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PARASITOID AGGREGATION AND THE STABILIZATION OF A SALT MARSH HOST–PARASITOID SYSTEM[1]

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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 "$\mathrm{CV}^2 > 1$" 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 (CV^2) 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, *Aonidiella 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 CV^2 from patterns of parasitism in 34 published studies, partitioning the CV^2 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

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density. They found values of the $\text{CV}^2 > 1$ 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 (Redfern 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) (Homoptera: 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 1982*a,* Cronin and Strong 1990*a,* 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 1982*a*). There are other factors that could potentially affect vulnerability, such as the age of the host eggs within the patch (Cronin and Strong 1990*b*). 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 cord grass *Spartina alterniflora* Loisel (Denno and Grissell 1979). In this subtropical climate both *Prokelisia* and *Anagrus* have multiple generations in a year. Populations of the planthopper 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 1982*b*).

Both the $\text{CV}^2 > 1$ 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 1990*a*). 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 1982*a*, 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 1990*a* 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 haphazardly 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 $P_i = PU_i$, 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_i 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_{1i} individuals are parasitized out of n_{2i} 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 $1 - e^{-aPU_i}$, where a is the attack rate of the parasitoid.The probability that n_{1i} are parasitized is

$$P(n_{1i} \mid n_{2i}, U_i) = \binom{n_{2i}}{n_{1i}} (e^{-aPU_i})^{n_{2i}-n_{1i}} (1 - e^{-aPU_i})^{n_{1i}}. \qquad (1)$$

Note that this is a conditional probability, depending on the value of U_i. To calculate the unconditional probability we integrate Eq. 1 over the distribution of U_i, to obtain

$$P(n_{1i} \mid n_{2i}) = \binom{n_{2i}}{n_{1i}} \frac{k^k}{\Gamma(k)} \int_0^\infty (e^{-aPu})^{n_{2i}-n_{1i}} (1 - e^{-aPu})^{n_{1i}} \times u^{k-1} e^{-ku}\, du. \qquad (2)$$

This equation can be further simplified, but because of rounding error (see Pacala and Hassell 1991) it is best evaluated in integral form, using numerical methods and various transformations (Press et al. 1986).

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

$$L = \sum_{i=1}^{M} \ln\left[\binom{n_{2i}}{n_{1i}} \frac{k^k}{\Gamma(k)} \int_0^\infty (e^{-aPu})^{n_{2i}-n_{1i}} (1 - e^{-aPu})^{n_{1i}} \times u^{k-1} e^{-ku}\, du\right]. \qquad (3)$$

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 parasitism rates among patches, can be found in Reeve and Murdoch (1985).

After obtaining maximum likelihood estimates of k and aP, we calculated asymptotic 95% confidence intervals for k by inverting the likelihood ratio test (Bickel and Doksum 1977). These intervals were derived using the asymptotic distribution of the likelihood ratio test statistic, which approaches a χ^2 distribution with 1 df as the number of samples becomes large.

In the model we use to estimate k and the CV^2, it is assumed that the number of parasitoids visiting a patch is large enough that we may accurately approximate their distribution using a continuous (i.e., gamma) random variable. As overall parasitoid densities decrease, however, this assumption will break down and the estimates will become increasingly biased, underestimating the true k and hence overestimating the CV^2 (see also Hassell et al. 1991:576). To examine our estimates for this potential source of bias, we plotted the CV^2 vs. aP, a measure of the overall density of parasitoids, for both the natural and experimental patches. If parasitoid densities are low enough to cause bias, then we would expect to see a sharp increase in the CV^2 for low parasitoid densities.

TABLE 1. Maximum likelihood estimates of k, aP, and the CV^2 for natural patches of hosts, with n the number of patches.

