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Spatial and temporal variation in the parasitoid assemblage of an exophytic polyphagous caterpillar

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Abstract. 1. Over 3400 larvae of the polyphagous ground dwelling arctiid *Grammia geneura* were sampled and reared over seven generations in order to characterise its parasitoid assemblage and examine how and why this assemblage varies over time and space at a variety of scales.

2. The total parasitoid assemblage of 14 species was dominated both in diversity and frequency by relatively polyphagous tachinid flies.

3. Both the composition of the parasitoid assemblage and frequency of parasitism varied strikingly among and within sampling sites, seasons, and years.

4. Overall rates of parasitism increased consistently over the duration of caterpillar development.

5. Within sampling sites, parasitism rates were non-random with respect to habitat structure and caterpillar behaviour for the most abundant parasitoid species.

6. The large variability in parasitoid assemblage structure over space and time in this system may be a function of local host population abundance, habitat-specific parasitism, and indirect interactions between *G. geneura* and other Macrolepidoptera through shared oligophagous and polyphagous parasitoids.

Key words. *Grammia geneura*, parasitoid, parasitoid community ecology, spatio-temporal heterogeneity, Tachinidae.

Introduction

The importance of spatial and temporal variability in species interactions has become increasingly obvious to ecologists and evolutionary biologists in recent years (Kalasa & Pickett, 1991; Thompson, 1994, 1997, 1999; Hanski & Gilpin, 1997). This is especially evident in studies of interactions between parasitoids and their hosts (e.g. Hassell *et al*., 1991; Ives, 1995; Lei & Hanski, 1997). Spatial heterogeneity in attack rate and the presence of host refuges have repeatedly been shown to stabilise parasitoid–host interactions in both theoretical models (Hassell & May, 1973; Hassell *et al*., 1991) and empirical studies (Pacala & Hassell, 1991). Such heterogeneity has also been implicated as an important factor influencing the diversity of communities of parasitoids and hosts (Holt, 1977, 1984; Klopfer & Ives, 1997) and determining their evolutionary interactions (Hartvigsen & Levin, 1997; Hochberg & van Baalen, 1998).

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Empirical studies of the extent of spatio-temporal variation in parasitoid assemblages and its role in shaping parasitoid–host interactions have lagged far behind theoretical work (Bernstein, 2000), however recent interest in the ecology of natural parasitoid communities promises to reduce this gap in understanding parasitoid–host interactions (e.g. Redfern *et al*., 1992; Roland & Taylor, 1997; Le Corff *et al*., 2000). Still, most data sets focus on economically important pests and their enemies, systems that are often characterised by high levels of human disturbance and may not typify the majority of ecological interactions (e.g. Cornell & Hawkins, 1993; Shaw, 1994). Most studies on natural systems have involved galling and leaf-mining insects, their hosts, and their enemies (e.g. Tscharntke, 1992; Kato, 1994; Memmot *et al*., 1994; Abrahamson & Weis, 1997), due primarily to the ease of sampling and rearing insects with these life histories (Shaw, 1994). These studies have also tended to focus on either temporal variation among generations and/or years (e.g. Kato, 1994) or geographic variation over one or two generations (Schönrogge *et al*., 1995; Stone *et al*., 1995) but rarely both. It is unlikely that the results of such studies can be extrapolated to the majority of phytophagous insects,

which feed exophytically, due to the marked differences in the diversity, frequency, and character of parasitoids that attack these different host guilds (Hawkins *et al*., 1990; Hawkins, 1994). Empirical studies of the spatio-temporal heterogeneity in parasitism of exophytic herbivores over a variety of scales are necessary to assess the extent of this variation and its importance in determining population interactions and the structure of host–parasitoid assemblages (Lei & Hanski, 1998; Doak, 2000; Ives & Hochberg, 2000; Teder *et al*., 2000).

In the work reported here, the tachinid-dominated larval parasitoid assemblage of a native exophytic generalist herbivore, *Grammia geneura* (Strecker) (Lepidoptera: Arctiidae), is described. A multi-scale spatial and temporal sampling programme was used to examine how this parasitoid assemblage varies across space and time, and what this variation can reveal about the ecological forces that shape the interactions between *G. geneura* and its parasitoids.

Although flies in the family Tachinidae are often important parasitoids of larval Lepidoptera (Schaffner & Griswold, 1934; Brodmann *et al*., 1997), relatively few studies of community organisation and patterns of parasitism have focused on this group. The wide host ranges characteristic of many tachinid species (Belshaw, 1994) suggest that their ecological interactions with hosts are likely to differ significantly from most well-studied parasitoid–host systems that involve relatively specialised parasitic wasps (Godfray, 1994). Recent studies of tachinid communities have demonstrated strong effects of habitat on the spatial distribution of searching females (Belshaw, 1992) and parasitism rates of hosts (Roland & Taylor, 1997). This spatial structure in habitat use, along with tendencies towards polyphagy and plasticity (O'Hara, 1985; Belshaw, 1994; Feener & Brown, 1997), suggests that tachinid complexes may be ideal systems in which to examine spatial and temporal heterogeneity in parasitoid–host interactions.

Materials and methods

The host study system

Grammia geneura is an arctiine moth with ground-dwelling larvae. The species is distributed in the south-western United States and northern Mexico at elevations of 1000–2000 m in semi-arid grassland and woodlands. *Grammia geneura* is exceptionally polyphagous. In Arizona (south-west U.S.A), it has been recorded feeding on plants belonging to 50 different families (Singer, 2000). In south-eastern Arizona, *G. geneura* is bivoltine. Adults mate and fly from late May to early July, and apparently lay eggs freely in leaf litter in suitable microhabitats ($\approx$1000 eggs per female; M. Singer, unpublished). The larvae develop through six to eight stadia during the summer rainy season, feeding on a wide variety of herbaceous annuals and perennials, and emerge as adults in early August to November. Again, eggs are laid in suitable microhabitats along drainages, and the larvae develop to intermediate stadia (typically fourth or fifth) before overwintering. These larvae complete their development in the spring (February–May) after the winter rains have produced a flush of vegetation and the temperature increases. Though early instars are probably somewhat limited in their mobility, late instars are highly mobile and commonly feed on over 10 individual plants of multiple species during a single day (Singer, 2000). Populations of *G. geneura* fluctuate strikingly in abundance among years, sometimes reaching outbreak numbers of up to 10 individuals per m^2 (J. O. Stireman and M. S. Singer, unpublished).

