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Porter, E E
Hawkins, Bradford A.

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The influence of varying spatial heterogeneity on the refuge model for coexistence of specialist parasitoid assemblages

Eric E. Porter and Bradford A. Hawkins

Models of host–parasitoid dynamics often assume constant levels of spatial heterogeneity in parasitoid attack rate, which tends to stabilize the interactions. Recently, authors have questioned this assumption and shown that outcomes of simple host–parasitoid models change if spatial heterogeneity is allowed to vary with parasitoid density. Here, we allow spatial heterogeneity to vary with either parasitoid density or percent parasitism in a model designed to explain specialist parasitoid coexistence on insect hosts with various levels of refuge. By examining this model we can evaluate the effect of varying spatial heterogeneity on a more complex model in which spatial heterogeneity is not considered the primary determinant of persistence. By modeling communities with one host and two parasitoid species, we show that the probability of species persistence for the competitively inferior parasitoid depends on the assumed relationship between spatial heterogeneity and both parasitoid density and percent parasitism. The probability of parasitoid coexistence is generally lower when spatial heterogeneity varies with parasitoid demographics. We conclude that the conditions for which host refuge promote specialist parasitoid coexistence are less common that proposed by the original model. Finally, we compared a model in which spatial heterogeneity varies with percent parasitism to data from laboratory trials and find a reasonable fit. We conclude that the change in spatial heterogeneity strongly influenced the outcome of the laboratory trials, and we suggest more research is necessary before researchers can assume constant spatial heterogeneity in future models.

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).

Insect species are often attacked by a suite of parasitoid species. Recently, parasitoid ecologists began asking how this seemingly homogeneous resource, the host species, can support a rich diversity of parasitoids. Based on a synthetic analysis of parasitoid assemblages throughout Great Britain and later the globe, Hawkins and colleagues suggested that host feeding-niches influence the number of parasitoids that a host species can support (Hawkins and Lawton 1987, Hawkins 1988, 1994). This conclusion lead to mathematical models that describe how host refuges from parasitism can lead to parasitoid coexistence, including a model describing how specialist parasitoid assemblages can coexist on a single host species (Hochberg and Hawkins 1992, 1993). These models consider the effect of global proportional refuges in that the refuges are absolute and do not distinguish among parasitoid species (Hochberg and Holt 1995). To examine the influence of refuge on parasitoid coexistence, we conducted a laboratory experiment in which we varied the amount of refuge for a host species and monitored the dynamics of two parasitoid species restricted to that host. We found little evidence that a host refuge can lead to increase the chance of parasitoid coexistence (Porter and Hawkins 2003). Our results suggest that a fundamental assumption of the refuge model and many related models, that

spatial heterogeneity in parasitoid attack rate is constant with respect to parasitoid density and percent parasitism, is not valid in at least some systems. Here, we relax this assumption by simulating the effect of several potential relationships between spatial heterogeneity and parasitoid density or percent parasitism and incorporating these relationships into the original refuge model for specialist parasitoids.

Spatial heterogeneity was first incorporated into host–parasitoid models because insects are often found in discrete patches with variable densities and parasitism rates. The term 'spatial heterogeneity' has been used to define many specific patterns, but the general idea is that higher spatial heterogeneity indicates a greater aggregation of risk of parasitism (Bernstein 2000, Hassell 2000). This form of probabilistic refuge differs from proportional refuge in that each the refuge acts independently for each parasitoid species, and parasitoid coexistence is possible when probabilistic refuges do not overlap (Wilson et al. 1996). By incorporating this variability into basic Nicholson-Bailey models, May (1978) and Hassell (1978) showed that spatial heterogeneity could stabilize host–parasitoid dynamics. In these models, spatial heterogeneity is incorporated as the constant k, known as the clumping parameter of the negative binomial distribution. Later, Hassell and Pacala (1990) and Hassell et al. (1991) proposed the $CV^2 > 1$ rule (CV^2 is the reciprocal of k), which states that if the coefficient of variation in parasitoid search time among patches is greater than 1, then spatial heterogeneity is sufficient to stabilize otherwise unstable host–parasitoid interactions. Their arguments made the assumptions that spatial heterogeneity is a characteristic of the particular host–parasitoid system and is constant through time. Nicholson-Bailey models have been extended to identify conditions for coexistence of two parasitoid species on one host based on aggregation of parasitism risk (May and Hassell 1981, Klopfer and Ives 1997), and these multiple-parasitoid models stress the influence of parasitoid distribution patterns on the impact of interspecific competition.

Lynch (1998), following Driessen and Visser (1997), argued that spatial heterogeneity is likely to vary systematically as parasitoid density changes. Lynch showed that when spatial heterogeneity varies as a linear function of parasitoid density, simple Nicholson-Bailey host–parasitoid models become more or less stable depending on the direction of the relationship. He showed that when spatial heterogeneity decreases with increased parasitoid density, host–parasitoid interactions tend to be less stable, whereas increasing spatial heterogeneity with increased parasitoid density stabilizes the interactions. Because Nicholson-Bailey models also form the basis of the Hochberg and Hawkins refuge models (Hochberg and Hawkins 1992), the assumption of constant spatial heterogeneity may lead to inaccurate conclusions for the refuge models as well.

