoids (Schaffner and Griswold 1934, as cited in Sheehan 1994), and tropical communities in which Janzen (1995; tropical dry forest, Costa Rica) recorded ~7% parasitism by tachinids vs. 3–4% by all Hymenoptera, and Gentry and Dyer (2002; tropical wet forest, Costa Rica) recorded 14.7% by tachinids and 12.5% by Hymenoptera. The parasitism rates found in this study were moderate (~15%), falling between the values reported by these other studies, but maximum parasitism rates of many host species were >50%. In addition, the levels of parasitism reported here must be considered underestimates because larvae were removed from potential parasitism when transferred from the field to the laboratory

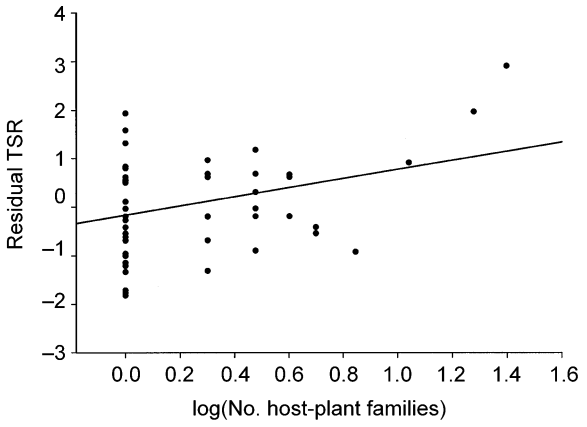

FIG. 5. The relationship between residual TSR (after effects of sample size were removed) and the number of host plant families each host species was recorded to feed upon (least-squares linear regression).

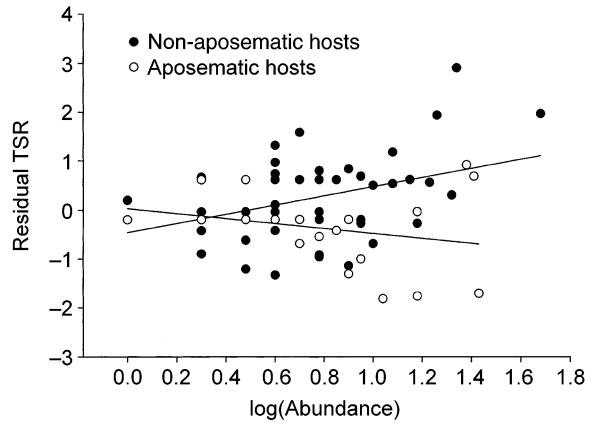

FIG. 7. Regressions of residual TSR against abundance for aposematic (adjusted $R^2 = 0.056$, $F_{1,27} = 2.673$, $P = 0.114$, regression coefficient = −0.509) and non-aposematic hosts (adjusted $R^2 = 0.112$, $F_{1,68} = 17.581$, $P < 0.000$, regression coefficient = 0.978).

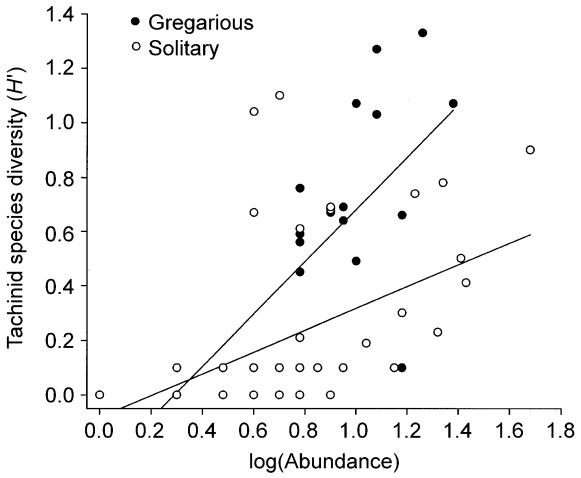

FIG. 8. Regressions of tachinid species diversity (H') against log(host abundance) for gregarious and solitary hosts (gregarious, adjusted $R^2 = 0.605$, $F_{1,28} = 45.35$, $P = 0.000$; solitary, adjusted $R^2 = 0.278$, $F_{1,67} = 27.14$, $P < 0.001$).