Sampling sites

Individuals of *G. geneura* were sampled from 10 sites in south-eastern Arizona (Table 1) in the vicinity of the Santa

Table 1. Sites in south-eastern Arizona from which *Grammia geneura* were collected from spring (March to May) 1996 to summer (July to September) 1999. Numbers indicate the number of times that each site was sampled in that season, x denotes sites that were surveyed for caterpillars but where populations were absent or at very low densities. – indicates sites that were not examined in that season/year.

		Sampling period							
Site	Elevation to nearest 25 m	1996 spring	1996 summer	1997 spring	1997 summer	1998 spring	1998 summer	1999 spring	1999 summer
Ash Creek	1225	2	1	3	3	5	3	2	x
Redington Pass	1275	2	x	2	x	4	–	1	–
Gardener Canyon	1225	2	1	x	x	x	x	x	x
Pena Blanca Lake	1125	1	x	x	x	x	x	–	x
Canelo Hills	1525	–	1	–	x	x	1	x	x
Upper Box Canyon	1525	–	–	–	–	–	2	1	x
Lower Box Canyon	1125	–	–	–	–	–	2	–	x
Arivaca	1075	2	–	–	x	x	x	x	1
Temporal Gulch	1275	–	–	1	x	1	x	–	x
Oracle	1375	–	–	2	–	x	x	1	–

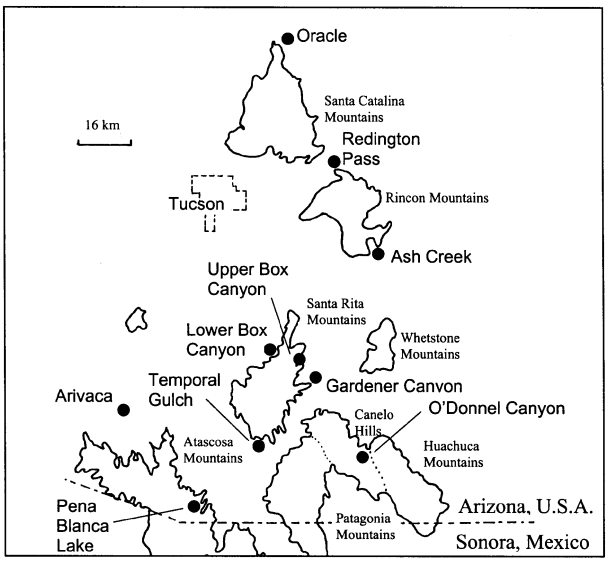

Fig. 1. Sampling sites of *Grammia geneura* in south-eastern Arizona (U.S.A) in relation to major mountain ranges. Lines around mountain ranges indicate the approximate extent of the range relative to surrounding valleys and plains.

Catalina, Rincon, Santa Rita, Huachuca, and Atascosa mountain ranges (32°N, 110°W) (Fig. 1). These sites range in elevation from 1050 to 1550 m and are dominated by mesquite-live oak savanna. Precipitation (≈ 300–600 mm) in this semi-arid region is divided nearly equally between winter rains (November–March) and the summer *monsoon* (July–September). This creates two major growing seasons during the year, the cooler, more temperate spring, and the warmer, more tropical summer.

Sampling methods

Scouting trips were conducted each year from 1996 to 1999 in February to April and again in July to August to locate dense populations of *G. geneura* larvae. Sampling sites were selected to maximise geographic coverage within the study area. The location of dense populations was highly variable, so few sites were sampled continuously over all generations and/or years (Table 1). When a population was located, the average developmental stage of the caterpillars was assessed and samples were either collected immediately or left for future collecting. In general, only late instars (sixth to eighth) were collected in order to maximise the opportunity for larvae to be parasitised in the field prior to removal. At most sites, collecting was concentrated in an area of ≈0.6 ha, within which either all of the late-instar caterpillars that could be located were collected or as many as could be found and processed in a 5–8-h period. The search area was expanded (≈ 1 ha) in sites where *G. geneura* densities were low in order to increase sample sizes. Sampling was conducted by walking slowly along transects in the sampling area and scanning the ground and low vegetation. When possible, sites were sampled several times within a season over the prolonged duration of activity of the caterpillars (Table 1).

In order to examine the effects of location, host plant, and caterpillar behaviour on parasitism, a suite of ecological variables was recorded for each individual collected, including the individual's behaviour (immobile, feeding, walking), the substrate on which it was found (ground or plant species), and the micro-habitat in which it was found (open versus canopy covered). Individuals were also classified by size on a scale of 1 to 5 (smallest to largest), the density of neighbouring caterpillars, and the presence of any tachinid eggs or cuticular blemishes. Caterpillar density was determined by the number of individuals located in a 1-m^2 circle centred on the caterpillar that was collected. This measure was used due to the difficulty of gathering (or effectively counting) all caterpillars within a sampling area during some sampling periods and the sporadic distribution of individuals at several sampling sites. This measure ignores the area with no caterpillars, and thus does not truly estimate their overall density. The total number of caterpillars collected at a particular site was used as an additional, coarser measurement of density.

Individual caterpillars were collected in plastic vials, given an identification number, and transported to an environmental chamber (28 °C, LD 16:8 h) at the University of Arizona. They were placed in covered 180-ml plastic cups with ≈1.0 g of synthetic wheat-germ based diet (Yamamoto, 1969). Food was replenished and frass removed every other day until caterpillars entered the prepupal stage. The number, identity, and date of emergence of all parasitoids were noted and the parasitoids were either killed and prepared as vouchers or used to maintain a laboratory colony. Parasitoids were identified by J. O. Stireman, N. E. Woodley (Systematic Entomology Laboratory, USDA; Tachinidae), J. E. O'Hara (Canadian National Collection; Tachinidae), J. B. Whitfield (University of Arkansas, *Cotesia*), and N. Zitani (University of Wyoming; *Meteorus*). Voucher specimens of all species were deposited at the University of Arizona Insect Collection.

Analysis

In order to examine the diversity of the parasitoid assemblage and the completeness of the sampling programme, 100 randomisations of the data were performed and a parasitoid species accumulation curve was computed using EstimateS (Colwell & Coddington, 1994; Colwell, 1997). This program also computed a series of statistical estimators of true species richness, such as ICE (Incidence-based Coverage Estimator; Lee & Chao, 1994) and Jack2 (Burnham & Overton, 1978), which were used to evaluate the adequacy of the sampling.