For that reason, we use a method similar to Lynch's in order to examine the influence of simple linear relationships between spatial heterogeneity and parasitoid density on the refuge model for specialist parasitoids. In this sense, the models described here serve as an extension of Lynch's work to examine the influence of varying spatial heterogeneity on a more complex host–parasitoid model.

In our laboratory studies we found a strong relationship between spatial heterogeneity in percent parasitism and average percent parasitism (Porter and Hawkins 2003). In general, when percent parasitism rose above 50–70%, spatial heterogeneity decreased dramatically. This basic trend is illustrated in the relationship between parasitoid pressure (acP) and spatial heterogeneity in attack rate from a compilation of field and laboratory studies (Hassell and Pacala 1990) (Fig. 1). Further, spatial heterogeneity in percent parasitism must decline as percent parasitism approaches one because all of the patches will have the same parasitism rate. Thus, as average percent parasitism becomes very high, spatial heterogeneity in attack rate can be expected to decline, depending on the relationship between attack rate at percent parasitism. To evaluate the influence of such relationships between spatial heterogeneity and percent parasitism, we simulate the effect of varying spatial heterogeneity with percent parasitism on the refuge model in two ways. First, we model the effect of simple linear relationships between percent parasitism and spatial heterogeneity. In one model we set k to increase linearly with percent parasitism from a range of initial values. Then, we set k to increase only after percent parasitism reaches 0.5, which assumes that spatial heterogeneity will only decrease when parasitoid
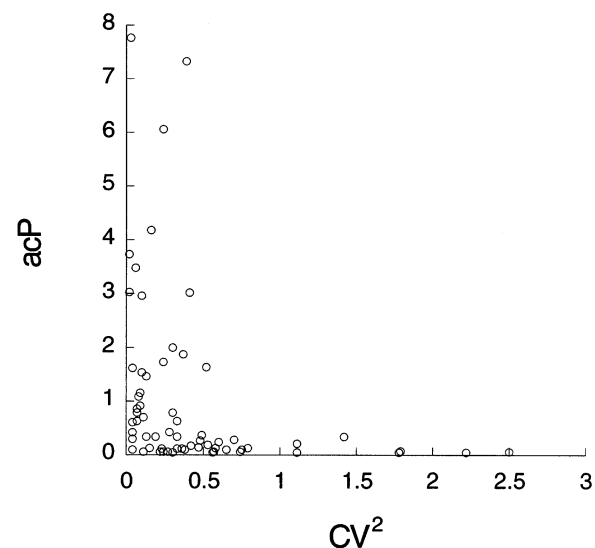

Fig. 1. The relationship between parasitoid pressure (acP) and spatial heterogeneity in attack rate compiled from field and laboratory studies (data from Hassell and Pacala 1990).

attack rates are fairly high. Finally, we use the specific relationship between percent parasitism and spatial heterogeneity found in the experimental trials and compare the simulation results with data from laboratory trials. The goal of this analysis is to identify the potential effect of variation in spatial heterogeneity on the conditions for coexistence in the refuge model for specialist parasitoid assemblages. The analysis also serves as an extension of Lynch's proposition that variation in spatial heterogeneity may have important implications for stability in many models that rely on spatial heterogeneity to stabilize interactions.

The model

The original refuge model for specialist parasitoids

The models are all based on the Hochberg and Hawkins (1992, 1993) model for specialist parasitoid assemblages. For simplicity, we initiate each simulation with only two parasitoid species. In this model, both specialist parasitoids attack one host species. The parasitoids are ranked in descending competitive superiority from $j = 1$ to $j = 2$, and the parasitoid densities are represented by S_1 and S_2. The average probability that a host will escape parasitism by each parasitoid species is given by s_1 and s_2. The difference equations for host (N) and both specialist parasitoids (S) are

$$N(t+1) = FN(t)d[N(t)][\alpha + (1 - \alpha)(s_1 s_2)]$$

$$S_1(t+1) = FN(t)d[N(t)](1 - \alpha)(1 - s_1)s_2$$

$$S_2(t+1) = FN(t)d[N(t)](1 - \alpha)(1 - s_2)$$

$$s_1 = \left[1 + \frac{aS_1(t)}{k[1 + aFN(t)(1 - \alpha)/\eta]}\right]^{-k}$$

$$s_2 = \left[1 + \frac{aS_2(t)}{k[1 + aFN(t)(1 - \alpha)/\eta]}\right]^{-k}$$

where
F = finite rate of increase for the host = 5
$d[N(t)] = 1/[1 + N(t)(F - 1)/Q]$, the proportion of hosts surviving intraspecific competition
Q = environmental carrying capacity of host population = 10^7
α = proportion of hosts inaccessible to parasitism (varied from 0 to 0.95)
a = per capita searching efficiency of parasitoid $y = 0.1$
η = maximum number of hosts attacked per parasitoid = 20
k = clumping parameter of the negative binomial distribution of parasitoid searching

The assumptions of the model are discussed in Hochberg and Hawkins (1993). Briefly, host refuge is modeled under the assumption that a fixed proportion of host species is not available for parasitism. Also, there is a dominance hierarchy among the parasitoid species in interference competition such that one parasitoid species sweeps through the host population, and the second parasitoid species can only attack the hosts that were not attacked by the first. Finally, and critically, it is assumed that both parasitoid species are functional specialists that do not attack alternate hosts.

