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## HOST-PARASITOID COEXISTENCE AND EGG-LIMITED ENCOUNTER RATES

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*Abstract.*—Most models of host-parasitoid interactions consider parasitoid attack rates or, more accurately, encounter rates to be limited by the ability of the parasitoids to find suitable hosts. Some models extend this limitation to include the length of time it takes a parasitoid to handle each host. Here we consider host-parasitoid dynamics in the context of parasitoid encounter rates being limited by the number of eggs that each parasitoid has to lay when the host is at high densities and by the ability of individual parasitoids to find hosts when the host is at low densities. Although the encounter rate function we obtain is mathematically equivalent to previously obtained encounter rate functions that include handling time, the stability properties of the resulting host-parasitoid system have heretofore not been fully explored. Our analysis indicates in the absence of host density self-regulating mechanism that the well-known condition in which host-parasitoid interactions cannot be stable unless the proportion of hosts escaping attack has a sufficiently clumped distribution (i.e.,  $k \leq 1$  in the negative binomial model, where  $k$  is the negative binomial parameter) still applies and that the intrinsic growth rate of the parasitoid population must exceed the intrinsic growth rate of the host population by a factor that both is greater than one and increases as the degree of clumping associated with the proportion of hosts that escape attack increases (i.e., as  $k \rightarrow 0$  in the negative binomial model).

Considerable effort over the past two decades has been devoted to understanding how insect parasitoids can be so effective in suppressing the abundance of insect pests in biological control programs. Recently, the theory of host-parasitoid interactions has focused on whether heterogeneity in parasitoid encounter rates is sufficient for the regulation of host populations (May 1978; Hassell and May 1988; Hassell and Pacala 1990; Hochberg and Lawton 1990; Pacala et al. 1990; Hassell et al. 1991; Ives 1992*b*; Murdoch et al. 1992). In these analyses the underlying assumption is that the rate at which female parasitoids encounter and attack their hosts is limited by the efficiency with which they are able to search for their hosts (a search-limited encounter rate). At high host densities, however, we might expect the encounter rate of female parasitoids to be limited by the number of eggs they can produce (an egg-limited encounter rate).

Here we analyze the more general situation in which the encounter or, equivalently, the attack rate of female parasitoids has both egg-limited and search-limited components. In this analysis we demonstrate that a high degree of spatial heterogeneity is insufficient on its own to stabilize the interaction between parasitoids and otherwise unregulated hosts in a discrete time model. In particular, we

demonstrate that stability also requires the intrinsic per capita rate of increase of the host population, denoted by  $\lambda$ , to be bounded below by one and above by a constant that is less than the maximum growth rate of the parasitoid population (i.e., the number of eggs—or egg clutches, in the case of gregarious parasitoids— $\beta$ , produced by each parasitoid female multiplied by the proportion—or number— $c$ , of females that emerge from a parasitized host), which we assume to be greater than one (i.e.,  $\beta c > 1$ ), a result that is similar to one recently obtained by Hochberg and Holt (1995). Further, we demonstrate that this upper bound on  $\lambda$  decreases toward the lower bound of unity as the spatial heterogeneity tends toward its most extreme. In effect, we demonstrate that any rule for determining when spatial variation is sufficiently heterogeneous to produce stable host-parasitoid interactions, including the  $CV^2 > 1$  rule (i.e., coefficient of variation rule; see Hassell and Pacala 1990; Hassell et al. 1991; Pacala et al. 1990), should be modified to include a condition that the host growth rate  $\lambda$  be less than an appropriate fraction of the maximum parasitoid growth  $\beta c$ . Finally, we demonstrate that the more the encounter rate of female parasitoids is dominated by egg limitation rather than search efficiency at moderate to low host densities, the more effective the parasitoid will be as a biological control agent of the host in question.

#### EGG-LIMITED ENCOUNTER RATES

Egg limitation will arise in different ways, depending on the biology of the parasitoid species. Pro-ovigenic parasitoids—those that emerge with a fixed complement of mature eggs—are implicitly egg limited whenever host density is sufficiently high that the ratio of the average time,  $T_h$ , it takes these parasitoids to locate and handle their hosts to the total time,  $T$ , that they have available to search for hosts is greater than their complement,  $\beta$ , of eggs, that is, whenever  $\beta < T/T_h$ . The more common synovigenic parasitoids—those that continue to mature eggs throughout their adult lives—experience daily egg limitation when the number of nonparasitized hosts encountered on a particular day exceeds the daily rate of egg maturation (e.g., Collins et al. 1981; Yamada 1987; Trudeau and Gordon 1989). Egg limitation has been recognized to be an important factor influencing the oviposition strategy of parasitoids (e.g., Iwasa et al. 1984; Lessells 1985; Mangel 1987; Godfray 1994). Yet, despite the fact that many parasitoids that have been so successful in biological control have low rates of daily egg maturation (Yamada 1988), the importance of egg limitation has been largely ignored in both biological and modeling studies. Further, Price's (1975) argument that parasitoids evolve fecundity to match their lifetime expectancy of host encounters does not preclude the widespread occurrence of egg limitation in parasitoids, because of variations in host density through time and space and because egg limitation may often be a consequence of constraints on nutritional intake, which itself is adversely affected by selective pressures on, for example, strategies to avoid predation and to find mates.

