PARASITOID AGGREGATION AND THE STABILIZATION OF A SALT MARSH HOST-PARASITOID SYSTEM

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Abstract. We examine a salt marsh host–parasitoid system, consisting of the planthopper Prokelisia marginata and its egg parasitoid Anagrus delicatus, for evidence of stabilizing parasitoid behavior. We first determine if there is sufficient parasitoid aggregation to potentially stabilize the Prokelisia–Anagrus interaction, using methods that infer parasitoid behavior from the spatial pattern of parasitism. We then test a basic assumption implicit in theory, that the degree of parasitoid aggregation is invariant with respect to changes in overall host and parasitoid density, and through time. Our results suggest that Anagrus behavior should, in theory, exert a consistent stabilizing effect on Prokelisia–Anagrus dynamics.

Using field experiments, and direct sampling of the spatial distribution of parasitoids, we then try to determine if parasitoid aggregation is in fact responsible for the heterogeneous pattern of parasitism observed in the field. The results of these studies indicate that there is insufficient parasitoid aggregation to account for this heterogeneity. Instead, factors such as the degree of tidal inundation, or the age of host eggs, may cause host patches to differ in their vulnerability to parasitoid attack.

Key words: aggregation; behavior; parasitoid; salt marsh; stability.

INTRODUCTION

A central theme in the theory of host–parasitoid systems is the link between parasitoid foraging behavior and the stability of the host–parasitoid interaction. One of the first forms of parasitoid behavior identified as stabilizing was an aggregative response by the parasitoid to the host, in which patches containing more hosts receive more parasitoids (Hassell and May 1973, 1974). Later on, the list was broadened to include aggregation of the parasitoids independent of host density (May 1978, Murdoch et al. 1984, Chesson and Murdoch 1986), in which the parasitoids are simply clumped across patches, and even inverse aggregation, where parasitoids are least common in the most dense patches of hosts (Hassell 1984). Models have also been developed that combine more than one type of these behaviors (Chesson and Murdoch 1986, Reeve et al. 1989, Pacala et al. 1990, Hassell et al. 1991). An important recent development in the theory is a unified criterion, the “cv2 > 1” rule, for determining the amount of aggregation, of any type, sufficient to stabilize the system (Pacala et al. 1990, Hassell et al. 1991). According to this rule, if the coefficient of variation squared (cv2) in the density of searching parasitoids per individual host is > 1, then the system will be stable.

Influenced by these theoretical results, numerous field studies have examined the relationship between parasitism rates and the density of hosts in a patch, the rationale being that if parasitism rates were either directly or inversely density dependent, this indicated stabilizing aggregative behavior by the parasitoid. Recent reviews have found significant direct relationships in about one-quarter of all studies, significant inverse ones in another quarter, with the remaining studies showing no relationship (Lessells 1985, Stiling 1987, Walde and Murdoch 1988). These results suggest that parasitoids aggregate in response to host density in at least some systems. Far fewer studies, however, have looked for evidence that parasitoids are aggregated independent of host density. If this type of aggregation were occurring, one would expect parasitism rates to be extremely heterogeneous across host patches (Murdoch et al. 1984, Reeve and Murdoch 1985, Pacala and Hassell 1991). Initial efforts to detect this type of parasitoid aggregation examined qualitatively the distribution of parasitism rates across patches, for two examples of successful biological control, the olive scale, Parlatoria oleae, and the California red scale, Aonidella aurantii (Murdoch et al. 1984, Reeve and Murdoch 1985). These studies found little evidence for heterogeneity in parasitism rates across patches. Using similar methods, however, Driessen and Hemerik (1991) found strong heterogeneity, enough to be stabilizing, in parasitism rates of Drosophila inhabiting stinkhorns. Pacala and Hassell (1991) have also found evidence for aggregation independent of host density in a number of systems. Using maximum likelihood methods, they estimated the cv2 from patterns of parasitism in 34 published studies, partitioning the cv2 into two components; the first involving the aggregative response of the parasitoid to host density (direct or inverse), and the second aggregation independent of host density.
density. They found values of the $cv^2 > 1$ in 9 of the 34 studies, and among the studies that satisfied the rule, aggregation independent of host density was the main source of stability. In two recently published case studies using the same methods, aggregation independent of host density was found to be important in one system (Redfearn et al. 1992) and insignificant in another (Jones et al. 1993).