The number following the description of the parameters indicates the value we use for most simulations. These values are thought to lie within reasonable bounds for naturally occurring systems and are equivalent to the base values used in Hochberg and Hawkins (1993). The only parameters that varied in most analyses were k and α. We also explored the effect of varying initial parasitoid densities for each model. Models were run for 1000 generations, and we report the final value for S_2 as a proportion of Q. This value is interpreted as a relative likelihood of persistence for the competitively inferior parasitoid. This interpretation assumes that the likelihood of persistence is dependent on the size of the host population such that if Q is very large a low final S_2 may still have a high chance of persistence. In every case, the value of S_2 stabilized by $t = 1000$ (S_2 at $t = 1000$ was within 0.001 of S_2 at $t = 999$), or S_2 showed no tendency to stabilize. Cases of instability are discussed when relevant. All models were evaluated with Berkeley Madonna Version 8.0.1 (Macey and Oster 2000).

Effects of different relationships between k and parasitoid demography

There is no consensus regarding the relationship between k and parasitoid density or percent parasitism. To date we can only conclude that the relationship is probably system specific, and no single set of assumptions can adequately represent all systems. Therefore, we present a series of possible relationships and model how these relationships affect the conclusions from the original models that assume constant spatial heterogeneity.

Spatial heterogeneity varies linearly with parasitoid density

First, we examine the effect of simple relationships suggested by Lynch (1998). As a measure of spatial heterogeneity Lynch used the coefficient of variation (CV), which is equivalent to reciprocal of the square root of k. In these models CV varies as a linear function of parasitoid density (in our case the summed
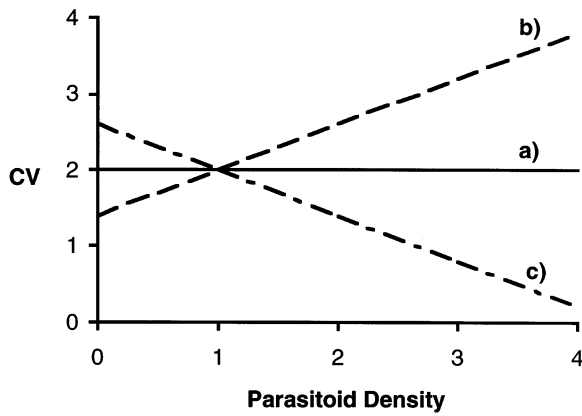
Fig. 2. Possible linear relationships between parasitoid density and spatial heterogeneity in attack rate defined as the reciprocal of the square root of k. This function of k is equivalent to the coefficient of variation (CV) used by Lynch (1998). Each of the following relationships were evaluated in refuge models: a) constant heterogeneity, b) increased heterogeneity with increased parasitoid density and c) decreased heterogeneity with increased parasitoid density.

density of both parasitoid species). The slope of this relationship (b) determines the change in degree of spatial heterogeneity as parasitoid density changes. Because spatial heterogeneity has the potential to either increase or decrease as parasitoid density increases depending on the behavioral response of the parasitoids (Driessen and Visser 1993), we model the following relationships (Fig. 2). First, we assume that spatial heterogeneity is constant ($b = 0$) and run the models using a range of k. This model is equivalent to the original Hochberg and Hawkins models with the exception that only two parasitoid species are introduced. Second, we assume that spatial heterogeneity increases as parasitoid density increases with a slope of $b = 0.3$. Finally, we assume that spatial heterogeneity decreases as parasitoid density increases with a slope of $b = -0.3$. These slopes represent the range of values used in Lynch's analysis and are thought to represent a reasonable range of ecologically relevant values.

For these models we followed the methods of Lynch (1998) in which k is determined by the function $g(S)$ as follows:

$$CV = g(S_1 + S_2)$$

$$k = (1/CV)^2$$

$$g(S_1 + S_2) = 2CV * \left[\frac{\exp(bx)}{1 + \exp(bx)} \right]$$

where:

$$x = \left(\frac{(S_1 + S_2) - (S_1 + S_2)^*}{(S_1 + S_2)^*} \right)$$

The equilibrium density, $(S_1 + S_2)^*$ is determined as the sum of S_1 and S_2 at $t = 1000$ assuming a constant k for each initial value of k. Initial densities of S_1 and S_2 are equal for each trial, and changing the initial ratio of S_1 to S_2 has no effect on the final value of S_2 in any model. Initial values of S_1 and S_2 are set at $0.5 \times (S_1 + S_2) - 1$. We also explore the effect of varying initial S_1 and S_2 for each model. For this and each of the remaining sets of simulations we use the following range of initial values for k: 0.1, 0.25, 0.5, 0.75, and 1. These values of k range from very high spatial heterogeneity rarely measured in field studies ($k = 0.1$) to moderate spatial heterogeneity thought to be high enough to stabilize simple 1 host – 1 parasitoid systems ($k = 1$). No models show any potential for parasitoid coexistence when k is greater than 1. We also use a range of host refuge levels from 0 to 0.95 at increments of 0.05.

