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# DYNAMICAL CONSEQUENCES OF OPTIMAL HOST FEEDING ON HOST–PARASITOID POPULATION DYNAMICS

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This study examines the influence of various host-feeding patterns on host-parasitoid population dynamics. The following types of host-feeding patterns are considered: concurrent and non-destructive, non-concurrent and non-destructive, and non-concurrent and destructive. The host-parasitoid population dynamics is described by the Lotka-Volterra continuous-time model. This study shows that when parasitoids behave optimally, i.e. they maximize their fitness measured by the instantaneous per capita growth rate, the non-destructive type of host feeding stabilizes host-parasitoid dynamics. Other types of host feeding, i.e. destructive, concurrent, or non-concurrent, do not qualitatively change the neutral stability of the Lotka-Volterra model. Moreover, it is shown that the pattern of host feeding which maximizes parasitoid fitness is either non-concurrent and destructive, or concurrent and non-destructive host feeding, depending on the host abundance and parameters of the model. The effects of the adaptive choice of host-feeding patterns on host-parasitoid population dynamics are discussed. © 1997 Society for Mathematical Biology

**Introduction.** It is believed that behavioral decisions of parasitoids may have a strong impact on host-parasitoid population dynamics. The effects of various behavioral decisions of parasitoids on host-parasitoid population dynamics were recently studied: searching for food versus ovipositing (Křivan and Sirot, 1997), searching for healthy hosts versus superparasitizing (Sirot and Křivan, 1997), ovipositing versus host feeding (Jervis and Kidd, 1986; Yamamura and Yano, 1988; Kidd and Jervis, 1991b; Murdoch *et al.*, 1992; Briggs *et al.*, 1995; Jervis and Kidd, 1995). Since host feeding (i.e. the consumption of host haemolymph by the adult female parasitoid) may have a major impact on host mortality, host-feeding parasitoid species may prove to be good biological control agents (Kidd and Jervis, 1989). Host feeding was also studied in the framework of dynamic state variable models (Collier *et al.*, 1994; Houston *et al.*, 1992). These models predict the

existence of a threshold egg load below which host feeding occurs. While these predictions qualitatively agree with earlier experimental results (Collier *et al.*, 1994), which showed that probability of host feeding declines with the egg load, a similar experiment by Rosenheim and Rosen (1992) does not show such a relationship.

In other work (Jervis and Kidd, 1986), the following types of host feeding were considered: concurrent, non-concurrent, destructive and non-destructive. Concurrent feeding means that the female parasitoid uses the same host individual for both feeding and oviposition, while non-concurrent means that different hosts are used. Destructive host feeding means that hosts die because of the host feeding, while in the case of non-destructive host feeding, hosts survive. Surveying known facts about 64 species of hymenopteran parasitoids, earlier work (Jervis and Kidd, 1986) showed that the most common host-feeding patterns to appear are: non-concurrent and destructive (42 species), and concurrent non-destructive (11 species). Some parasitoids also develop a mixed strategy: concurrent non-destructive/nonconcurrent destructive (eight species), or concurrent non-destructive/nonconcurrent non-destructive (three species). The decision of a parasitoid whether to host feed or to oviposit represents a tradeoff: host feeding increases the number of eggs produced, but it may decrease the number of ovipositions if host feeding is non-concurrent.

Effects of various host-feeding patterns on population dynamics were discussed earlier (Kidd and Jervis, 1989). The underlying dynamics was described by the discrete-time Nicholson-Bailey model. Based on a series of simulations, they concluded that "host-feeding behavior is unlikely to contribute to population regulation" since their models exhibit unstable oscillations of increasing amplitude as in the original Nicholson-Bailey model. This result supports the idea of Flanders (1953) that host feeding results in a low persistence of the parasitoid population when hosts are scarce and produces population oscillations of high amplitude. A similar result was also obtained (Briggs et al., 1995), which found that host feeding per se does not affect stability of a host-parasitoid system described by a continuous-time Lotka-Volterra model. However, they showed that if the parasitoid mortality rate is a decreasing function of the egg load, then the model may stabilize. Moreover, the input of nutrients from a non-host source has a stabilizing effect, while the use of host material for maintenance is destabilizing. Previously (Yamamura and Yano, 1988), the Lotka-Volterra continuous-type model with time delay was considered. In this model, host feeding increased the speed of convergence of trajectories to an equilibrium.

