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Combining different forms of parasitoid aggregation: effects on stability and patterns of parasitism

John D. Reeve, B. L. Kerans and Peter L. Chesson

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We present two models which blend different forms of parasitoid search behavior; aggregation independent of host density, and in response to host density. In the first model (Model A) parasitoid and host densities on a patch are assumed to be positively correlated, while in the second model (Model B) the parasitoids have a linear regression on host density, with an associated error term. In Model A, the dynamics were least stable when host and parasitoid were perfectly correlated. In Model B, the slope of the regression had only a moderate effect on stability, while large amounts of error strongly promoted stability. These results suggest that a weak and noisy aggregative response by the parasitoid may be strongly stabilizing, while a strong relationship between parasitoid and host density can sometimes produce instability. As a strong relationship also produces spatial density-dependence in parasitism rates, such a pattern in the field need not indicate stabilizing forms of parasitoid behavior.

J. D. Reeve, B. L. Kerans and P. L. Chesson, Dept of Zoology, Ohio State Univ., 1735 Neil Ave., Columbus, OH 43210, USA.

Introduction

The aggregative response of parasitoids to patches of their hosts has been reckoned an important component of host-parasitoid dynamics, in part because of its potential stabilizing effects (Hassell 1978). The first form of aggregation identified as stabilizing in models was aggregation in response to host density, in which foraging parasitoids either spend more time in patches of high host density, or more individuals find such patches (Hassell and May 1973, 1974). This would seem a sensible strategy for exploiting a patchily distributed resource, and versions of optimal foraging theory tailored to parasitoids have predicted such behavior (Cook and Hubbard 1977, Hubbard and Cook 1978, Comins and Hassell 1979, Iwasa et al. 1981). Provided the parasitoids are not strongly egg-limited, or limited by handling time, this form of aggregation should also generate a positive correlation between parasitism rate and patch density (Hassell 1982, Lessells 1985), a pattern found in roughly one-third of field studies (Morrison and Strong 1980, Lessells 1985, Walde and Murdoch 1988).

A second form of stabilizing behavior, aggregation independent of host density, occurs when parasitoids are clumped or aggregated in space in a manner unrelated to local host density (May 1978, Chesson and Murdoch 1986). While highly stabilizing, this type of aggregation predicts *no* correlation between parasitism rate and patch density (Murdoch et al. 1984, Chesson and Murdoch 1986), a pattern also found in roughly one-third of the field studies. The remaining one-third of the studies show an inverse relationship between parasitism and host density; this pattern could be generated by either type of aggregation if the parasitoids were sufficiently egg- or handling-time limited.

Real parasitoids are not likely to aggregate either purely in response to host density, or independently of host density. Their behavior will be a mixture of the two types of behavior, with the different types of aggregation representing endpoints along a continuum. Indeed,