When $b = 0$ the models are identical to the Hochberg and Hawkins (1993) refuge models and represent the reference models. One can evaluate the effect of various relationships between k and parasitoid demography by comparing simulation results to those found in Fig. 3. In this model the competitively inferior parasitoid (S_2) is most likely to survive when k is small (high spatial heterogeneity) and when refuge levels are intermediate. The results of this model are not dependent upon initial values of N, S_1 or S_2. The final value of S_2 is stable for all cases with the following exceptions. When $k = 0.75$
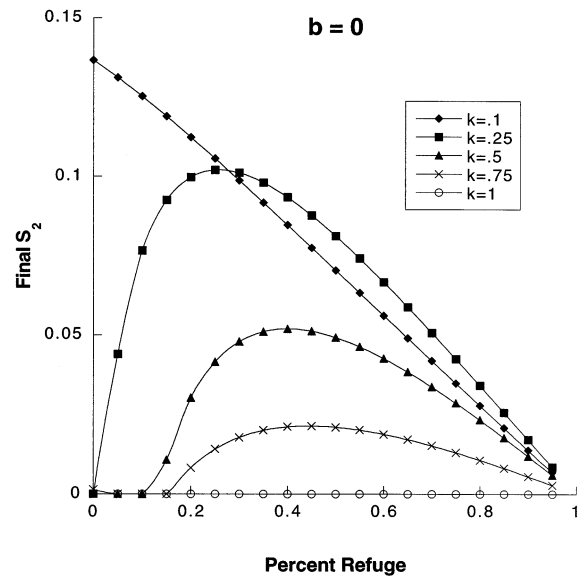

Fig. 3. Results of simulations assuming that spatial heterogeneity remains constant throughout the simulations. This model is identical to the Hochberg and Hawkins model for specialist parasitoids. Final density for the competitively inferior parasitoid (S_2) is measured as the percent of carrying capacity for the host (Q). As final S_2 decreases the likelihood of extinction increases for S_2.

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and $\alpha = 0$, S_2 continues to vary at $t = 1000$ but dips below 1 several times, indicating the parasitoid would certainly drop out of the system. Also when $k = 0.5$ and $\alpha = 0$, S_2 continues to vary at $t = 1000$, but it drops below 1 during the simulations, indicating certain extinction.

When spatial heterogeneity increases linearly with parasitoid density ($b = 0.3$), the results of the simulations are similar to the original model when refuge levels are higher than 25%, but the models become less predictable at low refuge levels (Fig. 4). As initial parasitoid densities ($S_1 + S_2$) increase final S_2 tends to decrease (Fig. 5a). At low refuge levels ($< 20\%$ for $k = 0.75$ and $< 15\%$ for $k = 0.5$) the final density of the inferior competitor is very sensitive to starting conditions (Fig. 5b), and the models become unstable when initial k is high (Fig. 5b). Final S_2 is sensitive to initial densities for higher refuge levels as well, but the change is less severe and initial parasitoid densities must be very high to change the results qualitatively. In general, final S_2 becomes more dependent on the starting values when k is high and refuge is low, and at very low refuge levels (< 0.15) and low initial parasitoid densities the models are unstable.

When spatial heterogeneity decreases linearly with parasitoid density ($b = -0.3$), the pattern is again similar to the original models at higher refuge levels (Fig. 6). In this case the conditions for coexistence are very sensitive to initial parasitoid density regardless of the initial spatial heterogeneity (Fig. 7). In fact, in many cases ($S_1 + S_2$) must start at roughly 50% of Q in order

a)

k = 0.25, b = 0.3

b)

k = 0.75, b = 0.3

Fig. 5. The influence of initial parasitoid density ($S_1 + S_2$) on the final density of the inferior competitor, S_2, when $b = 0.3$. The legend indicates the host refuge level simulated for initial spatial heterogeneities of a) $k = 0.25$ and b) $k = 0.75$. When ($S_1 + S_2$) is low, the models are unstable at low refuge levels.

to keep S_2 from certain extinction. Also, the refuge level does not strongly influence the effect of initial parasitoid densities such that initial parasitoid density becomes a primary determinant of parasitoid coexistence when $b = -0.3$.
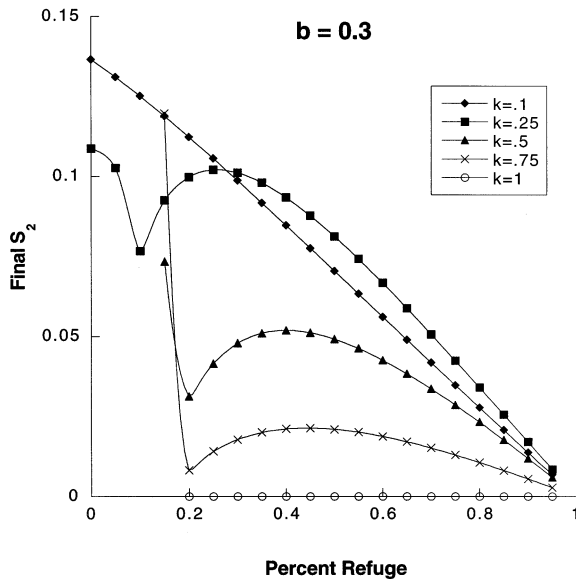