In the present paper, we want to compare the effects of various hostfeeding patterns on host-parasitoid population dynamics described by the Lotka-Volterra continuous-time model. We assume that parasitoids behave in order to maximize their fitness as measured by an instantaneous per-capita growth rate. We find the optimal host-feeding strategy for each host-feeding pattern, and we study the effects of optimal behavioral decisions of parasitoids on host-parasitoid population dynamics. Our model predicts that, while the destructive type of host feeding has little influence on host-parasitoid dynamics, non-destructive host feeding strongly affects the population dynamics, and may lead to a stable equilibrium. We also discuss the effect of adaptive selection of host-feeding patterns on host-parasitoid population dynamics.

Fitness and Optimal Host Feeding. In this section, we describe parasitoid fitness with respective to various host-feeding patterns. The host abundance is denoted by x and the parasitoid abundance by y. By  $\lambda$ , we denote the search rate of a parasitoid, u denotes the probability that upon an encounter with a host a parasitoid will host feed, e is the net energy (or protein, depending on the currency used) gained from feeding on one host, o is the energy needed for producing one egg, and s is the maintenance energy needed in unit of time. If N is the number of hosts required to be fed on to satisfy energy demands (i.e. maintenance and egg production) of a parasitoid in unit of time, following earlier work (Jervis and Kidd, 1986), we have

$$N = \frac{s + oE}{e}$$

where E is the number of eggs produced in a unit of time. Assuming that during a unit of time a parasitoid will encounter  $\lambda x$  hosts, and it will host feed on them with probability u, the total number of hosts which will be host fed is

$$N = \lambda u x$$
.

We note that in the above derivation, we neglect the time which a parasitoid devoted to handling one host. If  $\lambda ux$  is smaller than the maintenance energy s, no eggs are produced. This gives the maximum number of eggs E produced in a unit of time:

$$E = \max\left\{\frac{\lambda uxe - s}{o}, 0\right\}.$$

First, we consider the case of non-concurrent host feeding. In this case, a parasitoid upon an encounter with a host either host feeds or oviposits provided it has some eggs. We assume that parasitoids that do not have

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eggs always feed on hosts upon an encounter. Neglecting the time delay between egg production and oviposition, the maximum number of ovipositions in unit time is limited by the number of encounters with hosts and the number of eggs produced. If host feeding and oviposition are mutually exclusive (which is the case in non-concurrent host feeding), only hosts that are not host fed may be oviposited. Since the number of hosts encountered in unit time by a single parasitoid which are not host fed is  $(1 - u)\lambda x$ , the maximum number of ovipostions in unit time is constrained by the number of eggs produced and the number of hosts encountered which can be oviposited, i.e.

$$\min\left\{\max\left\{\frac{\lambda uxe-s}{o},0\right\},(1-u)\lambda x\right\}.$$

Now, we consider concurrent host feeding. In this case, parasitoids may both host feed and oviposit in the same host. Since all encountered hosts may be oviposited, the maximum number of ovipositions in unit time is

$$\min\left\{\max\left\{\frac{\lambda uxe-s}{o},0\right\},\lambda x\right\}.$$

We define fitness as the number of offsprings produced by an average parasitoid in unit time. This means that only those ovipositions which lead to the emergence of a new parasitoid add to parasitoid's fitness. In what follows, we consider the following host-feeding patterns: non-concurrent and destructive (ND), non-concurrent and non-destructive (NN), and concurrent and non-destructive (CN). We do not consider concurrent and destructive host feeding since, in this case, oviposited hosts are also host fed, which necessarily reduces fitness of this rarely observed host-feeding pattern (Jervis and Kidd, 1986).