Likelihood ratio χ^2 tests were used to determine whether maximum parasitism rates were significantly different among sites and years (using JMP IN 3.1.5; SAS Institute

Inc., 1989–1999). The maximum parasitism rates were defined as the highest rate of parasitism over all collections within a site per generation. In these analyses, the total rate of parasitism and the rate of parasitism for each of the three dominant parasitoids were compared among sites within a year and among years within sites. The density dependence of parasitism was assessed by performing linear regressions of parasitism rate by two measures of host density: mean density per m^2 and total number of caterpillars per collection. Preliminary observations suggested that the level of parasitism varied considerably over time within a single season. To test whether this pattern was significant, the rate of parasitism between the first and last samples was compared for all sites in which multiple collections were made, using a paired *T*-test with arcsin-transformed proportions.

To examine how patterns of parasitism within sites varied with ecological and behavioural characteristics of hosts, a stepwise binomial analysis of deviance with a binary response variable (parasitised, not parasitised) was conducted using generalised linear modelling techniques in GLIM 3.77 (McCullagh & Nelder, 1983; Crawley, 1993). Site–year samples were analysed individually due to the large variance in parasitoid abundance and composition over space and time. Samples characterised by low rates of parasitism ($< 10\%$) or small numbers of caterpillars collected, which would make detection of patterns impossible (e.g. spring 1996), were not analysed. Separate models were analysed for each parasitoid species. Factors included in the models were host behaviour, habitat, density, and substrate (see above). Comparisons of the residual deviance with the residual degrees of freedom for each model indicated that in no case were the data overdispersed (Crawley, 1993). Bonferroni corrected αs were used in analyses that employed multiple non-independent comparisons.

Results

Parasitoid diversity

Three thousand, four hundred and eighty-four *Grammia geneura* individuals were collected over the course of the study, of which 527 (15%) were found to be parasitised by one or more species of parasitoid. Fourteen species of endoparasitoid were reared, including nine tachinids and five Hymenoptera, one of which was a hyperparasitoid (*Perilampus hyalinus*) of the tachinid *Carcelia reclinata* (Table 2). Both the observed curve of cumulative species richness and the plot of cumulative richness by sample size generated by the 100 randomisations of the data set approached an asymptote at ≈ 2500 individuals (Fig. 2). All richness estimators calculated in EstimateS (e.g. ICE, ACE, Chao1,2, Jack1,2, Alpha, Shannon, Simpson; see Colwell, 1997, and references therein) for the complete data set varied less than one species from the observed total of 13 primary parasitoids. Hence, the sampling was

Table 2. The parasitoids reared from *Grammia geneura* in the seven generations of the study and the maximum per cent parasitism in any one sample ($n > 25$) across all sampling sites within each of the two yearly generations. The column Greg. indicates whether the parasitoid was solitary (S), gregarious (G), or facultatively gregarious (S-G). Eclosion refers to whether the parasitoid emerged from the host larva (L), late larva (LL), prepupa (PP), or pupa (P). Numbers in parentheses refer to parasitism rates from samples where $n < 25$. Tachinid taxa indicated in bold represent species that have not previously been reared from the genus *Grammia* (previously *Apantesis*). There are no published parasitoid records for *G. geneura*.

			Maximum per cent parasitism across all sampling sites						
			1996		1997		1998		1999
Parasitoid species	Greg.	Eclosion	Spring	Summer	Spring	Summer	Spring	Summer	Spring
Tachinidae									
Exorista mella (Walker)	S-G	PP-P	2.7	0	35.6	0	47.7	0	3.0
Carcelia reclinata (Ald. & Webb.)	S-G	LL-PP	0	78.3	25.5	24.0 (57.1)	0	14.5	9.8
Chetogena tachinomoides (Twnsd)	S-G	LL-P	0	0	7.8	0	2.0	3.8	2.5
Chetogena edwardsii (grp.) (Williston)	S-G	PP-P	0	0	2.3	0.5	9.8	2.1	4.5
Chetogena scutellaris (Wulp)	S-G	LL-P	0	0	0	0	4.2	1.2	2.4
Chaetogaedia monticola (Bigot)	S	P	1.3	0	1.0	0	0	5.1 (8.3)	0
Lespesia aletiae (Riley)	S-G	L-P	0	12.5	0	0.5	0	16.7	0
Lespesia archippivora (Riley)	S-G	L-PP	0	0	0	0	2.0	0	0
Archytas lateralis (Macquart)	S	P	0	0	0	0	0	2.1 (8.3)	0
Braconidae									
Cotesia nr. *phobetri* (Rohwer)	G	LL	7.5	0	45.8	0	0	0	0
Meteorus arizonensis (Muesebeck)	S	L	1.3	0	0	0	0	(4.76)	(33.3)
Ichneumonidae									
Ophion sp.	S	PP	0	8.7	0	16.7	0	1.3	0
Erigorgus sp.	S	P	0	0	0	0	2.0	0	0
Perilampidae									
Perilampus hyalinus Say	S	(P)	0	0	0	0	0	(10.0)	0

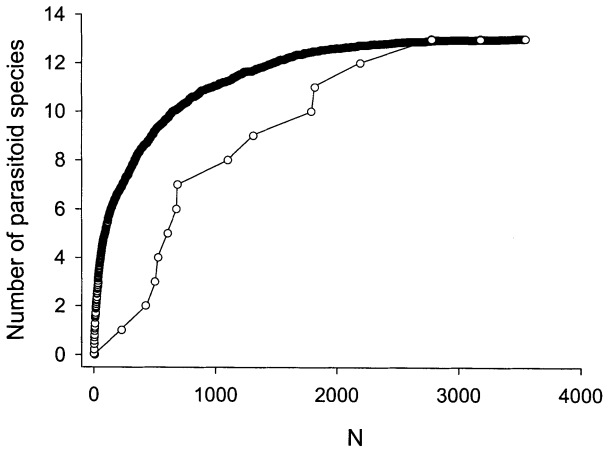

Fig. 2. The observed parasitoid species accumulation curve by sampling effort of *Grammia geneura* (top curve), and a plot of the mean richness by sample size generated from the randomised data set (–○–).

complete enough to reveal the vast majority of parasitoids attacking this host within the sampling area.