b = 0.3

Fig. 4. Results of simulations models assuming a linear relationship ($b = 0.3$) between spatial heterogeneity and parasitoid density ($S_1 + S_2$). Units are the same as Figure 3.2. Missing data points indicate conditions that caused instability in the models.
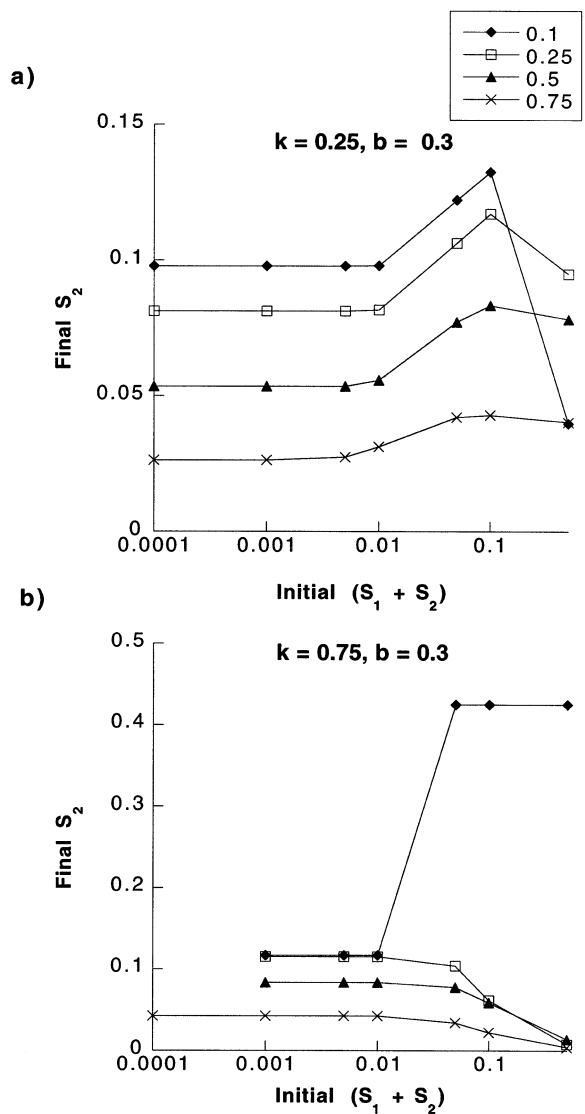
k varies as a function of percent parasitism

In our laboratory experiments spatial heterogeneity varied more closely with percent parasitism than with parasitoid density directly. To evaluate this relationship, we allow spatial heterogeneity to decrease linearly
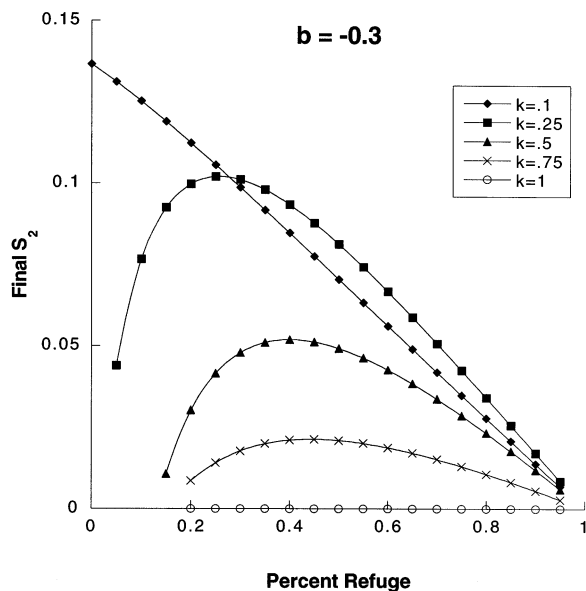
Fig. 6. Results of simulations models assuming a linear relationship (slope = − 0.3) between spatial heterogeneity (*CV*) and parasitoid density ($S_1 + S_2$). Units are the same as Figure 3. Missing data points indicate conditions that caused instability in the models.
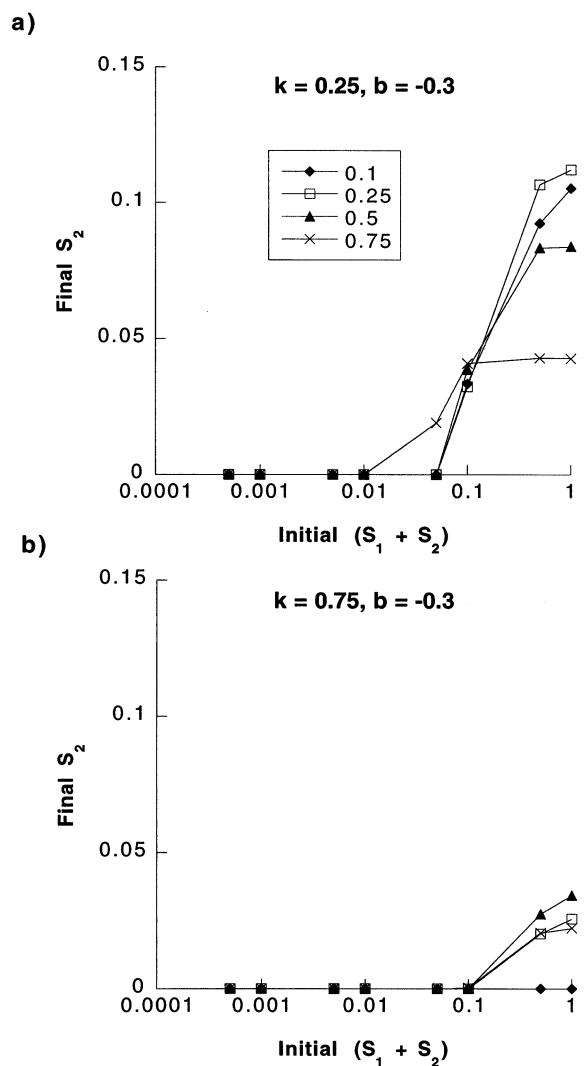