In this short article, we fill a gap in the stability analysis of the dynamics of host-parasitoid interactions by assuming that egg-limited parasitoid encounter

rates come into effect at moderate to high host densities. It is surprising that this gap has continued to exist until now given that the foundations for an egg-limited encounter rate in solitary parasitoids attacking hosts with nonoverlapping generations were laid by Thompson (1924), a decade before the appearance of the search-limited encounter rate model of Nicholson and Bailey (1935). We speculate that the primary reason for the neglect of Thompson's egg-limited approach by Nicholson and Bailey in the 1930s and by population ecologists over the past several decades is due to the fact that Thompson's model (as elaborated in the appendix) does not support an equilibrium in which both the parasitoid and host are nonzero (i.e., a nontrivial equilibrium), although on rare occasions Thompson's model has been used in simulation studies of host-parasitoid interactions (e.g., Münster-Swendsen and Nachman 1978). Analyses of population dynamics typically focus on investigating the stability properties of nontrivial equilibria, often ignoring the fact that the dynamics of systems without nontrivial equilibria yield insights into the nonequilibrium dynamics of such systems and into related systems where nontrivial equilibria do exist (see Getz and Pickering 1983 for an example of this in the context of microparasitic diseases).

#### MODEL FORMULATION

Both the Thompson and Nicholson-Bailey models are special cases of the following formulation, which holds either for solitary parasitoids that lay one egg in each attacked host or for gregarious parasitoids that lay a given clutch size of eggs in each attacked host. Here,  $N_t$  and  $P_t$  are the respective densities of hosts and female parasitoids in generation  $t$ ,  $c > 0$  is the average number (or fraction, if we are thinking of solitary parasitoids) of female parasitoids that emerge from each attacked host,  $\lambda > 0$  is the intrinsic per capita growth rate of the host in the absence of parasitism,  $\epsilon_t$  is the mean rate at which hosts are encountered by parasitoids in generation  $t$ ,  $f(\epsilon)$  is the proportion of hosts that escape parasitism in each generation, and the dynamics satisfy the equation

$$\begin{aligned} N_{t+1} &= \lambda N_t f(\epsilon_t) \\ \text{and} \quad P_{t+1} &= c N_t (1 - f(\epsilon_t)) \end{aligned} \tag{1}$$

(cf. the formulation outlined in Hassell 1978). In the Nicholson-Bailey model the search-limited encounter rate is

$$\epsilon = aP, \tag{2}$$

where  $a > 0$  is interpreted as an "area of discovery" or search parameter (Nicholson and Bailey 1935; Hassell 1978; May 1978). Expression (2) is derived under the assumption that the number of encounters between parasitoids and hosts is directly proportional to the number of hosts (which implicitly assumes that eggs are never limiting). In the Thompson model the egg-limited encounter rate is

$$\epsilon = \beta P/N. \tag{3}$$

It is derived under the assumption that each parasitoid lays an average of  $\beta$  eggs (or clutches, in the case of gregarious parasitoids), and parasitoid encounter rates with hosts are either limited by the actual number of eggs that females are able to produce (Thompson 1924; Varley et al. 1974) or critically influenced by daily egg load (Yamada 1988; Trudeau and Gordon 1989; Minkenberget al. 1992). The search- and egg-limited encounter rates are special cases of the following mean encounter rate function:

$$\epsilon = \frac{a\beta P}{(\beta + aN)} \quad (4)$$

(in the search-limited case  $\beta \rightarrow \infty$ , and in the egg-limited case  $a \rightarrow \infty$ ). Since the mean encounter rate function is the average number of encounters of each host and parasitoids, while the functional response  $g$  used in predation theory is the mean number of hosts encountered by each predator (i.e., the relationship between  $g$  and  $\epsilon$  is given by  $g = \epsilon N/P$ ), it follows directly that the encounter rate function (eq. [4]) is equivalent to a Holling Type II response function (Holling 1959).

Further, equation (4) has been derived in the context of insect parasitism and predation from a time allocation point of view (Holling 1959; Royama 1971) with parameter  $a = a'T$  and the ratio  $a/\beta = a'T_h$ , where the parameters  $T$  and  $T_h$  are as defined above and the parameter  $a'$  is a search rate parameter (see also Hassell 1978). Under this interpretation  $\beta = T/T_h$  is an upper bound to the encounter rate set by the maximum number of hosts that a parasitoid can handle if it devotes no time to search. For many parasitoids, however, the handling time is so short (less than 1 min) that egg limitation is a far more reasonable interpretation of the parameter  $\beta$  than is the maximum number of hosts that can be handled in the available time. For example, as pointed out by Abrams (1990), estimates of  $T_h$ , derived by fitting an expression of equation (4) to laboratory data, do not correspond to handling times that can be obtained through direct observation. Note that Hassell and May (1973) suggested that handling time in parasitoids could be interpreted as egg limitation, but handling time continues to be the dominating concept for interpreting Type II functional response forms of parasitoid encounter rates.

