

Behavioral Stabilization of Host-Parasite Population Dynamics

MARC MANGEL

*Section of Zoology and Center for Population Biology,
University of California, Davis, California 95616*

AND

BERNARD D. ROITBERG

*Behavioral Ecology Research Group and Centre for Pest Management,
Department of Biological Sciences, Simon Fraser University,
Burnaby, British Columbia, Canada V5A 1S6*

Received September 9, 1991

We demonstrate that individual behavior can stabilize classical (Nicholson-Bailey) host-parasite population dynamics. Our model assumes that hosts can be divided into at least two phenotypes and that parasites either do not attack one of the phenotypes or attack them facultatively. The former case corresponds to a behavioral refuge (Hassell, 1978) and it is known that other kinds of refuges lead to stability of population dynamics. Behavioral refuges can stabilize the population dynamics in the same way that spatial refuges do. When parasites attack hosts facultatively within the year, strange attractors may arise in the year-to-year population dynamics, in response to the nonlinear nature of the facultative response to the distribution of host densities. © 1992 Academic Press, Inc.

1. INTRODUCTION

Models for host-parasite interactions from one of the classical basis of population biology (e.g., Hassell, 1978). For hosts and parasites with a single generation per year, the general model takes the form

$$\begin{aligned} H(y+1) &= RH(y) f_0(H(y), P(y)) \\ P(y+1) &= rH(y) [1 - f_0(H(y), P(y))] \end{aligned} \quad (1.1)$$

which $H(y)$ is the number of unparasitized hosts at the start of year y , f_0 is the fecundity of hosts that escape parasitism, $f_0(h, p)$ is the fraction of hosts escaping parasitism when host and parasite populations are h and p , r is the number of parasites at the start of year y , and r is a measure

of the conversion of attacks on hosts into parasites in the next year (Table I).
 The Nicholson-Bailey (Hassell, 1978) model corresponds to choosing $f_0(h, p)$ to be the zero-term of the Poisson process, independent of host population size, so that

$$(1.2) \quad f_0(h, p) = \exp(-aP(y)),$$

where a is the searching efficiency of the parasite and can be related to physiological variables such as flight speed and detection abilities (Mangel

TABLE I
 Models, Symbols, and Interpretations

| Symbol | Interpretation |
|--|---|
| $H(y)$ | Number of hosts in year y |
| R | Fecundity of hosts that escape parasitism |
| $f_0(h, p)$ | Fraction of hosts escaping parasitism when host and parasite populations are h and p |
| $P(y)$ | Number of parasites in year y |
| r | Conversion rate of attacks into parasites in the next year |
| a | Searching efficiency of the parasite |
| Standard between-Year Model | |
| $H(t, y)$ | Number of hosts at time t within the season in year y |
| $P(t, y)$ | Number of parasites at time t within the season in year y |
| β | Relative fitness of parasite offspring emerging from host type 2 ($\beta > 1$) |
| H_T | Total number of hosts at the start of a season |
| $\gamma_1(H_T)$ | Fraction of hosts of type 1 when the total host population at the start of the year is H_T |
| $\gamma_2(H_T)$ | $1 - \gamma_1(H_T)$ |
| ω_1, ω_2 | Parameters for density dependence of hosts in that number of hosts of type 2 at the start of season = $\omega_2(1 - \exp(-\omega_1 H_T))$ |
| "Facultative" Parasite within-Year Model | |
| r, R, a | As above |
| $H(t, y), P(t, y)$ | As above |
| $\gamma_1(H_T), \beta$ | As above |
| T | Length of season |
| α | Within-season encounter rate ($a = \alpha T$) |
| λ_i | Probability of encountering a host of type i in a single period of search within the season |
| H_s | Parasite mortality while searching |
| H_{ov} | Parasite mortality while ovipositing |

and Clark, 1988). The assumption underlying (1.2) is that parasites encounter hosts according to random search.

One of the paradoxes of this simple and reasonable biological model is that it leads to oscillations of increasing magnitude, followed by extinction of one or both species. A typical behavior of the Nicholson-Bailey model (Hassell, 1978, p. 16ff) is that the populations show lagged oscillations, with the peaks and troughs in parasite population size lagging those in host population size until the parasite population is extinct, at which point the host population explodes.