The distribution of parasitoid abundances over the entire study suggested that the parasitoid assemblage could be divided into three functional groups (Fig. 3): core parasitoids that are likely to rely heavily on *G. geneura* as a principal host and effect high rates of parasitism (e.g. *Exorista mella*), peripheral parasitoids that are responsible for somewhat lower rates of parasitism and may use *G. geneura* facultatively when it is abundant and other hosts are unavailable or rare (e.g. *Chetogena scutellaris*; Stireman, 2001), and incidental parasitoids that attack *G. geneura* rarely and incidentally (e.g. *Archytas lateralis*). This classification does not necessarily reflect which parasitoids are distributed most widely or associated most commonly with *G. geneura*, but rather uses discontinuities in the total number of hosts attacked to indicate distinct classes of probable influence on the host.

Temporal and spatial variability among sites

Variability in the presence and abundance of each parasitoid species was striking across sites and years for both the spring (Fig. 4) and summer (Fig. 5) generations. Over all sampling periods, there were no sites in which an identical complement of parasitoid species was found. Nor was there complete congruence of any parasitoid assemblages among years within a site. A regression of the number of parasitoid species reared against the number of caterpillars collected in each site (in each year) indicated that 74% of the total variance in parasitoid species richness among collections was due to local population density and/or sample size ($n = 25$, $F = 34.3$, $P < 0.001$; Fig. 6).

Maximum parasitism rates varied significantly across sites over all generations (except summer 1997 when only one site was sampled; Table 3). Much of this variability was due to the three core parasitoids, which varied widely in their abundance among sites. For example, in 1997 *Cotesia* nr. *phobetri* achieved parasitism rates of >40% in samples

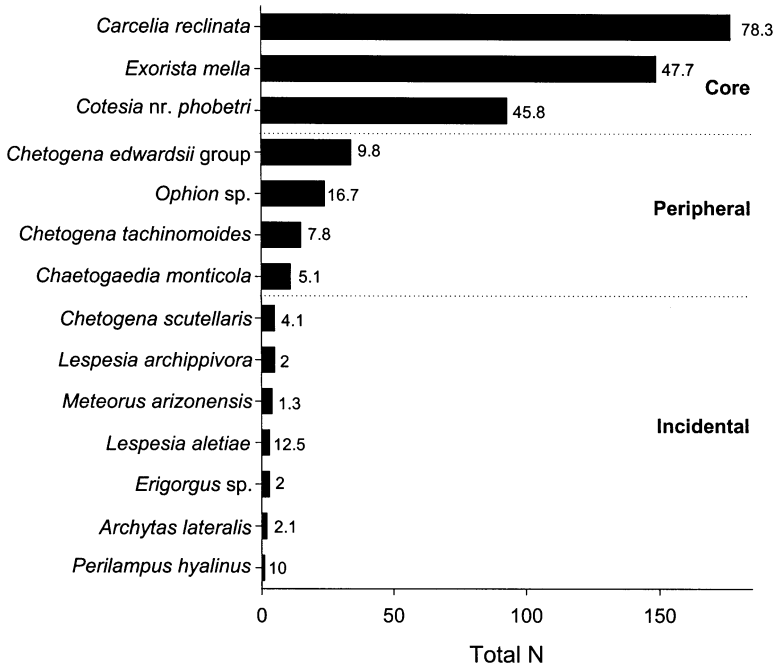

Fig. 3. Absolute numbers of hosts attacked by each parasitoid species, divided into classes of ecological importance. Numbers beside the bars indicate the maximum per cent parasitism by this species in any sample.