In this paper, we examine in depth a salt marsh host–parasitoid system, consisting of the planthopper Prokelisia marginata (Van Duzee) (Hemiptera: Delphacidae) and its minute egg parasitoid Anagrus delicatus Dozier (Hymenoptera: Mymaridae), for evidence of stabilizing parasitoid behavior. Our first objective is to determine if there is sufficient parasitoid aggregation, independent of host density, to potentially stabilize the Prokelisia–Anagrus interaction. We concentrate our search on this type of aggregation alone, because previous field and laboratory behavioral studies have amply demonstrated that the other forms of aggregation do not occur in the Prokelisia–Anagrus system (Stiling and Strong 1982a, Cronin and Strong 1990a, 1993, Strong 1989, Stiling et al. 1991). There is some evidence that aggregation independent of host density does occur in this system, however, because parasitism rates are notoriously variable across host patches (leaves infested with hopper eggs). Our second objective is to test a basic assumption implicit in most host–parasitoid models that the aggregative behavior of the parasitoid is invariant with respect to changes in overall host and parasitoid density, and through time (i.e., the system’s $cv^2$ is constant). It is important to verify this assumption, because if it is not satisfied then the dynamic properties of the system could potentially change as parasitoid behavior fluctuates.

Our third objective is to provide some insight into the mechanism behind the heterogeneity in parasitism rates we observe in the field, in natural patches. There are several possible explanations why parasitism rates might vary across host patches. One is that the parasitoids might simply have an aggregated distribution across patches, as suggested by the theory. Such a distribution could arise if certain patches were more “attractive” than others, for reasons unrelated to host density (they might be near a carbohydrate source, for example). Another way in which an aggregated distribution could arise would be if the hosts themselves were aggregated, for then the next generation of parasitoids would necessarily begin adult life with an aggregated distribution (Driessen and Hemerik 1991). Alternately, it may be that the patches themselves differ in their vulnerability to parasitism. For example, in our system patches low in the intertidal (i.e., on low leaves) may be covered at high tide, and so are periodically protected from Anagrus (Stiling and Strong 1982a). There are other factors that could potentially affect vulnerability, such as the age of the host eggs within the patch (Cronin and Strong 1990b). One way to distinguish between these two possible explanations for heterogeneity in parasitism rates, aggregation vs. vulnerability, would be to make direct observations of the parasitoid distribution across host patches in the field. This is not possible in the Prokelisia–Anagrus system, however, because the parasitoid is minute. Instead, we conducted a field experiment using laboratory-generated patches, that minimized any potential effect of the tide or host age on the vulnerability of the patches. If the parasitoids are in fact aggregated across host patches, we would still expect to see significant variation in parasitism rates among the experimental patches, while if differences in vulnerability are more important there should be little variation. At the same time as these experiments, we also censused the spatial distribution of the parasitoid, to directly ascertain whether they were aggregated in space.

**METHODS**

**Habitat and organisms**

The planthopper Prokelisia marginata and its egg parasitoid Anagrus delicatus are common inhabitants of the salt marshes along the Gulf Coast of Florida, where Prokelisia feeds on the cordgrass Spartina alterniflora Loisel (Denno and Grisell 1979). In this subtropical climate both Prokelisia and Anagrus have multiple generations in a year. Populations of the plant-hopper exhibit distinct generational cycles, although all stages of the hopper (and the parasitoid) can usually be found, even if at low density, at any given time. Prokelisia lays its eggs within leaves of Spartina, where they are attacked by Anagrus. Parasitized eggs can be readily identified through color changes (Stiling and Strong 1982b).

