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The effects of plant dispersion and prey density on parasitism rates in a naturally patchy habitat

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Abstract Despite extensive research on parasitoid-prey interactions and especially the effects of heterogeneity in parasitism on stability, sources of heterogeneity other than prey density have been little investigated. This research examines parasitism rates by three parasitoid species in relationship to prey density and habitat spatial pattern. The herbivore *Itame andersoni* (Geometridae) inhabits a subdivided habitat created by patches of its host plant, *Dryas drummondii*, in the Wrangell Mountains of Alaska. *Dryas* colonizes glacial moraines and spreads clonally to form distinct patches. Habitat subdivision occurs both on the patch scale and on the larger spatial scale of sites due to patchy successional patterns. *Itame* is attacked by three parasitoids: an ichneumonid wasp (*Campeletis* sp.), a braconid wasp (*Aleiodes* n. sp.), and the tachinid fly (*Phyrxe pecosensis*). I performed a large survey study at five distinct sites and censused *Itame* density and parasitism rates in 206 plant patches for 1–3 years. Parasitism rates varied with both plant patch size and isolation and also between sites, and the highest rates of overall parasitism were in the smallest patches. However, the effects of both small- and large-scale heterogeneity on parasitism differed for the three parasitoid species. There was weak evidence that *Itame* density was positively correlated with parasitism for the braconid and tachinid at the patch scale, but density effects differed for different patch sizes, patch isolations, and sites. At the site scale, there was no evidence of positive, but some indication of negative density-dependent parasitism. These patterns do not appear to be driven by negative interactions between the three parasitoid species, but reflect, rather, individual differences in habitat use and response to prey density. Finally, there was no

evidence that parasitism strongly impacted the population dynamics of *Itame*. These results demonstrate the importance of considering habitat pattern when examining spatial heterogeneity of parasitism and the impacts of parasitoids.

Key words Host-parasitoid interactions · Habitat patchiness · Spatial heterogeneity · Tritrophic interactions

Introduction

Much of the past work on parasitoid-prey systems has concentrated on examining the influence of prey density on parasitoid behavior and parasitism rates (Hassell 1978; Lessells 1985; Stiling 1987; Hassell and May 1988; Walde and Murdoch 1988; Pacala et al. 1990; Reeve 1990; Pacala and Hassell 1991; Jones et al. 1994). More recently, increasing attention has been given to tritrophic interactions, with emphasis on the effects of plant quality, phytochemistry, plant morphology, and plant community diversity (Price et al. 1980; Barbosa and Letourneau 1988; Craig 1994). However, little work has addressed how features of habitat structure such as plant patch size and dispersion impact parasitoid-prey interactions (but see Sheehan and Shelton 1989; Segarra-Carmona and Barbosa 1992; Cronin and Strong 1999). Given the recent identification of the importance of density-independent heterogeneity in parasitism in many systems (Hassell and Pacala 1990; Hassell et al. 1991; Pacala and Hassell 1991), study of the tritrophic effects of habitat structure provides an interesting and important avenue for research.

One of the most important factors influencing habitats for parasitoids and their prey are host plants (the ‘hosts’ of parasitoids are referred to as ‘prey’ throughout this paper to avoid confusion with ‘host plants’). Habitat structure can alter insect movement rates and the probability that patches will be discovered and therefore is likely to contribute to heterogeneity in parasitism

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(Hassell and Southwood 1978; Price et al. 1980; Maguire 1983; Bach 1984; Kareiva 1987; Sheehan and Shelton 1989; Cronin and Strong 1999). Thus, parasitoid behavior and parasitism rates will likely be influenced by a combination of prey attributes such as density and prey resource attributes such as abundance and dispersion. When considering parasitism within this tritrophic context, a number of predictions can be made about the distribution of parasitism among patches. Here I concentrate on three important predictions:

- (1) Rates of parasitism may increase in patches of higher prey density (direct density dependence) because parasitoids are attracted to, congregate in, or remain longer in higher-prey-density patches (Hassell 1978) as is predicted by optimal-foraging theory (Cook and Hubbard 1977; Hubbard and Cook 1978).
- (2) Rates of parasitism may decrease with increasing prey density (inverse density dependence). This could be due to a lack of aggregation in high-prey-density patches due to 'spreading the risk' behavior (Strong et al. 1990). On the other hand, it could occur despite aggregation in high-prey-density patches if this aggregation is countered by the effects of pseudointerference (Free et al. 1977; May 1978; Reeve and Murdoch 1985; Taylor 1993) or limitations imposed by handling time or egg availability (Lessells 1985; Stiling 1987; Taylor 1993), all of which decrease parasitoid efficiency in exploiting high prey densities.
- (3) Rates of parasitism may be linked to and increase with increasing prey resources (e.g., larger plant patch size) rather than prey density itself (Sheehan and Shelton 1989). This prediction arises as an extension of the resource concentration hypothesis (Root 1973) to parasitoids searching for the resource base of their prey. Thus, these parasitoids may be more likely to find or less likely to leave large or concentrated patches of such a resource (Sheehan and Shelton 1989) leading to higher rates of parasitism in these patch types.

While predictions 1 and 2 are clearly at odds with one another, prediction 3 could coincide with either, depending on the relationship between prey density and prey resources.

Support for all three of these predictions can be found in the literature. Studies examining the impacts of prey density on parasitism rates find that direct and indirect density dependence, as well as density independence, are all common (see Lessells 1985; Stiling 1987; Walde and Murdoch 1988 for reviews). There is also some indication that response to density may be sensitive to the spatial scale of investigation (Heads and Lawton 1983; Walde and Murdoch 1988). The few studies directly examining tritrophic impacts of prey resource abundance on parasitoid behavior or parasitism rates have found positive effects of prey resource on parasitism (Sheehan and Shelton 1989; Cappuccino 1992; Segarra-Carmona and Barbosa 1992). Furthermore, a number of research-

ers have shown that habitat subdivision can disrupt predator-prey interactions by impacting predators more than prey (Huffaker 1958; Kareiva 1987; Roland 1993; Kruess and Tschurutke 1994), suggesting that predators and parasitoids may accumulate in or more efficiently exploit prey in large habitat patches.

Here, I examine the interactions of *Itame andersoni* (Geometridae) (henceforth *Itame*), an insect herbivore, and its three parasitoid species living in a habitat composed of discrete plant patches. *Itame* inhabits patches of its early successional host plant, *Dryas drummondii* (Rosaceae) (henceforth *Dryas*), which forms an essentially two-dimensional habitat that naturally varies from small, clearly separated patches surrounded by rocks and gravel to extensive, continuous monocultures. Areas inhabited by *Dryas* are also subdivided on a larger spatial scale by river channels, later successional vegetation, or uncolonized moraine. This habitat subdivision provides an excellent opportunity to examine direct effects of habitat spatial structure as well as *Itame* density on parasitism rates and to compare these factors at two spatial scales.