Since host and parasite populations are observed to persist in the field and laboratory, the simple Nicholson-Bailey model cannot represent the actual situation. Furthermore, understanding host-parasite dynamics is important for biological control. For this reason, the stabilization of host-parasite dynamics has received considerable previous attention; we briefly review some previous work in the next section. After this review, we begin the development of our own models, which are based on the linkage between events that happen within generations and those which occur between generations. Population ecology and population genetics typically focus exclusively on the between-generation events, completely ignoring within-generation factors. However, host choice behavior by individual parasitoids (a within-generation event) can lead to stabilization of the Nicholson-Bailey model by creation of a "behavioral refuge." Our work also shows that populations of optimally behaving parasites may lead to host choice patterns which show great diversity. That is, an optimality mechanism can generate variability of behavior, especially if a range of environmental conditions exists and the conditions are linked from one year to the next (as they are by population dynamics).

2. PREVIOUS WORK

The observed persistence of host and parasite populations in natural and laboratory situations has lead many investigators to study means of stabilizing the population dynamics. This can clearly be done by incorporating density dependence into the host dynamics, or both host and parasite dynamics (Beddington *et al.*, 1978). Two other methods that we briefly discuss are models based on spatial heterogeneity and models based on behavior.

Models Based on Spatial Heterogeneity (Patchiness)

Perhaps the most famous of the models based on spatial heterogeneity is the one due to May (1978). May's model can be derived simply by assuming that the parameter a in (1.2) has a distribution caused by spatial

behave facultatively in their attacks on hosts. In particular, there is often a within-season dynamics to host choice: early in the season, only the first phenotype is attacked but later in the season both are. In particular, such individual behavior generates a time $t^* (0 \leq t^* \leq T)$ such that for $t < t^*$, only host type 1 is attacked.

Methods for determining t^* are described in the next two sections. In addition to assuming that only host type 1 is attacked before t^* , we assume that for times greater than t^* hosts are attacked at a rate proportional to their initial abundance and that there is no mortality of hosts during the season. That is, when $t < t^*$, hosts of type 1 disappear at a rate proportional to their abundance and hosts of type 2 do not disappear at all. When $t > t^*$ hosts of each type are parasitized according to their initial abundances. With these assumptions, the dynamics of parasites do not change from (3.1), but the host dynamics become

$$(3.2) \quad \begin{cases} \frac{d}{dt} H^1(t, y) = \begin{cases} -\alpha P(0, y) H^1(t, y) \\ -\alpha \left(\frac{H^1(0, y) + H^2(0, y)}{H^1(0, y) P(0, y)} \right) H^1(t, y) \end{cases} & \text{for } t < t^* \\ & \text{for } t \geq t^* \end{cases} \\ \frac{d}{dt} H^2(t, y) = \begin{cases} 0 \\ -\alpha \left(\frac{H^1(0, y) + H^2(0, y)}{H^2(0, y) P(0, y)} \right) H^2(t, y) \end{cases} & \text{for } t < t^* \\ & \text{for } t \geq t^* \end{cases}$$

These equations can be solved directly to give

$$(3.3) \quad \begin{aligned} H^1(t, y) &= H^1(0, y) \exp(-\alpha P(0, y) t) \exp \left(\frac{-\alpha P(0, y) H^1(0, y) + \alpha H^2(0, y)}{H^1(0, y) P(0, y) + H^2(0, y)} t \right) \\ H^2(t, y) &= H^2(0, y) \exp \left(\frac{-\alpha P(0, y) H^2(0, y) + \alpha H^1(0, y)}{H^2(0, y) P(0, y) + H^1(0, y)} t \right) \end{aligned}$$

