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Coexistence of specialist parasitoids with host refuges in the laboratory and the dynamics of spatial heterogeneity in attack rate

Eric E. Porter and Bradford A. Hawkins

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There is a well documented relationship between parasitoid species assemblage size and host feeding niche. Parasitoid assemblage size peaks on hosts thought to have intermediate levels of physical refuge. We examined the influence of refuges on parasitoid coexistence using pairs of specialist parasitoids in a controlled laboratory environment. Using physical barriers we excluded parasitoids from 0, 25, 50 or 75% of the hosts to simulate host refuge. We found no evidence that host refuges can promote parasitoid coexistence in a simplified laboratory environment. Results were similar whether pairs of parasitoid species were competitively disparate or competitively similar. Our results suggest that spatial heterogeneity in parasitoid attack rate was not sufficient to maintain parasitoid coexistence regardless of host refuge, and we argue that the level of spatial heterogeneity necessary to promote coexistence is rare in nature. We conclude that in most systems the coexistence of specialist parasitoids cannot be explained by a host refuge effect.

E. E. Porter and B. A. Hawkins, Dept of Ecology and Evolutionary Biology, Univ. of California, Irvine, CA 92697, USA. Present address for EEP: Dept of Zoology, Miami Univ., Oxford, OH 45056, USA (portere@muohio.edu).

Parasitoids are one of the most biologically diverse groups of organisms (Lasalle and Gauld 1993, Godfray 1994), yet community ecologists are just beginning to understand the patterns of diversity and what factors are involved in maintaining parasitoid diversity (Hawkins and Sheehan 1994). To date, the most robust pattern identified is the relationship between parasitoid diversity and host feeding niche. Based on published accounts of British insect communities, Hawkins and Lawton (1987) described the relationship between host feeding niche and parasitoid diversity, defined here as the number of parasitoid species that attack a particular host species. They argued that feeding niche measures the extent of host concealment, a form of host refuge. By this definition, external feeders such as folivorous caterpillars have the least refuge and root feeders have the most, and parasitoid diversity peaks on hosts with intermediate refuge levels, such as leaf miners and gall makers. As an example, some gall maker parasitoids can only attack relatively small galls because they are limited by ovipositor length, leaving larger galls completely protected (Weis and Abrahamson 1985, Price and Clancy 1986). The relationship between parasitoid assemblage size and host feeding niche found in Britain was confirmed in a data set comprising more than 2000 host species from around the world (Hawkins 1994).

Hochberg and Hawkins (1992, 1993) developed a mathematical model to explore mechanisms that may explain the relationship between host feeding niche and parasitoid diversity, focusing on the presumed relationship between host feeding niche and refuge. The theory suggested that intermediate refuge levels promote parasitoid diversity by maintaining sufficient host popula-

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tion densities to sustain large numbers of parasitoids. If there is too little refuge, parasitoids can reduce host population densities to very low levels, thereby limiting the supply of hosts available for parasitoid population growth. At the other extreme, high refuge levels limit parasitoid diversity by exposing too few hosts to sustain parasitoid populations. Thus, the model predicts parasitoid diversity patterns of the same shape and magnitude as found in the empirical data. This theoretical framework was subsequently used as a basis for theoretical investigations into optimal use of parasitoids as biological control agents (Hawkins et al. 1993) and the evolution of host refuges (Hochberg and Holt 1995, Hochberg 1997).

To date, research on refuge theory has been restricted to correlative studies and theory. Clearly, theoretical work has advanced more rapidly than experimental tests of the models' assumptions. It is impractical to manipulate the feeding biology and therefore refuge of individual insects in the field, which makes field experiments on host refuges difficult. On the other hand, refuges can be manipulated in the laboratory simply by preventing parasitoid access to different proportions of host populations. We established a laboratory system in which the level of host refuge is manipulated using physical barriers that exclude hosts from potential parasitism while other sources of variability are minimized. Using this system, we examine the assumptions of refuge theory without confounding factors such as environmental variability and host phylogeny. Here we report the results of two experiments designed to test the conclusions of the theory for specialist parasitoids. For each experiment we tracked the population dynamics of two parasitoid species and one host species. The experiments differed mainly in the competitive disparity between the parasitoid species.