I censused *Itame* population densities and determined parasitism rates in *Dryas* patches at several distinct sites over multiple years. I used these data to examine the effects of patch size, patch isolation, site, and *Itame* density on parasitism rates for each of the three parasitoid species. Because patterns of habitat use or responses to prey density could be driven by interactions among the parasitoids (e.g., direct interference, superparasitism), I looked for correlations between parasitism by the three species. Finally, I examined the impacts of parasitism on *Itame* populations. This study stands out because it simultaneously investigates prey density and habitat structure as sources of heterogeneity that may impact parasitism rates. Furthermore, it does this for three parasitoid species, thereby addressing the generality of effects in a very simple but natural system, consisting of a monophagous prey inhabiting a patchy monoculture of its host plant.

Materials and methods

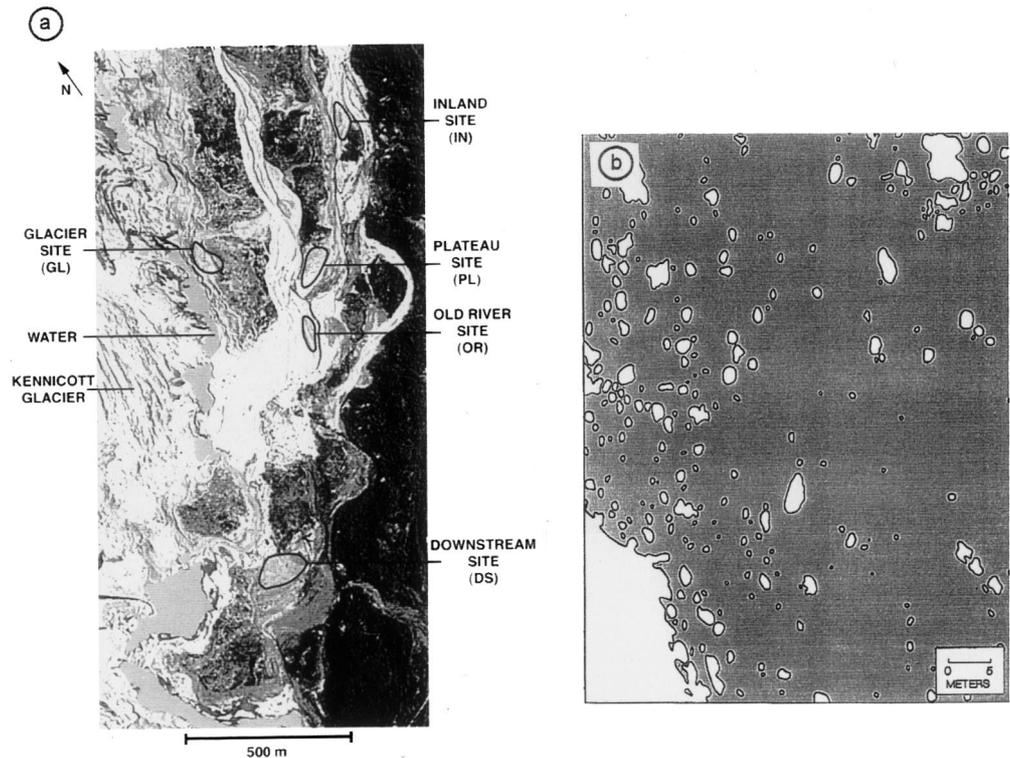
Natural history and study system

I conducted this research in the Wrangell Mountains near McCarthy, Alaska (61° N, 143° W). My studies were all confined to the east margins of the Kennicott Glacier (Fig. 1a).

The host plant, *Dryas*, is an early successional shrub that grows on glacial moraine and river bars. Its growth form is low and creeping with foliage height of approximately 5 cm. It forms distinct patches on gravel, rock, and silt substrates (see Fig. 1b for scale of patchiness). At later successional stages, these patches grow together and eventually form extensive mats which are then overgrown by later successional species. In many locations *Dryas* exists in an almost complete monoculture.

In this system, habitat subdivision not only occurs on the small patch-to-patch scale but also on a larger scale due to patchy successional patterns. The glacial retreat at the study site has left a landscape consisting of dry run-off channels interspersed with older vegetation 'islands.' The dry channels and lower benches tend

Fig. 1 **a** Study region and five survey sites (modified from aerial photograph taken by AeroMap U.S.). **b** Section of one site demonstrating scale of patchiness (*Dryas* patches are shown in white)



to harbor younger populations of *Dryas* than the older and higher 'island' areas. Thus there is a mosaic of very recent run-off channels with little or no *Dryas* (or other plant growth), older channels with young, patchily distributed *Dryas*, 'island' areas with older patchy and/or continuous growth of *Dryas*, and 'island' areas in later successional stages that are being taken over by shrubs and trees (Fig. 1a).

I. andersoni is univoltine. Caterpillars hatch from overwintering eggs in early to mid May shortly after snowmelt. All larval instars feed on the foliage of *D. drummondii*. *Itame* was the only abundant herbivore on *Dryas* at my study sites from 1990 to 1996 and appears to be a specialist on *Dryas* in this region. Fifth-instar caterpillars pupate under rocks or in the litter beneath *Dryas* patches in mid June to mid July. Adults emerge about 2 weeks after pupation. Eggs are laid singly in leaf litter, on foliage, and predominantly in gravel and rocks both under and surrounding *Dryas* patches.

I. andersoni is attacked by three parasitoids: an ichneumonid wasp (*Campeletis* sp.), a braconid wasp (*Aleiodes* n. sp.), and the tachinid fly, *Phyrxe pecosensis*, Townsend (specimens are deposited at the Cornell Entomology Collections). All of these parasitoids are solitary with only one adult emerging from an individual *Itame*. Host specificity for the two wasps is unknown. The tachinid is a generalist parasitoid with a wide host range over its own range (R. Hoebcke, personal communication), although there are no data on other hosts at my study site.

The two wasps oviposit internally in second- and possibly also third-instar larvae, while tachinids lay external and easily identifiable eggs on fifth-instar larvae. Braconids mummify caterpillars during the fifth instar. Mummies form on *Dryas* foliage, old inflorescence stalks, and rocks; braconids overwinter in the mummies and emerge the following year in late May to early June. Ichneumonid larvae emerge from fifth-instar *Itame* once they have entered a short period of prepupation inactivity at their pupation sites; larvae then spin silk cocoons and overwinter to emerge the following late May to early June. Tachinid larvae emerge from *Itame* pupae approximately 10 days after pupation. They pupate nearby and the adult flies emerge in late July to early August. The activities of the adults during the remainder of the year are presently unknown. Although multiple tachinid eggs may be laid on a

caterpillar, I never observed more than one individual successfully emerging from a host. On rare occasions I found wasps emerging from larvae that carried tachinid eggs, indicating that the tachinid engages in superparasitism. Because I cannot identify larvae parasitized by the wasps until mummification or larval emergence, I do not know whether the two wasp species also engage in superparasitism nor whether the tachinid is ever successful in its superparasitism.