Fig. 7. The influence of initial parasitoid density ($S_1 + S_2$) on the final density of the inferior competitor, S_2, when $b = -0.3$. The legend indicates the host refuge level simulated for initial spatial heterogeneities of a) $k = 0.25$ and b) $k = 0.75$. When ($S_1 + S_2$) is low, the models are unstable at low refuge levels.

as percent parasitism increases. We explore the effect of such a relationship using the following assumptions (Fig. 8). First, we use a simple linear relationship in which *k* increases as percent parasitism increases with a slope of 1 (a from Fig. 8). With this relationship *k* is between 1.1 and 2 when percent parasitism is 1.0. We expect *k* to be high in most systems if all hosts are attacked suggesting that the slope is gentle enough that it may underestimate the chance of extinction for S_2. Next, we again use a slope of 1, but we assume that spatial heterogeneity is constant until percent parasitism is 0.5 (b from Fig. 8). This non-linear relationship more accurately reflects the shape of the relationship found in laboratory trials (Porter and Hawkins 2003). Finally, we cap spatial heterogeneity at $k = 2$ and assume that *k* increases linearly from its initial value to 2 but only after half of the hosts are attacked (c from Fig. 8). In this case, spatial heterogeneity is moderately low when percent parasitism is 100%, and the slope of the relationship between *k* and percent parasitism is generally steeper than the previous model (b).

When *k* increases linearly with percent parasitism, the likelihood of persistence for S_2 is reduced in all cases when compared to models with constant *k* and equivalent initial conditions (Fig. 9). The other obvious effect of this relationship is that the likelihood of persistence peaks at higher refuge levels than the original models, usually between 0.5 and 0.7. In fact, when ∝ is greater than 0.25, extinction of S_2 is nearly inevitable. This shift can be attributed to the fact that

percent parasitism varies more drastically at low refuge levels, and maximum percent parasitism decreases with increasing refuge level. Also, with this relationship, initial spatial heterogeneity must be high ($k = 0.1$ or 0.25) for S_2 to persist at any refuge level. Final S_2 is independent of initial parasitoid densities in each model that simulates a relationship between spatial heterogeneity and percent parasitism.

Trials that assume decreasing spatial heterogeneity when percent parasitism is greater that 0.5 give similar results to the original models (Fig. 10a). The only obvious difference is that the peak in final S_2 shifts to higher refuge levels under these conditions. Again, maximum percent parasitism is highest at low refuge levels,
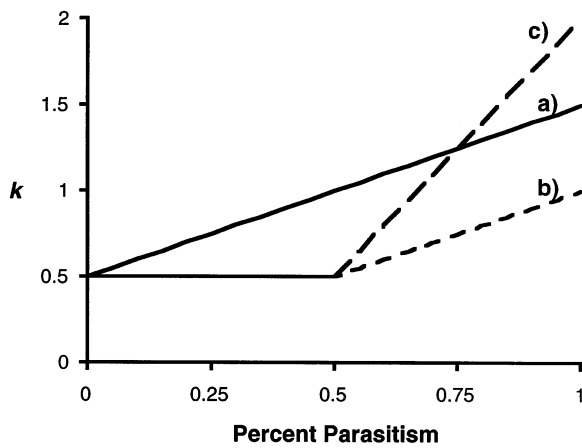
Fig. 8. Possible relationships between percent parasitism and spatial heterogeneity in attack rate that were evaluated in refuge models. Note the slope of the curves for (c) is different for each initial spatial heterogeneity modeled. See text for a detailed explanation of each relationship.

which makes the effect of decreased spatial heterogeneity greatest at low refuge levels.

The final model is similar to the previous one except the slope of the relationship between k and percent parasitism is generally steeper. We set the slope such that k increases linearly with percent parasitism to a maximum of $k = 2$. Thus, the specific slope for each simulation depends on the initial k. The increased slope has a dramatic effect on final S_2 (Fig. 10b). In these simulations refuge levels need to be particularly high for S_2 to persist unless the initial value of k is extremely low. Likelihood of persistence drops dramatically for refuge levels below 0.5 unless k is 0.1.
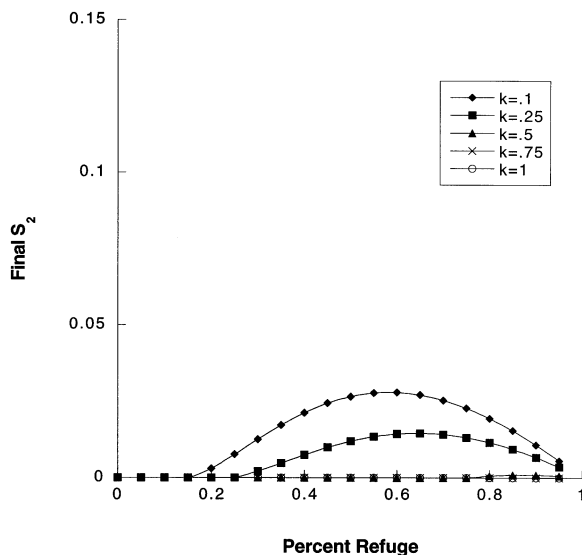