According to refuge theory, whereas generalist parasitoids coexist with minimal spatial heterogeneity in attack rate among population patches, coexistence of specialist parasitoids requires a high degree of spatial heterogeneity. Spatial heterogeneity is commonly used as a stabilizing parameter in host–parasitoid models (May 1978, Pacala et al. 1990, Hassell et al. 1991). This type of heterogeneity can be measured in two ways. First, one can directly measure the coefficient of variation in percent parasitism among patches (CV^2). It is this variation in relative risk of parasitism among patches that determines stability in models that assume spatial heterogeneity (Hassell 2000). Second, one can measure the coefficient of variation in parasitoid density among patches (CV_p^2). The latter measure is more difficult to determine because it requires maximum likelihood estimation of parameters, unless one has observations of parasitoid activity in each patch (Pacala and Hassell 1991, Reeve et al. 1994), and it is a less complete estimate of spatial heterogeneity (Taylor 1993). Nonetheless, workers often estimate CV_p^2 because its reciprocal is the clumping parameter (k) that is used as the measure of aggregation in mathematical models. It has been suggested that host–parasitoid dynamics will be stable if $CV_p^2 > 1$ (May 1978, Hassell et al. 1991), and most estimates of spatial heterogeneity are reported in this context. The relationship between CV^2 and CV_p^2 depends on the assumptions regarding the distribution of parasitoid attack rates within patches (Ives 1995, Gross and Ives 1999).

It is not obvious that the necessary conditions for coexistence in specialist refuge models are common in nature. The models require a reduction in interspecific competition through any mechanism (Hochberg and Hawkins 1993). Although they mention other potentially important mechanisms, in their models Hochberg and Hawkins only explored the effect of increased spatial heterogeneity, which leaves more hosts available for parasitism and reduces interspecific competition. They used the form of spatial heterogeneity in their models that is commonly used to model single host-parasitoid dynamics. Our arguments focus on spatial heterogeneity as the primary mechanism for reduced interspecific competition and leave other mechanisms for further work. In order for spatial heterogeneity to stabilize refuge models for specialist parasitoids CV^2 must be greater than one, which is rare among published field and laboratory measurements to date (Pacala and Hassell 1991). Also, the models assume that spatial heterogeneity is constant regardless of host or parasitoid density. Reeve et al. (1994) found no relationship between spatial heterogeneity and either host density or parasitoid density in a field study. In contrast, Tregenza et al. (1996) and Visser et al. (1999) found negative relationships between spatial heterogeneity and parasitoid density in separate laboratory experiments. Further, Lynch (1998) questioned the assumption of constant spatial heterogeneity and showed that the stability of host–parasitoid models can be altered if spatial heterogeneity is not constant. Because of the potentially crucial link between spatial heterogeneity and the coexistence of specialized parasitoids in refuge theory, we also counted the number of parasitoids and hosts that emerged from each vial (patch) in all replicates. These data allowed us to identify the relationships between CV^2 and a number of population parameters, including percent parasitism, average number of parasitoids per patch, and average number of hosts per patch. Using these relationships we tested the common assumption that spatial heterogeneity is invariant with respect to host and parasitoid density.

Methods

Experimental organisms

The host species for all experiments was the pomace fly,

Drosophila melanogaster. Fly stocks were obtained from Dr. Laurence Mueller (Univ. of California, Irvine). They had been cultured under laboratory conditions without substantial inbreeding for more than 10 years. Stock flies were reared in our laboratory from 1997 through the initiation of the first experiment (September 1999). These flies typically develop from egg to adult in 9–16 d. The stocks showed no ability to resist parasitism even when selected for increased encapsulation levels (unpubl.), although other *D. melanogaster* populations have evolved resistance in controlled environments (Fellowes et al. 1998).

The parasitoid wasps *Asobara persimilis* (Hymenoptera: Braconidae), *Leptopolina boulardi* and *Leptopolina heterotoma* (Hymenoptera: Eucoilidae) were maintained as stocks in our laboratory for at least 1 year (12 or more generations) prior to all experiments. Dr. Peter Chabora (Queens College, City Univ. of New York) provided the *L. boulardi* and *L. heterotoma* strains. Dr. Jaques van Alphen (Univ. of Leiden, the Netherlands) provided the *A. persimilis* strain. All parasitoids used in these experiments oviposit in 2nd to 3rd instar hosts and emerge from host pupae. Typical generation times in the laboratory range from 18 to 27 d, depending on the species and temperature. These species are relatively well studied and have been used in a number of laboratory experiments (Carton et al. 1976, van Strien-van Liempt and van Alphen 1981).