A gregarious hyperparasitoid wasp attacks both the braconid and tachinid. However, the impact of hyperparasitism was not examined in this study because the hyperparasitoid appears to oviposit in braconid mummies or tachinid pupae, while I collected caterpillars. Thus hyperparasitoids never had access to the individuals that I reared. Other natural enemies of *Itame* include ants, spiders, ground beetles, and birds.

My studies were conducted at five sites along the east margin of the Kennicott Glacier during the summers of 1992–1994. Sites were chosen as areas where *Itame* occurred and were delineated by natural features (e.g., extent of *Dryas* growth, gravel banks, forested areas, and where patchy areas merged into regions of huge continuous *Dryas* mats) (Fig. 1a). When areas of the glacial margin were last seasonally flooded (due to spring run-off or glacial outburst floods) is not known and it is therefore difficult to determine the ages of my sites. However, data on when areas were last permanently flooded do exist and likely correlate well with the relative ages of *Dryas* sites (Rickman and Rosenkrans 1997). These data suggest the following hierarchy of site ages: DS (dry after 1937), PL (dry before 1957), IN (dried sometime in the period 1948–1960), OR (dry after 1957), and GL (lake at site in 1964).

Effects of habitat spatial structure and prey density on parasitism

Field methods

A survey study was used to examine relationships between plant patch size and isolation, *Itame* caterpillar densities, and parasitism rates by the three primary parasitoids. I followed patches of the host plant over multiple years to gain information on within-year

Table 1 The number of patches from which rearing data on parasitism were collected. Classifications are based on patch area in 1993 (for site designations, see Fig. 1)

Year	Site	Patch type					
		Small isolated	Small surrounded	Medium isolated	Medium surrounded	Large	Extra-large
1992	OR	1	2	3	4	4	–
	GL	2	5	5	17	9	10
1993	PL	6	4	6	4	6	4
	DS	4	1	4	6	3	2
	IN	3	3	3	7	6	6
	OR	3	4	6	7	6	–
	GL	7	7	11	15	10	10
1994	DS	0	2	2	6	6	5
	IN	3	5	4	6	6	6
	OR	4	4	8	8	6	–
	GL	7	12	10	13	10	6

and between-year patterns of population change and parasitism rates. Data are from patches at two sites for 1992, five sites for 1993, and four sites for 1994 (see Table 1). I chose patches on the basis of size and isolation categories. At each site I surveyed patches in four size categories based on their size in 1993 (small: $<0.30 \text{ m}^2$, medium: $0.30\text{--}1.56 \text{ m}^2$, large: $2.73\text{--}20 \text{ m}^2$, extra-large: $>150 \text{ m}^2$). Patch areas were estimated as ellipses based on their major and minor diameters. All patches surveyed in 1992 were measured that year. Patches added in 1993 were measured in 1993, and all patches were again measured in 1994. For those patches measured only in 1992 and 1994, 1993 areas were estimated as the average of the two areas. Mean size of large patches was $7.14 \pm 3.82 \text{ m}^2$ (mean \pm 1 SD).

Small- and medium-sized patches were further classified as either isolated or surrounded. To measure isolation, in 1994 I recorded distances to and areas of all other patches with an edge within 2 m of the edge of small and medium survey patches. The whole area of any patch whose edge was within this 2-m distance was included. I then summed the areas of these neighbors. Since a larger survey patch encompasses a larger area by this measurement, I divided summed neighbor areas by the area surveyed. This measure of isolation was used to classify patches into two categories (isolated $<0.20 \leq$ surrounded) separated at the median isolation value. Large and extra-large patches seldom occurred as isolated and were therefore all classified as surrounded.

I was unable to consider extra-large patches in their entirety because (1) they were so large, and (2) they did not always form many distinct patches at a site. Thus, at some sites, multiple $3 \times 3 \text{ m}$ plots were placed within extra-large patches and were used as units for investigation. Plots were subjectively spread in an even pattern among the extra-large patches available or across the area spanned by one extra-large patch.

Itame densities were measured each year when the majority of individuals at a site were fourth and fifth instars. Within both large patches and extra-large survey plots, three 0.25-m^2 quadrats were randomly chosen for censusing. Densities were measured by counting all individuals in a patch (for small and medium patches) or in each of the three 0.25-m^2 quadrats (for large and extra-large patches). Densities were calculated as the number of caterpillars per patch area in the year of the census for small and medium patches or as the average density of the three sampled quadrats for large and extra-large patches.

Each year, fifth-instar caterpillars, if present, were collected from each survey patch. In 1992, collection numbers varied widely (maximum=37). In 1993, a maximum of 15 caterpillars were collected from small and medium patches and a maximum of 10 from each quadrat in the large and extra-large patches. In 1994, a maximum of 15 were collected from each patch. In large and extra-large patches, if there were not five individuals suitable for collection in one quadrat, additional individuals were collected from other quadrats where available or from the patch as a whole. Collections from quadrats within large and extra-large patches were grouped for analysis.

Caterpillars were reared in petri dishes (≤ 5 per dish) at ambient temperature. They were fed field collected *Dryas* ad libitum. Caterpillars and pupae were usually checked every other day and dates of mummification and parasitoid emergence were recorded. In 1992 and 1993, all pupae of *Itame* and parasitoids were returned to their patches of origin.

Both pre- and post-pupation mortality (aside from that caused by parasitoids) were quite low in captive populations (e.g., for 1992: 2.5% of 966 caterpillars reared). In calculating the percentage of caterpillars parasitized or pupating, those individuals that died from unknown causes either before or after pupation or parasitoid emergence were removed from the analysis.

Sample sizes for parasitism data varied between patch types, sites, and years due both to growth of initially small patches into medium-sized patches and because some patches had no individuals suitable for collecting and rearing (Table 1).

Caveats

Many complications exist in the accurate measurement of rates of parasitism from field data (Van Driesche 1983). Estimates that only consider successful emergence of parasitoids will underestimate the actual mortality caused by parasitoids since some parasitism will kill the host without also resulting in successful parasitoid emergence. Although I found little evidence of this in the fifth instars I reared, it could be an important factor at earlier instars. Furthermore, if parasitism alters prey behavior, it may in turn alter the probability of the prey being found by the researcher or another predator (Van Driesche 1983). Although I cannot rule out behavioral changes, observations do not suggest that they were a major problem in my study system. Individuals parasitized by the ichneumonid and tachinid did not show any noticeably deviant behavior, while individuals carrying braconid parasitoids only became inactive about 24 h prior to mummification. Additionally, all three parasitoids were found at background levels in samples of caterpillars that had immigrated into extirpated patches (P. Doak, unpublished data) suggesting that movement behavior was neither increased nor decreased by parasitism. Finally, measured parasitism rates may also differ from actual rates due to the death of some parasitoid individuals through multi- or superparasitism.