Note that these equations reduce to the previous, simpler form under appropriate simplifying assumptions (e.g., host type 2 never attacked or host types are identical). The total number of unparasitized hosts at the end of the season is $H^1(T, y) = H^1(0, y) \exp(-\alpha P(T, y))$. Assuming that they contribute equally to the production of offspring, the total number of hosts at the start of the next season is

$$(3.4) \quad H^T(0, y + 1) = R[H^1(T, y) + H^2(T, y)].$$

Similarly, the parasite population at the start of the next season is composed of parasites emerging from host type 1 and those emerging from

host type 2. Assuming that the latter are less likely to emerge than the former, by a factor of β , we have

$$P(0, y + 1) = r[H_1(0, y) - H_1(T, y)] + \beta r[H_2(0, y) - H_2(T, y)]. \quad (3.5)$$

Our description of host population dynamics will be complete once we specify how the numbers of host types 1 and 2 are related to the total host population at the start of the season. We assume that

$$H_i(0, y + 1) = \gamma_i(H_i(T, y) + 1). \quad (3.6)$$

In this equation, the γ_i are functions of total host population; we require only that they are positive and that they sum to 1. The simplest case is density-independent production of phenotypes, in which the γ_i are constants. This is the proportional refuge model of Hassell (1978). A specific model of density-dependent production of phenotypes is described below.

The intraseasonal description of host dynamics is now complete. In the next two sections, we investigate the effects of different assumptions about the determination of t^* on the dynamics of host and parasite populations.

4. POPULATION DYNAMICS FOR "HARD-WIRED" PARASITIDS: A BEHAVIORAL REFUGE

The simplest assumption about t^* is that it equals either 0 or T . When t^* equals 0, the model (3.2)-(3.6) simplifies to the usual Nicholson-Bailey model. When $t^* = T$, hosts of type 2 are never attacked. We could state that such parasitoids are "hard-wired" to reject host type 2, regardless of the conditions of abundance of the two host types. This is a behavioral refuge, akin to the spatial refuges described by Hassell. The effect of this kind of behavioral refuge will be the weakest when the distribution of host phenotypes in one season depends upon total host population. An example of a density-dependent production of phenotypes is

$$\gamma_2(H^T) = \omega_1(1 - \exp(-\omega_2 H^T)), \quad (4.1)$$

where ω_1 and ω_2 are parameters; as host population declines, more and more hosts are of type 1 (and thus subject to parasitism). This functions could arise, for example, if crowding of offspring decreases their size (e.g.,

Danthanarayanan *et al.*, 1982).

5. POPULATION DYNAMICS FOR "FACULTATIVE" PARASITIDS AND HOSTS

We now turn to the situation in which t^* is determined by facultative behavior of the parasitoids (Mangel and Clark, 1988). To do this, we model the within-season host choice behavior of the parasite, assuming that it is not egg-limited (cf. Mangel, 1987). Hassell (1987) stresses the importance of taking into account "spatial and other forms of within-generation variability in survival" (p. 705) and our objective is to follow this program by studying behavior as a source of within-generation variability. Facultative oviposition behavior is clearly one of the most important sources of within-generation variability.

We assume that the season lasts T periods and that in each period the parasitoid encounters at most one host. We can relate the encounter rate to the parameter α as follows. First, when there is only one host present, assuming random search gives

$$\Pr\{\text{encounter a single host in a single period}\} = 1 - \exp(-\alpha) \quad (5.1)$$

so that the probability of encountering one of H_T hosts in a single period is

$$\Pr\{\text{parasite encounters one of } H_T \text{ hosts in a single period}\} = p(H_T) = 1 - \exp(-\alpha H_T) \quad (5.2)$$

We assume that hosts are encountered according to their initial densities; the probability that a host of type i ($i = 1$ or 2) is encountered is

$$\lambda_i = \Pr\{\text{parasite encounters a host of type } i \text{ in a single period}\} = p(H^i_T) \cdot \left(\frac{H^i_T(0, \lambda^i)}{H^i_T(0, \lambda^i)} \right) \quad (5.3)$$