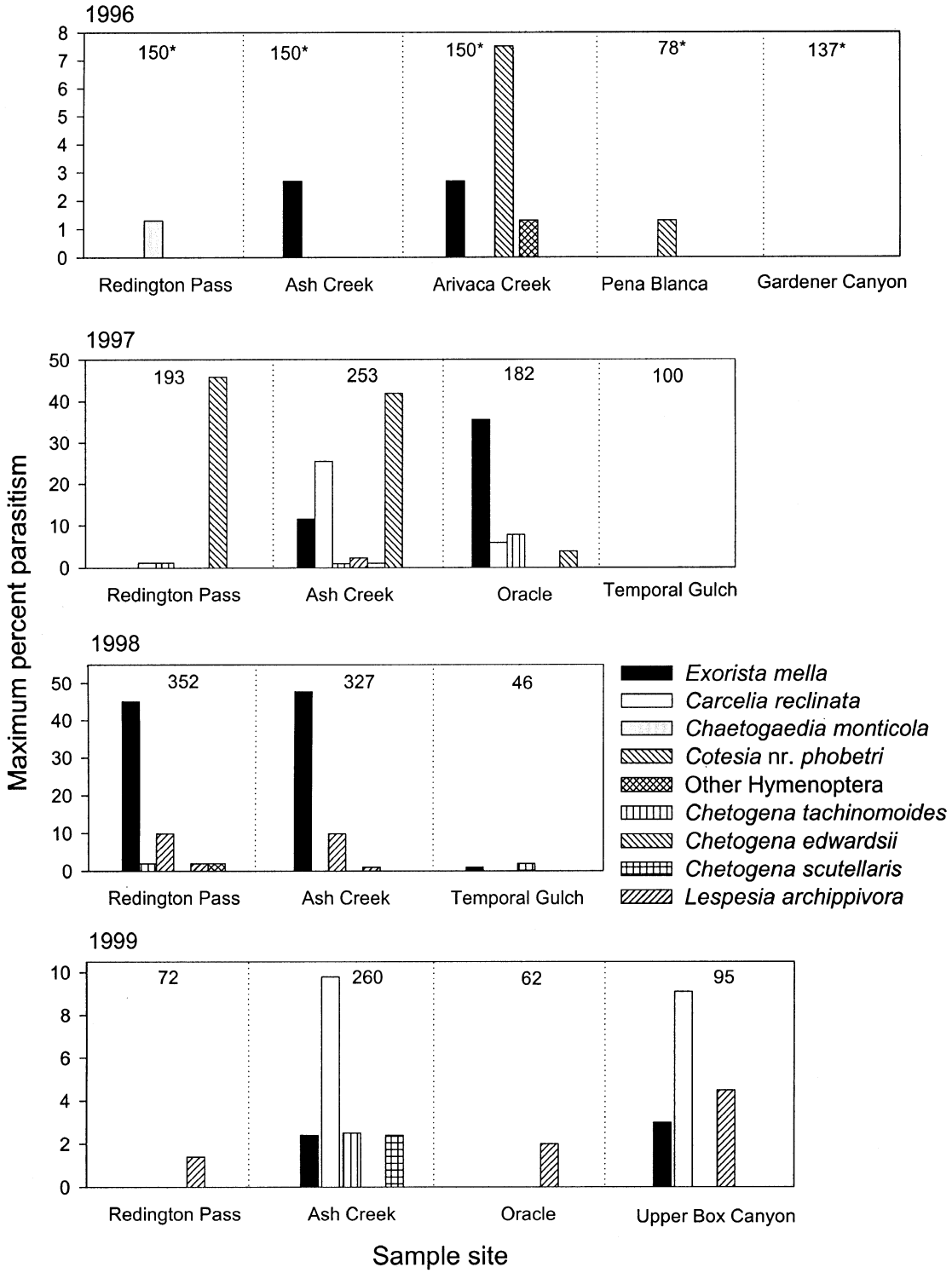

Fig. 4. Maximum parasitism rates of the parasitoids attacking the spring generation of *Grammia geneura* for each site sampled over 4 years. Numbers above each set of columns indicate the total sample size for that site–year combination. *The total number of caterpillars collected in 1996 was twice the number indicated, but half were not reared.

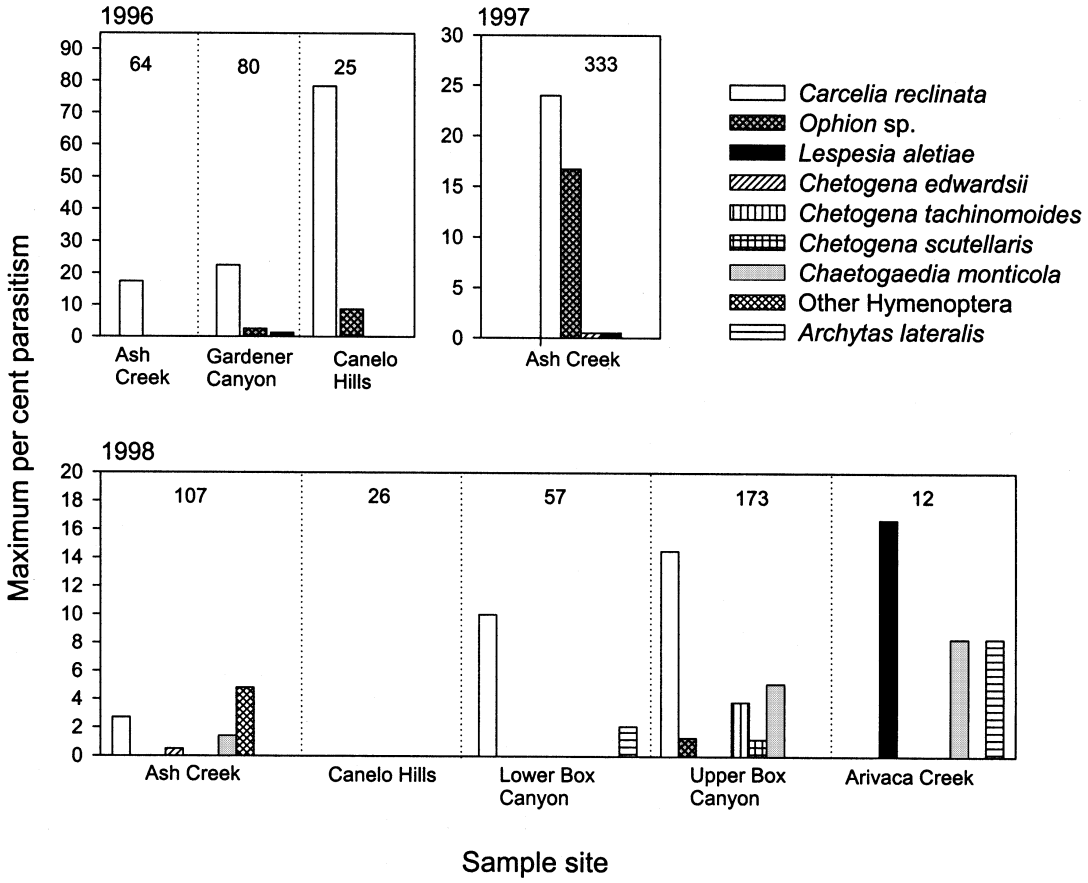

Fig. 5. Maximum parasitism rates of the parasitoids attacking the summer generation of *Grammia geneura* for each site sampled over 3 years. Numbers above each set of columns indicate the total sample size for that site–year combination.

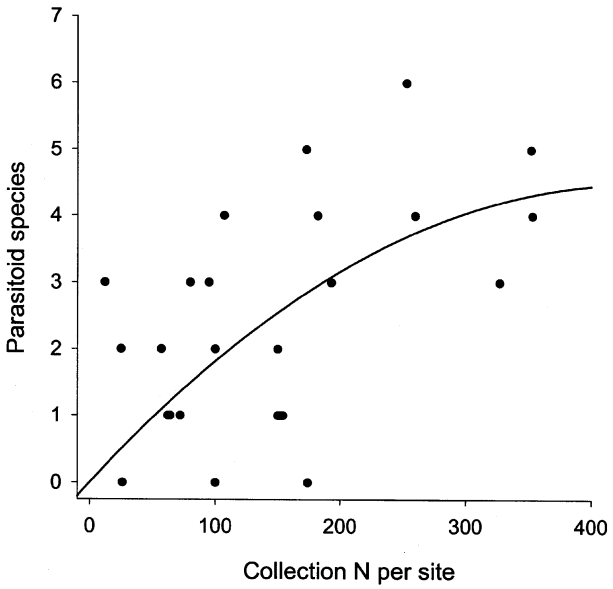

Fig. 6. A quadratic regression of the number of parasitoid species reared against the number of hosts sampled per collection ($R^2 = 0.744$, $n = 25$, $F = 33.5$, $P < 0.001$).

from Redington Pass and Ash Creek but was rare at the Oracle site and absent from Temporal Gulch (Fig. 5).

The variation among years within a site was even more striking than the variation between sites (Figs 4 and 5). For those sites sampled in multiple years, significant differences were found in total maximum parasitism rates among years (Table 3). Again, this was due primarily to the three core parasitoids, though the presence and level of peripheral and incidental parasitoids also varied widely. The variability in parasitism rates among years was most evident at the two sites where *G. geneura* populations were large and consistent enough to be sampled for more than 2 consecutive years (Fig. 7). This variation in parasitism within a site showed no apparent relationship with *G. geneura* densities in the current or preceding year, as measured by the mean density or total number sampled (e.g. for Redington Pass, R^2 ranged from –0.34 to 0.13, $1.5 > F > 0.2$, $0.68 > P > 0.35$; but see below).