Week	k	95% CI for k	aP	CV^2	n
1	0.18	(0.03, 0.97)*	0.77	5.65	7
2	0.17	(0.07, 0.45)*	0.25	5.74	26
3	0.30	(0.07, 1.40)	0.17	3.31	16
4	2.96	(0.19, >20)	0.13	0.34	16
5	0.49	(0.07, >20)	0.24	2.05	9
6	0.10	(0.02, 0.38)*	1.02	10.51	9
7	0.19	(0.06, 0.55)*	0.36	5.38	15
8	0.68	(0.12, 4.20)	1.39	1.47	7
9†	...	...	...	...	11
10	0.32	(0.14, 0.75)*	1.59	3.08	19
11‡	>20	...	0.06	<0.05	12
12	0.22	(0.07, 0.69)*	0.16	4.63	21
13	0.31	(0.14, 0.66)*	0.83	3.23	32
14	0.58	(0.30, 1.09)	0.32	1.74	37
15	0.45	(0.27, 0.75)*	0.55	2.20	47
16	0.64	(0.39, 1.06)	0.67	1.55	47
17	0.54	(0.31, 0.93)*	0.72	1.86	48
18	0.38	(0.22, 0.63)*	0.60	2.66	51
19	0.71	(0.47, 1.10)	0.23	1.40	71
20	0.80	(0.54, 1.16)	0.72	1.26	80
21	1.75	(1.00, 3.14)*	1.74	0.57	61
22	0.32	(0.16, 0.56)*	2.98	3.09	48
23	0.34	(0.20, 0.54)*	0.32	2.96	58
24	0.30	(0.20, 0.46)*	0.29	3.28	77
25	0.72	(0.44, 1.18)	0.88	1.39	66
26	0.88	(0.45, 1.76)	2.34	1.14	43
27	0.86	(0.30, 2.88)	3.62	1.16	32
28	1.52	(0.19, >20)	0.72	0.66	9
29	0.47	(0.07, 5.47)	1.75	2.13	6

* 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.

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.

RESULTS

Heterogeneity in natural patches

Using the statistical method described above, we estimated k, aP, and the CV^2, for natural patches on each sample date, using individual leaves as the patch (Table 1). To check for potential bias, we then plotted the CV^2 vs. aP, using the sample dates as replicates (Fig. 1A). There was no indication of an increase in the CV^2 for low values of aP, our measure of parasitoid density, and we conclude that bias due to low parasitoid densities is probably minimal for the natural patches. More importantly, our data also suggest that the CV^2 is in-

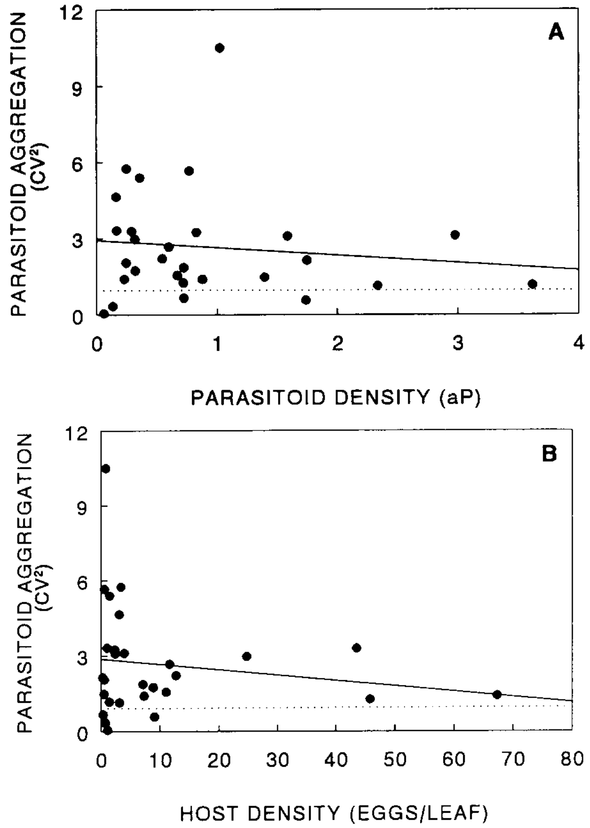

FIG. 1. The relationship between the cv^2 for natural patches of hosts and (a) the overall parasitism rate ($y = 2.931 - 0.298x$, NS), and (b) the mean number of host eggs per leaf ($y = 2.873 - 0.022x$, NS). The dotted line indicates a cv^2 value of 1, above which there is sufficient parasitoid aggregation to be stabilizing.

dependent of the overall density of parasitoids. Similarly, overall host density had no significant effect on the 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 cv^2 appear unbiased, is there sufficient heterogeneity to satisfy the cv$^2 > 1$ rule? In accord with anecdotal evidence that parasitism rates are extremely variable in this system, we found values of 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 cv$^2 > 1$. Using the dates as replicates, a 95% confidence interval for the cv^2 is (1.800, 3.522), which indicates that the overall mean cv^2 is also significantly greater than one. Fig. 2 illustrates the pattern of parasitism rates for one sample date (week 20), for which the 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 cv^2 for any seasonal or other temporal patterns (Fig. 3). Although the cv^2 fluctuated through time, there was no apparent seasonal pattern, nor any obvious relationship between the 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 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 cv^2, and in fact we see exactly this pattern, with the 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 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 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 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 cv^2 is (0.250, 0.826), indicating that the overall mean 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 cv^2 vs. wasp density yielded a pattern similar to Fig. 4, with the cv^2 increasing sharply at low densities, and low values of