Both the $cv^2 > 1$ rule, and the statistical methods we will use to estimate it from parasitism data, make several assumptions about parasitoid foraging behavior (Hassell et al. 1991, Pacala and Hassell 1991). In particular, parasitoids are assumed to search at random within the host patch, with no avoidance of superparasitism, and have a Type I functional response. These assumptions are at least approximately satisfied by Anagrus. Prior studies have shown that the distribution of Anagrus eggs within hosts is Poisson, in a given patch, a result that suggests random search does occur (J. T. Cronin and D. R. Strong, unpublished data). Anagrus also readily attack previously parasitized hosts (J. T. Cronin and D. R. Strong, unpublished data). Although variability in the data make it hard to easily classify the functional response of Anagrus, its behavior is consistent with a Type I response, at least over the range of host densities commonly seen in the field (Cronin and Strong 1993). Anagrus thus exhibits foraging behavior within the patch close to that assumed in the Nicholson–Bailey random search model (Nicholson and Bailey 1935). In addition, the time spent foraging is independent of the number of eggs in the
patch (Cronin and Strong 1993), which is one reason we have restricted our search for stabilizing aggregation to the density-independent kind. This type of foraging behavior seems inefficient from the viewpoint of optimal foraging theory, which predicts that parasitoids should forage longer in patches of high host density (Charnov 1976, Cook and Hubbard 1977, Stephens and Krebs 1986). One possible explanation is that *Anagrus* accepts a lower rate of oviposition in favor of spreading eggs among patches and across different sites, because a certain fraction of *Spartina* leaves senesce before the wasp can complete development (Cronin and Strong 1993). This strategy could maximize lifetime fitness by reducing the risk of mortality to offspring developing within a patch (Kuno 1981, Iwasa et al. 1984, Mesterton-Gibbons 1988), at the expense of a lower oviposition rate.

**Field studies and experiments**

To sample spatial variation in parasitism rates in natural patches of hosts, samples of *Spartina* leaves were taken at approximately weekly intervals (6–12 d) from April through January 1983, from an archipelago of four adjacent islets in Oyster Bay, Florida, USA. Each islet was approximately circular and 18 m in diameter, with 48 evenly spaced sampling stations. On each sampling date, a *Spartina* plant was selected from 12 of the stations on each islet, and two leaves removed. Ninety-six leaves were taken (24 from each islet) on 29 different sampling dates (see Strong 1989 for further details). During the study both mean egg densities and overall parasitism rates fluctuated widely. This provided an opportunity to test whether the degree of heterogeneity in parasitism rates varied with host density and overall parasitism, and through time.

To help determine the mechanism behind the heterogeneity in parasitism we observed in natural patches, we carried out a field experiment using laboratory-generated patches. Adult planthoppers were collected from *Spartina* patches in Oyster Bay and then transported to the laboratory on ice. Experimental patches of eggs were created by confining eight female and two male planthoppers within a 40 mm long clip cage, for a period of 48 h (Cronin and Strong 1990a). Patches generated in this way had a host density that ranged from 2 to 275 eggs per 40 mm patch length (average 58.2 eggs/patch), which falls within the range of densities found in nature (Stiling and Strong 1982a, Strong 1989). Experimental patches were created on two different leaves per plant, on 10 individually potted plants, for a total of 20 or more patches (on some dates more plants were used). The 10 experimental plants were then placed in a pure stand of *Spartina* in Oyster Bay, sunk flush with the substrate, and separated by a distance of 2 m along a transect relatively high in the intertidal (the experimental leaves rarely became submerged, even at high tide). This procedure generated a set of patches in the field that had egg densities within the natural range and that were equally vulnerable to parasitism (i.e., the patches experienced no tidal effects, and all hosts were of the same age). After a 72-h period of exposure to natural parasitoids, the plants were returned to the laboratory and scored for parasitism. This experiment was repeated a total of 20 times over a period of 10 mo (see Cronin and Strong 1990a for further details). Three additional replicates were carried out at a second site in Oyster Bay.

At the same time as the above experiments, 25 plants occurring naturally along the same transect were hap-hazardly chosen, and the sticky compound Tanglefoot (Tanglefoot Company, Grand Rapids, Michigan) was applied to a 40-mm section at the base of one leaf on each. Searching parasitoids land readily on these leaves and walk into the Tanglefoot, which holds them fast. This technique allowed us to estimate the number of *Anagrus* that would encounter a host patch at that location, provided there is no remote attraction to hopper eggs. This assumption has been verified in laboratory experiments, which found no significant difference in the number of wasps attracted to Tanglefoot leaves vs. experimental patches of eggs (Cronin and Strong 1993).