#### ANALYSIS AND RESULTS

An interpretation of the behavior of the model described by equation (1), with equation (4) cast in terms of egg-limited encounter rates at high host densities, has heretofore not been considered. Before we proceed with a general analysis, it is worth noting that for parasitoids with a fixed complement of eggs  $\beta$ , the magnitude of  $a$  determines how rapidly egg limitation sets in as host density increases (the larger the value of  $a$ , the more rapidly it sets in). At some points in the analysis we will consider what happens to the value of equilibria as  $a \rightarrow \infty$ . This approach does not conform to the interpretation of  $a$  as a proportion of the total host population vulnerable to each parasitoid during its lifetime search.

Strictly speaking, this interpretation is incorrect: the case in which  $a > 1$  can theoretically occur and would imply that parasitoids traverse some of the same areas several times and others not at all while searching at random to produce a total area of search that is greater than the area containing the host population. Note, however, that the real quantity of importance in determining the trade-off between egg and search limitation is the ratio  $\beta/a$  so that increasing  $a$  has mathematically the same effect as decreasing  $\beta$ .

Standard techniques can be used to study the existence of coexistence equilibria and their stability properties under the general and biologically reasonable assumption that the greater the mean encounter rate, the lower the proportion of hosts that escape encounter (see the appendix).

From the analysis in the appendix and from an evaluation of the signs of the two factors in the factorization of the egg-limitation constraint introduced there (see eq. [A16]), we conclude the following regarding the dynamics of equations (1), assuming a Holling Type II mean encounter rate (eq. [4]) and the negative binomial form

$$f(\epsilon) = \left(1 + \frac{\epsilon}{k}\right)^{-k} \quad (5)$$

for the escape function  $f(\epsilon)$ , where  $k > 0$  is the negative binomial aggregation parameter. (This is the form most commonly used to model nonrandom, or aggregated, encounter rates between parasitoids and their hosts. The degree of aggregation increases with decreasing  $k$ ; see Hassell 1978; May 1978; May and Hassell 1988.)

First, we conclude that host-parasitoid interactions modeled by equations (1) cannot be stable unless the distribution of host-parasitoid encounters is sufficiently aggregated (eq. [A15] implies that  $0 < k \leq 1$ ) and the maximum per capita growth rate  $\beta c$  of the parasitoid population is sufficiently greater than the per capita growth rate  $\lambda$  of the host population (for given  $\lambda$  eq. [A16] in the appendix can only be satisfied if  $\beta c$  exceeds  $\lambda$  by a certain amount, where the lower bound for  $\beta c$  is given by eq. [A18]; see fig. 1). It has been drawn to our attention by a reviewer that Hochberg and Holt (1995) independently derived the result that if the maximum growth of the parasitoid population is less than  $\lambda$ , then the interaction is unstable and the host grows without bound. Hochberg and Holt, however, do not provide a precise way to estimate the bound on host growth rate, as we do with equation (A18).

Second, as the degree of spatial heterogeneity increases ( $k \rightarrow 0$ ), the per capita growth rate  $\lambda$  of the host population must decline if a stable host-parasitoid interaction is to be maintained. Further, as spatial heterogeneity becomes extreme, stability can be maintained only if  $\lambda$  approaches one.

Third, as eggs become less limiting ( $\beta$  increases), the bound on the size of the per capita growth rate  $\lambda$  of the host population increases until, in the pure search-limited extreme ( $\beta \rightarrow \infty$ ), the only constraint on stability is that sufficient spatial heterogeneity should exist (i.e.,  $0 < k \leq 1$ ).