Refuge experiments

Two separate experiments were conducted. For both experiments host refuges were fixed at 0%, 25%, 50% and 75%. In the first experiment, the parasitoids *Asobara persimilis* and *Leptopolina boulardi* were paired together in communities with the host. *L. boulardi* had a distinct competitive advantage because *A. persimilis* emerges earlier than *L. boulardi* and has higher mortality by the time they are allowed to oviposit. The second experiment paired *L. heterotoma* and *L. boulardi*. The congeneric parasitoids were expected to have similar competitive abilities, and there were no apparent life history characteristics suggesting a strong competitive disparity. By testing different parasitoid combinations, effects of differences in host use resulting from differences in parasitoid biology could be identified. Refuge theory does not explicitly account for the magnitude of differences in competitive abilities among parasitoid species.

We expected to record evidence of coexistence in some refuge treatments if the assumptions of refuge theory were correct. Further, refuge theory predicts maximum coexistence in the intermediate refuge level (50%). We used the number of generations that both parasitoids coexisted and the stability of population dynamics for the less abundant parasitoid species as measures of the refuge effect.

Experimental communities were set up within plexiglass cages measuring 20 cm wide, 15 cm tall, and 25 cm deep. Two cages were used for each replicate community. One cage contained all of the adult flies that emerged from the previous generation and the other contained adult parasitoids (both species) that emerged from the previous generation. At the beginning of every generation 8 vials were placed into each fly cage. Vials were 10 cm tall and 3.5 cm in diameter and filled with 20 ml of host medium, a mixture of water, sucrose, brewers yeast and agar. Typically, no more that 350 insects successfully emerged from each vial. For the experimental treatments some vials were designated refuge vials. These vials were never exposed to parasitoids. Only host flies could emerge from refuge vials. The remaining vials were exposed to parasitoid adults for 24 h while host larvae were typically in the 2nd instar.

Refuge theory assumes host self-limitation, which was ensured in this system. During the final larval instar, *D. melanogaster* crawl up the sides of vials and pupate. Eight days after eggs were collected, the host diet was removed. The base of each vial was removed and replaced with 2 sheets of wax paper. Eight days after egg collection, we removed the wax paper and the remaining food, and we inserted agar and clean wax paper. Therefore, only flies that pupated by day 8 successfully emerged as adults (either flies or parasitoids). Ultimately, the number of pupation sites within vials limited the number of hosts (and parasitoids) that could emerge from each vial.

Four refuge treatments were used for both experiments. Eight exposed vials were used for 0% refuge treatments, 6 exposed vials and 2 refuge vials for 25% refuge, 4 exposed vials and 4 refuge vials for 50% refuge and 2 exposed vials and 6 refuge vials for 75% refuge. There were 3 replicates of each refuge treatment in the *A. persimilis–L. boulardi* experiment and 5 replicates of each refuge treatment in the *L. heterotoma–L. boulardi* experiment. Parasitism rates were allowed to reach high levels in an attempt to hasten identification of the dynamics of the interactions.

To determine whether the refuge treatment had any significant effect on duration of coexistence, one-way, fixed model analyses of variance were performed for each experiment. A simple effect of refuge does not in itself imply that refuge leads to parasitoid coexistence. It is also important to track the dynamics of the individual parasitoid species for signs of stabilizing dynamics. Because refuges were likely to allow the competitively superior parasitoid species to survive indefinitely, we were only interested in the dynamics of the inferior competitor. The population trajectories of

the inferior competitor were clear in every case, and time series analyses were not performed.

Experimental protocols

Initially, each community was stocked with 8 vials containing ca 200 2nd instar *D. melanogaster* and 17 adults (12 females and 5 males) of each parasitoid species. The vials were cleared of all parasitoids and removed from cages after 24 h. After 8 d, the diet in each vial was replaced with agar, and fresh host diet was placed into the host cages every other day until the hosts were allowed to oviposit into fresh vials. For the *A. persimilis–L. boulardi* experiment, the number of adult flies emerging from each vial was recorded daily from day 9 to 16, and all flies were put into new population cages. For the *L. heterotoma–L. boulardi* experiment, fly populations were estimated by counting the number of empty pupal cases in each vial at day 16. For both experiments, parasitoid abundance per vial was estimated by counting the number of healthy pupal cases at day 16. Once all flies had emerged, the exposed vials were placed into separate population cages for parasitoid emergence. On days 28 and 29 hosts were given fresh yeast and food in order to increase egg deposition. On day 30 fresh vials with diet and a drop of fresh yeast (in solution with water and acetic acid) were added to the host cages for oviposition and removed 24 h later. After 48 h, the exposed vials were placed into parasitoid cages for 24 h to allow parasitoids to oviposit. Replicates were terminated when the population of any species reached zero females.