A final concern with my sampling methods is that my measurements of prey density are for fifth-instar caterpillars while both wasps oviposit in second and possibly third instars. Therefore, I do not know the actual prey densities encountered by ovipositing wasps.

Analysis

I analyzed parasitism data using linear mixed models. For each parasitoid species alone and for the three species combined, I ex-

amined the effect of site, patch identity (nested within site), year, patch size, patch isolation, and caterpillar density on percent parasitism for a patch. Patch identity, site and all two-way interactions with site were treated as random effects in the models. I used PROC MIXED (SAS 1992) because it offers the most appropriate analysis for unbalanced data (C. McCulloch, personal communication). PROC MIXED provides traditional type III *F*-tests for fixed effects and restricted maximum likelihood estimates of the random effects (SAS Institute, technical report P-229). I used likelihood ratio tests to examine the significance of random effects. While likelihood ratio tests are inherently two-tailed, variance components should be tested as one-tailed. To adjust for this, I calculated a critical *P*-value for an α which is twice the desired α level (Stram and Lee 1994; C. McCulloch, personal communication).

Initial analyses examined significance of main effects, all two-way interactions and all variance components. Random effects estimated to be zero or found to be non-significant, as well as non-significant interaction terms were dropped from models. The results I present are for the reduced models. Scatterplots and residual plots were visually examined to judge the adequacy of model assumptions. Special attention was given to equalizing the variance of residuals with respect to the number of caterpillars reared from a patch, so that patches with small or large numbers reared did not exert an especially large influence on the analysis. Model assumptions were best met when percent parasitism for each parasitoid species was transformed to $1/(\% \text{ parasitism} + 0.5)$. Density was transformed to $\ln(\text{density} + 1)$.

Contrasts were computed to compare main effect means and the effect of density was examined for different patch types. Sequential Bonferroni corrections (Rice 1989) with experimentwise $\alpha = 0.05$ were used to guard against inflated type-I errors brought about by multiple, non-independent contrasts.

Interactions among parasitoids

Although very little is known about the biology of the parasitoid species studied, I could examine whether there was any evidence for interactions among them. If patterns of habitat use or responses to density were due to direct interference among the different parasitoid species, I would expect to find negative correlations between parasitism rates by the different species. However, negative correlations between species could also result from: (1) past interference which has led to the evolution of resource partitioning, (2) indirect interference, such as that for enemy-free space if the parasitoids share natural enemies, and (3) differences in parasitoid distribution, resulting from e.g., different habitat preferences, dispersal abilities, habitat-specific survival probabilities. I examined the data for negative correlations by performing pairwise Pearson correlations on percent parasitism by the three parasitoid species at the patch level. Analyses included only plant patches with ≥ 3 individuals reared. I also performed partial correlations correcting for the effects of site, patch size, patch isolation, and $\ln(\text{caterpillar density})$. A negative correlation in this analysis would rule out option 3 and indicate that some type of interference (current, past, or indirect) is likely occurring. Sequential Bonferroni corrections for multiple comparisons were computed for the three correlations calculated within each year.

Impact of parasitoids on *Itame* populations

The survey data described above were also used to examine the population-level impacts of parasitism on *Itame*. I first examined whether the parasitoids appeared capable of effecting population change by performing Pearson correlations between the change in density from one year to the next, $\ln(\text{Itame density year 2}/\text{density year 1})$, and the percent mortality in year 1 caused by each parasitoid species individually, as well as by all species combined. I did this analysis separately for the 49 patches at the OR and GL sites for which I had 1992–1993 data and the 126 patches (DS, IN, OR, and GL sites) for which I had data from the 1993–1994 transition. Sequential Bonferroni corrections were computed.

Table 2 Results of linear mixed-model analysis of percent parasitism by the ichneumonid wasp. Model: $1/(\% \text{ ichneumonid} + 0.5) = \text{constant} + \text{year} + \text{patch type} + \ln(\text{density} + 1) + \text{site} + \text{patch}(\text{site}) + (\text{site} * \text{year})$. Denominator degrees of freedom differ because non-significant random effects were dropped from the model

Fixed effects				
Source	<i>df</i>	<i>F</i>	<i>P</i>	
Year	2,4	5.30	0.0751	
Patch type	5,154	2.15	0.0627	
Density	1,154	0.00	0.9445	
Random effects				
Source	Estimate	SE	<i>G</i>	<i>P</i>
Site	0.0152	0.0153	24.58	<0.0005
Patch(site)	0.0205	0.0098	4.91	<0.0250
Site*year	0.0069	0.0072	3.98	<0.0500
Residual	0.0893	0.0102		

I further examined the influence of parasitism on *Itame* population change by comparing an ANCOVA model examining the influence of site, patch size, patch isolation, and $\ln(\text{density in year 1})$ on $\ln(\text{density year 2}/\text{density year 1})$ to a similar model including a term to correct for the percent of individuals surviving parasitism [$=\ln(\text{density year 1} \times \text{percent surviving parasitism})$] in place of $\ln(\text{density in year 1})$ to determine if including the effect of parasitism improved the model. I performed these tests separately for the 1992–1993 and 1993–1994 transitions.

Results

Effects of habitat spatial structure and prey density

Ichneumonid

An initial analysis of parasitism by the ichneumonid showed a significant patch size by isolation interaction. Because not all patch sizes occur as both surrounded and isolated, this interaction necessitated the combination of these two main effects into a new variable, 'patch type,' with six levels, so that least-squares means could be calculated.

Patch type had a marginally significant effect on percent parasitism by the ichneumonid wasp (Table 2) with a trend towards higher parasitism rates in larger patches (Fig. 2a). However, pairwise comparisons revealed no significant differences between individual patch types (Table 3). Parasitism differed among sites, and there was a significant site by year interaction (Table 2); however, despite fluctuations in parasitism rates between years, sites tended to retain their relative rankings (Fig. 3). Parasitism did not vary significantly with *Itame* density (Table 2).