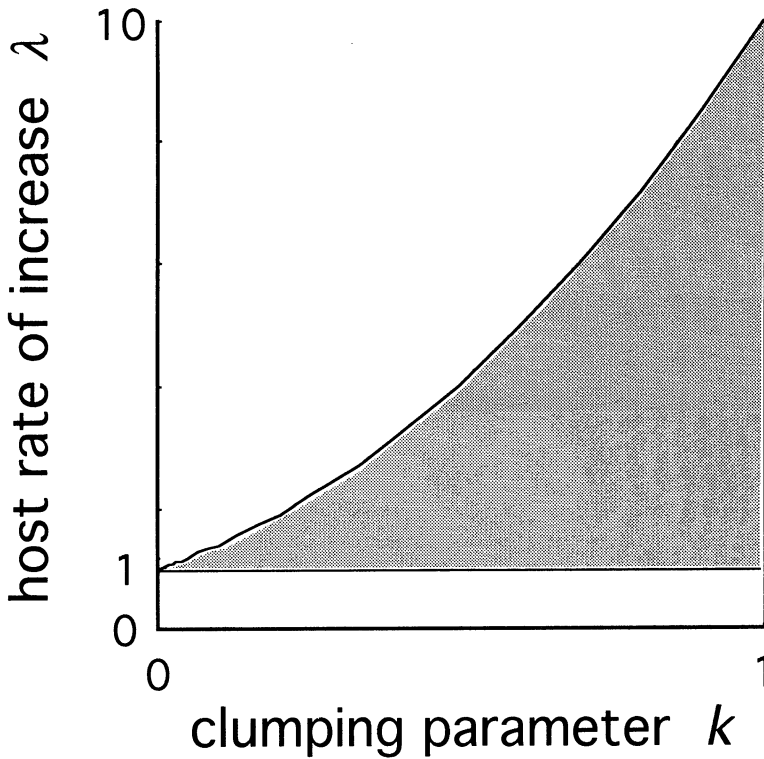


FIG. 1.—The egg limitation stability constraint for the negative binomial case (eq. [A16]) plotted in terms of the negative binomial aggregation coefficient  $k$  and the per capita growth rate parameter  $\lambda$  of the host population for a parasitoid maximum per capita growth rate of  $\beta c = 10$ . The conditions for stability of equations (1) require that  $\lambda$  lie between the egg-limitation constraint and the line  $\lambda = 1$  and, from the escape function constraint (eq. [A15]), that  $k \leq 1$ . The hatched area is the only region in  $k - \lambda$  parameter space that simultaneously satisfies all three of these constraints. Similar figures can be obtained for other values of  $\beta c$ . Note that the value of  $\lambda$  at the intersection of the egg limitation and the constraint  $k = 1$  is always  $\beta c$  for all values of  $\beta c > 1$ .

Finally, as search becomes less limiting ( $a$  increases in eq. [4]), irrespective of whether the escape function is a negative binomial or some other valid model, the nontrivial equilibrium ( $N^*, P^*$ ) approaches the origin (i.e., as  $a \rightarrow \infty$  in eq. [A2]  $N^*$  and  $P^* \rightarrow 0$ ; see fig. 2). Thus, the more efficient parasitoids become at searching out their hosts, the more the host-parasitoid encounter rate will be egg limited at moderate and low host densities and the more suppressed the equilibrium host population will be if the interaction is stable.

Although a purely egg-limited encounter rate is an unrealistic assumption at low host densities, our analysis suggests, and simulation indicates (fig. 3), that under some circumstances highly search-efficient parasitoids are able to drive the host population to extinction, even if they only have a finite number of eggs to lay. We should also bear in mind that the prediction of equilibrium values close to zero in a strongly egg-limited deterministic model (i.e., a model in which the

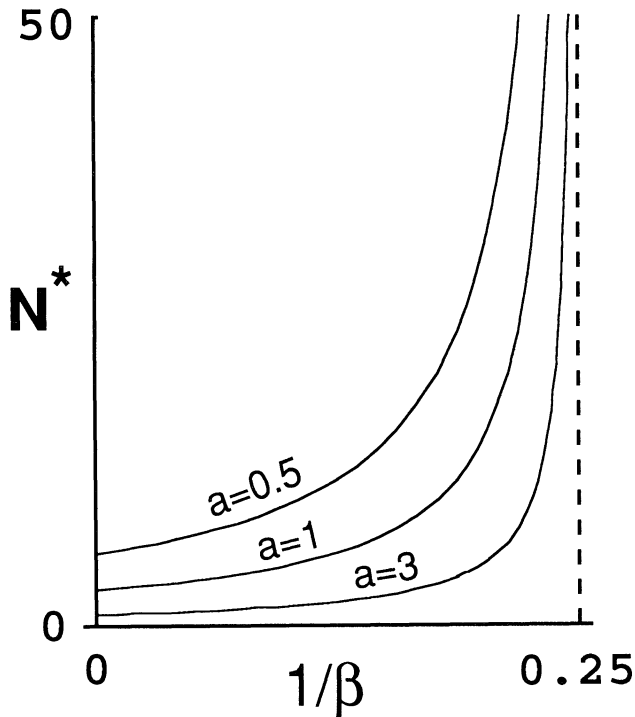


FIG. 2.—The nontrivial equilibrium values  $N^*$  of the host population, as a function of the inverse values of the egg limitation parameter  $\beta$  ranging from the critical value  $\bar{\beta}$  to the case of unlimited eggs  $\beta \rightarrow \infty$  (i.e.,  $1/\beta \rightarrow 0$ ), plotted for the indicated values of the search parameter  $a$ . For these graphs we have selected  $f(\epsilon) = 1/(1 + \epsilon)$  (i.e., the negative binomial escape function, as discussed later in the text, with clumping parameter  $k = 1$ ),  $\beta = 10$ ,  $c = 0.5$ , and  $\lambda = 2$ , while the vertical dotted line represents the asymptotic value  $\bar{\beta} = 0.25$ . The value of  $N^*$  at  $1/\beta = 0$  corresponds to the case of a purely search-limited encounter rate. As the population becomes less search limited with increasing values of  $a$ , the values of  $N^*$  decrease toward 0.

ratio  $a/\beta$  in eq. [4] is relatively large) implies a high probability of extinction of populations modeled by an equivalent stochastic model.