We make the following assumptions. First, we assume that the energy gain from destructive host feeding is higher than from non-destructive feeding, i.e.

$$e_D > e_N$$

where  $e_D$  denotes the net energy gained from feeding on a host when host feeding is destructive, and similarly for  $e_N$ . Second, we assume that non-destructive feeding has no ill effects on the parasitoid's developing progeny.

For a fixed host abundance x and host-feeding strategy u, the number of ovipositions in unit time, i.e. the parasitoid's fitness, is given by (the

subindex refers to the type of host-feeding pattern considered)

$$f_{\rm ND}(x,u) = \min\left\{\max\left\{\frac{\lambda uxe_D - s}{o}, 0\right\}, (1 - u)\lambda x\right\},\$$
  
$$f_{\rm NN}(x,u) = \min\left\{\max\left\{\frac{\lambda uxe_N - s}{o}, 0\right\}, (1 - u)\lambda x\right\},\$$
  
$$f_{\rm CN}(x,u) = \min\left\{\max\left\{\frac{\lambda uxe_N - s}{o}, 0\right\}, \lambda x\right\}.$$

We assume that parasitoids behave so as to maximize their fitness with respect to host feeding, and for each host abundance, we define the maximal parasitoid fitness

$$F_i(x) = \max_{0 \le u \le 1} f_i(x, u), \qquad i = \text{ND}, \text{NN}, \text{CN}.$$

Thus,  $F_i(x)$  is the maximal possible fitness of a parasitoid measured through the number of offspring produced in unit of time. The values of u which maximize  $f_i(x, u)$  define the optimal strategy of parasitoids with respect to host feeding.

We set

$$u_D^1 = \frac{s}{\lambda x e_D},$$
  

$$u_N^2 = \frac{o\lambda x + s}{\lambda x e_N},$$
  

$$x_D^1 = \frac{s}{\lambda e_D},$$
  

$$x_N^1 = \frac{s}{\lambda e_N},$$
  

$$x_D^2 = \frac{s}{\lambda (e_D - o)},$$
  

$$x_N^2 = \frac{s}{\lambda (e_N - o)}.$$

Since fitness functions  $f_i$ , i = ND, NN, CN are piecewise linear in u, it is easy to determine the optimal strategy for each type of host feeding. For



Figure 1. Maximal fitness for various host-feeding patterns plotted as a function of host abundance. In A, the parameters are such that  $o < e_N e_D / (e_D - e_N)$ , which leads to the existence of the critical host abundance  $x^*$  such that below it, non-concurrent and destructive host feeding gives the highest fitness, while above it, the concurrent and non-destructive host feeding is the best choice. For  $o > e_N e_D / (e_D - e_N)$ , see B. In this case, the non-concurrent and destructive host-feeding pattern gives the highest parasitoid fitness.

non-concurrent and destructive host feeding, the optimal strategy is as follows (see Appendix A and Fig. 1).

• If  $x < x_D^1$ , then  $F_{ND}(x)$  is identically zero since the energy obtained through host feeding does not meet the amount of energy necessary for the maintenance, and no eggs are produced. Consequently, the optimal strategy  $u_{opt}$  cannot be uniquely determined; thus,  $0 \le u_{opt} \le 1$ .

In this case, there must be another source of energy (like pollen, honeydew, etc.) which allows parasitoids to survive. Whether a parasitoid will host feed or not may depend on the distribution of the alternative food type. If a parasitoid encounters hosts when searching for the alternative food type, it is likely that it will host feed on them (i.e.,  $u_{opt} = 1$ ). If the alternative food is located at a place where are no hosts, parasitoids will have no possibility to host feed.