Fig. 9. When k varies linearly with percent parasitism (slope = 1), final values of S_2 are always lower than comparable results assuming constant spatial heterogeneity.
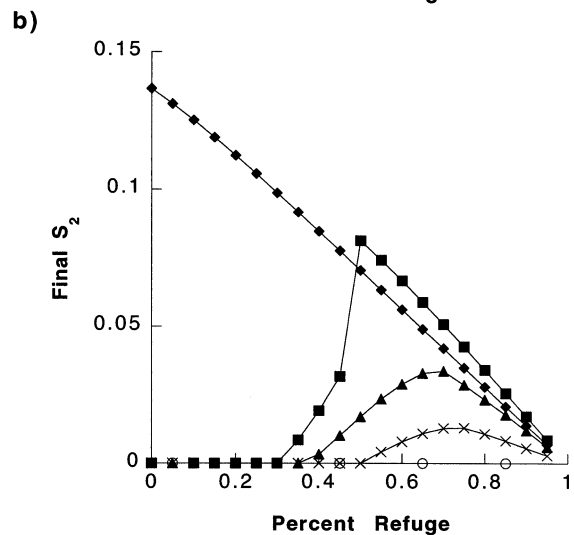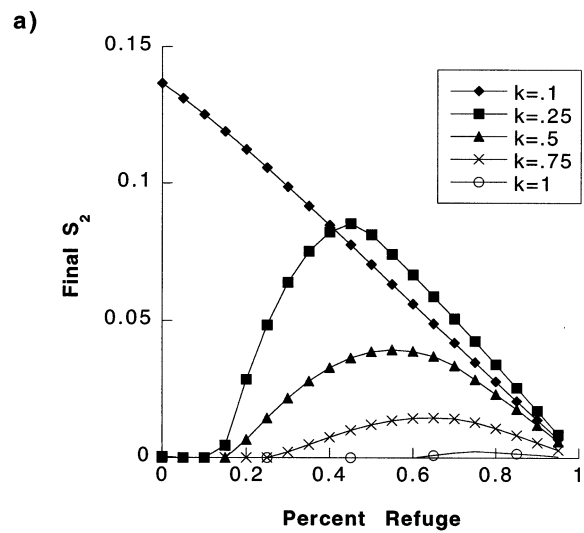

Fig. 10. In simulations that use a linear increase in k when parasitism rates are greater than 50%, the slope of the curve has a strong influence on the conditions for stability. When the slope is 1 (a), the final results are similar to models assuming constant k. When she slope is greater (b), for most initial k coexistence requires high refuge levels.

The relationship as measured in laboratory experiments

We use the relationship found in a series of laboratory experiments that allowed us to fit a relationship between k and percent parasitism. The equation $\ln(k) = -4.235 + 9.291 \times \arcsin\sqrt{\text{percent parasitism}}$ explains 67.5% of the variation in k. When this function is incorporated into the Hochberg and Hawkins (1992) refuge model, the competitively inferior parasitoid species is predicted to go extinct in 6 generations, depending on the refuge level. The models qualitatively predict the outcome of laboratory trials with similar initial conditions ($Q = 2500$, $S_1 = 17$, $S_2 = 17$; Fig. 11). In
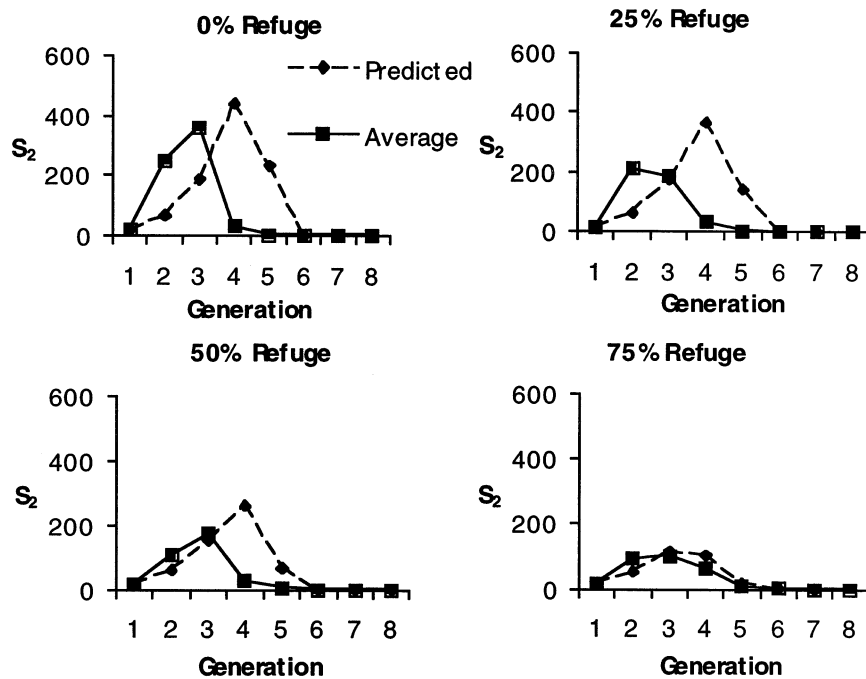
Fig. 11. Comparison of average results from laboratory experiments and the predictions of refuge models that allow k to vary with percent parasitism.

each case, the model predicts extinction time to within 1 generation of the actual data. Also, the accuracy of the models tends to increase as refuge levels increase. We attribute this trend to the increased stability of high refuge systems. Models that simulate decreasing spatial heterogeneity with increasing percent parasitism show a tendency to become less stable at lower refuge levels. This instability may be reflected in the inability of the model to accurately predict parasitoid densities at low refuge levels.