#### DISCUSSION

In the majority of discrete time search-limited encounter rate models, the incorporation of spatial heterogeneity in the form of either density-dependent or density-independent aggregation of parasitoid encounter rates promotes the stability of host-parasitoid interactions (Bailey et al. 1962; Chesson and Murdoch 1986; Pacala et al. 1990; Ives 1992*b*). Thus, the effect of spatial heterogeneity on the dynamics of host-parasitoid interactions has frequently been considered the most important factor accounting for the persistence of the biological control of exotic pests through parasitoid introductions (Beddington et al. 1978; May and Hassell 1988). By aggregating the risk of parasitoid encounter (e.g., spatial distribution,

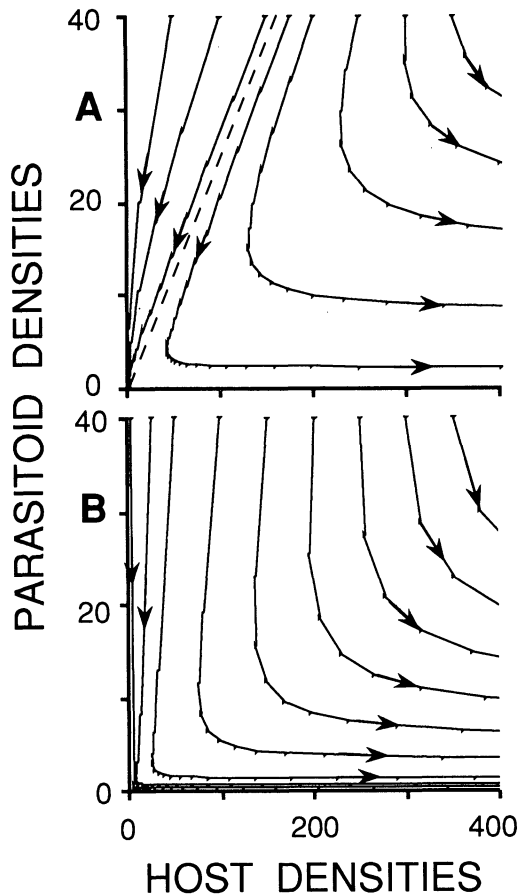


FIG. 3.—Graphs of the negative binomial distribution of encounter rates with population parameters  $\lambda = 1.3$ ,  $\beta = 2$ ,  $c = 0.5$ . *A*, Parameter  $k = \infty$ . For the egg-limited encounter rate model under a random or Poisson distribution of parasitoid encounter rates (i.e.,  $k = \infty$ ), trajectories (i.e., solutions to eqq. [1] and [3]) starting at initial parasitoid population densities of  $P_0 = 40$  approach the trivial equilibrium (0,0) for initial host densities  $N_0 = 50$ , 100, and 150, and head toward  $(\infty, \infty)$  for initial host densities  $N_0 = 175$ , 200, 250, 300, and 350. *B*, Parameter  $k = 0.5$ . For the egg-limited encounter rate model with a high degree of parasitoid aggregation with respect to the host (i.e.,  $k = 0.5$ ), trajectories starting at initial parasitoid population densities of  $P_0 = 40$  eventually head toward  $(\infty, \infty)$ , irrespective of the host density, even though those with relatively high initial parasitoid-to-host ratios pass very close to zero.

host instar distribution), heterogeneity induces temporal density dependence on the parasitoid population through a reduction in the per capita efficiency of aggregated parasitoids that waste time in encountering previously parasitized hosts (Taylor 1993a). Although  $k < 1$  always induces stability in these discrete time models, Taylor (1993b) has pointed out that the degree of stability (or characteristic return time) does not continue to increase with more extreme levels of hetero-

generity (i.e., as  $k \rightarrow 0$ ). Further, if overcompensating self-limitation is incorporated into the host model, aggregated parasitoid encounter rates (i.e.,  $k < 1$ ) are no longer able to stabilize the host population unless parasitoid reproductive rates are sufficiently large (Hochberg and Lawton 1990).

Our analysis of an encounter rate model that includes search- and egg-limited encounters as special cases implies that a sufficient degree of spatial heterogeneity coupled with a sufficient degree of efficiency in the ability of female parasitoids to search out their hosts (i.e., parasitoids that remain egg limited at relatively low densities) will account for host and parasitoid systems persisting at relatively low densities, providing the per capita growth rate of the host species is suitably bounded. The importance of a bound on the growth rate of the host has been found by Hassell (1980) in the context of a host-parasitoid model in which the aggregation parameter  $k$  is a linear function of host density. Further, our analysis of a combined search- and egg-limited encounter rate model requires that the underlying host reproductive rate  $\lambda$  should not be too much larger than one, especially for highly aggregated systems where  $k$  is close to zero (note in the appendix the constraint  $\lambda < \lambda_k \rightarrow 1$  as  $k \rightarrow 0$ ).