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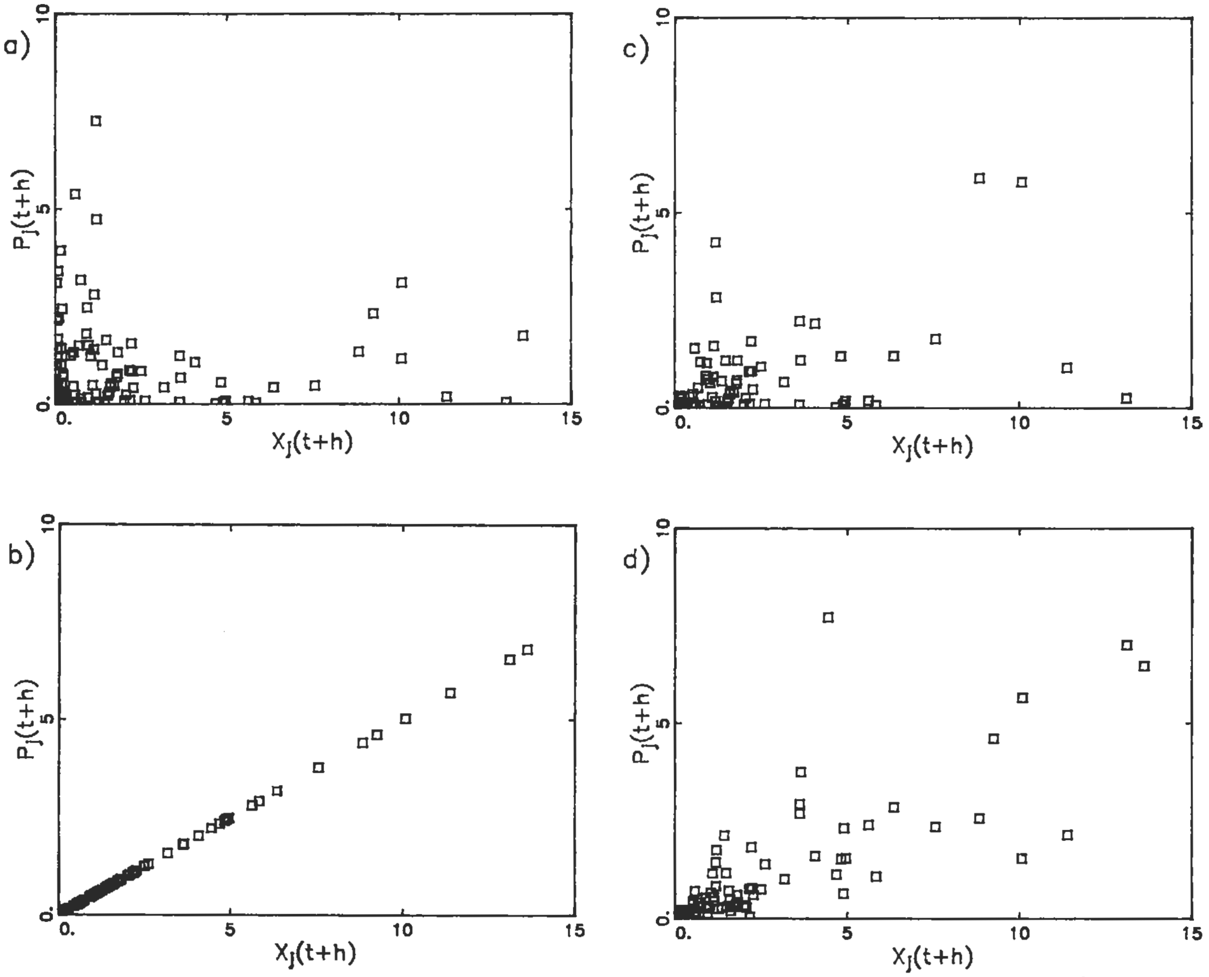

Fig. 1. The joint distribution of $X_j(t+h)$ and $P_j(t+h)$ for Model A and B, for $X(t) = 2$ and $P(t) = 1$. (a) Model A for $\varrho^2 = 0$ and $k = 0.5$, (b) Model A for $\varrho^2 = 1$ and $k = 0.5$, (c) Model B for $\varrho^2 = 1$, $k = 0.5$, and $m = 0.5$, (d) Model B for $\varrho^2 = 1$, $k = 2$, and $m = 0.5$.

Chesson and Murdoch (1986) describe a general class of models which incorporate both types of aggregation. They separate the aggregative response of the parasitoid into two parts, regression and error. The regression part of their formulation describes how the average density of parasitoids changes with the number of hosts per patch, while an error term describes how parasitoid density varies about this average value. They classify as "pure regression" those models which incorporate only aggregation in response to host density, since parasitoid densities are determined solely by patch density. "Pure error" models are those which incorporate only aggregation independent of host density.

In this paper, we examine the dynamic behavior of two models which incorporate both types of aggregation, in simple and biologically plausible forms. One model (Model A) assumes that host and parasitoid densities on a patch are correlated, with the correlation ranging form zero to one. In this model the error and regression components of parasitoid behavior are inversely related; as the correlation is varied from zero ton one the model changes from pure error (no relationship between parasitoid and host density) to pure regression (a linear relationship). It is shown that a high correlation between parasitoid and host, implying a strong response by the parasitoid to host density, acts to destabilize the dynamics. A second model (Model B) uses the basic framework of Chesson and Murdoch (1986), and further assumes that parasitoid density has a linear regression on host density, with an error term independent of the regression component of the model. In this model stability arises mainly from the error term, not the regression term. In both models, a pattern of density-dependent parasitism is most apparent when the dynamics are *unstable*, not stable.