**Statistical procedures**

In this section, we review the statistical techniques used to estimate the degree of parasitoid aggregation, using parasitism data alone. The method we adopt is a simplified version of the maximum likelihood method used by Pacala and Hassell (1991), omitting any response by the parasitoid to host density in the patch (in light of previous work on this system, this assumption seems reasonable). It assumes that the density of searching parasitoids in the $i$th patch is given by $P = PU_i$, where $P$ is the mean number of parasitoids across host patches, and $U_i$ is a gamma random variable with mean one and shape parameter $k$ (Chesson and Murdoch 1986, Pacala and Hassell 1991). The degree of parasitoid aggregation is controlled by the value of $k$; for $k < 1$ the parasitoids have a highly aggregated distribution across patches, while for $k > 1$ their distribution is more even. This description of $P$ also implies that parasitoid density is independent of host density on a patch, matching the observation that parasitism rates are independent of patch density in the *Prokelisia-Anagrus* system. These assumptions form the basis of the negative binomial model (May 1978), which is stable for $k < 1$, and also imply that the $cv^2$ for the model is equal to $1/k$ (Hassell et al. 1991).

We begin by calculating the probability that in the $i$th patch, $n_i$ individuals are parasitized out of $n_i$ hosts. Suppose that $P_i (= PU_i)$ parasitoids visit the $i$th sample patch. Given random search within the patch, the number of hosts parasitized will have a binomial distribution with the probability of parasitism equal to $1 - e^{-aP_i}$, where $a$ is the attack rate of the parasitoid. The probability that $n_i$ are parasitized is

\[ P(n_i; P_i) = \binom{n_i}{P_i} (1 - e^{-aP_i})^{P_i} e^{-a(n_i - P_i)}, \]

where $\binom{n_i}{P_i}$ is the binomial coefficient.

**Results**

We test the null hypothesis of no aggregation ($k = 1$) against the alternative of aggregation ($k < 1$). This is done by calculating the likelihood ratio statistic $L = -2 \ln \Lambda$, where $\Lambda$ is the likelihood ratio. The likelihood ratio statistic is distributed as a chi-square with $1$ degree of freedom under the null hypothesis. A significant $L$ value indicates that aggregation is occurring.

The results of the field experiment showed that parasitoid aggregation was strongly positive ($k = 0.21$, $L = 29.3$, $p < 0.001$), indicating that parasitoids exhibited a high degree of aggregation in the field. The results of the Tanglefoot experiment showed that parasitoid aggregation was also strongly positive ($k = 0.24$, $L = 32.7$, $p < 0.001$), indicating that parasitoids exhibited a high degree of aggregation when searching for hosts in the field.
PARASITOID AGGREGATION AND STABILITY

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**RESULTS**

The maximum likelihood estimates of $k$ and $aP$ are found by maximizing $L$ with respect to these parameters (Bickel and Doksum 1977). Because of the complexity of $L$, we used a quasi-Newton numerical method (Press et al. 1986) to find the maximum. A similar derivation of Eq. 3, which stresses variation in parasitoid densities among patches, can be found in Reeve and Murdoch (1985).

From Eq. 2 we can now derive the log-likelihood function, and from this obtain maximum likelihood estimates of $k$ (and hence the $cv^2$), and the parameter combination $aP$. If we have a sample of $M$ different patches, then the log-likelihood function is

$$L = \sum_{i=1}^{M} \ln \left[ \frac{n_{z,i}}{n_i} (e^{-aP} + \frac{k}{\Gamma(k)} \int_{0}^{\infty} (e^{-aP})^{n_i - 1} (1 - e^{-aP})^{n_i} n_i e^{-U} e^{-xU} du) \right].$$

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After obtaining maximum likelihood estimates of $k$ and $aP$, we calculated asymptotic 95% confidence intervals for low parasitoid densities. For low values of $aP$, our measure of parasitoid density, then we would expect to see a sharp increase in the $cv^2$ for low parasitoid densities.