Spatial heterogeneity and its correlates

Spatial heterogeneity was measured every generation in all replicates as the coefficient of variation squared (CV^2), which was calculated as: (variance in attack rate among exposed vials)/(mean attack rate for exposed vials)^2. Two measures of host density were collected. First, we measured the number of adult hosts that emerged from the previous generation, which we assume was correlated to the total number of eggs laid in exposed vials. This is not necessarily a good determinant of the number of larvae available for parasitism because many larvae failed to develop due to intraspecific competition. Second, we counted the total number of apparently healthy pupae that attached to the sides of exposed vials. Parasitoid density was measured as the total number of parasitoid adults that emerged from the previous generation. Neither estimate based on the previous generation's adult density accounted for mortality before oviposition. The number of parasitoids per host was estimated from the number of adults that emerged in the previous generation. Finally, percent parasitism was estimated as the number of parasitoid pupae per vial/total pupae per vial. Because estimates of parasitoid density per vial were based on pupal number, it was not possible to distinguish between the parasitoid species.

Using simple linear regression, we identified the relationships between CV^2 and both estimates of host density, parasitoids/host, parasitoid density and average percent parasitism. We also identified the relationships between average percent parasitism and both estimates of host density, parasitoids per host and parasitoid density. The data for the two experiments were pooled for the spatial heterogeneity analyses because the relationships were similar for both. For all analyses, CV^2, total pupae, parasitoids/host and parasitoid density were $\log_e$ transformed and percent parasitism was arcsine-transformed. Regressions were performed using the data from individual refuge treatments and pooled across treatments. The refuge treatment was likely to affect spatial heterogeneity, because the number of patches depended on the number of exposed vials: 8 for 0% refuge, 6 for 25% refuge, 4 for 50% refuge and 2 for 75% refuge.

Results

There was no effect of refuge on the duration of parasitoid coexistence for either parasitoid combination: *L. boulardi* and *A. persimilis* ($F_{3,11} = 2.246$, $P = 0.160$, Fig. 1) or *L. boulardi* and *L. heterotoma* ($F_{3,19} = 1.628$, $P = 0.223$, Fig. 2). Also, there was no evidence to suggest that two parasitoid species could persist in the system under any host refuge treatment. In all trials either the hosts went extinct (0% refuge

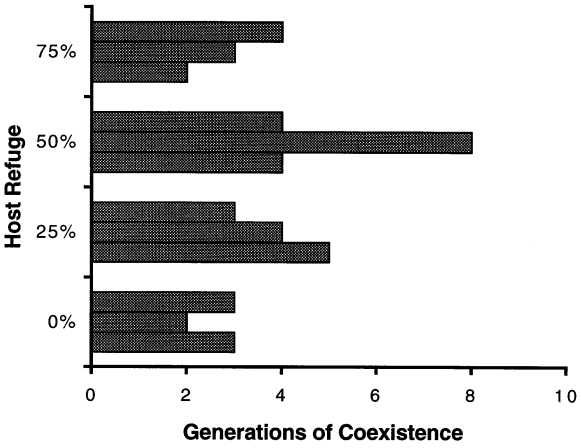

Fig. 1. Duration of coexistence under different host refuge levels for the parasitoids *Asobara persimilis* and *Leptopolina boulardi*. In this experiment *L. boulardi* was the competitively superior species.