Models

We begin by assuming that the spatial redistribution of host and parasitoid occurs first within a generation,

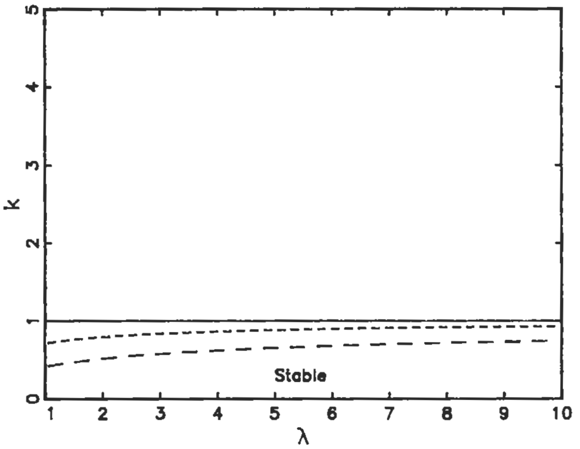

Fig. 2. Stability boundaries for Model A. -- $\varrho^2 = 0.75$, --- $\varrho^2 = 0.5$, — $\varrho^2 = 0$.

from time to to t+h, followed by host reproduction and parasitism from t+h to t+1 (this is a standard assumption of host-parasitoid models). In the first model we will examine, Model A, a bivariate version of the gamma distribution is used to model the redistribution of hosts and parasitoids across patches (Johnson and Kotz 1972: 220). The distribution describes the density of hosts and parasitoids on the jth patch after migration, namely X_j (t+h) and P_j (t+h), given the spatial correlation ϱ^2 between host and parasitoid (always non-negative), their mean densities X(t) and P(t) at time t, and a shape parameter k. As in the univariate gamma distribution, k describes the degree of clumping in both host and parasitoid; $k < 1$ implies that both organisms are strongly clumped, with patches having either very low or high densities. A. Ives (pers. comm.) has also used this distribution to describe patch apparency for two competing species.

The effect of correlation on the joint distribution of $X_j(t+h)$ and $P_j(t+h)$ is shown in Fig. 1, using variates drawn from the bivariate gamma distribution. When $\varrho^2 = 0$, the density of parasitoids on a patch is independent of the host density, and we observe only a scatter of $X_j(t+h)$ and $P_j(t+h)$ values (Fig. 1a). When $\varrho^2 = 1$ parasitoid and host density are linearly related, however, and lie on a straight line through the origin (Fig. 1b). Intermediate values of ϱ^2 yield lines of intercept $\beta_0 = (1 - \varrho^2)P(t)$ and slope $\beta_1 = \varrho^2 P(t)/X(t)$ (Johnson and Kotz 1972). The marginal densities of $X_j(t+h)$ and Pj (t+h) are univariate gamma with means X(t) and P(t), and common shape parameter k.

The bivariate gamma distribution, while analytically tractable, also makes the assumption that the regression and error components of parasitoid aggregation are inversely related: as ϱ^2 is increased the model varies from pure error to pure regression, and it is not possible to increase the error about the regression, without decreasing the slope. It also assumes that the marginal distributions of both host and parasitoid density have a common shape parameter (i.e., k). In the second model we will examine, Model B, both these assumptions are relaxed. As in Model A, we assume that the marginal distribution of hosts is gamma, with mean X(t) and shape parameter m. We then specify that the number of