In conclusion, the analysis presented here provides further support for the claim that the effects of parasitoid aggregation on the dynamics of host-parasitoid interactions are very much dependent on the construction of the models themselves. More important, our analysis leads us to question whether the assumption that parasitoid encounter rates are determined purely by limitations in searching efficiency, irrespective of whether or not the underlying distributions of the populations are aggregated, should underpin more elaborate discrete time host-parasitoid models that include, for example, interference competition or host self-regulation (Beddington et al. 1978; Hassell 1978; May and Hassell 1988; Hochberg and Lawton 1990; Ives 1992a). Similarly, we question the generality of a purely search-limited encounter rate in population models that underlie more sophisticated behavioral and evolutionary analyses (Mangel and Roitberg 1992; van Baalen and Sabelis 1993). In the future, it may be prudent to pay more attention to potential effects of egg limitation when considering both the dynamic behavior of host-parasitoid interactions and biological aspects of parasitoid encounter rates.

#### ACKNOWLEDGMENTS

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#### APPENDIX

##### EQUILIBRIUM AND STABILITY ANALYSES

The assumptions we make are that the escape function  $f(\epsilon)$  is positive and is monotonically decreasing from unity for positive  $\epsilon$ . This assumption implies that  $df/d\epsilon < 0$  and that  $f_{(\epsilon)}^{-1}$  is positive and has a single value for all  $\epsilon > 0$ .

## EQUILIBRIA

At an equilibrium ( $N^*, P^*$ ), the general model (eqq. [1]) reduces to the equations

$$\epsilon^* = f^{-1}\left(\frac{1}{\lambda}\right)$$

and

$$P^*/N^* = c\left(1 - \frac{1}{\lambda}\right).$$

If the encounter rate has the Holling Type II form (eq. [4]) and the per capita host population growth rate satisfies  $\lambda > 1$  (i.e., the host population increases in the absence of parasitoids), then it is easily shown that the above two equilibrium equations have the following positive solution.

GENERAL CASE.

$$N^* = \frac{\beta\lambda f^{-1}(1/\lambda)}{a\beta c(\lambda - 1) - a\lambda f^{-1}(1/\lambda)} \quad (\text{A2a})$$

and

$$P^* = \frac{\beta c(\lambda - 1)f^{-1}(1/\lambda)}{a\beta c(\lambda - 1) - a\lambda f^{-1}(1/\lambda)}, \quad (\text{A2b})$$

provided that

$$\beta > \beta^c = \frac{\lambda f^{-1}(1/\lambda)}{c(\lambda - 1)}. \quad (\text{A3})$$

For comparison, an assumption of a purely search-limited encounter rate (eqq. [2])—that is, letting  $\beta \rightarrow \infty$  in equation (A2)—yields the following search-limited equilibrium (Hassell 1978; May 1978).

SEARCH-LIMITED CASE.

$$N^* = \frac{\lambda f^{-1}(1/\lambda)}{ac(\lambda - 1)} \quad (\text{A4a})$$

and

$$P^* = \frac{f^{-1}(1/\lambda)}{a}. \quad (\text{A4b})$$

We note from equations (A2) that  $N^*$  is a minimum when the encounter rate is purely search limited and increases without bound as  $\beta$  decreases from  $\infty$  to  $\tilde{\beta}$  (fig. 1). In contrast, in trying to solve equations (A1) for a purely egg-limited encounter rate (eq. [3]), a solution will not exist except in the singular case

$$\beta c\left(\frac{\lambda - 1}{\lambda}\right) = f^{-1}\left(\frac{1}{\lambda}\right),$$

when the ratio  $P^*/N^*$  is specified but not the actual values of  $P^*$  and  $N^*$  themselves. (In this case the equilibrium set is a line rather than a point and, from eq. [A3], the identity  $\tilde{\beta} \equiv 1$  must hold.)

## STABILITY

The next step in using analytical techniques to understand the dynamical properties of host-parasitoid interactions modeled by equations (1) is to evaluate the stability properties of its equilibrium solutions, of which there are at most two: the trivial equilibrium  $(\tilde{N}, \tilde{P}) = (0, 0)$  and the nontrivial equilibrium  $(\hat{N}, \hat{P}) = (N^*, P^*)$  expressed in equations (A2), which are in the positive quadrant provided that  $a > 0$ ,  $c > 0$ ,  $\lambda > 1$ , and  $\beta > \tilde{\beta}$ .

By considering the linearization of equations (1) around either the trivial or the nontrivial

equilibrium solution, it is easily demonstrated (e.g., May 1978; Edelstein-Keshet 1988) that the equilibrium is stable if the solutions  $\mu$  to the eigenvalue equation

$$\left\{ \mu^2 - \left[ \lambda f + N \frac{df}{d\epsilon} \left( \lambda \frac{\partial \epsilon}{\partial N} - c \frac{\partial \epsilon}{\partial P} \right) \right] \mu - c \lambda N \frac{df}{d\epsilon} \frac{\partial \epsilon}{\partial P} \right\}_{(\hat{N}, \hat{P})} = 0 \tag{A5}$$

have moduli (absolute value for real numbers or magnitude for complex numbers) that are less than one. Further, the equilibrium is unstable if one of the two solutions has a modulus greater than one (i.e.,  $|\mu_i| > 1$  for  $i = 1$  and/or 2), while the case in which  $|\mu_1| \leq 1$  and  $|\mu_2| = 1$  requires a higher than linear order analysis to resolve the local stability characteristics of the equilibrium in question.