We also assume that oviposition in a host of type 1 increments the lifetime reproduction of the parasitoid by 1 unit and that oviposition in a host of type 2 increments the lifetime reproduction by $\beta > 1$ units. We define expected lifetime reproduction from t to T by

$$F(t) = \max E\{\text{accumulated reproduction through ovipositions between } t \text{ and } T\}, \quad (5.4)$$

where the maximum is taken over the facultative behavior of oviposition in host type 2. (It is easy to show that to maximize expected lifetime reproduction, the parasite will always oviposit in host type 1.) Finally, we assume that while searching the parasite has a probability of mortality μ_s

and while ovipositing a probability of mortality μ_{ov} ; we generally expect that $\mu_{ov} > \mu_s$. With these assumptions, $F(t)$ satisfies

$$F(t) = (1 - \lambda_1 - \lambda_2)(1 - \mu_s)F(t+1) + \lambda_1\{1 + (1 - \mu_{ov})F(t+1)\} \\ + \lambda_2 \max\{\beta + (1 - \mu_{ov})F(t+1); (1 - \mu_s)F(t+1)\} \quad (5.5)$$

with the condition that $F(T) = 0$. The three terms on the right-hand side of (5.5) correspond to (i) no host is encountered in period t , (ii) a host of type 1 is encountered in period t , and (iii) a host of type 2 is encountered in period t .

In writing (5.5), we assume that the parasite behaves throughout the season according to the host densities at the start of the season. That is, there is no facultative adjustment of behavior according to changing host distributions *within* seasons, but only *between* seasons.

Equation (5.5) is solved backwards in time (Mangel and Clark, 1988) starting at $t = T - 1$ and generates both the expected lifetime reproduction $F(t)$ and the facultative behavior of the parasite, through the maximization step in (5.5). We define t^* as the value of t such that the facultative behavior is to reject host type 2 for all times before t but to accept it for all times after t . The time t^* will depend upon the densities of hosts and upon the life history parameters β , μ_{ov} , μ_s and the ecological parameters α , $H_1(0, y)$, $H_2(0, y)$, and T . It is possible to derive an analytical formula for t^* (Mangel, 1992). The most important point, however, is that t^* will generally be a nonlinear function of $H_1(0, y)$ and $H_2(0, y)$, and when this is incorporated into (3.3), the between-year dynamics of hosts and parasites change.

6. RESULTS

We have now described three models for the between-season dynamics of hosts and parasites (Table I). These are the standard Nicholson-Bailey model (with parameters r , R , and a), the proportional refuge of "hard-wired" model (with parameters r , R , a , γ_1 , and γ_2 and possibly ω_1 and ω_2), and the "facultative" model (with parameters r , R , a , γ_1 , γ_2 , T , μ_s , μ_{ov} , and β). In this section, we provide illustrative descriptions of the dynamics. To begin, consider the case in which the allocation of hosts to the two phenotypes is independent of the total host population. That is, at the start of each season, the number of hosts of type 1 is $\gamma_1 H^T(0, y)$ and the remaining hosts are type 2. For purposes of illustrating the range of dynamic behaviors, we fix all parameters except for γ_1 . The values we choose are: $F(0, 1) = 50$, $H^T(0, 1) = 500$, $T = 20$, $R = 2$, $r = 1$, $\beta = 0.1$, $\mu_s = 0.001$, $\mu_{ov} = 0.2$, $\alpha = 0.0001$.