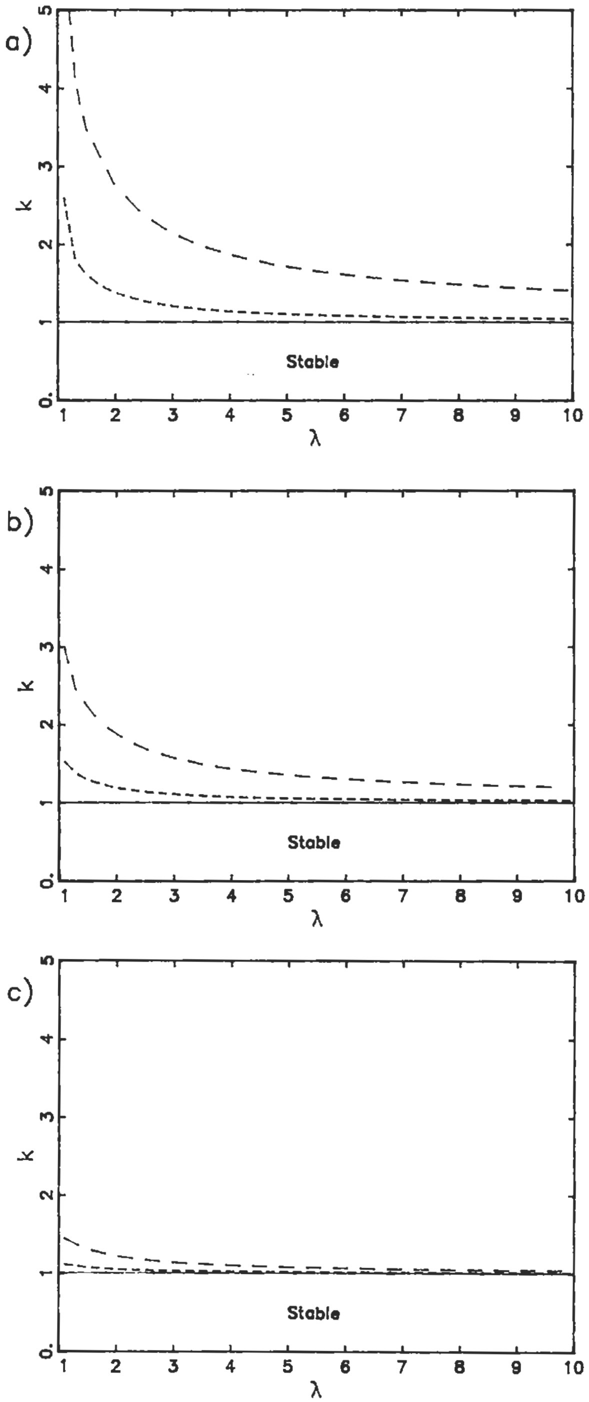

Fig. 3. Stability boundaries for Model B. (a) m = 0.5, (b) m = 1, (c) m = 4. -- $\varrho^2 = 1$, --- $\varrho^2 = 0.5$, — $\varrho^2 = 0$.

parasitoids on the jth patch is given by

$$Pj(t+h) = \left\{(1-\varrho^2)P(t) + \frac{\varrho^2 P(t)}{X(t)} X_j(t+h)\right\} U_j(t+h). \quad (1)$$

As in Model A, the parameter ϱ^2 varies between zero and one. The quantity $U_j(t+h)$ is defined to be a gamma random variable with mean 1 and shape parameter k, independent of $X_j(t+h)$, and can be thought of as the error component of the model (see Chesson and Murdoch 1986). The smaller the value of k, the more skewed the distribution of $U_j(t+h)$, and the more error in the parasitoid's aggregative response to host density. The above definition for $P_j(t+h)$ ensures that the regression of $P_j(t+h)$ on $X_j(t+h)$, i.e., the expected value of $P_j(t+h)$ given $X_j(t+h)$, is the same as for Model A. As ϱ^2 varies from zero to one the model shifts from a pure error model with a regression slope of zero, to one which includes both regression and error components. Unlike Model A, the error component $U_j(t+h)$ is always present with the same coefficient of variation, regardless of the value of ϱ^2. This provides a useful contrast with the Model A, and will help illustrate the important role of the error term in generating stability.

Fig. 1c and 1d show some variates from Model B, for $m = 0.5$, $k = 0.5$ and $k = 2$, and for $\varrho^2 = 1$. Unlike Model A, which is pure regression for this value of ϱ^2, the values of $P_j(t+h)$ become increasingly spread out as $X_j(t+h)$ increases, especially for $k = 0.5$. This pattern occurs because of the multiplicative way the error term is incorporated in Eq. (1).

Dynamics within a patch: the Nicholson-Bailey model

After dispersal has occurred, we assume that the dynamics on the patch are described by the Nicholson-Bailey model (Nicholson and Bailey 1935), so that

$$\begin{aligned} X_j(t+1) &= \lambda X_j(t+h) e^{-\alpha P_j(t+h)} \\ P_j(t+1) &= X_j(t+h)\{1 - e^{-\alpha P_j(t+h)}\}. \end{aligned} \quad (2)$$