Most linear regression analyses of per cent parasitism against *G. geneura* density across sites (within years) indicated no significant relationship ($R^2 = 0.05$–0.66, $F = 0.43$–3.2, all NS), however in spring 1997 a significant, positive relationship was found between the total parasitism

Table 3. A summary of χ^2 analyses of variation in maximum parasitism rates among all sites within a given year, and among years for spring samples of Ash Creek and Redington Pass. Likelihood ratio χ^2 values are reported for comparisons between sites for total parasitism rates and variation in the rates of the three core parasitoids found in this study. na = years in which a species was not present. $^{**}P < 0.01$, $^{***}P < 0.001$, NS = not significant (Bonferroni corrected $\alpha = 0.0125$).

	Likelihood ratio χ^2				
Sample date/site	Number of sites	Total parasitism	*E. mella*	*C. reclinata*	*C.* nr. *phobetri*
1996 Spring	5	26.2***	NS	na	28.1***†
1997 Spring	4	66.4***	131.9***	20.2***	78.9***
1998 Spring	3	12.9**	14.1**	na	na
1999 Spring	4	12.0**	NS	14.0**	na
1996 Summer	3	40.2***	na	32.1***	na
1998 Summer	5	35.8***	na	26.0**†	na
96–99 Spring, Ash Creek		45.4***	19.9***	44.3***	101.8***
96–99 Spring, Redington Pass		75.3***	82.8***	na	142.1***

†In these analyses, 20% of expected values of cells were <5 and the χ^2 values may be inflated.

rate and the total number of caterpillars sampled per site (Table 4). *Grammia geneura* was extraordinarily abundant in spring 1996 and parasitism rates were so low (averaging $<2\%$) that any effect of host density on parasitism rates is likely to have been obscured. When years were combined and the data from spring 1996 were excluded from the analysis, significant, positive relationships emerged between total parasitism rate and both of the density measurements examined (Table 4). These patterns held at a finer scale for each of the core parasitoids, although they differed depending on which measure of *G. geneura* density best explained parasitism rate (Table 4). Summer samples were too limited to be useful in examining these patterns.

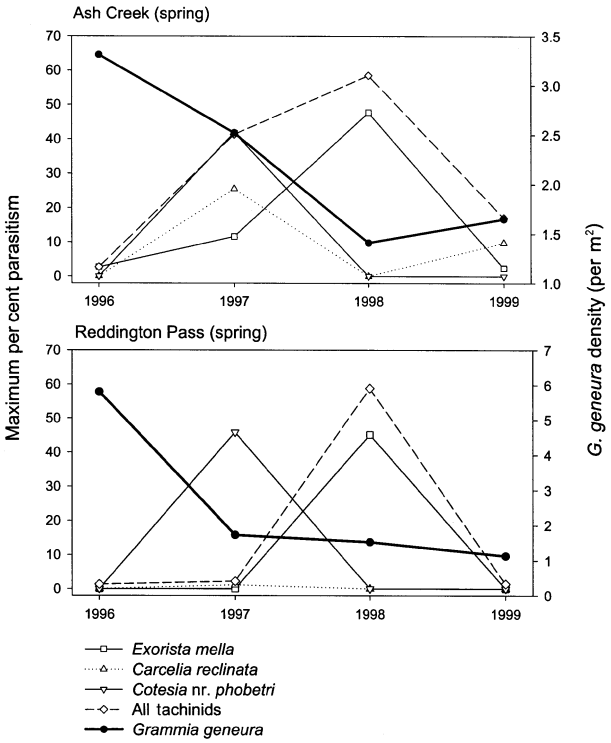

Fig. 7. Rates of parasitism by core parasitoids and density of *Grammia geneura* in the spring generation at Ash Creek and Redington Pass over 4 years.

Within-generation temporal variation

Parasitism rates by core parasitoids were found to increase significantly over time within a single season across sites (paired *t*-test on arcsin-transformed proportions, d.f. = 10, $T = -3.3159$, $P < 0.005$; Fig. 8). In general, levels of parasitism by core parasitoids increased greatly at later sampling dates, this pattern being most pronounced in the spring. A comparison of the first date on which collected caterpillars produced silk (in preparation for pupation) for parasitised and unparasitised individuals indicated that this pattern was not due to prolonged development of parasitised hosts, at least for *C. reclinata* ($t = 0.86$, $n = 35$, $P =$ NS).

Within-site variation

The analyses of deviance of the ecological factors associated with parasitism within sites revealed a number of behavioural and habitat-related correlates for each of the core parasitoids (Table 5). The likelihood of parasitism was found to vary significantly with host behaviour when sampled (feeding or immobile), and its interaction with other variables, for several of the collections analysed. These significant effects were generally a consequence of higher parasitism rates of stationary individuals rather than of individuals that were observed feeding or walking.

The habitat in which a host was collected also influenced its probability of parasitism. Caterpillars collected under the canopy of trees and large shrubs were significantly

Table 4. A summary of regression analyses of parasitism rates against two measures of host density for all parasitoids together and each core parasitoid separately. The top row shows results from within-year analyses. The bottom four rows show results from spring collections lumped across years, with the exclusion of 1996. *P*-values shown in bold are significant with a Bonferroni corrected α of 0.0125.

	N/0.6 ha			Mean/m^2		
Parasitoid	R^2	F	P	R^2	F	P
Total parasitism (1997)	0.92	35.5	$<$ **0.01**	0.77	9.8	0.052
Total parasitism (all years except 1996)	0.63	15.1	$<$ **0.005**	0.61	13.8	$<$ **0.005**
Exorista mella (all years except 1996)	0.56	11.6	$<$ **0.01**	0.02	0.2	NS
Carcelia reclinata (all years except 1996)	0.06	0.6	NS	0.63	15.4	$<$ **0.005**
Cotesia nr. *phobetri* (all years except 1996)	0.04	0.4	NS	0.60	13.6	$<$ **0.005**

more likely to have been parasitised by *E. mella* than were caterpillars found in open habitat (Table 5). This result held for two sites (Redington Pass and Ash Creek) in 1998, and the same pattern was revealed for the ichneumonid *Ophion* sp. in the summer generation (Ash Creek). A significant interaction between habitat and substrate was found for *C. reclinata* in both spring and summer generations. In the spring, caterpillars found on plants in the open were more likely to have been parasitised by this tachinid, whereas in the summer generation caterpillars found on plants under the canopy of trees were more likely to have been parasitised. Caterpillars collected on the ground were more likely to have been parasitised by *C. reclinata* if there were no neighbouring individuals (substrate–density interaction). There was no relationship between the host plant from which a caterpillar was collected and parasitism by any parasitoid species, and no positive relationship between density and parasitism rates within sites. There was also no relationship between parasitism rates by any of the parasitoid species and host size based on the rough classification.