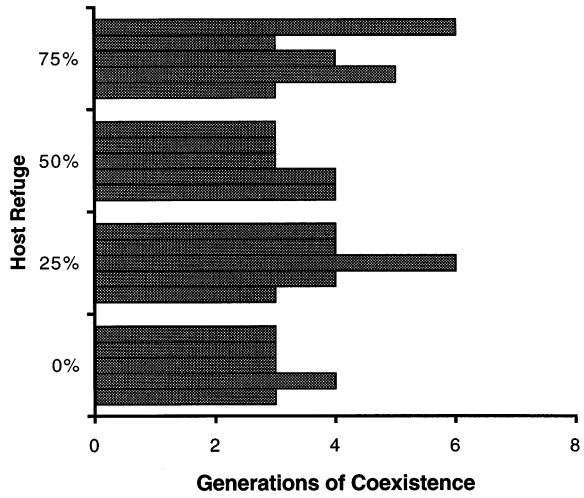

Fig. 2. Duration of coexistence under different host refuge levels for the parasitoids *Leptopolina heterotoma* and *Leptopolina boulardi*.

only) or *L. boulardi* was the only parasitoid species to survive (e.g. Fig. 3 and 4). In nearly every case the density of the weaker competitor (*A. persimilis* or *L. heterotoma*) peaked in the 2nd or 3rd generation and then rapidly declined to zero. The sole exception was the B replicate of the 50% *A. persimilis–L. boulardi* experiment. In this case *A. persimilis* competed effectively until the 6th generation, when a population explosion in *L. boulardi* eventually drove *A. persimilis* to extinction (Fig. 3). In this replicate, both fly and *L. boulardi* density were unusually low until the 5th generation.

CV^2 was not constant throughout the experiments. Table 1 shows the variation of CV^2 explained with simple linear regressions by both estimates of fly density, parasitoid density, the number of parasitoids per fly, and percent parasitism. Percent parasitism explained the most variation in CV^2 ($R^2 = 0.675$; Fig. 5) indicating that spatial heterogeneity was strongly influenced by average percent parasitism. Table 2 shows the variation of percent parasitism explained with simple linear regressions by fly density, parasitoid density, and the number of parasitoids per fly. Parasitoid density explained the most variation in percent parasitism ($R^2 = 0.462$; Fig. 6).

Discussion

We found no evidence that host refuges facilitate specialist parasitoid coexistence. The parasitoid species that went extinct showed extreme drops in population size after an initial population increase, suggesting very unstable dynamics under the experimental conditions. Further, there was no obvious effect of competitive ability in the experiments. The inferior competitor quickly went extinct regardless of the difference of magnitude in competitive abilities. It is unlikely that any pair of parasitoid species would be able to coexist

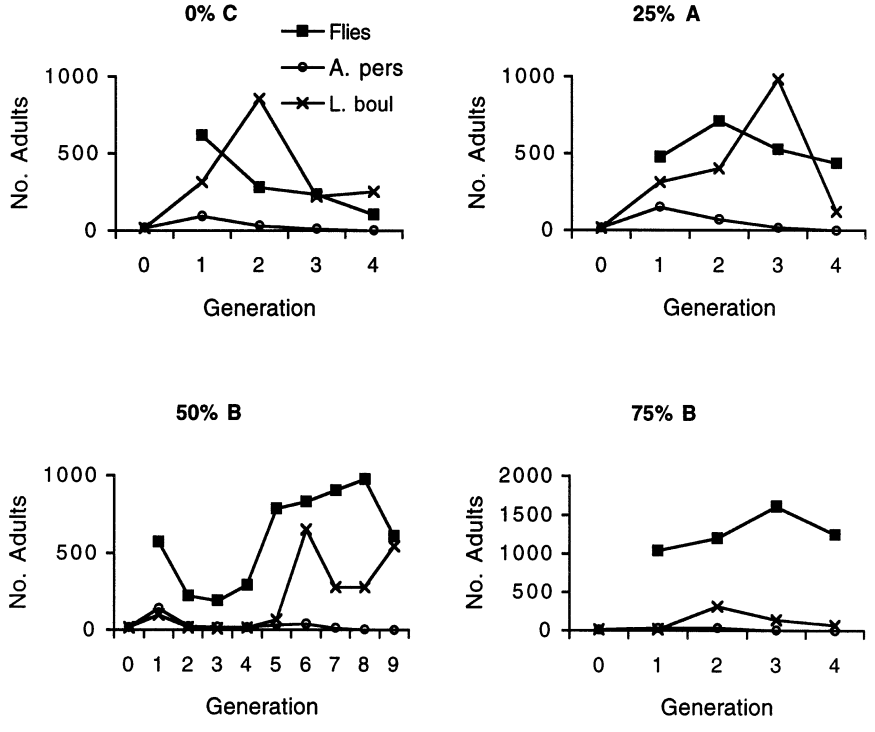

Fig. 3. Examples of dynamics for the 4 refuge treatments in the *A. persimilis–L. boulardi* experiment. Letters after the refuge level indicate specific replicate represented.