Here α is the attack rate of the parasitoid, which searches at random within the patch, and λ the finite rate of increase for the hosts. We are interested in the dynamics of mean host and parasitoid density, X(t) and P(t), and these quantities may be found by taking the expected value of both sides of Eq. (2). More specifically, we find X(t+1) and P(t+1) using the formulae

$$\begin{aligned} X(t+1) &= \lambda E[X_j(t+h) e^{-\alpha P_j(t+h)}] \\ P(t+1) &= X(t) - E[X_j(t+h) e^{-\alpha P_j(t+h)}], \end{aligned} \quad (3)$$

where the expectation is carried out using the joint distribution of $X_j(t+h)$ and $P_j(t+h)$. In the case of Model A, this is done using the bivariate gamma distribution for $X_j(t+h)$ and $P_j(t+h)$, and has an analytic answer (see Appendix). After substituting the scaled densities $x(t) = \alpha X(t)$ and $p(t) = \alpha P(t)$, we find that

$$\begin{aligned} x(t+1) &= \lambda x(t) \left\{1 + \frac{p(t)}{k}\right\}^{-k-1} \left\{1 + \frac{(1-\varrho^2)p(t)}{k}\right\} \\ p(t+1) &= x(t) \left\{1 - \left\{1 + \frac{p(t)}{k}\right\}^{-k-1} \left\{1 + \frac{(1-\varrho^2)p(t)}{k}\right\}\right\}. \end{aligned} \quad (4)$$

The resulting model resembles the negative binomial model of May (1978), and in fact collapses to it for $\varrho^2 = 0$. For $\varrho^2 = 1$ the model is also close to the negative binomial, except that the equations involve the $-k-1$ power, not the $-k$ power. Chesson and Murdoch (1986) present a class of pure regression models which lead exactly to the negative binomial.

Fig. 2 depicts the local stability boundaries of the model given by Eq. (4), as a function of λ, k, and ϱ^2 (see Appendix for further details). For $\varrho^2 = 0$ we have the standard negative binomial model, which is stable for $k < 1$, regardless of the value of λ (May 1978). As ϱ^2 is increased the boundary moves downward, until for $\varrho^2 = 1$ no stability is possible. Thus as we move along a continuum from pure error to pure regression, the model becomes *less* stable, although moderate values of correlation ($\varrho^2 = 0.5$) still allow a fairly large region of stability.

For Model B we were unable to find a neat analytic result, although some simplification is possible. Recall that the definition of $P_j(t+h)$ includes the error random variable $U_j(t+h)$, which is defined to be independent of $X_j(t+h)$. This independence means that we may evaluate Eq. (3) in two steps, by first averaging with respect to the distribution of $U_j(t+h)$, and then the distribution of $X_j(t+h)$ (see Appendix for further details). Define the integral I, where I is a function of ϱ^2, k, m, x(t), and p(t):

$$I = \int_0^\infty u \left\{1 + \frac{(1-\varrho^2)p(t) + \frac{\varrho^2 p(t)}{x(t)} u}{k}\right\}^{-k} \frac{(m/x(t))^m}{\Gamma(m)} u^{m-1} e^{(-m/x(t))u} \, du. \quad (5)$$

The model can then be written simply as

$$\begin{aligned} x(t+1) &= \lambda I(\varrho^2, k, m, x(t), p(t)) \\ p(t+1) &= x(t) - I(\varrho^2, k, m, x(t), p(t)) . \end{aligned} \quad (6)$$

Here k is the shape parameter of the error variable $U_j(t+h)$, while m is the shape parameter of the distribution of $X_j(t+h)$, the density of hosts per patch. The integral I must be evaluated numerically, for $\varrho^2 \neq 0$. For $\varrho^2 = 0$, Model B is equivalent to the negative binomial