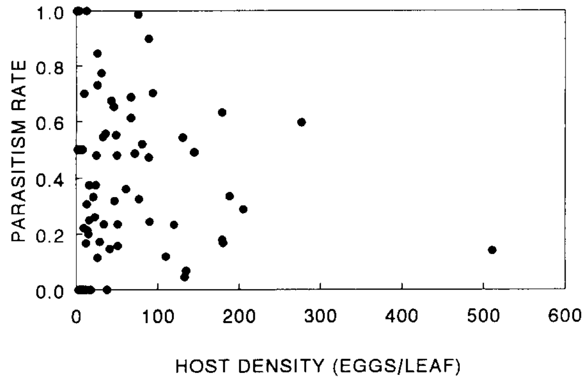

FIG. 2. Parasitism rates vs. host density for Week 20 of the island data set.

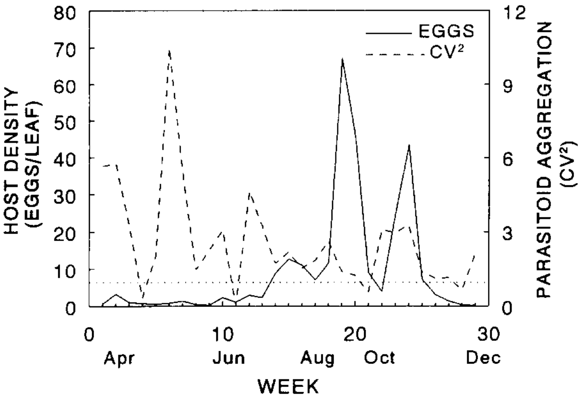

FIG. 3. Mean host-egg density and the CV^2 for natural patches, during the 29 wk of the study. For one date (Week 9) we were unable to estimate the CV^2 (see Table 1). The dotted line indicates a CV^2 value of 1.

the CV^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 aP and mean wasp density ($R^2 = 0.33$, $P = .003$), which suggests that aP 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 CV^2, we can use the quantity $1/k_{nb}$ with this data as a measure of the degree of aggregation (small values of $1/k_{nb}$ imply a weakly aggregated distribution, large values a highly aggregated one). Using the different dates as replicates, a 95% confidence interval for $1/k_{nb}$ is (0.121, 0.475), in close agreement with the CV^2 values obtained for the experimental patches (see Table 2). Both analyses imply that *Anagrus* are at most weakly aggregated in space.

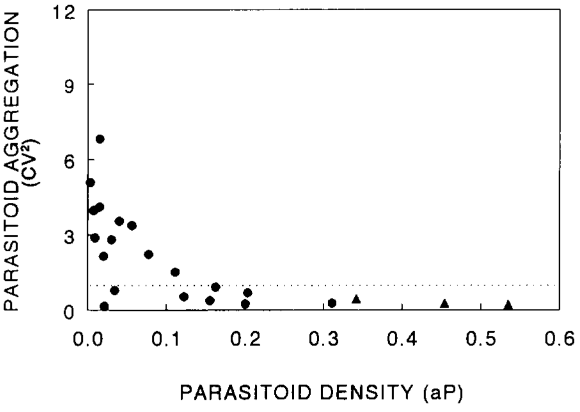

FIG. 4. The relationship between the CV^2 for experimental patches and overall parasitism rate, for data from the first (●) and second (▲) site at Oyster Bay. For clarity, a single point at (0.01, 43.869) is omitted from the graph. We did not attempt a linear regression. The dotted line indicates a CV^2 value of 1.

TABLE 2. Maximum likelihood estimates of k, aP, and the CV^2 based on experimental patches of hosts, with n the number of patches.