In the case of the trivial equilibrium  $(\hat{N}, \hat{P}) = (0, 0)$ , since  $f(0) = 1$  and, from equation (4),  $\partial \epsilon / \partial P|_{(0,0)} = a$  and  $\partial \epsilon / \partial N|_{(0,0)} = 0$  holds for the general case and its search-limited extreme but not for the egg-limited extreme. In the latter case, the eigenvalue equation (A5) reduces to

$$\mu(\mu - \lambda) = 0. \tag{A6}$$

Thus, for the combined search- and egg-limited encounter function (eq. [4]) with  $a > 0$  and  $\beta > 0$ , including the purely search-limited case  $\beta \rightarrow \infty$ , the origin is always unstable when  $\mu = \lambda$  for all  $\lambda > 1$ . In this case, the origin (0,0) is a saddle point rather than an unstable center (since one of the eigenvalues has a modulus less than one, i.e.,  $\mu = 0$ ) so that it is possible for the parasitoid to approach zero while the host grows without bounds. This can be shown through numerical simulation when the nontrivial equilibrium  $(N^*, P^*)$  is unstable and the host and parasitoid populations oscillate with increasing amplitude until, because of numerical limits of computers in representing small numbers, the parasitoid population becomes zero.

For the purely egg-limited extreme ( $a \rightarrow \infty$ ), it follows from equation (3) that  $\partial \epsilon / \partial P = \beta / N$  and  $\partial \epsilon / \partial N = -\beta P / N^2$  so that the coefficient of the linear term in the eigenvalue equation (A5) explicitly involves the ratio  $P/N$ , which has no defined value at  $(\hat{N}, \hat{P}) = (0, 0)$ . In this case, the stability properties of  $(\hat{N}, \hat{P}) = (0, 0)$  can be rather complicated, with some solutions being attracted to the origin and others escaping to  $(\infty, \infty)$ , depending on the particular value of the initial ratio  $P_0/N_0$  (fig. 3).

Before we go on to analyze the stability of the nontrivial equilibrium  $(N^*, P^*)$ , we note from equations (4) that when  $P \neq 0$ ,

$$\frac{\partial \epsilon}{\partial P} = \frac{\epsilon}{P} \tag{A7}$$

and

$$\frac{\partial \epsilon}{\partial N} = \frac{-\epsilon^2}{\beta P},$$

and from the first equation in (A1) that  $f(\epsilon^*) = 1/\lambda$ . Thus, it follows directly from equation (A5) that the stability eigenvalues associated with the nontrivial equilibrium  $(N^*, P^*)$  satisfy the equation

$$\mu^2 - \left[ 1 + \phi^* \left( \frac{f^{-1}(1/\lambda)}{\beta c} + \frac{1}{\lambda} \right) \right] \mu + \phi^* = 0, \tag{A8}$$

where

$$\phi^* = \frac{\lambda^2}{\lambda - 1} f^{-1}(1/\lambda) \left( -\frac{df^*}{d\epsilon} \right) > 0, \tag{A9}$$

$df^*/d\epsilon = (df/d\epsilon)|_{\epsilon^*} < 0$ ,  $\lambda > 1$ , and  $f^{-1}(\cdot) > 0$ .

Further, since  $[f^{-1}(1/\lambda)/c\beta + 1/\lambda] > 0$ , it follows directly from the Schur-Cohn condi-

tions (e.g., May 1978; see also Edelstein-Keshet 1988, sec. 2.8) that both eigenvalues  $\mu$  have a modulus less than one in equation (A8) if

$$1 > \phi^* > \phi^* \left( \frac{f^{-1}(1/\lambda)}{\beta c} + \frac{1}{\lambda} \right). \quad (\text{A10})$$

Satisfaction of the left-hand inequality depends directly on the form of the escape function  $f(\epsilon)$ .

ESCAPE FUNCTION CONSTRAINT.

$$\phi^* < 1. \quad (\text{A11})$$

The right-hand inequality in equation (A10) implies the following constraint.

EGG LIMITATION CONSTRAINT.

$$\frac{f^{-1}(1/\lambda)}{\beta c} + \frac{1}{\lambda} - 1 < 0. \quad (\text{A12})$$

For  $\lambda > 1$ , this constraint is always satisfied for sufficiently large values of  $\beta$ .