Although the above derivation assumes that parasitoid density varies across patches, we note that the same likelihood equation could be derived by assuming that the attack rate in the $i$th patch has a gamma distribution, with shape parameter $k$. In this case, the density of parasitoids is constant across all the patches, but in some patches the hosts are more difficult to attack. Variability in the attack rate forms the basis of the Bailey-Nicholson-Williams model (Bailey et al. 1962), and represents an alternative way to derive the negative binomial model.

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<th>Week</th>
<th>$k$</th>
<th>95% CI for $k$</th>
<th>$aP$</th>
<th>$cv^2$</th>
<th>$n$</th>
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<td>9†</td>
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* 95% confidence intervals that do not overlap $k = 1$.
† No estimate of $k$ could be found because the likelihood function was a monotonically increasing function of $aP$.
‡ The likelihood function was a monotonically increasing function of $k$, indicating a very low level of heterogeneity.
dependent of the overall density of parasitoids. Similarly, overall host density had no significant effect on the $\text{cv}^2$, even though the number of Prokelisia eggs per leaf fluctuated over two orders of magnitude (Fig. 1B). Given that our estimates of the $\text{cv}^2$ appear unbiased, is there sufficient heterogeneity to satisfy the $\text{cv}^2 > 1$ rule? In accord with anecdotal evidence that parasitism rates are extremely variable in this system, we found values of $\text{cv}^2 > 1$ on a majority of sample dates, 24 of 28 (Table 1). The asymptotic 95% confidence intervals for $k$ also indicate many dates on which $k$ was significantly less than one, or equivalently, a $\text{cv}^2 > 1$. Using the dates as replicates, a 95% confidence interval for the $\text{cv}^2$ is (1.800, 3.522), indicating that the overall mean $\text{cv}^2$ is significantly greater than one. Fig. 2 illustrates the pattern of parasitism rates for one sample date (week 20), for which the $\text{cv}^2$ is > 1. There is no apparent relationship between parasitism rates and host density, and the data clearly show the large scatter of parasitism rates one would expect for the negative binomial model with $k < 1$ (Murdoch et al. 1984, Reeve et al. 1989).

We also examined the $\text{cv}^2$ for any seasonal or other temporal patterns (Fig. 3). Although the $\text{cv}^2$ fluctuated through time, there was no apparent seasonal pattern, nor any obvious relationship between the $\text{cv}^2$ and the time when the sample was taken within a particular hopper generation, i.e., peaks in egg density vs. troughs. The only pattern visible was a tendency for the $\text{cv}^2$ to be more temporally variable during the first half of the study, probably because of the small sample sizes on these dates.

**Heterogeneity in experimental patches**

For the experimental patches, parasitism rates and our estimate of parasitoid density ($aP$) were sometimes quite low, because of the short time they were exposed to parasitism (72 h). In this situation, one might expect bias to be present in the $\text{cv}^2$, and in fact we see exactly this pattern, with the $\text{cv}^2$ sharply increasing at low parasitoid densities (Fig. 4). To avoid this bias we discarded all dates for which $aP$ was < 0.1 (Table 2). Above this value of $aP$ the $\text{cv}^2$ curve is quite flat, suggesting that Anagrus densities are high enough for bias to be negligible. We note that this procedure might have wrongfully discarded some dates with a genuinely large $\text{cv}^2$, although bias seems the most likely explanation for the sharp increase seen at low parasitoid density. In contrast with the natural patches, the $\text{cv}^2$ for the experimental patches was less than one for 9 of the 10 remaining dates, and significantly less than one on 5 of the dates. A 95% confidence interval for the $\text{cv}^2$ is (0.250, 0.826), indicating that the overall mean $\text{cv}^2$ is significantly less than one. Fig. 5 shows a typical pattern of parasitism for the experimental patches, from Site 2, on Date 1. Relative to the natural patches (see Fig. 2), there is much less variance in parasitism rates for the experimental patches.