• If  $x \ge x_D^1$ , then  $u_{opt} = (o\lambda x + s)/(\lambda x(e_D + o))$  and  $F_{ND}(x) = (\lambda xe_D - s)/(e_D + o)$ . In this case, the egg production rate equals the encounter rate with hosts which are not host fed.

The strategy for non-concurrent and non-destructive host feeding is obtained from the optimal strategy for non-concurrent and destructive host feeding by replacing index D by N.

The optimal strategy for concurrent and non-destructive host feeding depends on the relation between o and  $e_N$ . First, we assume  $e_N > o$ , which means that feeding on one host is sufficient to produce more than one egg. Under this assumption, the optimal strategy is as follows (see Appendix A).

- If  $x < x_N^1$ , then the optimal strategy is not uniquely determined,  $0 \le u_{opt} \le 1$  and  $F_{CN}(x) = 0$ , which means that no eggs are produced because hosts are scare.
- If  $x_N^1 \le x \le x_N^2$ , then  $u_{opt} = 1$  and  $F_{CN}(x) = (\lambda x e_N s)/o$ . In this case, the number of hosts is too small to produce enough eggs to oviposit each encountered host due to the loss of energy which goes to the maintenance. A convenient strategy for parasitoids would be to obtain additional energy to cover the maintenance cost from non-host food sources which would allow for higher egg production and for a higher parasitoid growth rate.
- If  $x > x_N^2$ , then the optimal strategy is not uniquely determined,  $u_N^2 \le u_{opt} \le 1$  and  $F_{CN}(x) = \lambda x$ . The number of ovipositions is limited by the number of hosts available for oviposition rather than egg production. In this case, the egg production rate exceeds the oviposition rate if  $u_{opt} > u_N^2$ , which would lead to the growth of the egg load in ovaries. It is therefore reasonable to assume that if parasitoids have small (or zero) egg load, then they may increase host feeding (i.e.  $u_{opt}$ may be higher than  $u_N^2$ ), which will increase the average egg load. If the average egg load reaches the maximum storage capacity of ovaries, then  $u_{opt} = u_N^2$  since, in this case, the number of eggs produced will balance the number of eggs deposited keeping the egg load constant.

Second, we assume that feeding on one host is not sufficient to produce one egg, i.e.  $e_N \leq o$ , which gives the following optimal strategy (see Appendix A).

- If  $x < x_N^1$ , then  $0 \le u_{out} \le 1$  and  $F_{CN}(x) = 0$  due to the host scarcity.
- If  $x \ge x_N^1$ , then  $u_{opt} = 1$  and  $F_{CN}(x) = (\lambda x e_N s)/o$ . In this case, the oviposition rate is always limited by the egg production.

Effects of Host-Feeding Patterns on Population Dynamics. In this section, we study the effects of host-feeding patterns on host-parasitoid population dynamics. We assume that parasitoids host feed optimally, i.e. they maximize their fitness, and for a given parasitoid species, the host-feeding pattern is fixed. The underlying population dynamics is of the Lotka-Volterra continuous time.

Non-concurrent and destructive host feeding. This host-feeding pattern is the most common type observed among hymenopteran parasitoids (Jervis and Kidd, 1986). All encounters of a parasitoid with hosts are lethal for hosts either due to oviposition or host feeding, i.e. the functional response is  $\lambda x$ . Assuming that a parasitoid lays one egg per host, which gives to rise  $F_{\rm ND}(x)$  new parasitoids in a unit of time, we get the following continuoustime dynamics:

$$x' = x(a - \lambda y),$$
  

$$y' = F_{ND}(x)y - my.$$
(1)

Here, a is the intrinsic per-capita growth rate of hosts, and m is the intrinsic per-capita mortality rate of parasitoids. Thus, we do not consider any density dependence in the growth of the host population.