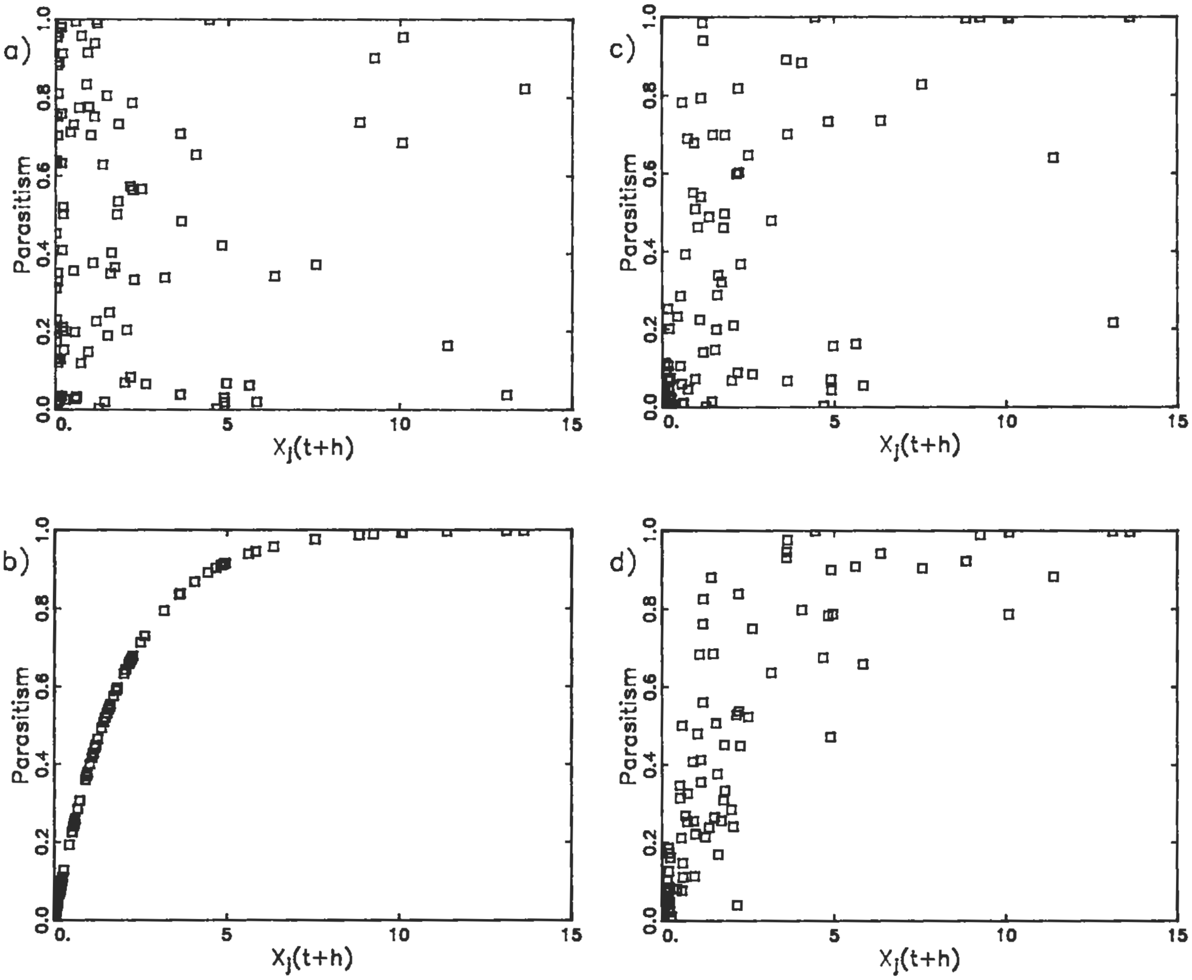

Fig. 4. Patterns of parasitism produced by the data in Fig. 1, assuming Nicholson-Bailey parasitism and $\alpha = 1$. (a) Model A for $\varrho^2 = 0$ and $k = 0.5$, (b) Model A for $\varrho^2 = 1$ and $k = 0.5$, (c) Model B for $\varrho^2 = 1$, $k = 0.5$, and $m = 0.5$, (d) Model B for $\varrho^2 = 1$, $k = 2$, and $m = 0.5$.

model, regardless of the value of m. For $\varrho^2 = 1$ and $k = \infty$ Model B is equivalent to Model A for $\varrho^2 = 1$.

Fig. 3 shows the local stability boundaries for Model B, for three different values of the host shape parameter m. For $m = 0.5$ and 1 the boundaries are shifted upwards for $\varrho^2 > 0$, especially for small λ; for $m = 4$ the effect of ϱ^2 is negligible. These results indicate that aggregation in response to host density can add to the stability of the model, but the effect depends sensitively on the skewness of the host distribution. This is because large m implies a quite narrow distribution of host densities on the patch, so that the response of the parasitoid to local host density can only be small. The main source of stability in model is the error term $U_j(t+h)$, because no stability is possible for large values of k, which imply small amounts of error. Thus, it is the error component of parasitoid search, not the regression one, which contributes most to stability in Model B.