Braconid

Patch size had a marginally significant effect on braconid parasitism with smaller patches displaying slightly higher parasitism rates (Table 4, Fig. 2b). Isolated patches tended to have higher parasitism than surrounded

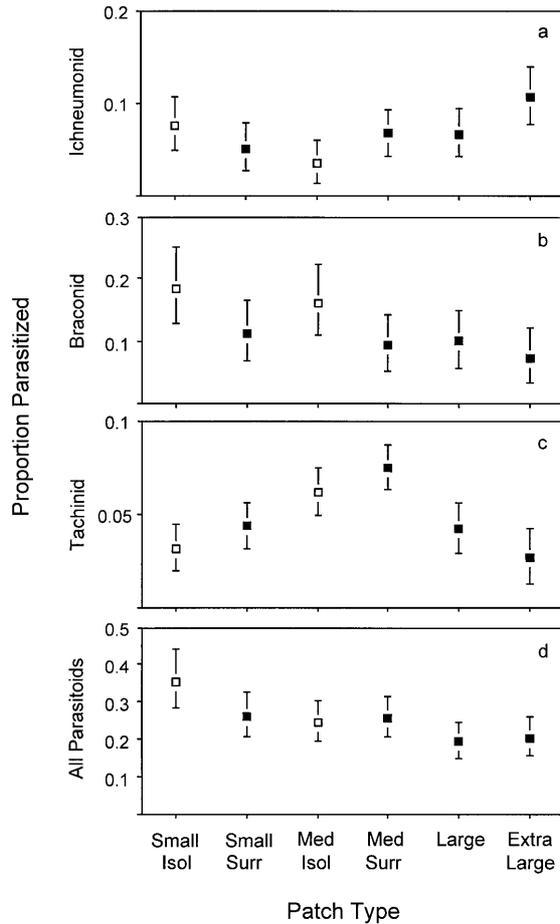
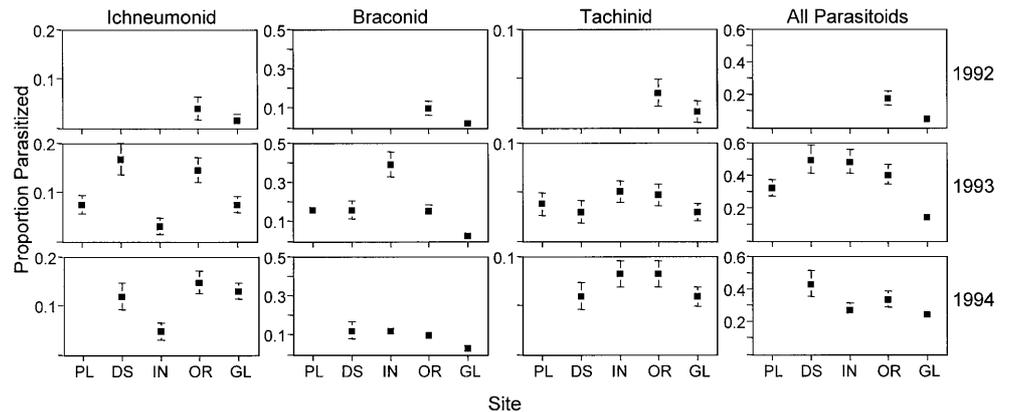


Fig. 2 Mean \pm 1 SE proportion parasitized (back-transformed least-squares means and best predicted values) from linear mixed models for the effect of patch type on the proportion of individuals parasitized. *Open squares* are isolated patches, *filled squares* are surrounded patches. The patch size by isolation interaction is not significant for the braconid or tachinid (*Isol* isolated, *Surr* surrounded as defined in the text)

patches although the main isolation effect was not significant while the site by isolation interaction was (Table 4); in all cases, isolated patches had higher rates of parasitism, but contrasts revealed no significant differences within sites. A significant site by year interaction (Table 4)

Fig. 3 Mean \pm 1 SE proportion parasitized (back-transformed best-predicted values from linear mixed models) by site and year



stemmed from the significantly higher parasitism at the IN site in 1993 compared to 1994 ($F_{1,4}=38.65$, $P=0.0034$) while the other sites did not significantly differ in parasitism rate between years (Fig. 3). In all cases parasitism showed a positive relationship with density; however, this relationship was not significant within sites or for all sites combined (Table 4).

Tachinid

Although rates of tachinid parasitism were very low in general, they did differ significantly between patch types, between years, and over densities (Table 5). Medium-sized patches had significantly higher rates of parasitism than extra-large patches (Table 3; Fig. 2c). Surrounded patches had higher parasitism than isolated patches (Fig. 2c, Table 5), and overall there was a positive effect of density on parasitism by the tachinid. However, examination of the significant isolation by density interaction revealed that the overall effect was largely driven by a positive and significant relationship of density and parasitism for the isolated patches ($t=-3.27$, $P=0.0012$), while surrounded patches showed a very weak and non-significant negative relationship with density. Parasitism by the tachinid also increased over the 3-year period but did not differ between sites (Fig. 3, Table 5).

A complication arises for the measurement of parasitism for the tachinid since collection of fifth instars occurred prior to the completion of all parasitism. This problem is most likely to contribute to site effects since *Itame* phenology differs between sites, and collection dates varied more between than within sites (Doak 1997). It is much less likely to contribute greatly to the differences observed between patch types and densities within sites.

Total parasitism

Examination of total parasitism can provide a better picture of how impacts of the three parasitoid species jointly influence *Itame* populations. Due to a significant in-

Table 3 Pairwise comparisons of percent parasitism by patch size for the braconid and for the tachinid, and patch type for the ichneumonid and for all parasitoids combined

Patch size comparison		Braconid (<i>df</i> =1,150)		Tachinid (<i>df</i> =1,350)	
		<i>F</i>	<i>P</i>	<i>F</i>	<i>P</i>
Small	Medium	0.85	0.3581	6.55	0.0109
Small	Large	3.12	0.0795	0.09	0.7632
Small	Extra-large	6.85	0.0098	0.49	0.4847
Medium	Large	1.36	0.2448	3.62	0.0580
Medium	Extra-large	4.63	0.0331	7.32	0.0072*
Large	Extra-large	1.05	0.3070	0.99	0.3208
		Ichneumonid (<i>df</i> =1,154)		Total parasitism (<i>df</i> =1,342)	
		<i>F</i>	<i>P</i>	<i>F</i>	<i>P</i>
Small surrounded	Medium surrounded	0.62	0.4333	2.55	0.1112
Small surrounded	Large	0.53	0.4674	13.34	0.0003*
Small surrounded	Extra-large	4.93	0.0278	9.15	0.0027*
Medium surrounded	Large	0.00	0.9841	7.30	0.0072*
Medium surrounded	Extra-large	2.99	0.0856	3.78	0.0526
Large	Extra-large	2.86	0.0930	0.18	0.6736
Small surrounded	Small isolated	1.01	0.3162	0.09	0.7591
Medium surrounded	Medium isolated	2.95	0.0880	5.79	0.0166

*Significantly different after sequential Bonferroni correction with experimentwise $\alpha=0.05$

Table 4 Results of linear mixed-model analysis of percent parasitism by the braconid wasp. Model: $1/(\% \text{braconid} + 0.5) = \text{constant} + \text{year} + \text{size} + \text{isolation} + \ln(\text{density} + 1) + \text{site} + \text{patch}(\text{site}) + (\text{site} \times \text{year}) + (\text{site} \times \text{isolation}) + [\text{site} \times \ln(\text{density} + 1)]$