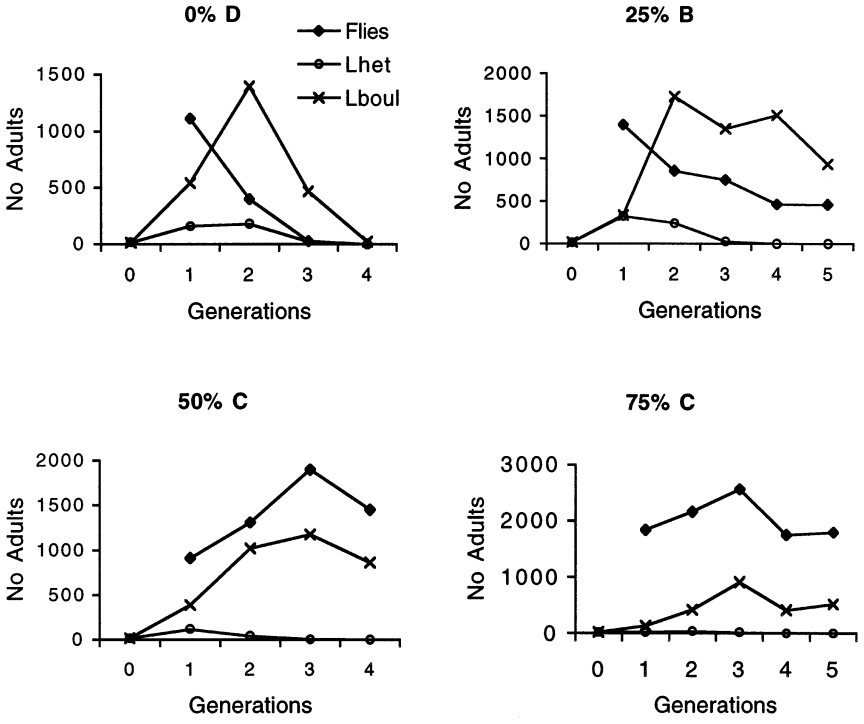

Fig. 4. Examples of dynamics for the 4 refuge treatments in the *L. heterotoma–L. boulardi* experiment. Letters after the refuge level indicate specific replicate represented.

in the laboratory environment described here. Clearly, at least one of the assumptions of the refuge models was not satisfied in the experiment.

The CV^2 for percent parasitism among vials was consistently low throughout the experiment. Indeed, the experiment was not set up to encourage high CV^2.

Table 1. The relationships between the spatial heterogeneity (ln CV^2) and host density, exposed hosts, ln (parasitoids/host), ln (parasitoid density), and arcsin sqrt (percent parasitism). For each treatment, we list number of replicates (N), slope of relationship, variance explained (R^2), and P-value. The data are pooled across refuge experiments.

Factor	Refuge	N	Slope	R^2	P
Host density	All	145	−0.001	0.068	0.002
	0%	30	0.001	0.134	0.046
	25%	38	−0.001	0.013	0.504
	50%	40	−0.003	0.439	<0.001
	75%	37	−0.136	0.136	0.025
Exposed hosts	All	129	−0.007	0.007	0.351
	0%	30	−0.001	0.042	0.275
	25%	32	−0.004	0.269	0.002
	50%	35	−0.001	0.033	0.294
	75%	32	0.001	0.011	0.569
Ln (parasitoid/host)	All	145	−0.592	0.121	<0.001
	0%	30	−0.434	0.253	0.005
	25%	38	−0.847	0.251	0.001
	50%	40	−1.238	0.330	<0.001
	75%	37	−2.207	0.193	0.007
Ln (parasitoid density)	All	145	−1.064	0.294	<0.001
	0%	30	−0.948	0.470	<0.001
	25%	38	−1.127	0.369	<0.001
	50%	40	−1.153	0.474	<0.001
	75%	37	−1.391	0.209	0.004
Arcsin sqrt (percent parasitism)	All	145	−9.291	0.675	<0.001
	0%	30	−6.677	0.659	<0.001
	25%	38	−10.916	0.864	<0.001
	50%	40	−8.940	0.780	<0.001
	75%	37	−10.116	0.593	<0.001