Spatial patterns of parasitism

The spatial pattern of parasitism is a frequent object of study in real host-parasitoid systems, in part because of its potential connection to stability. In particular, some forms of aggregation in response to host density can stabilize host-parasitoid dynamics (Hassell and May 1973, 1974), and this type of parasitoid behavior will also produce spatial density-dependence in parasitism rates. As we have seen in Models A and B, however, linear forms of aggregation do not generate stability unless supplemented by error. What pattern of parasitism is produced by these two models? Fig. 4 illustrates the pattern of parasitism which would be obtained from the data in Fig. 1, assuming that the fraction parasitized within a patch is $1\text{-}e^{-\alpha P_j(t+h)}$. For the pure error version of Model A, we observe only a scatter of points, as would be expected (Fig. 4a). For the pure regression form of that model, a strong pattern of spatial density-dependence is produced (Fig. 4b). Thus, in Model A spatial density-dependence is most apparent when the model is *unstable,* not stable. Fig. 4c and 4d show the pattern for Model B, corresponding to the data in Fig. 1c and 1d. Parasitism rates are both density-dependent and highly scattered, because both forms of aggregation are present, but the pattern of density-dependence is clearest for $k = 2$ (Fig. 4d). For small λ both values of k would yield stability (see Fig. 3a), but with $k = 0.5$ more stable than $k = 2$. For larger k Model B would eventually become unstable, and the spatial pattern of parasitism would approach that shown in Fig. 4b, where spatial density-dependence is strong. Therefore, strong density-dependence in Model B, like Model A, indicates unstable dynamics.

Discussion

Our results suggest that aggregation independent of host density, i.e. clumping or error in the parasitoid distribution, contributes strongly to stability. A linear response by the parasitoids to host patch density does not generate stability, unless it is combined with error in the parasitoid's response. Why do these results differ from earlier ones, which stressed the stabilizing effects of aggregation in response to host density (Hassell and May 1973, 1974)? Stability occurs in these earlier models because of the strongly non-linear response of the parasitoid to host density, with high host density patches receiving many more parasitoids than low density ones. No error is involved in these models. In contrast, the models here begin with a situation in which parasitoid and host distributions are unrelated, i.e. pure error. As the parasitoid distribution becomes more strongly related to the host distribution (ϱ^2 increases), more parasitoids are found in high density patches, but the response is always linear and cannot alone generate stability. What stability is present in Model A and B arises mainly from the error term, not the response of the parasitoid to host density.

It seems likely that the behavior of real parasitoids will combine both an aggregative response to host density, and a substantial error component, as in the models in this paper. For example, Smith and Maelzer (1986) studied the response of the parasitoid *Aphytis melinus* to fruit with different densities of its host, the California red scale (*Aonidiella aurantii*). Although *Aphytis* were observed more frequently on high density fruit, the response was weak, highly variable, and failed to produce density-dependence in parasitism rates. Waage (1983) found essentially the same result with the parasitoid *Diagdegma* searching for caterpillars of its host, *Plutella xylostella.* In both systems error formed a large component of the parasitoid's aggregative response, and would need to be included in any realistic model. Another possibility in real systems is the combination of a non-linear aggregative response *and* an error component. No models of case have been developed, as yet, but it seems likely that this form of parasitoid behavior would be very stabilizing.

As we have seen, unstable linear forms of parasitoid aggregation can easily generate density-dependence in parasitism rates. The stable models examined by Hassell and May (1973, 1974) would also produce this result. Thus, density-dependence in parasitism rates need not imply a stabilizing form of aggregation in response to host density. To distinguish between stable and unstable forms the actual aggregative response would probably be needed, i.e., the number of parasitoids found at a given density of hosts (see Waage 1983, Smith and Maelzer 1986). On the other hand, if the pattern of parasitism is density-independent, then a sufficiently stabilizing amount of error would produce highly heterogeneous parasitism, across patches (see Fig. 4a). This heterogeneity could be detected using a χ^2 test of heterogeneity, and further examined by determining the actual frequency distribution of parasitism rates (Murdoch et al. 1984, Reeve and Murdoch 1985). At present, no precise methods exist for the likely case where both forms of aggregation are combined. A highly scattered pattern of parasitism (as in Fig. 4c) would indicate substantial error in the parasitoid's aggregative response, and in theory should increase stability. It is ironic that most field studies have ignored the scatter found in patterns of parasitism, when in fact this might be an important source of stability.