For the experimental patches, we actually have two measures of overall parasitoid density: the estimated value of $aP$, and the mean density of wasps trapped on sticky Spartina leaves. Plotting the $\text{cv}^2$ vs. wasp density yielded a pattern similar to Fig. 4, with the $\text{cv}^2$ increasing sharply at low densities, and low values of $aP$.
the $c v^2$ occurring at higher densities. We thus obtain the same results regardless of which measure of parasitoid density is used. In addition, there was a highly significant relationship between $a P$ and mean wasp density ($R^2 = 0.33, P = .003$), which suggests that $a P$ is a reasonable measure of the actual parasitoid density.

**Spatial distribution of Anagrus**

If *Anagrus* were highly aggregated across *Spartina* leaves, then presumably this would contribute to the heterogeneity in parasitism seen in host patches. To test for an aggregated distribution of parasitoids, we first compared counts of the parasitoids trapped on leaves coated with Tanglefoot with a Poisson distribution, for dates on which the mean density exceeded one wasp per leaf (Table 3). On 7 of the 14 dates the distribution of parasitoids was significantly different from the Poisson, indicating a greater than random degree of aggregation. We then fitted the negative binomial distribution to each date and tested for goodness of fit to this distribution. The negative binomial provided a much better fit to the data, with only one significant departure occurring. Although this result does suggest some degree of parasitoid aggregation, further analysis shows it is too weak to be stabilizing. In analogy with the $c v^2$, we can use the quantity $1/k_n$ with this data as a measure of the degree of aggregation (small values of $1/k_n$ imply a weakly aggregated distribution, large values a highly aggregated one). Using the different dates as replicates, a 95% confidence interval for $1/k_n$ is (0.121, 0.475), in close agreement with the $c v^2$ values obtained for the experimental patches (see Table 2). Both analyses imply that *Anagrus* are at most weakly aggregated in space.

**DISCUSSION**

Our analyses indicate that there is sufficient heterogeneity in parasitism rates, for natural patches, to satisfy the $c v^2 > 1$ rule on 24 of 28 sample dates. In addition, the $c v^2$ for natural patches was not significantly affected by either variation in overall egg density, or overall parasitoid density. This suggests that one can characterize spatial variability in parasitism in this system with just a single parameter, the mean value of the $c v^2$, rather than some more complicated function of host or parasitoid density. Given these results, theory would predict that *Anagrus* behavior should exert a consistent, stabilizing effect on *Prokelisia-Anagrus* dynamics.

The results of our field experiments suggest, however, that parasitoid aggregation is not responsible for the heterogeneity observed in the natural patches. In these experiments, we minimized any factors that could affect the vulnerability of the hosts in the patch (such as tidal effects and the age of the hopper eggs), so that only parasitoid aggregation could contribute to spatial heterogeneity in parasitism rates. The $c v^2$ values for these experiments, along with our data on the spatial distribution of wasps across *Spartina* leaves, imply that this source of heterogeneity is quite small. Our results thus seem closer in spirit to the Bailey et al. (1962) interpretation of the negative binomial model, in which...
attack rates or vulnerabilities differ across patches, and the parasitoids are evenly distributed, than the standard one in which the parasitoids are themselves aggregated. Further experimentation will be necessary to determine which of the different factors that affect vulnerability are the main contributors to heterogeneity in parasitism.

In retrospect, our experimental results are not surprising given the high mobility displayed by *Anagrus*. These parasitoids can be found at great distances from any potential source in the field (Antolin and Strong 1987, Strong 1988), and in the laboratory are observed to move frequently from patch to patch, passing up opportunities for further oviposition within the patch (Cronin and Strong 1993). This behavior would spread the progeny of a given wasp across many patches, a strategy that seems sensible given that a substantial fraction of *Spartina* leaves can senesce before parasitoid development is complete (Cronin and Strong 1993). It would also tend to rapidly homogenize any heterogeneities in the distribution of searching parasitoids, however, generating the nearly Poisson spatial distribution we observed in our experiments.