Discussion

The analysis of the accumulation curve of parasitoid species richness indicates that the vast majority of parasitoids of *G. geneura* within the study area was recovered. Any parasitoid species not detected were likely to be extremely rare. The total of 13 primary parasitoids reared over the course of the study is high relative to the average parasitoid species richness for exophytic Lepidoptera recorded by Hawkins (1994) for studies reporting sample sizes between 500 and 10 000 (mean $\pm$ SE $= 8.14 \pm 0.67$, median $= 7$), despite the fact that the parasitoid assemblage was examined over only a small part of the range of *G. geneura* and only late-instar larval parasitoids were sampled.

The parasitoid assemblage of *G. geneura* was dominated by tachinid flies both in composition (nine out of 13 species excluding the hyperparasitoid) and overall parasitism rates (although see *Cotesia* nr. *phobetri*; Fig. 3). This tachinid species richness is significantly higher than the mean recorded for other exophytic Lepidoptera (with comparable sample sizes) based on Hawkins's (1994) host–parasitoid database (mean $\pm$ SE $= 3.42 \pm 0.38$, $P < 0.05$), however as tachinid flies are largely diurnal (Clausen, 1940), tend to attack large insect hosts (Arnaud, 1978), and often dominate parasitoid assemblages of hairy host species (Herting, 1960; Parry, 1995; Zolubas *et al.*, 2001), *G. geneura* has the characteristics that make it a preferred host for tachinid parasitism. The wide host range of many tachinid species may predispose them to attack a polyphagous host such as *G. geneura* that is distributed unpredictably over space and time. Hairy caterpillar species have been found to support more polyphagous parasitoids than have smooth caterpillar species (Sheehan, 1991, 1994), suggesting that this trait may be responsible for the large number of generalist tachinids that attack *G. geneura*. These characteristics are also likely to account for the relative paucity of specialist parasitoids in this system. Host associations are not well known for many of the parasitoids reared from this study, but only one species, *Carcelia reclinata*, appears to be a specialist on *G. geneura* and related polyphagous arctiids (Arnaud, 1978).

Within-site variability

The significant associations between host immobility and the substrate on which hosts were found (ground) and parasitism probably do not reflect the searching behaviour of female parasitoids. Rather, both of these patterns probably reflect inactivity or sluggishness of the caterpillars due to parasitoid development (Godfray, 1994). The measure of habitat, however, was probably at a coarse enough scale relative to caterpillar movement that the associations between canopy-covered habitats and parasitism by *E. mella* and *Ophion* sp. reflect true differences in the probability of parasitoid attack. This is supported by an analysis of the distribution of caterpillars bearing tachinid

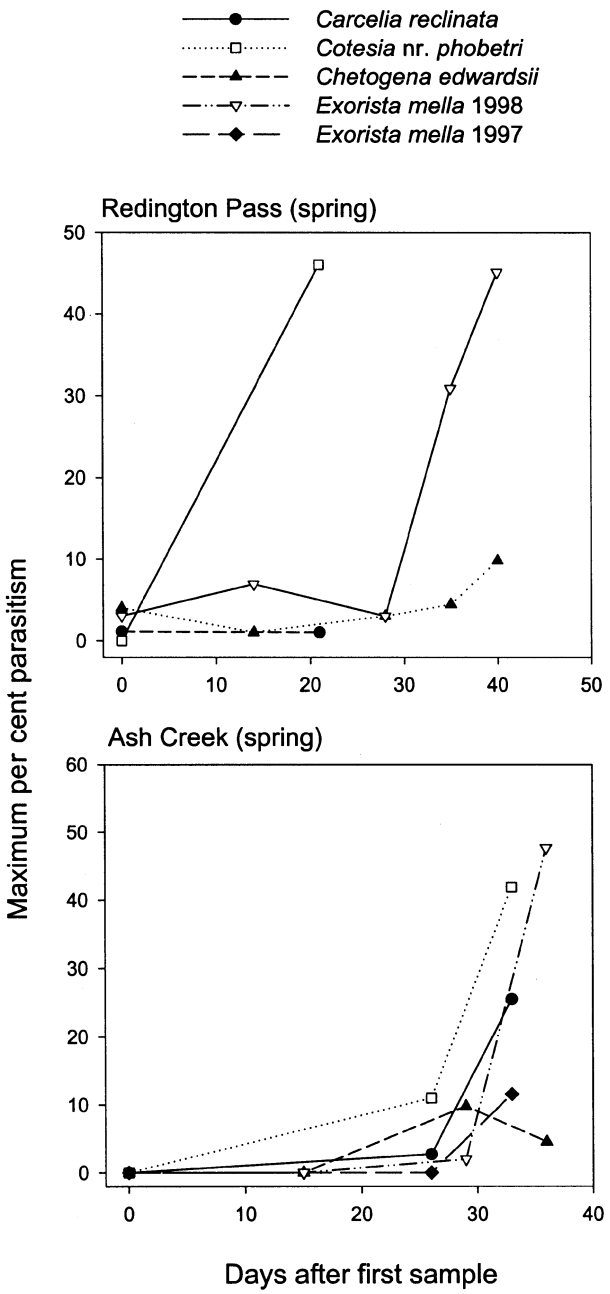

Fig. 8. Parasitism rates by core parasitoids of *Grammia geneura* over the course of the spring generation at Ash Creek and Redington Pass in 1997 and 1998.

eggs (*E. mella* and *Chetogena* spp.) on their cuticles. Caterpillars located in canopy-covered habitats were significantly more likely to bear visible tachinid eggs than were those in open habitats for both Ash Creek and Redington Pass (1998; Fisher's exact test, both $P < 0.05$).