The dynamics of (1) is described for  $x > x_D^1$  by

$$x' = x(a - \lambda y),$$
  

$$y' = y \left( \frac{\lambda x e_D - s}{e_D + o} - m \right),$$
(2)

and for  $x \leq x_D^1$  by

$$x' = x(a - \lambda y).$$
  

$$y' = -my.$$
(3)

It is proved in Appendix B that trajectories of (1) are closed curves centered at the neutrally stable equilibrium of (2):

$$E^{2} = \left(\frac{m(e_{D}+o)+s}{e_{D}\lambda}, \frac{a}{\lambda}\right);$$



Figure 2. For non-concurrent and destructive host feeding, equilibrium  $E^2$  is surrounded by closed curves. In this case, host feeding does not qualitatively influence the neutral stability of the underlying Lotka-Volterra model. Parameters are as follows: a = 1.5,  $\lambda = 1$ ,  $e_D = 2$ , o = 1, m = 0.5, s = 1.

see Fig. 2. Qualitatively, trajectories look the same as for the classical Lotka-Volterra model. If a trajectory moves in the part of the space where  $x > x_D^1$ , the egg production rate is  $(\lambda x e_D - s)/(e_D + o)$  and the probability of host feeding is  $(o\lambda x + s)/(\lambda x (e_D + o))$ . The ratio of ovipositions/feeding attacks

$$\frac{1 - u_{\text{opt}}}{u_{\text{opt}}} = \frac{\lambda x e_D - s}{o \lambda x + s} \qquad \text{for } x \ge x_D^1$$

is declining with declining host abundance, which corresponds to observations (Kidd and Jervis, 1991b).

If  $x < x_D^1$ , no eggs are produced because all energy available is used for maintenance, and the parasitoid population is declining, which reduces the pressure on the host population that can recover.

Concurrent and non-destructive host feeding. In this case, only those hosts which are parasitized will die since host feeding is non-destructive. Assuming that each parasitoid lays one egg per host, the functional response is given by the number of ovipositions  $F_{\rm CN}(x)$ , which is also the numerical response. This leads to the following model:

$$x' = ax - F_{CN}(x)y,$$
  

$$y' = F_{CN}(x)y - my.$$
(4)

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First, we assume that  $e_N > o$ , i.e. feeding on one host leads to the production of more than one egg. The dynamics of (4) driven by the optimal strategy is described for  $x > x_N^2$  by

$$x' = x(a - \lambda y),$$
  

$$y' = y(\lambda x - m),$$
(5)

for  $x_N^1 \leq x \leq x_N^2$  by

$$x' = ax - \frac{\lambda x e_N - s}{o} y,$$
  
$$y' = \frac{\lambda x e_N - s}{o} y - my,$$
 (6)

and for  $x < x_N^1$  by

$$\begin{aligned} x' &= ax, \\ y' &= -my. \end{aligned} \tag{7}$$

If the host abundance is below  $x_N^1$ , then the host population is growing since parasitoids do not have enough energy to produce eggs. Thus, all trajectories for which the initial host abundance is below  $x_N^1$  enter in a finite time the region  $x > x_N^1$  and stay there forever. Equation (5) has equilibrium

$$E^5 = \left(\frac{m}{\lambda}, \frac{a}{\lambda}\right)$$

and (6) has equilibrium

$$E^{6} = \left(\frac{mo+s}{e_{N}\lambda}, \frac{a(mo+s)}{e_{N}\lambda m}\right).$$

If

$$m < \frac{s}{e_N - o},\tag{8}$$

then  $E^5$ ,  $E^6$  are to the left of the line  $x = x_N^2$  and  $E^6$  is globally asymptotically stable for (4); see Appendix C and Fig. 3A. The mechanism which drives trajectories to the stable equilibrium is the following. If a trajectory of (4) reaches the line  $x = x_N^2$  below the point  $y = a/\lambda$  from the left, then it will cross this line, and in the region  $x > x_N^2$ , it will move along a Lotka-Volterra cycle centered at  $E^5$ . Since equilibrium  $E^5$  is to the left of