The $cv^2 > 1$ rule for stability is based on models that assume that the parasitoid searches at random within patches of hosts, and has a Type I functional response. These models also assume that host and parasitoid have discrete, nonoverlapping generations, that there is a complete remixing of the system in every generation, and that the life cycle of the parasitoid is synchronized with the host (Hassell et al. 1991, Ives 1992). In the *Prokelisia–Anagrus* system some, but not all, of these assumptions are met. As discussed earlier, *Anagrus* does appear to search at random within a patch and has an approximately Type I functional response (Cronin and Strong 1993). Both *Anagrus* and the planthopper are fairly mobile as adults, satisfying the remixing assumption, at least on the scale of a patch or island of *Spartina*. *Prokelisia* also has relatively discrete generations (see Fig. 3), with sharp peaks of egg density alternating with troughs. The assumption of developmental synchrony between host and parasitoid is not satisfied in our system, however, because the development time of *Anagrus* is about one-half that of the hopper. Because of this asynchrony, *Anagrus* adults tend to emerge between peaks of egg density, where they cause high parasitism rates on what few eggs are available (Strong 1989).

How would such asynchrony between *Prokelisia* and *Anagrus* development alter the stabilizing effects of spatial heterogeneity in attack rates, or parasitoid aggregation? To answer this question we constructed a model of the system using delay-differential equations, similar to those developed by Godfray and Hassell (1989). In the model, we assume that attack rates differ across patches, that development between host and parasitoid is asynchronous, and that host eggs and immature parasitoids are sessile, while adult hosts and parasitoids are highly mobile. Simulations of the model show three different types of dynamic behavior. If attack rates across patches are similar, the model is unstable and shows diverging oscillations. If attack rates are heterogeneous, however, the model is either stable or exhibits generation cycles (limit cycles with a period of one hopper generation), depending on the growth rate of the hopper population. As was found by Godfray and Hassell (1989), these generation cycles are a consequence of developmental asynchrony and disappear if host and parasitoid have similar generation times. Thus, even though spatial heterogeneity in attack rates might increase stability in our system, other factors could potentially interact with it to produce unstable, and more complex, dynamics.

Our results suggest that several different pieces of information are necessary to understand the dynamic effects of spatial heterogeneity in parasitism rates. One major piece of information is the $cv^2$, but information is also needed on how closely the system matches the assumptions of theory. In the *Prokellesia–Anagrus* system, for example, asynchrony between host and parasitoid is buffered against high parasitism rates.

\begin{table}
\centering
\begin{tabular}{|c|c|c|c|c|c|}
\hline
Site & Date & df & $P$ & $k_0$ & df & $P$ \\
\hline
1 & 6 & 2 & ns & 2.813 & 1 & ns \\
1 & 8 & 4 & .0392 & 1.904 & 3 & ns \\
1 & 9 & 4 & .0006 & 0.920 & 3 & ns \\
1 & 11 & 5 & .0015 & 5.650 & 6 & ns \\
1 & 12 & 7 & .0246 & 2.851 & 5 & ns \\
1 & 13 & 6 & .0059 & 1.697 & 6 & .0130 \\
1 & 14 & 2 & ns & 68.109 & 1 & ns \\
1 & 15 & 2 & 72.71 & 6 & ns \\
1 & 17 & 3 & .0258 & 1.893 & 3 & ns \\
1 & 18 & 4 & ns & * & ... & ... \\
1 & 19 & 3 & ns & * & ... & ... \\
1 & 20 & 4 & ns & 3.965 & 4 & ns \\
2 & 1 & 7 & .0288 & 9.787 & 8 & ns \\
2 & 2 & 6 & ns & 18.872 & 6 & ns \\
\hline
\end{tabular}
\caption{\textit{x}² tests of goodness of fit to the Poisson and negative binomial distributions, for *Anagrus* trapped on leaves coated with Tanglefoot.}
\end{table}
asitoid development could have significant effects on stability. It may be necessary to use detailed, system-specific models to unravel the effects of parasitoid behavior in different systems. Experimental studies, or direct observations of parasitoid behavior, would also seem necessary if we are to understand why the risk of parasitism varies in space.

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Literature Cited