The increasing rate of parasitoid attack over the course of a single generation within sampling sites is perhaps the strongest pattern observed in the data. The pattern is consistent across years and across parasitoid taxa (Fig. 8). The lack of a relationship between parasitism and host size, and the observation that parasitised caterpillars did not differ from unparasitised individuals in the timing of pupation, suggest that this pattern was not due to parasitoid preferences for larger hosts or delayed development. This lag has been recorded in previous studies of parasitoid communities (e.g. Felland, 1990) and may be a general phenomenon of many parasitoids that attack later developmental stages of hosts in seasonal environments. It is unclear whether this pattern is due to an aggregational response or parasitoid reproduction in this system. The lag in parasitism may stabilise population dynamics of *G. geneura* by providing a temporal refuge from parasitoid attack (Munster-Swendsen & Nachman, 1978).

Seasonal variability

The difference in the composition of the parasitoid assemblages attacking the spring and summer generations of *G. geneura* is probably a consequence of the distinct abiotic and biotic environments that characterise these two growing seasons in south-eastern Arizona. Only *Carcelia reclinata*, the specialist, was found at appreciable levels in both generations, though it appeared to be active predominantly in summer. This species is recorded to overwinter as a larva inside the diapausing host larva (Sellers, 1943), leading to the observed pattern of high levels of parasitism in some spring samples. The distinctiveness of the parasitoid assemblage between seasons may be responsible for the relatively diverse assemblage attacking *G. geneura*. This suggests that host species that undergo multiple generations within a year may be expected to exhibit larger complements of parasitoid species, especially in environments with multiple growing seasons, as in south-eastern Arizona (Hawkins & Gagné, 1989).

Between-site variability

Although there are many differences among sampling sites, a few primary factors are indicated that may explain much of the variation in parasitoid assemblage structure and levels of parasitism among sites and years: the density of *G. geneura* populations, the distribution of canopy and open habitats, and the presence of alternative hosts. The first is suggested by the significant effect of collection size (reflecting density in part) on parasitoid species richness and the effect of density on the total rate of parasitism (e.g. 1997). The second is suggested by the repeated effect of habitat on the probability of parasitism in the within-site analyses. Several other tachinid species (as well as parasitic wasps) have been shown to exhibit spatial structure in parasitism rates depending on the distribution and size of forest fragments (Roland & Taylor, 1997; Cappuccino *et al.*, 1998). Weseloh

Table 5. A summary of the significant terms in the analysis of deviance models examining the effect of within-site ecological variables on the probability of parasitism by the core parasitoids of *Grammia geneura*. $*P < 0.05$, $**P < 0.01$, NS = no significant factors at $\alpha = 0.05$.

Species	Site	Year, season	Factor†	d.f.	χ^2
Cotesia nr. *phobetri*	Ash Creek	1997, Spring	Behaviour	1	8.03**
Cotesia nr. *phobetri*	Ash Creek	1997, Spring	Behaviour × habitat	2	8.13*
Exorista mella	Oracle	1997, Spring	Behaviour × density	2	9.53**
Exorista mella	Ash Creek	1998, Spring	Habitat	1	6.88**
Exorista mella	Redington Pass	1998, Spring	Habitat	1	3.85*
Carcelia reclinata	Ash Creek	1997, Spring	Substrate × density	1	5.18*
Carcelia reclinata	Ash Creek	1997, Spring	Substrate × habitat	1	4.75*
Carcelia reclinata	Ash Creek	1996, Summer	Substrate × habitat	1	8.61**
Carcelia reclinata	Upper Box Canyon	1998, Summer	Behaviour	1	5.39*
Ophion sp.	Ash Creek	1997, Summer	Habitat	1	5.21*

†For explanation of factor, see methods.

(1972, 1974, 1982) also demonstrated a strong influence of host microhabitat on parasitism rates by tachinids in another hairy polyphagous caterpillar, the gypsy moth *Lymantria dispar*.

All of the tachinids reared from this study, and probably also the hymenopterans, frequently use other lepidopteran hosts present in these habitats (Stireman, 2001; J. O. Stireman, unpublished). This suggests that the composition of the parasitoid assemblage and the levels of parasitism in particular locations are partly a function of the presence and abundance of alternate hosts of these parasitoids. For example, the tachinid *Chaetogaedia monticola* Bigot is a frequent parasitoid of the arctiid *Pygarctia roseicapitis* (Neumoegen) (Stireman, 2001). In sites where this arctiid species was abundant, the number of *G. geneura* found to be parasitised by *C. monticola* (e.g. Upper Box Canyon, 1998) was relatively high. Similarly, *Chetogena edwardsii* (group) achieved parasitism rates in *G. geneura* of almost 10% at or near sites with the lasiocampid *Malacosoma incurvum* (Edwards), and parasitism was greatest by *C. reclinata* in a site (Canelo Hills, 1996) shared with the arctiid *Estigmene acrea* (Drury). This overlap in host use may result in apparent competition, in which potential host species that co-exist in the same habitats have a negative effect on each other through a shared parasitoid (Holt, 1977; Holt & Lawton, 1994).

Some evidence is provided that the core parasitoids in this system respond to *G. geneura* population density over large spatial scales, either through aggregation or local reproduction. The significant associations between host density and parasitism rates in 1997, and for the combined data set (excluding 1996 samples), indicate that the core parasitoids of *G. geneura* are more abundant in high-density patches of this host. The observation that the core parasitoids differed in the measure of host density that best explains parasitism rates (Table 4) may reflect differences in foraging behaviour with respect to the distribution of hosts and the scale at which each parasitoid responds to host density. For example, *Exorista mella*, which exhibited increased parasitism in response to the total number of caterpillars collected per site, may respond to density at a coarser scale than either *Carcelia reclinata* or *Cotesia* nr. *phobetri*, which exhibited a positive relationship with the mean number of hosts per square metre (probably in part reflecting small-scale patchiness).

In general, it is suggested here that the high level of variability in the parasitoid assemblage and parasitism rates of this host is due to its variable population density (e.g. effects of collection size and density on parasitoid richness and parasitism rates), its occupation of a variety of microhabitats (i.e. canopy covered and open), and the dominance of the parasitoid assemblage by generalist tachinid flies, which are able to use alternate hosts. It is difficult, however, to infer how important these factors are in determining patterns of variation in parasitism among phytophagous insects generally without comparative analyses of spatial and temporal patterns of parasitism in other exophytic species that vary in these traits. Such studies are rare, but growing in number, and it is hoped that the patterns revealed and ecological hypotheses raised here will spur further empirical examination of the causes of spatial and temporal variation in host–parasitoid interactions.

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