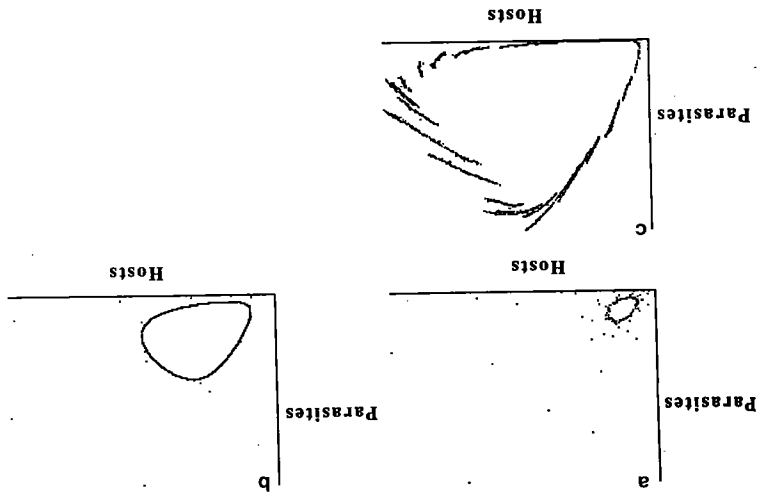


FIG. 1. Host-parasite phase planes for varying values of γ_1 . (a) The phase plane for the model with "facultative" parasites when $\gamma_1 = 0.5$ (for "hard-wired" parasites, the model predicts a stable steady state). Note that a limit cycle is present. (b) The phase plane for the model with "hard-wired" parasites (proportional refuge model) when $\gamma_1 = 0.75$. The stable steady state, obtained when $\gamma_1 = 0.5$ is replaced by a limit cycle. (c) The phase plane for the model with "facultative" parasites when $\gamma_1 = 0.75$. The limit cycle is replaced by a "strange" attractor with apparent discontinuities.

When $\gamma_1 = 0.5$, the proportional refuge model leads to a nonzero, stable steady state for both parasites and hosts. The phase plane for the model with "facultative" parasites when $\gamma_1 = 0.5$ leads to a stable limit cycle (Fig. 1). When γ_1 increases to 0.75, the phase plane for the proportional refuge model now has a limit cycle. The phase plane for the model with "facultative" parasites when $\gamma_1 = 0.75$ shows that the limit cycle is replaced by a "strange" attractor with apparent discontinuities (Ruelle, 1989). This appears to be an example of a general bifurcation that occurs for

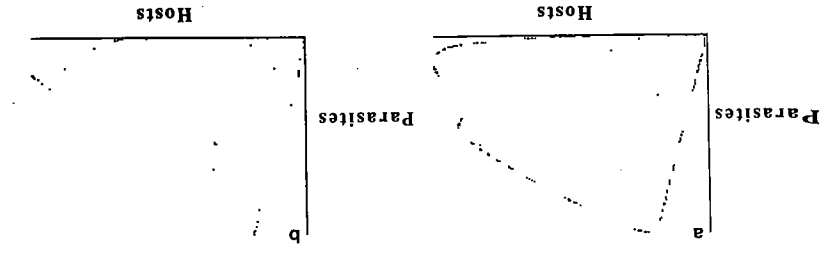


FIG. 2. Host-parasite phase planes when $\gamma_1 = 0.9$. (a) For "hard-wired" parasites, the limit cycle seen when $\gamma_1 = 0.75$ is replaced by a strange attractor. (b) The strange attractor seen for "facultative parasites" is replaced by one with even fewer points.

FIG. 3. The distribution of t^* over 10,000 generations, for different values of $\gamma_1 = 0.5$ (a), 0.6 (b), 0.75 (c), or 0.9 (d).