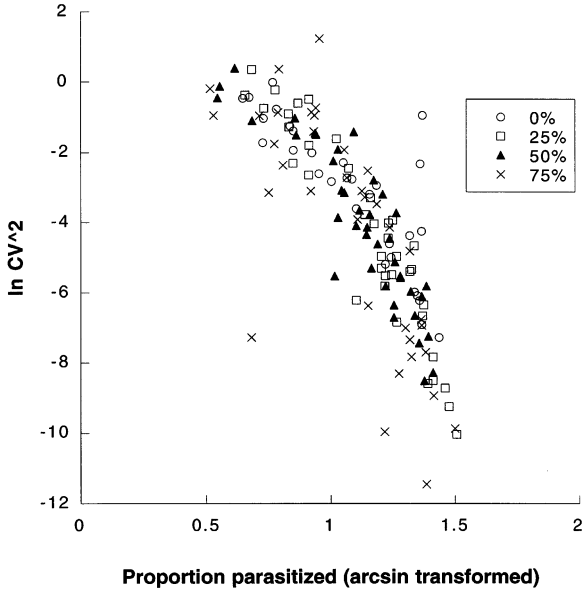

Fig. 5. The relationship between average percent parasitism and spatial heterogeneity in attack rate for both refuge experiments. The data are distinguished by refuge treatment and pooled across refuge experiments.

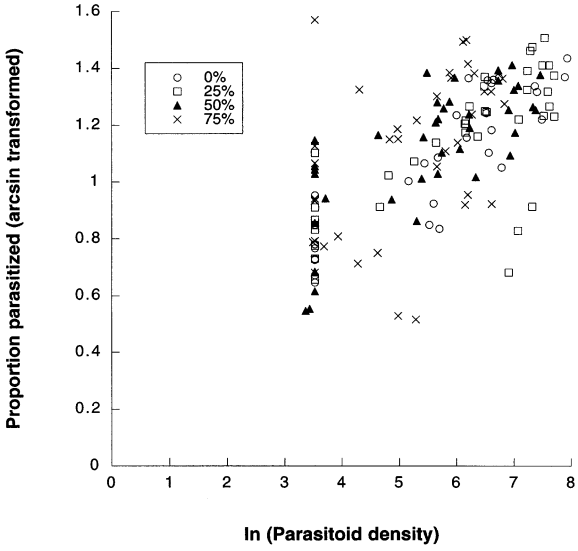

Fig. 6. The relationship between parasitoid density and percent parasitism for both experiments combined. The data are distinguished by refuge treatment and pooled across refuge experiments.

Patchiness was incorporated into the system only to stabilize the population dynamics enough to distinguish the effects of refuges. The degree of instability in the dynamics suggests that the lack of spatial heterogeneity overwhelms any effects that might arise from refuges. Refuge theory predicts high parasitoid diversity only for relatively high levels of spatial heterogeneity (Hochberg and Hawkins 1992, 1993). In order to maintain such spatial heterogeneity levels, the experiment would probably require physical barriers among patches, as has been done for two-species predator–prey (Huffaker 1958) and parasitoid–host systems (Pimentel et al. 1963).

We found a distinct negative relationship between percent parasitism and CV^2, which further complicates attempts to satisfy the spatial heterogeneity assumption of the refuge models. Percent parasitism was also related to parasitoid density, and it appears that spatial

Table 2. The relationships between arcsin sqrt (percent parasitism) and host density, exposed hosts, ln (parasitoids/host) and ln (parasitoid density). For each treatment, we list number of replicates (N), slope of relationship, variance explained (R^2), and P-value. The data are pooled across refuge experiments.