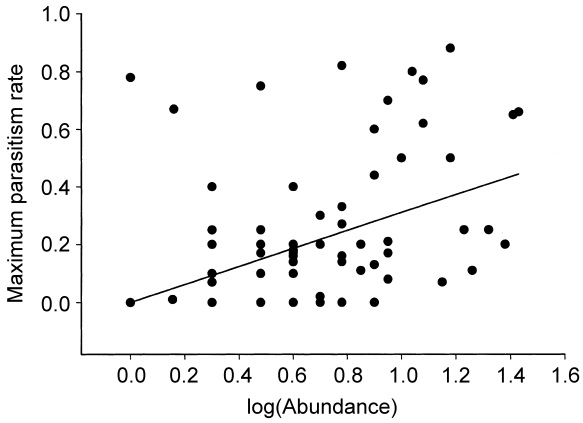

FIG. 9. A regression of maximum parasitism rate due to tachinids against log(host abundance) ($R^2 = 0.325$, $F_{1,75} = 37.174$, $P < 0.001$). See Table 3 for full model statistics.

(see Van Driesche 1983 for additional problems with estimating parasitism rates). The complete parasitoid assemblages for most host species are probably also considerably larger than indicated by this data set, given the strong, nonasymptoting relationship between sample size and tachinid species richness.

Taxonomy

The phylogenetic lability of host associations within the Tachinidae (Stireman 2001, 2002*a*), the wide host ranges of many species, and the lack of a relationship between tachinid species richness and local or global diversity of host family all suggest that host phylogeny is unlikely in itself to be of major importance in determining patterns of tachinid species richness among host species. However, there are more subtle effects that traits correlated with phylogeny may have on TSR. For example, if many tachinid species are habitat specialists, as has been suggested by several authors (Belshaw 1994, Sheehan 1994), and if phylogenetically related hosts are likely to feed in similar habitats, then the effects of evolutionary history and habitat may be difficult to separate. Likewise, related species of hosts often tend to share certain traits (e.g., hairiness) and thus effects of these traits may be confounded with effects of phylogeny (or other characteristics correlated with phylogeny such as physiology). The high TSR of Arctiidae (which are all hairy), however, is likely due in large part to their hairiness. Haired species from

TABLE 3. *F* ratios from the stepwise regression and ANCOVA analysis of factors listed in Table 1 on maximum percentage of parasitism in any collection (where total *N*/[no. collections] = 3 and total $N \geq 10$) and mean percentage of parasitism across collections (where total $N \geq 10$ and no. collections > 1).

	Maximum parasitism				Mean parasitism			
	TAC		HYM		TAC		HYM	
Factor	df	*F*	df	*F*	df	*F*	df	*F*
Log sample size	1, 37	2.430	1, 37	0.080	1, 53	**7.817****†	1, 39	0.434
Log abundance	1, 51	**23.13****†	1, 37	0.224	1, 39	0.295	1, 39	0.325
Host family	6, 37	0.068	6, 51	**3.147***†	6, 39	0.308	6, 39	1.210
Plant type	2, 51	2.088†	2, 37	1.979	2, 53	2.214†	2, 39	1.508
Height	2, 37	0.943	2, 37	1.171	2, 39	0.250	2, 39	0.810
Diet breadth	1, 37	0.002	1, 37	0.170	1, 39	1.460	1, 39	0.005
Morphology	2, 51	**3.923***†	2, 37	0.342	2, 53	**3.551***†	2, 39	0.518
Appearance	1, 37	1.033	1, 37	0.074	1, 53	**4.733***†	1, 39	1.176
Gregariousness	1, 51	**5.091***†	1, 37	1.887	1, 39	0.082	1, 39	1.834
Body size	3, 37	0.087	3, 37	0.024	3, 39	0.072	3, 39	0.000
Adjusted R^2 of final model:		0.415		0.172		0.230		NS

Notes: *F* ratios are reported from ANOVA/ANCOVA analyses with $N = 57$, df = 1–2 for maximum parasitism; and $N = 59$, df = 1–2 for mean parasitism. *F* ratios in bold type indicate significant effects; asterisks indicate the level of significance: * $P < 0.05$; ** $P < 0.01$; NS, not significant.

† Included in final ANCOVA model.