Fixed effects				
Source	<i>df</i>	<i>F</i>	<i>P</i>	
Year	2,4	1.63	0.3041	
Size	3,150	2.51	0.0607	
Isolation	1,4	3.04	0.1561	
Density	1,4	2.58	0.1832	
Random effects				
Source	Estimate	SE	<i>G</i>	<i>P</i>
Site	0.0000			
Patch(site)	0.0271	0.0115	6.18	<0.0125
Site×year	0.0182	0.0129	17.31	<0.0005
Site×isolation	0.0161	0.0140	5.48	<0.0125
Site×density	0.0045	0.0040	9.29	<0.0025
Residual	0.0957	0.0113		

teraction of patch size and isolation, these two effects were combined into the variable 'patch type'. Overall parasitism varied significantly with patch type, and there was a significant density by patch type interaction (Table 6). Considering only surrounded patches, small patches had higher parasitism rates than large and extra-large patches and medium patches had higher parasitism than large patches (Table 3; Fig. 2d). These relationships appeared most similar to those for the braconid and thus may have been driven by braconid parasitism. There was a significant patch type by density interaction; however, I found no significant effect of density on parasitism either overall (Table 6) or within patch types. Total parasitism

differed significantly between sites and there was a significant site by year interaction (Table 6, Fig. 3).

Density effects at the site level

All of the previous analyses examined the effects of *Itame* density at the patch level. However, if population processes operate at a higher spatial scale such as sites, either due to mixing between patches by *Itame*, the parasitoids, or both, there may not be strong density effects at the smaller spatial scale of patches, while density may have an effect at the larger spatial scale. Plots of site-wide parasitism (total parasitized/total reared summed over all collections) versus mean site density (mean of all patch densities) (Fig. 4) do not indicate that parasitism was concentrated in places or at times of higher prey density. To the contrary, Pearson correlations indicated an overall negative relationship between density and total parasitism (Table 7).

Interactions among parasitoids

I found little evidence that interactions among the three parasitoid species significantly affect parasitism rates (Table 8). When effects of site, patch size, patch isolation, and caterpillar density were accounted for, there was a significant negative relationship between braconid and tachinid parasitism in 1993 (Table 8). This relationship was negative and marginally significant in 1994, but actually positive and non-significant in 1992 (Table 8). I

Table 5 Results of linear mixed-model analysis of percent parasitism by the tachinid fly. Model: $1/(\% \text{ tachinid} + 0.5) = \text{constant} + \text{year} + \text{size} + \text{isolation} + \ln(\text{density} + 1) + \text{isolation} \times \ln(\text{density} + 1) + \text{site}$

Fixed effects				
Source	df	F	P	
Year	2,350	7.31	0.0008	
Size	3,350	3.77	0.0110	
Isolation	1,350	11.40	0.0008	
Density	1,350	5.46	0.0201	
Isolation × density	1,350	11.03	0.0010	
Random effects				
Source	Estimate	SE	G	P
Site	0.0021	0.0024	2.65	<0.10
Residual	0.0793	0.0060		

Table 6 Results of linear mixed-model analysis of percent parasitism for all three parasitoids combined. Model: $1/(\% \text{ total parasitism} + 0.5) = \text{constant} + \text{year} + \text{patch type} + \ln(\text{density} + 1) + \text{patch type} \times \ln(\text{density} + 1) + \text{site} + \text{site} \times \text{year} + \text{site} \times \ln(\text{density} + 1)$

Fixed effects				
Source	df	F	P	
Year	2,4	4.14	0.1060	
Patch type	5,342	4.71	0.0004	
Density	1,342	0.29	0.5933	
Patch type × density	5,342	3.76	0.0025	
Random Effects				
Source	Estimate	SE	G	P
Site	0.0217	0.0238	12.63	<0.0005
Site × year	0.0186	0.0153	11.00	<0.0005
Residual	0.1521	0.0116		

found no significant correlations between parasitism by the ichneumonid and the other species (Table 8).

Impacts of parasitism on *Itame* populations

Parasitism rates on individual patches ranged from 0 to 100% for each of the three parasitoid species. Parasitism on a site level for a given year ranged from 3 to 32% for the ichneumonid, 2 to 47% for the braconid, and 1 to 15% for the tachinid. Total parasitism for sites ranged from 7 to 57%.

When all sites were considered together, there were no significant correlations between parasitism and population change for either the 1992–1993 or 1993–1994 transitions either for the parasitoid species alone or combined (Fig. 5). The strongest relationship was a positive correlation between total parasitism in 1993 and $\ln(\text{density}_{1994}/\text{density}_{1993})$, suggesting that caterpillar densities increased more in patches with greater parasitism; however, this relationship was not significant once sequential Bonferroni corrections were applied. Examination of the sites separately also failed to yield any significant correlations between parasitism and population change.

Comparison of the ANCOVAs explaining variation in $\ln(\text{density year 2}/\text{density year 1})$ showed that incorporating a correction for the percent surviving parasitism in

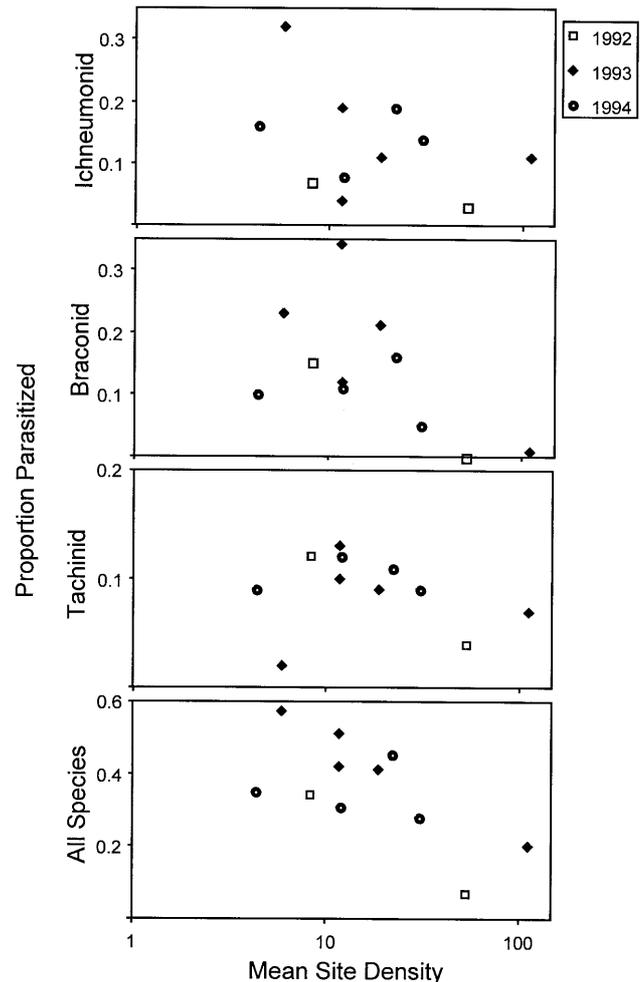


Fig. 4 Mean proportion of individuals parasitized per site for each year. Site densities were estimated as the mean of all patch densities for patches with parasitism data (plotted on a log scale). Pearson correlation and *P*-values are reported in Table 7

place of total *Itame* density actually led to poorer model fits (1992–1993: $r^2=0.702$ with $\ln(\text{density})$, $r^2=0.611$ with $\ln(\text{density} \times \% \text{ surviving})$; 1993–1994: $r^2=0.491$ with $\ln(\text{density})$, $r^2=0.387$ with $\ln(\text{density} \times \% \text{ surviving})$).