Factor	Refuge	N	Slope	R^2	P
Host density	All	146	0.000	0.006	0.333
	0%	30	−0.000	0.379	<0.001
	25%	38	0.002	0.002	0.795
	50%	40	0.000	0.372	<0.001
	75%	38	0.000	0.089	0.069
Exposed hosts	All	130	0.000	0.028	0.059
	0%	30	−0.000	<0.001	0.986
	25%	32	0.000	0.219	0.007
	50%	35	0.000	0.070	0.124
	75%	33	0.000	0.034	0.300
Ln (parasitoids/host)	All	146	0.085	0.312	<0.001
	0%	30	0.080	0.577	<0.001
	25%	38	0.090	0.391	<0.001
	50%	40	0.129	0.370	<0.001
	75%	38	0.224	0.319	0.002
Ln (parasitoid density)	All	146	0.119	0.462	<0.001
	0%	30	0.148	0.783	<0.001
	25%	38	0.115	0.527	<0.001
	50%	40	0.119	0.521	<0.001
	75%	38	0.112	0.225	0.002

heterogeneity decreases as an indirect function of increasing parasitoid density. We were not able to estimate CV_p^2 for the experiments because we had no estimates of parasitoid distributions among or within vials, and the techniques used to estimate CV_p^2 assume that parasitoids show a Poisson distribution within vials and a negative binomial distribution among vials. Nonetheless, it is the variation in attack rates among patches that determines the dynamics of host–parasitoid interactions (Hassell 2000). Therefore, if CV^2 decreases with increasing parasitoid density, then host–parasitoid dynamics will be more likely to destabilize with increasing parasitoid density.

We are aware of only two field studies that specifically identified the relationship between parasitoid density and spatial heterogeneity, and no general pattern emerged from these analyses (Jones et al. 1993, Reeve et al. 1994). Two other studies examined the relationship between parasitoid density and spatial heterogeneity in controlled environments, and both concluded that spatial heterogeneity decreases as parasitoid density increases (Tregenza et al. 1996, Visser et al. 1999). There are several potential explanations for the difference in conclusions between laboratory and field studies including differences in 1) behavior among parasitoid species, 2) complexity of environments, and 3) relative parasitoid densities studied. Jones et al. (1993) and Visser et al. (1999) used the same parasitoid species, *Trybliographa rapae* (Hymenoptera: Cynipoidae), which removes the possibility that differences in parasitoid behavior lead to different conclusions regarding the parasitoid density–spatial heterogeneity relationship. The laboratory studies used less complex habitats than are commonly found in nature, and it is possible that negative relationships between parasitoid density–spatial heterogeneity only occur in simplified environments. Finally, it is possible that the field studies failed to identify a decrease in spatial heterogeneity simply because parasitoid densities were too low to show an effect. If it is true that spatial heterogeneity decreases at high parasitoid densities, then models that assume constant spatial heterogeneity overestimate the boundaries for stability in host–parasitoid dynamics.

To assess the relevance of the relationship between parasitoid attack rate and spatial heterogeneity for refuge theory, we examined parasitism rates recorded in field studies. Hawkins (1994) searched for patterns in parasitoid attack rate using a database of 819 host species for which maximum parasitism rates were recorded. Maximum percent parasitism exceeded 80% in over 10% of the studies reported and exceeded 50% in nearly 40% of the cases. In addition, Hawkins (1994) found that the strongest relationship was between host feeding niche and maximum parasitism rate. Maximum parasitism rate was highest on leaf miners and gallers and lowest on stem borers and root feeders. Thus, the host feeding-niche most likely to have low spatial heterogeneity, due to the effect of parasitism rate, is also the niche most likely to have a rich parasitoid assemblage. In other words, the hosts most likely to fit within the necessary refuge range for coexistence of specialist parasitoids are the least likely to fit within the necessary range of spatial heterogeneity. We note that these data were not limited to specialist parasitoids and assume that generalists and specialists respond similarly to host-feeding niche.

Further, parasitism rates are often high at equilibrium in refuge models, depending on both refuge level and the assumed level of spatial heterogeneity. In general, the parasitism rate increases as refuge level decreases, and percent parasitism is often over 50% when the refuge level is 50% or less. Thus, if spatial heterogeneity decreases as percent parasitism increases, then the stability of refuge models is likely to be affected by this process.

Our results suggest that host refuges are unlikely to explain parasitoid richness patterns for specialist parasitoids because the necessary levels of spatial heterogeneity are probably rarely satisfied, especially among hosts with the richest parasitoid assemblages. Another variant of the host refuge model, using only generalist parasitoids, predicts high parasitoid richness with little spatial heterogeneity (Hochberg and Hawkins 1992, 1993). The importance of spatial heterogeneity varies in mixed models incorporating both generalist and specialist parasitoids, depending largely on the position of specialists in the competitive hierarchy. Further work is needed to evaluate the influence of host refuges on parasitoid richness of generalist parasitoids.

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