Site	Date	k	95% CI for k	aP	CV^2	n
1	2	2.74	(0.69, >20)	0.15	0.36	22
1	3	1.47	(0.52, 4.55)	0.20	0.68	16
1	6	0.67	(0.23, 1.90)	0.11	1.50	10
1	11	3.69	(1.52, 9.36)*	0.31	0.27	18
1	13	4.27	(1.22, >20)*	0.20	0.23	19
1	15	1.91	(0.56, 10.82)	0.12	0.52	17
1	20	1.11	(0.43, 2.87)	0.16	0.90	15
2	1	3.80	(1.99, 6.96)*	0.45	0.26	26
2	2	4.84	(2.14, 11.00)*	0.53	0.21	21
2	3	2.30	(1.04, 5.17)*	0.34	0.43	21

* 95% confidence intervals that do not overlap $k = 1$.

DISCUSSION

Our analyses indicate that there is sufficient heterogeneity in parasitism rates, for natural patches, to satisfy the CV$^2 > 1$ rule on 24 of 28 sample dates. In addition, the CV^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 CV^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 CV^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

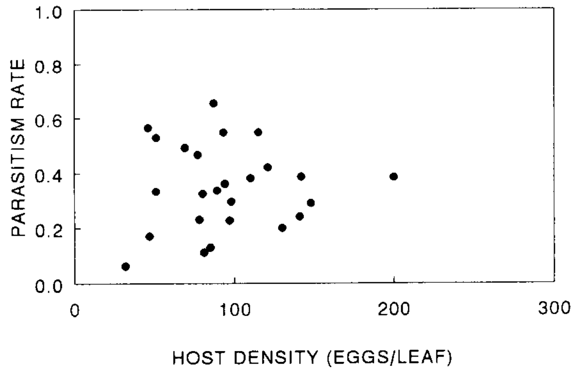

FIG. 5. Parasitism rates vs. host density for the experimental patches at Site 2, on Date 1.

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 $\mathrm{CV}^2 > 1$ 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 *Prokelisia–Anagrus* system, for example, asynchrony between host and par-

TABLE 3. χ^2 tests of goodness of fit to the Poisson and negative binomial distributions, for *Anagrus* trapped on leaves coated with Tanglefoot.

		Poisson		Negative binomial		
Site	Date	df	P	k_{ab}	df	P
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	6	NS	7.271	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

* The mean and variance were equal on these dates, indicating a distribution very close to the Poisson (i.e., $k = \infty$).

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

Antolin, M. F., and D. R. Strong. 1987. Long-distance dispersal by a parasitoid (*Anagrus delicatus*, Mymaridae) and its host. Oecologia (Berlin) **73**:288–292.

Bailey, V. A., A. J. Nicholson, and E. J. Williams. 1962. Interactions between hosts and parasites when some host individuals are more difficult to find than others. Journal of Theoretical Biology **3**:1–18.

Bickel, P. J., and K. Doksum. 1977. Mathematical statistics. Holden-Day, San Francisco, California, USA.

Charnov, E. L. 1976. Optimal foraging: the marginal value theorem. Theoretical Population Biology **9**:129–136.

Chesson, P. L., and W. W. Murdoch. 1986. Aggregation of risk: relationships among host–parasitoid models. American Naturalist **127**:696–715.

Cook, R. M., and S. F. Hubbard. 1977. Adaptive searching strategies in insect parasites. Journal of Animal Ecology **46**: 115–125.

Cronin, J. T., and D. R. Strong. 1990*a*. Density-independent parasitism among host patches by *Anagrus delicatus* (Hymenoptera: Mymaridae): experimental manipulation of hosts. Journal of Animal Ecology **59**:1019–1026.

Cronin, J. T., and D. R. Strong. 1990*b*. Biology of *Anagrus delicatus* (Hymenoptera: Mymaridae), an egg parasitoid of *Prokelisia* spp. (Homoptera: Delphacidae). Annals of the Entomological Society of America **83**:846–854.

Cronin, J. T., and D. R. Strong. 1993. Substantially submaximal oviposition rates by a mymarid egg parasitoid in the laboratory and field. Ecology **74**:1813–1825.

Denno, R. F., and E. E. Grissell. 1979. The adaptiveness of wing-dimorphism in the salt marsh-inhabiting planthopper, *Prokelisia marginata* (Homoptera: Delphacidae). Ecology **60**:221–236.

Driessen, G., and L. Hemerik. 1991. Aggregative responses of parasitoids and parasitism in populations of *Drosophila* breeding in fungi. Oikos **61**:96–107.

Godfray, H. C. J., and M. P. Hassell. 1989. Discrete and continuous insect populations in tropical enviroments. Journal of Animal Ecology **58**:153–174.

Hassell, M. P. 1984. Parasitism in patchy environments: inverse density dependence can be stabilizing. Journal of Mathematics Applied in Medicine and Biology **1**:123–133.