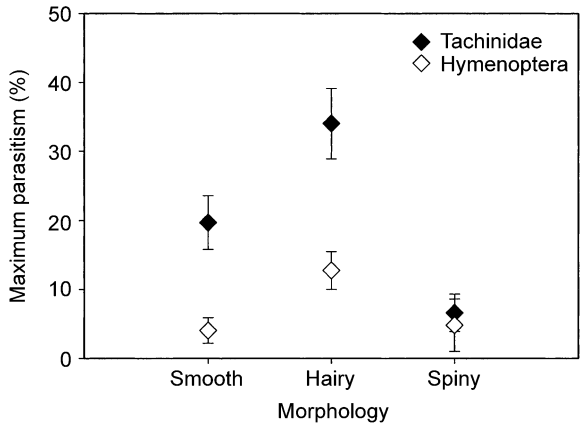

FIG. 10. The mean (±1 SE) maximum parasitism rates for host species relative to their defensive morphology, by tachinid and hymenopteran parasitoids. See Table 3 for statistics.

distantly related families also exhibit high TSR (e.g., Megalopygidae, Lasiocampidae, Apatelodidae) and share many genera and species of tachinid parasitoids with arctiids (e.g., *Chetogena* spp., *Carcelia* spp., *Lespesia aletiae*). The lack of significant effects of host family on TSR or tachinid diversity suggests that effects of phylogeny (by this crude measure) are overshadowed by the importance of broadly distributed morphological and ecological traits.

Although parasitism rates by tachinids varied among host families, much of this could be explained by the host traits measured. For example, low parasitism rates of Papilionoidea and Saturniidae by tachinids (both <10%) may reflect protection many of these caterpillars receive by feeding on noxious plants that may confer upon them a relative invulnerability to generalist parasitoids. Interestingly, the pattern for Hymenoptera is quite different, with not a single individual being reared from Notodontidae (where tachinids average 17% parasitism), and relatively high rates of parasitism of saturniid species (12.5%). The significant effect of host family on maximum parasitism rates by wasps suggests that phylogenetic history (or traits more closely associated with phylogeny than those examined here) may be relatively more important in determining patterns of host use for these parasitoids.

Sample size and abundance

Sample size is by far the most important factor in explaining variation in tachinid species richness among host species in this data set. It was responsible for >75% of the total variation among caterpillar species. The total number of parasitized hosts sampled reflects sampling error or bias in part. However, in the full regression model, abundance, along with its interactions with other variables, was a strong predictor of TSR and diversity (H'). Abundant hosts may be utilized by larger numbers of specialist parasitoid taxa because a large host population size lessens the likelihood of parasitoid extinction. They are also expected to support more generalists because they may be relatively easily located. The latter factor may be particularly true for tachinids given the potentially wide host ranges of many species.

When examined independently of sample size, host abundance had a strong effect on maximum parasitism rates by tachinids, explaining approximately one-third of the total variance among hosts (adjusted $R^2 = 0.325$). The presence of this effect on tachinid parasitism (along with the effect of sample size on mean parasitism by tachinids) and its absence on Hymenoptera parasitism may reflect differences in the proportion of generalist taxa in each of these groups. A significant number of generalist tachinid species possess the potential to attack a wide variety of hosts and may temporarily or locally focus their attacks on the most abundant host taxa through behavioral reinforcement. We suggest that, given their narrow host ranges, most hymenopteran parasitoids of larval Lepidoptera lack the physiological flexibility to respond to high densities of different caterpillar species in this manner. Thus, abundant hosts are subject to attack by both their specialist parasitoids (as argued above) and by generalists that possess the behavioral plasticity to opportunistically respond to high local densities of hosts.

Habitat

In contrast to several other studies examining correlates of parasitoid species richness among herbivorous insects (Askew 1980, Hawkins and Lawton 1987, Hawkins et al. 1990), we found little evidence that diversities of tachinid parasitoids were higher on tree-feeding hosts than hosts feeding on shrubs or herbs. The related measure of the height above the ground at which hosts were collected, which may represent a less subjective measure of habitat than plant growth form, also had no significant effect on TSR. Some other studies such as Mills' (1993) analysis of parasitoids of tortricid moths have also failed to find a relationship between parasitoid species richness (PSR) and plant growth form. Furthermore, Hawkins' (1994) analysis of PSR of dipteran parasitoids relative to plant growth form used by the host revealed only a small effect with an erratic progression from herbs to trees. The lack of increased TSR of tree-dwelling caterpillars in this study may be due to the type of habitat sampled. The mesquite–live-oak savanna habitats we sampled have a fairly stable herbaceous plant community that cannot be considered merely an early successional stage of the ecosystem (McPherson 1997). Given this stability, host diversity is likely to be only weakly associated with plant architecture if at all (our possibly biased sampling indicates no difference: herbs, 66 host species; shrubs, 42 host species; trees, 62 host species). If host diversity is not associated with plant architecture, then increased PSR on trees vs. shrubs or herbs may not be expected.