Discussion

Spatial heterogeneity in attack rate offers an important explanation for the persistence of host–parasitoid interactions. Certainly, attack rates often vary among patches in nature (Lessells 1985, Stiling 1987, Walde and Murdoch 1988), and this spatial heterogeneity may help stabilize interactions. However, the theory of spatial heterogeneity has advanced far beyond empirical tests of assumptions. It is still not clear that the conditions necessary for stability in host–parasitoid interactions due to spatial heterogeneity are commonly found in nature (Pacala and Hassell 1991). Perhaps more importantly, little attention has been paid to the effect of changes in spatial heterogeneity over time. It is reasonable to expect patterns of parasitism to change as parasitoid density changes, yet these changes have received little attention in the literature. It is difficult to monitor changes in parasitoid density in the field and relate these patterns to variation in percent parasitism,

which probably accounts for the lack of attention to this problem (Hassell 2000). Nonetheless, modelers have incorporated constant spatial heterogeneity as templates for more complex models in efforts to explain more specific and complex phenomena. We argue here that it is unlikely that spatial heterogeneity will remain constant with respect to parasitoid demography, and that this variability has the potential to drastically change the outcome of at least one such model, the refuge model for coexistence of specialist parasitoids.

Relaxing the assumption of constant spatial heterogeneity has a range of effects on refuge models, depending on the assumed underlying relationship between spatial heterogeneity and parasitoid demography. When one assumes a simple linear relationship between parasitoid density and spatial heterogeneity, the model results are less stable at low refuge levels. When refuge levels are high, parasitoid density cannot increase to levels that would alter the fundamental dynamics of the refuge models, but at low refuge levels, parasitoid density is more variable and can reach levels that have critical effects on spatial heterogeneity. When spatial heterogeneity is assumed to decrease with increasing average parasitism rates, the results are more variable. A simple linear decrease in spatial heterogeneity with increasing parasitism rates inevitably reduces the likelihood of persistence for the inferior parasitoid species. The effect of seemingly more realistic non-linear relationships between spatial heterogeneity and percent parasitism depends critically on the slope of the relationships. Models assuming gentle relationships have little effect on parasitoid coexistence, but steep relation-

ships virtually guarantee extinction for inferior parasitoids on host with low refuge levels. These results point to the fact that it is difficult to predict the effect of changes in spatial heterogeneity on host–parasitoid models, yet these effects can dramatically alter the predictions of these models.

Both Lynch's (1998) exploration of the single host–parasitoid dynamics and our results with a more complex model emphasize the need for detailed examinations into the influence of parasitoid demography on spatial heterogeneity in attack rate. Previous studies showed that it is possible to collect information on changes in spatial heterogeneity with parasitoid density in the field (Waage 1983, Driessen and Hemerik 1991), but these data are clearly difficult to collect. Laboratory trials in which known parasitoid densities are used to initiate trials can be used to quantify the influence of both parasitoid density and the resulting changes in percent parasitism on spatial heterogeneity in attack rate. Our laboratory experiments showed some evidence that spatial heterogeneity drops drastically as average percent parasitism increases, but the size of the habitat patches and the crowded cages offered little room for natural variation in attack rate. Future experiments must use large areas with highly dispersed patches in order to simulate natural conditions. Such larger scale experiments could help researchers evaluate the effect of parasitoid density by controlling initial parasitoid population sizes. Nonetheless, parasitoid species show a range of behavioral responses to changes in density (Ives 1995, Klopfer and Ives 1997, Hassell 2000), and no single system can provide a universal description of the relationship between parasitoid demography and spatial heterogeneity. Clearly, if parasitoid species respond differently to changes in host density, the outcome of competition could change dramatically. Therefore, these relationships need to be examined in a number of systems in an effort to identify meaningful patterns that can be used to classify relationships for various host–parasitoid systems.

We provide evidence that refuge theory can explain the coexistence of specialist parasitoids only under a limited range of conditions. The original model showed that high spatial heterogeneity was necessary for coexistence, and evidence from field studies suggests that these levels are rare in nature (Pacala and Hassell 1991). The laboratory trials showed that spatial heterogeneity is unlikely to remain constant as parasitoid density increased and provided no indication that even two parasitoid species can coexist for any refuge treatment. Finally, the models presented here indicate that variation in spatial heterogeneity generally reduces the likelihood of coexistence for multiple parasitoids. Still, the refuge model for generalist parasitoids may still offer an important explanation for parasitoid coexistence because this model predicts coexistence with much lower levels of spatial heterogeneity than the model for specialist parasitoids.

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