These analyses failed to provide any evidence that mortality caused by parasitoids plays a dominant role in stabilizing population change for *Itame*.

Discussion

Influence of *Itame* density on parasitism

At the scale of host plant patches, I find weak positive relationships between *Itame* density and parasitism for the braconid and the tachinid. These then translate into a weak overall relationship between total parasitism and prey density. A number of reviews of density effects on parasitism have found that in 48–66% of studies there is evidence of density dependence and in about half of these, there was direct rather than inverse density dependence (Lessells 1985; Stiling

Table 7 Pearson correlation coefficients, $r(P)$, between overall site densities and site-wide parasitism rates

	<i>n</i>	Ichneumonid	Braconid	Tachinid	All species
1993	5	-0.49 (0.40)	-0.74 (0.15)	+0.12 (0.87)	-0.97 (0.01*)
1994	4	+0.08 (0.92)	-0.11 (0.89)	+0.14 (0.86)	-0.01 (0.99)
1992–1994	11	-0.38 (0.25)	-0.57 (0.07)	-0.20 (0.56)	-0.67 (0.03)

*Significantly different after sequential Bonferroni correction with experimentwise $\alpha=0.05$

Table 8 Patch-level Pearson correlations, $r(P)$, between percentage parasitism by the different parasitoid species for all patches with ≥ 3 individuals reared

Full correlations						
	1992 (<i>n</i> =49)		1993 (<i>n</i> =118)		1994 (<i>n</i> =114)	
	Ichneumonid	Braconid	Ichneumonid	Braconid	Ichneumonid	Braconid
Braconid	-0.12 (0.47)		-0.13 (0.16)	-0.10 (0.29)		
Tachinid	-0.14 (0.38)	+0.22 (0.17)	-0.13 (0.16)	-0.03 (0.74)	-0.04 (0.71)	-0.14 (0.14)
Partial correlations correcting for effects of site, patch size, patch isolation, and ln(caterpillar density)						
	1992 (<i>n</i> =37)		1993 (<i>n</i> =118)		1994 (<i>n</i> =114)	
	Ichneumonid	Braconid	Ichneumonid	Braconid	Ichneumonid	Braconid
Braconid	-0.26 (0.13)		-0.05 (0.58)		-0.11 (0.24)	
Tachinid	-0.16 (0.35)	+0.17 (0.31)	-0.06 (0.001*)	-0.03 (0.001*)	+0.04 (0.67)	-0.17 (0.07)

*Significantly different after sequential Bonferroni correction with experimentwise $\alpha=0.05$

1987; Walde and Murdoch 1988). My results indicate possible weak direct density dependence. However, for the braconid, this relationship was only significant at one out of five sites, and for the tachinid, an opposite but non-significant relationship was actually seen for surrounded patches which probably compose the great majority of all host plant patches in most populations (personal observations).

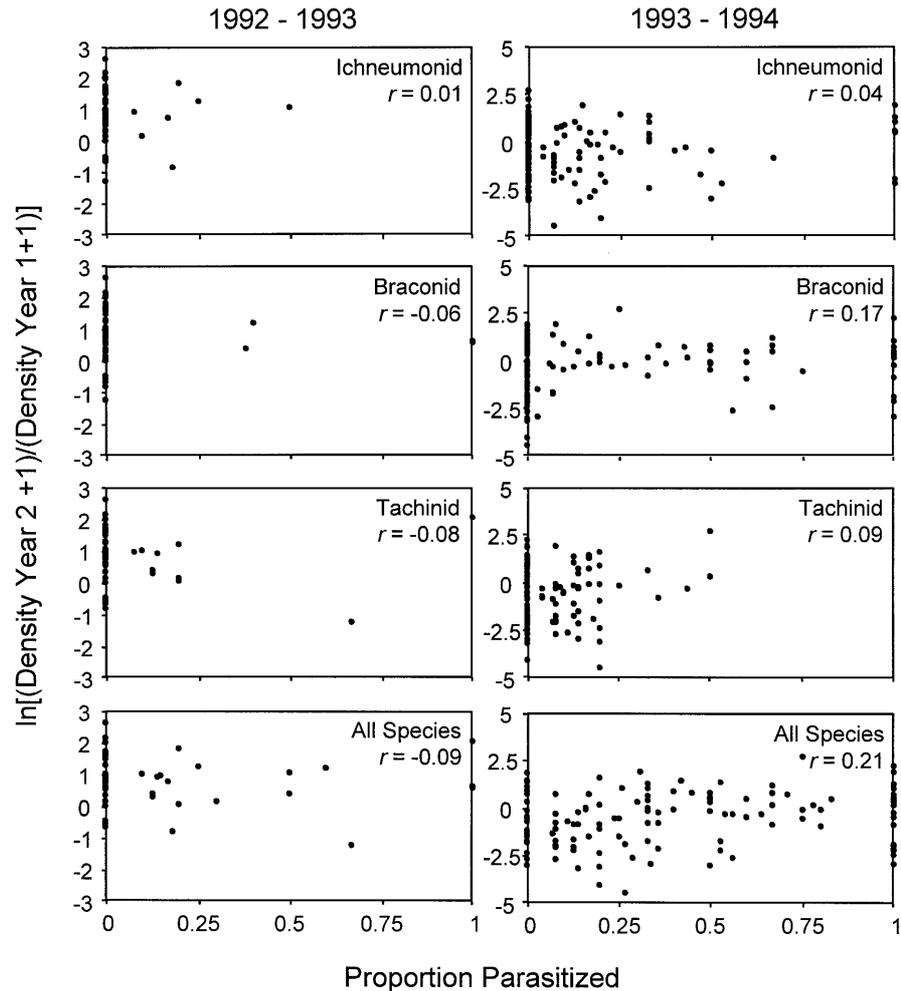
My examination of prey density effects at both the patch and site scale indicate that general conclusions about density effects can be greatly influenced by the choice of sampling regime. In particular, at the site scale, I find no indication of direct density dependence for any of the parasitoids and some evidence of inverse density dependence for the two wasp species and for all parasitism combined. In contrast, Walde and Murdoch (1988) found that studies conducted at larger spatial scales are more likely to find direct density dependence. They also reported that in the majority (17 of 21) of investigations where the same system was studied at two spatial scales, patterns of density dependence were consistent between scales. My results demonstrate that different sites as well as different sets of patch types may lead to differing conclusions about the density dependence of parasitism. Thus, in this system, density effects appear weak, are mediated by habitat type, and differ between spatial scales, allowing no clear generalities either within or between parasitoid species.