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Appendix

Derivation of the Models

For both Model A and B, we seek to calculate $E[X_j(t+h)e^{-\alpha P_j(t+h)}]$, the expected number of hosts surviving parasitism. This expectation is carried out using the joint distribution of $X_j(t+h)$ and $P_j(t+h)$. In Model A, $X_j(t+h)$ and $P_j(t+h)$ are assumed to have a bivariate gamma distribution with means $X(t)$ and $P(t)$, common shape parameter k, and a correlation of ϱ^2. We will use the moment generating function (mgf) for this distribution to calculate the expectation. The mgf for his distribution is

$$E[e^{s_1X_j(t+h) + s_2P_j(t+h)}] =$$

$$\left\{1 - \frac{s_1X(t)}{k} - \frac{s_2P(t)}{k} + \frac{(1-\varrho^2)s_1s_2X(t)P(t)}{k^2}\right\}^{-k}$$

where s_1 and s_2 are dummy parameters taking real values (Johnson and Kotz 1972). Taking the partial derivative with respect to s_1 on both sides, we get

$$\frac{\partial}{\partial s_1} E[e^{s_1 X_j(t+h) + s_2 P_j(t+h)}] = E[X_j(t+h) e^{s_1 X_j(t+h) + s_2 P_j(t+h)}]$$

$$= X(t) \left\{ 1 - \frac{s_1 X(t)}{k} - \frac{s_2 P(t)}{k} + \frac{(1-\varrho^2) s_1 s_2 X(t) P(t)}{k^2} \right\}^{-k-1}$$

$$\times \left\{ 1 - \frac{(1-\varrho^2) s_2 P(t)}{k} \right\} .$$

In order to evaluate the expectation for Model A, we simply substitute $s_1 = 0$, $s_2 = -\alpha$ into this equation.

For Model B, we first make use of the mgf for $U_j(t+h)$, which has a univariate gamma distribution with mean 1 and shape parameter k. We have

$$E[e^{sU_j(t+h)}] = \left\{ 1 - \frac{s}{k} \right\}^{-k}, \quad \text{(Mood et al. 1974)}$$

Using this expression, Eq. (2), and the independence of $U_j(t+h)$ and $X_j(t+h)$, we obtain

$$E[X_j(t+h) e^{-\alpha P_j(t+h)}] =$$

$$E\left[\left\{ 1 + \frac{(1-\varrho^2)\alpha P(t) + \frac{\varrho^2 \alpha P(t)}{X(t)} X_j(t+h)}{k} \right\}^{-k} \right]$$

where the expectation now involves only the distribution of $X_j(t+h)$. Using the distribution of $X_j(t+h)$, which is gamma with mean $X(t)$ and shape parameter m, and substituting the scaled densities $x(t) = \alpha X(t)$ and $p(t) = \alpha P(t)$, we obtain Eq. (5).

Stability analysis

The stability analysis for these systems is analytically straightforward, but numerically difficult. Consider a general host-parasitoid model whose dynamics are given by the equations

$$X(t+1) = f(X(t),P(t))$$
$$P(t+1) = g(X(t),P(t))$$

where f and g are functions of $X(t)$ and $P(t)$. Stability is determined by four quantities a, b, c, and d, defined by

$$a = \frac{\partial f}{\partial X(t)} \bigg|_{X^*,P^{*\prime}} \quad b = \frac{\partial f}{\partial P(t)} \bigg|_{X^*,P^{*\prime}}$$

$$c = \frac{\partial g}{\partial X(t)} \bigg|_{X^*,P^{*\prime}} \quad d = \frac{\partial g}{\partial P(t)} \bigg|_{X^*,P^*} .$$

Here X^* and P^* are equilibrium densities of host and parastioid, respectively. The system will be locally stable when $2 > 1 + ad - bc > |a + d|$ (May 1974, Reeve 1988). For both Model A and B, X^* and P^* were found from the system equations using a two-dimensional root-finding algorithm. Once X^* and P^* were determined, the stability criteria were also evaluated numerically. This can be particularly time-consuming in the case of the Model B, where a, b, c, and d are integrals.

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