Hassell, M. P., and R. M. May. 1973. Stability in insect host–parasite models. Journal of Animal Ecology **42**:693–736.

Hassell, M. P., and R. M. May. 1974. Aggregation in predators and insect parasites and its effect on stability. Journal of Animal Ecology **43**:567–594.

Hassell, M. P., R. M. May, S. Pacala, and P. L. Chesson. 1991. The persistence of host-parasitoid associations in patchy environments. I. A general criterion. American Naturalist **138**:568–583.

Ives, A. 1992. Density-dependent and density-independent parasitoid aggregation in model host-parasitoid systems. American Naturalist **140**:912–937.

Iwasa, Y., Y. Suzuki, and H. Matsuda. 1984. Theory of oviposition strategy of parasitoids. I. Effect of mortality and limited egg number. Theoretical Population Biology **26**: 205–227.

Jones, T. H., M. P. Hassell, and S. W. Pacala. 1993. Spatial heterogeneity and the population dynamics of a host–parasitoid system. Journal of Animal Ecology **62**:251–262.

Kuno, E. 1981. Dispersal and persistence of populations in unstable habitats: a theoretical note. Oecologia **49**:123–126.

Lessells, C. M. 1985. Parasitoid foraging: should parasitism be density dependent? Journal of Animal Ecology **55**:923–940.

May, R. M. 1978. Host-parasitoid systems in patchy environments: a phenomenological model. Journal of Animal Ecology **47**:833–844.

Mesterton-Gibbons, M. 1988. On the optimal compromise for a dispersing parasitoid. Journal of Mathematical Biology **26**:375–385.

Murdoch, W. W., J. D. Reeve, C. B. Huffaker, and C. E. Kennett. 1984. Biological control of olive scale and its relevance to ecological theory. American Naturalist **123**: 371–392.

Nicholson, A. J., and V. A. Bailey. 1935. The balance of animal populations. Part I. Proceedings of the Zoological Society of London 1935: 551–598.

Pacala, S., and M. P. Hassell. 1991. The persistence of host-parasitoid associations in patchy environments. II. Evaluation of field data. American Naturalist **138**:584–605.

Pacala, S. W., M. P. Hassell, and R. M. May. 1990. Host–parasitoid interactions in patchy environments. Nature **344**: 150–153.

Press, W. H., B. P. Flannery, S. A. Teukolsky, and W. T. Vetterling. 1986. Numerical recipes: the art of scientific computing. Cambridge University Press, New York, New York, USA.

Redfern, M., T. H. Jones, and M. P. Hassell. 1992. Heterogeneity and density dependence in a field study of a tephritid–parasitoid interaction. Ecological Entomology **17**: 255–262.

Reeve, J. D., B. L. Kerans, and P. L. Chesson. 1989. Combining different forms of parasitoid aggregation: effects on stability and patterns of parasitism. Oikos **56**:233–239.

Reeve, J. D., and W. W. Murdoch. 1985. Aggregation by parasitoids in the successful control of the California red scale: a test of theory. Journal of Animal Ecology **54**:797–816.

Stephens, D. W., and J. R. Krebs. 1986. Foraging theory. Princeton University Press, Princeton, New Jersey, USA.

Stiling, P. D. 1987. The frequency of density dependence in insect host–parasitoid systems. Ecology **68**:844–856.

Stiling, P. D., and D. R. Strong. 1982*a*. Egg density and the intensity of parasitism in *Prokelisia marginata* (Homoptera: Delphacidae). Ecology **63**:1630–1635.

Stiling, P. D., and D. R. Strong. 1982*b*. The parasitoids of the planthopper *Prokelisia marginata* (Homoptera: Delphacidae). Florida Entomologist **65**:191–192.

Stiling, P. D., A. Throckmorton, J. Silvanima, and D. R. Strong. 1991. Does spatial scale affect the incidence of density dependence? A field test with insect parasitoids. Ecology **72**:2143–2154.

Strong, D. R. 1988. Parasitoid theory: from aggregation to dispersal. Trends in Ecology and Evolution **3**:277–280.

———. 1989. Density independence in space and inconsistent temporal relationships for host mortality caused by a fairyfly parasitoid. Journal of Animal Ecology **58**:1065–1076.

Walde, S. J., and W. W. Murdoch. 1988. Spatial density dependence in parasitoids. Annual Review of Entomology **33**:441–466.