Influence of habitat structure on parasitism

My data suggest that plant patch size and isolation influence parasitism by all three species of parasitoid, although the patterns differ among species. Only the ichneumonid showed a tendency toward higher levels of parasitism in larger patches, while the braconid displayed the opposite trend, with the highest rates in small and isolated patches, and the tachinid had the highest rates of parasitism in medium-sized, surrounded patches (Fig. 2). These differences are of particular interest because all three species were responding to the same insect prey in the same simple habitat. Furthermore, I found the highest rates of overall parasitism in smaller plant patches (Fig. 2d).

Other researchers have also found direct relationships between parasitism and prey resources, but these studies have shown positive correlations between parasitism and resource quantity. Segarra-Carmona and Barbosa (1992) found that parasitism rates on a pod border were highest in larger plant patches and unrelated to prey insect abundance. Sheehan and Shelton (1989) found that leaving rates of an Aphidiid parasitoid were lower on larger host plant patches, perhaps explaining accumulation of parasitoids in these patch types. Cappuccino (1992) found parasitism rates positively related to the density of the resource of its prey (a gall insect) but not to prey density itself. These studies suggest that in cases where it is easier for a parasitoid to find the resource of its prey than the prey itself, parasitoids may accumulate in larger resource patches (Sheehan and Shelton 1989; Cappuccino 1992).

Fig. 5 The relationship between the proportion of individuals parasitized by the ichneumonid, the braconid, the tachinid, and all parasitoids combined and the proportional change in density from one year to the next (r values are for Pearson correlations)



In my system, larger plant patches do not correlate with higher *Itame* density and thus do not provide good targets for parasitoids seeking *Itame*. Medium-sized patches actually harbor the highest *Itame* densities (Doak, in press). While cueing in on medium-sized patches might be a good way to find *Itame*, only the tachinid showed higher levels of parasitism in these patches. Although my results do not support the proposed general pattern of parasitoid accumulation in larger resource patches (Price et al. 1980; Sheehan and Shelton 1989; Cappuccino 1992), or the concentration of parasitism in patch types most likely to harbor high *Itame* densities (Fig. 2), they do agree with other studies in pointing to the importance of direct influences of host plant patch size on parasitoids and parasitism.

Patch isolation has contradictory impacts on parasitism by the different parasitoid species; however, it appears that in the majority of cases, the trend is for small isolated patches to suffer higher parasitism than small surrounded patches (Fig. 2). One intriguing possibility is that the wasps may exhibit an optimal foraging strategy where oviposition effort is positively correlated with travel time (see Cronin and Strong 1999). The clear exception to this pattern is the tachinid which displays higher parasitism rates in surrounded patches. Two types

of parasitoid possibly exist in this system: those that disperse widely and adjust foraging behavior to foraging costs, and those that disperse less widely and therefore seldom encounter isolated patches.

These findings could result from interactions between the parasitoid species rather than responses to habitat; however, I did not find strong evidence for this (Table 8). When the partial correlations are considered, there is evidence of a negative association between the tachinid and braconid (Table 8b), suggesting the existence of some type of interference (present, past, or indirect). However, this relationship only existed in 1 out of 3 years, suggesting that consistent patterns of parasitism with habitat type cannot be explained by this association alone. Furthermore, the lack of correlation between ichneumonid parasitism and that by either of the other species suggests that it was responding to habitat variables rather than other parasitoid species.

My research does not address parasitoid behavior and therefore cannot sort out actual responses to habitat structure but only the results of it. Related to this is the fact that parasitoid responses may actually be to correlates of plant patch size and isolation. Patch size is positively correlated with age (Doak 1997), and patches may have characteristics (e.g., water stress, phytochemicals)

other than size that trigger parasitoid behavior (see Price et al. 1980; Barbosa and Letourneau 1988). Results of this observational study are unable to disentangle effects of habitat structure from strongly correlated factors.

The fact that parasitism by both the ichneumonid and braconid was significantly different between sites coupled with a lack of direct density dependence at the site scale suggests that aspects of sites other than prey density are highly likely to affect parasitism. Although environmental variability is often thought to influence species interactions, the variability considered is usually much greater than that which exists between my sites which all consist of the same simple plant community and are all less than 2 km from one another. Possible site effects in this system are proximity to other habitats with alternative prey (for generalist parasitoids) or food sources, more favorable microhabitat, a greater proportion of preferred habitat type, or differential impacts of mortality agents acting on the parasitoids.

Impacts of parasitism on *Itame* populations

In this system it appears that the three parasitoids of *Itame* exert little if any regulating force. Regulation of *Itame* populations may be through other factors such as intraspecific competition and resource limitation (Doak, in press), climatic variables, and/or action by natural enemies other than parasitoids. Parasitoid species may be effective at moderating population growth under some but not all conditions; this is suggested by the relatively high levels of parasitism at some low-density sites (especially DS) but low levels at the highest-density site. Despite the overwhelming similarity between sites, some sites could escape control through the inability of parasitoids to respond to high *Itame* densities or poorer conditions for parasitoid survival. Parasitoids may also have a stabilizing effect despite low parasitism rates, if parasitism is strongly aggregated (Hassel et al. 1991).

Conclusions

Whereas most theoretical work focuses on the interactions between parasitoids and their prey ignoring tritrophic interactions, my work indicates that habitat structure is likely important in influencing heterogeneity of parasitism rates over space. Clearly this research fails to give any general support to the three predictions posed earlier. Rather, I find the effects of prey density on parasitism rates to vary between species and to be mediated by habitat structure and scale of investigation even within species. I further find that only one (the ichneumonid) of the three parasitoids shows any tendency towards concentrating parasitism in larger habitat patches (supporting the resource concentration hypothesis). Overall parasitism rates are actually highest in small habitat patches, indicating that habitat patchiness may impact *Itame* more strongly than its parasitoids.

These results indicate that both the distribution and scale of sampling effort is likely to qualitatively alter conclusions about the relationship between prey density and parasitism. Sampling over a range of prey densities may not be adequate to illuminate a general pattern for a system. Rather, sampling over a variety of patch sizes and dispersions as well as in many sites is likely necessary to elucidate general patterns, if in fact these exist.

My work also suggests that it will be hard to generalize about parasitoid responses to habitats. I find different responses for three parasitoid species despite the fact that each is responding to the same prey species in the same, simple habitat. This will make it difficult to connect parasitoid-prey models to measurement of real habitat pattern without detailed data for every parasitoid-prey pair. Although parasitoid-prey theory has largely ignored specific effects of habitat structure, these effects may be critical to our understanding of many parasitoid-prey interactions.

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