We found no significant relationship between parasitism rate and host habitat. This lack of a strong significant effect supports Hawkins' (1994) finding that percentage of parasitism of exophytic herbivores exhibits no significant relationship with plant type.

Host plant range

As we hypothesized, host species that feed on a wide variety of plants were attacked by larger numbers of tachinid species. Sheehan (1994) found this same pattern for tachinids (but not for Hymenoptera) in northeastern U.S. forests and suggested that this pattern is consistent with the hypothesis that the colonization of new hosts by tachinids is limited by host-finding (Sheehan 1986, 1994). In this study, the pattern appears to be due to increased numbers of generalist tachinids on polyphagous hosts, including species such as *Chetogena scutellaris*, *C. tachinomoides*, *Exorista mella*, and *Lespesia aletiae*, which have all been reared from more than five families of Lepidoptera (Arnaud 1978). Caterpillars with large host-plant ranges are found in a greater variety of micro- and macrohabitats and may be more conspicuous to generalist parasitoids than specialized hosts (Sheehan 1994). In contrast, specialized hosts may be associated with more specialized tachinid parasitoids due to stronger selection for efficient host location. Although tachinids appear to be relatively insensitive to host physiology (Gauld et al. 1992, Belshaw 1994), chemical toxicity of specialized host species may limit the parasitoid species that attack them to primarily specialists (Price et al. 1980, Gauld and Gaston 1994). We found no significant interaction between effects of morphology and host range in our statistical models even though most of the highly polyphagous host species in the data set are hairy, suggesting that these effects are independent.

The absence of a significant effect of diet breadth on tachinid species diversity (H') is not inconsistent with the hypothesis presented above. Hosts that feed on many plant species in a variety of habitats will occasionally encounter generalist parasitoids or parasitoids of other host species, but these may be rare relative to their more specialized parasitoids, resulting in diversity indices similar to more host-plant specialized hosts.

Host defenses

The strong effect of host morphology (hairy, spiny, smooth) on tachinid species richness is one of the more novel results of this study. Sheehan (1994) also reported effects of caterpillar morphology on tachinid diversity, but his study revealed the opposite pattern, with smooth hosts experiencing relatively richer tachinid complexes. This difference may be due in part to the coding of the data. The current analysis suggests a trend towards lower TSR on hosts bearing spines (primarily saturniids and nymphalid butterflies). If these taxa are lumped with those bearing dense hairs as in Sheehan (1994), the effect of hairiness may be obscured. It is our hypothesis that hairy caterpillars support larger complexes of parasitoids because of their reduced susceptibility to predators. They provide ''enemy-free space'' (Jeffries and Lawton 1984, Gentry and Dyer 2002). Predation on caterpillars is often quite severe (Montllor and Bernays 1993) and the benefits of using hosts that have a high probability of surviving until a parasitoid can complete development are obvious. In addition, most of the species of hairy caterpillars reared in this study are not particularly cryptic, nor are they aposematic. This lack of crypsis may be due to relaxed selection by predators, but it may result in an increased apparency to polyphagous tachinids, which have been shown to rely heavily on visual cues (Monteith 1956, Weseloh 1980, Stireman 2002*b*). It might be expected that spiny hosts should confer the same benefit of reduced predation to parasitoids. However, few families containing ''spiny'' larvae are present in our data set, and we suspect that the lower TSR on spiny hosts may be a result of host physiology or other characteristics associated with phylogeny.

The effect of morphology on parasitism rates due to tachinids (both measures) can be explained in the same manner as the effect on TSR. Hairy hosts are less likely to be preyed upon and therefore are more likely to produce adult parasitoids, and they are generally more apparent than cryptic species. We found no indication that hairs provide an effective defense against tachinids as suggested by Sheehan (1994). To the contrary, several tachinid species reared in our study appear to be restricted to hairy host species and the most polyphagous species were often reared from hairy hosts. It is possible that the effect of morphology is due at least in part to hidden effects of species abundance. A relatively high proportion of all hosts that we collected are hairy (26% of those used in analyses), and many of these species were quite abundant. If parasitoids possess a means to overcome the morphological defenses of these hosts, then they may represent a very large pool of potential hosts sustaining high densities of these parasitoid species.