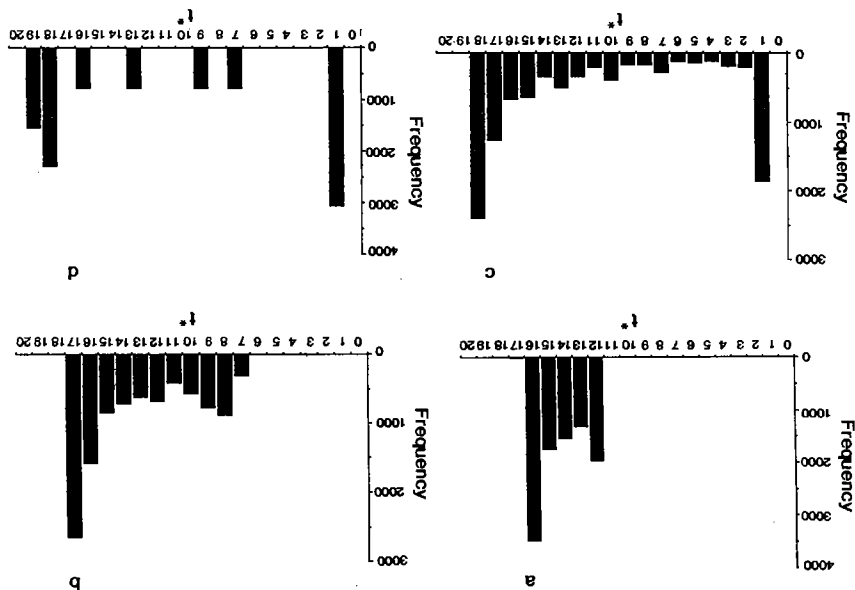
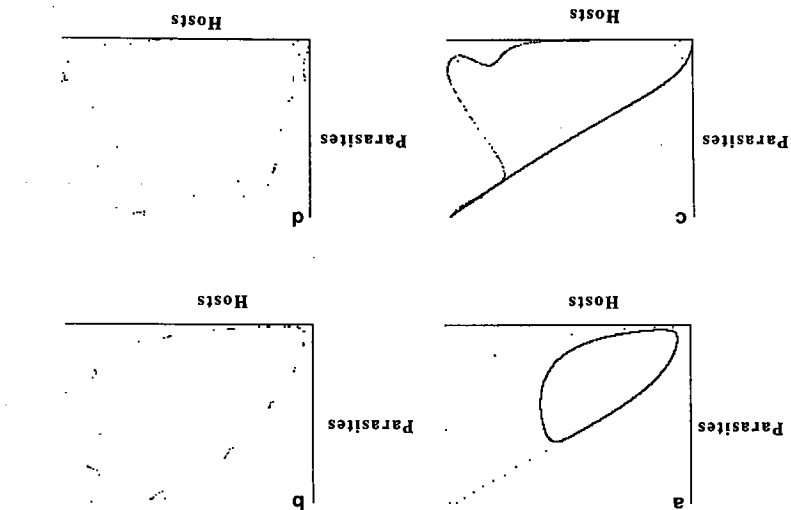


FIG. 4. Host-parasite phase planes when $\omega_2 = 0.5$, for the case of density-dependent distribution of host phenotypes. The parameter measuring the strength of density dependence is ω_1 . (a) "Hard-wired" parasites with $\omega_1 = 0.0005$, (b) "facultative" parasites with $\omega_1 = 0.0005$, (c) "hard-wired" parasites with $\omega_1 = 0.0001$, (d) "facultative" parasites with $\omega_1 = 0.0005$.



$\rho_1 = 0.5 + \epsilon$, for ϵ small but positive (A. Klebanoff, personal communication). When ρ_1 is increased to 0.9 (Fig. 2), both proportional refuge and facultative models have strange attractors. An effect of this nonlinear behavior is seen in the distribution of t^* (Fig. 3). Note that t^* can change considerably from one season to the next, depending upon the relative and absolute densities of host phenotypes. We thus predict, based on the optimality model, considerable field variation.

Finally, let us consider the case in which the distribution of hosts at the start of each year is density dependent. In particular, we assume that $\rho_2(H^t) = \omega_2(1 - \exp(-\omega_1 H^t))$. The parameter measuring the strength of density dependence is ω_1 . The parameter ω_2 measures the maximum fraction of hosts of the second phenotype. Here we also find that limit cycles and strange attractors may indeed arise for the proportional refuge model as well as for the model of "facultative" parasites (Fig. 4).

7. DISCUSSION

Our results show that individual behavior can stabilize the standard Nicholson-Bailey model. That is, spatial heterogeneity ("patchiness") is not needed to stabilize the interaction (cf. Comins and Hassell, 1979). In this regard, our work complements that of Ives and Dobson (1987), who found, using classical predator-prey equation dynamics, that individual behavior (anti-predator behavior) tends to decrease the oscillatory dynamics in model predator-prey systems. In our case, however, the results are more complicated. "Hard-wired" individual behavior, which leads to complete rejection of a certain phenotype of host essentially produces a refuge for hosts. This behavioral refuge is analogous to the spatial or temporal refuges described by Hassell (1978). Such a refuge leads to the most stabilization for the host-parasite dynamics. However, even in this case, the resulting dynamics can be chaotic if the distribution of host phenotypes is density dependent (Fig. 4). "Facultative" individual behavior leads to dynamics that are less stable than those corresponding to "hard-wired" behavior associated with the proportional refuge model. This is an example of a situation in which what is good for the individual, measured in terms of increased reproductive success, is bad for the population, measured in terms of stability or nearness to extinction.