#### NEGATIVE BINOMIAL ESCAPE FUNCTION

In equation (1), the spatial variabilities that arise in the densities of hosts and parasitoids because of, say, the structure of the environment, are generally reflected in the form of the escape function  $f(\epsilon)$  (Bailey et al. 1962; Hassell 1978; May 1978). Homogeneous environments (i.e., those in which parasitoids and hosts are distributed randomly in space and encounter one another at random) correspond to an escape function that is the zero term of a Poisson distribution (Nicholson and Bailey 1935; Hassell 1978; May 1978), namely,

$$f(\epsilon) = e^{-\epsilon}, \quad (\text{A13})$$

whereas the zero term of a negative binomial distribution with contagion or aggregation parameter  $k > 0$ , namely, equation (5), has been proposed for the escape function when the distribution of parasitoid encounter rates is aggregated in some way (Hassell 1978; May 1978). Note that as  $k \rightarrow \infty$ , the negative binomial equation (5) tends to the Poisson expression (eq. [A13]).

It is well known that for  $\lambda > 1$  the nontrivial equilibrium ( $N^*, P^*$ ) of equation (1) is unstable for the Poisson (eq. [A13]) and for the negative binomial attack functions when  $k > 1$  but is stable under conditions sufficiently clumped to ensure  $k < 1$  (eq. [5]; cf. Hassell 1978; May 1978). We now generalize these results by assessing constraints (A11) and (A12) when the escape function is a negative binomial.

In the case of the negative binomial, it follows from equation (5) that

$$f^{-1}(1/\lambda) = k(\lambda^{1/k} - 1) \quad (\text{A14a})$$

and

$$\frac{df}{d\epsilon} = -f(\epsilon)^{(k+1/k)}. \quad (\text{A14b})$$

Thus, the stability constraints for a negative binomial escape function are, from inequalities (A11) and (A12) (fig. 1), as follows:

ESCAPE FUNCTION CONSTRAINT.

$$\phi_k = k \left( \frac{\lambda^2}{\lambda - 1} \right) (\lambda^{1/k} - 1) \left( \frac{1}{\lambda} \right)^{(k+1/k)} < 1. \quad (\text{A15})$$

EGG LIMITATION CONSTRAINT.

$$\psi_k = \lambda^{(k+1/k)} - \left( \frac{\beta c}{k} + 1 \right) \lambda + \frac{\beta c}{k} < 0. \quad (\text{A16})$$

Since  $\phi_1 = 1$  and standard calculations can be used to show that  $d\phi_k/dk > 0$  for  $k > 0$ , it follows that the inequality  $\phi_k < 1$  holds for all  $0 < k < 1$  and, conversely, equations (1) are unstable for  $k > 1$ . Therefore, we need only consider the egg limitation constraint  $\psi_k < 0$  for  $0 < k \leq 1$  to identify conditions under which stable coexistence of host and parasitoid occur.

For  $k = 1$ , the egg limitation constraint  $\psi_1 < 0$  reduces to the quadratic constraint  $\lambda^2 - (\beta c + 1) + \beta c < 0$  that, by standard quadratic theory, implies that  $1 < \lambda < \beta c$  (fig. 1). Perhaps the easiest way to understand the egg limitation constraint in terms of  $k \in (0, 1)$  is to define  $n = 1/k$  and consider solutions to the equation

$$\psi_{1/n} = \lambda^{n+1} - (n\beta c + 1)\lambda + n\beta c = 0 \quad (\text{A17})$$

that define the boundaries of inequality (A16). Clearly,  $\lambda = 1$  is a solution for all  $n$ , so that  $(\lambda - 1)$  is a factor. Division by this factor and setting the remaining factor to zero implies that other solutions  $\lambda$  to polynomial equation (A17) satisfy the equation

$$\lambda^n + \lambda^{n-1} + \dots + \lambda^2 + \lambda - n\beta c = 0$$

or, after rearrangement of terms,

$$\frac{1}{n} \sum_{i=1}^n \lambda^i = \beta c. \quad (\text{A18})$$

Note that the quantity  $\beta c$  is the upper limit to the reproductive value of a parasitoid—it is the maximum number of eggs a female can lay (or maximum number of clutches in the case of gregarious parasitoids) multiplied by the fraction (or number) of females that will emerge from each host and survive to become reproductive adults. Thus, we assume that  $\beta c > 1$ , otherwise the parasitoid population cannot grow even under the most optimal (i.e., low parasitoid density or density-independent) conditions. Note that the left-hand side of equation (A18) equals one when  $\lambda = 1$ . Further, it is an increasing function of  $\lambda$  and of  $n$  (since  $\lambda > 1 \Rightarrow \lambda^{i+1} > \lambda^i$  for  $i = 1, 2, 3, \dots, n$ ). Thus, it follows that for each integer  $n$ , equation (A18) has a unique positive solution  $\lambda_n$  satisfying  $\lambda_1 = \beta c$ ,  $\lambda_{n+1} < \lambda_n$ , and  $\lambda_n \rightarrow 1$  as  $n \rightarrow \infty$ . (The last condition follows from the fact that if  $\lambda_n > 1 + \delta$  for some  $\delta > 0$  and all  $n > n_\delta$ , then the left-hand side of eq. [A18] is unbounded as  $n \rightarrow \infty$ .)

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