Our findings that aposematic hosts tend to support less diverse tachinid assemblages, especially in relation to abundance, is somewhat unexpected. Most chemical defenses that caterpillars advertise with bright coloration are thought to be directed against vertebrate (and possibly invertebrate) predators (Bowers 1993, Dyer 1995, 1997). However, Gauld and Gaston (1994) and Barbosa (1988) presented broad evidence for detrimental effects of chemically ''nasty'' plants on parasitoid development. Even so, none of the examples cited by these authors involved tachinid flies, which are believed to be relatively insensitive to toxins and physiological defenses (Gauld et al. 1992). It is possible that toxins deposited in the cuticle of aposematic caterpillars may deter egg-laying female parasitoids or damage neonate larvae attempting to burrow into the

host. The potential effects of sequestered plant toxins on parasitoid survival, especially generalists, need to be explored more thoroughly for both the Hymenoptera and Tachinidae. If aposematic hosts are attacked primarily by specialized tachinids that have evolved physiological resistance to toxins, this relationship, along with increased use of abundant non-aposematic hosts by generalist tachinids, may be responsible for the observed interaction between abundance and coloration.

Gregarious hosts tended to exhibit a greater diversity of tachinids and higher maximum parasitism rates as predicted by the hypothesis that they may be more easily located by parasitoids. The strong interaction between gregariousness and abundance indicates that common gregarious hosts support especially large assemblages of tachinid species, which is also consistent with this host-location hypothesis. In addition, it suggests the possibility that parasitoids of abundant gregarious hosts may be less likely to become locally extinct than those attacking solitary hosts. The lack of a relationship between host gregariousness and parasitism by wasps was unexpected, and may be due to the low and variable parasitism rates by Hymenoptera in this system. The effects of gregariousness on tachinid diversity and parasitism rates may be somewhat underestimated as individuals were summed independently in calculations of sample size.

Conclusions

The significant factors identified in the analyses of this data set represent both the evolutionary forces that have shaped tachinid parasitoid assemblages on Lepidoptera and the ecological forces that influence patterns of parasitoid diversity and frequencies of parasitism among hosts. Host characteristics that appear to be most important in explaining variation in tachinid species richness among hosts are abundance, morphology (hairiness), host-plant range, appearance (aposematism), and gregariousness. Host phylogeny is unlikely to be important itself (in terms of cocladogenesis with tachinids or associations between tachinid diversity and species richness of host clades), although host characteristics correlated with phylogeny may have important effects on parasitoid diversity. In contrast to previous studies, the host-plant growth form used by caterpillars was not found to explain a significant amount of variation in tachinid species richness.

The large spatial and temporal variance in parasitism among host collections in this study limits our power to identify significant correlates of parasitism levels among species. However strong effects of host abundance and host morphology on parasitism rates are likely to reflect the opportunistic use by generalist tachinid species of abundant hosts and the increased suitability for all parasitoids of hosts with effective defenses against predators. The relationship between TSR and parasitism rates supports our finding that the number of species that can use a host and the frequency of attack are influenced by the same host characteristics (in part), and that ecological refuges of hosts may differ for particular tachinid species (i.e., parasitism by different species is additive to some degree).

Although a few factors may influence the number of specialist tachinid species per host (e.g., abundance and perhaps phylogeny), the host characteristics examined here largely determine how generalist tachinids are distributed among hosts. The effects of abundance, host plant range, aposematism, and possibly morphology and gregariousness are due to either a limitation of the number of generalist tachinid species (aposematism), or the support of additional generalist species (abundance, host range). This suggests that, in contrast to studies involving more specialized host–parasitoid relationships, the variation in parasitoid species richness among hosts in this community of herbivores is likely dominated by ecological forces rather than historical ones. In particular, the nature of the interaction between herbivores, their food plants, and their predators is linked to the prevalence (Price et al. 1980, Barbosa et al. 2001) and community structure (Hawkins 1994) of parasitoid–host interactions. The precise magnitude and community consequences of such multitrophic linkages may be most apparent by examining local ecological communities as we have done here.

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APPENDIX

A table listing caterpillar traits and associated tachinid parasitoids is available in ESA's Electronic Data Archive: *Ecological Archives* E084-007-A1.