Our models involve a number of additional parameters, which are used to characterize the within-season environment and behavior of the parasite. All of these parameters can be measured in the laboratory or field cages. Parameter estimation and testing of the theory can be decoupled because they occur on different time scales (individuals vs populations).

ACKNOWLEDGMENTS

The work of MM was partially supported by NSF Grant BSR 91-17603 and by the Center for Population Biology, University of California, Davis, and that of BDR by NSERC for Population Biology. This work was started at Bamfield Marine Station, which we thank for its hospitality, while MM was a Visiting Professor of Biology at Simon Fraser University. We thank P. E. Bradshaw, Colin Clark, Jin Yoshimura, Don Strong, and Ron Vdenberg for helpful conversations.

REFERENCES

- BEDDINGTON, J. R., FREE, C. A., AND LAWTON, J. H. 1978. Characteristics of successful natural enemies in models of biological control of insect pests, *Nature* **273**, 513-519.
- CHESSON, P. L., AND MURDOCH, W. W. (1986). Aggregation of risk: Relationships among host-parasitoid models, *Am. Nat.* **127**, 696-715.
- COHEN, J. E., AND NEWMAN, C. M. 1989. Host-parasite relations and random zero-sum games: The stabilizing effect of strategy diversification, *Am. Nat.* **133**, 533-552.
- COMINS, H. N., AND HASSELL, M. P. 1979. The dynamics of optimally foraging predators and parasitoids, *J. Animal Ecol.* **48**, 335-351.
- DANTHANARAYANA, W., HAMILTON, J. G., AND KHOUR, S. 1982. Low-density larval crowding in the light brown apple moth *Ephyhysa posttiana* and its ecological significance, *Entomol. Exp. Appl.* **31**, 353-358.
- DEBUZZE, D., AND THOULOSSE, J. 1986. Statistics to find spatial and temporal structures in populations, in "Pest Control: Operations and Systems Analysis in Fruit Fly Management" (M. Mangel *et al.*, Eds.), pp. 263-282, Springer-Verlag, New York.
- HASSELL, M. P. 1978. "The Dynamics of Arthropod Predator Prey Systems," Princeton Univ. Press, Princeton, NJ.
- HASSELL, M. P. 1987. Detecting regulation in patchily distributed animal populations, *J. Animal Ecol.* **56**, 705-713.
- HASSELL, M. P., AND MAY, R. M. 1973. Stability of insect host-parasite models, *J. Animal Ecol.* **42**, 693-726.
- HASSELL, M. P., AND MAY, R. M. 1988. Spatial heterogeneity and the dynamics of parasitoid-host systems, *Am. Zool. Fenn.* **25**, 55-61.
- HASSELL, M. P., AND WAGE, J. K. 1984. Host-parasitoid population interactions, *Am. Rev. Entomol.* **29**, 89-114.
- IVES, A. R., AND DOBSON, A. P. 1987. Antipredator behavior and the population dynamics of simple predator-prey systems, *Amer. Nat.* **130**, 431-447.
- MANGEL, M. 1987. Oviposition site selection and clutch size in insects, *J. Math. Biol.* **25**, 1-22.
- MANGEL, M. 1992. Descriptions of super parasitism by optimal foraging theory, evolutionarily stable strategies, and quantitative genetics, *Evol. Ecol.* **6**, 152-169.
- MANGEL, M., AND CLARK, C. W. 1988. "Dynamic Modeling in Behavioral Ecology," Princeton Univ. Press, Princeton, NJ.
- MAY, R. M. 1978. Host-parasitoid systems in patchy environments: A phenomenological model, *J. Animal Ecol.* **47**, 833-843.
- PACALA, S. W., HASSELL, M. P., AND MAY, R. M. 1990. Host-parasitoid associations in patchy environments, *Nature* **344**, 150-153.
- RUELE, D. 1989. "Chaotic Evolution and Strange Attractors," Cambridge Univ. Press, Cambridge, UK.

Printed by Catherine Press, Ltd., Tempelhof 41, B-8000 Brugge, Belgium