Figure 3. For concurrent and non-destructive host feeding, equilibrium  $E^6$  is globally asymptotically stable if it is to the left of the line  $x = x_N^2$  (A). In this simulation,  $e_N = 2$ ; other parameters are the same as those given in Fig. 2. If  $E^6$  is to the right of the line  $x = x_N^2$  (B), then trajectories converge from outside to the largest Lotka-Volterra cycle of (5) which is to the right of the line  $x = x_N^2$ . In this simulation, m = 1.5 and other parameters are the same as those given in Fig. 2.

the line  $x = x_N^2$ , the trajectory will necessarily return to the region  $x < x_N^2$  where it is attracted by  $E^6$ . In this way, trajectories will converge to  $E^6$ , and host feeding has a stabilizing effect. At the equilibrium, the egg deposition rate equals *m*, and parasitoids will play pure strategy (u = 1), i.e. they will host feed upon each encounter with a host.

If  $m > s/(e_N - o)$ , then  $E^5$ ,  $E^6$  are to the right of the line  $x = x_N^2$ , and it is proved in Appendix C that the qualitative behavior of trajectories

depends on initial conditions. If the initial condition belongs to the set bounded by the largest Lotka-Volterra cycle of (5) which is to the right of the line  $x = x_N^2$ , then the corresponding trajectory will follow a Lotka-Volterra cycle of (5) (see the small amplitude cycle in Fig. 3B). If initial conditions are outside this set, the corresponding trajectory will converge to the largest Lotka-Volterra cycle which is to the right of the line  $x = x_N^2$ ; see Fig. 3B. In this case, host feeding has a partially stabilizing effect on population dynamics in the sense that there exists a bound on population fluctuations. The amplitude of maximal fluctuations is proportional to the distance of  $E^5$  from the line  $x = x_N^2$ . This distance is given by

$$\frac{m(e_N-o)-s}{\lambda(e_N-o)}$$

For example, fluctuations in the host-parasitoid population dynamics increase with increasing instantaneous predator mortality rate m.

If we assume  $e_N \leq o$ , the host-parasitoid dynamics is described by (6) for  $x > x_N^1$ , by (7) for  $x \leq x_N^1$ , and all trajectories converge to  $E^6$  which is globally stable; see Appendix C.

Non-concurrent and non-destructive host feeding. In this case, only those hosts which are oviposited will die, which leads to the following host-parasitoid dynamics:

$$x' = ax - F_{NN}(x)y,$$
  

$$y' = F_{NN}(x)y - my.$$
(9)

The dynamics of (9) driven by the optimal strategy is described for  $x > x_N^1$  by

$$x' = ax - \frac{\lambda x e_N - s}{e_N + o} y,$$
  
$$y' = y \left( \frac{\lambda x e_N - s}{e_N + o} - m \right),$$
 (10)

and for  $x \leq x_N^1$  by (7). System (9) has a globally asymptotically stable equilibrium which is the equilibrium of (10) (see Appendix C):

$$E^{10} = \left(\frac{m(e_N+o)+s}{e_N\lambda}, a\frac{m(e_N+o)+s}{e_N\lambda m}\right).$$

Trajectories qualitatively look the same as those in Fig. 3A. Host feeding stabilizes, in this case, the Lotka–Volterra dynamics. At equilibrium, partial preferences for host feeding appear since

$$u_{\rm opt} = \frac{mo+s}{m(e_N+o)+s}.$$

Effects of Adaptive Host Feeding on Population Dynamics. In this section, we will assume that the host-feeding patterns may be adaptive. This means that the host-feeding pattern which gives the highest fitness should be selected. We find which type of host-feeding pattern gives the maximum fitness. We note that

$$f_{\rm ND}(x,u) \ge f_{\rm NN}(x,u), f_{\rm CN}(x,u) \ge f_{\rm NN}(x,u)$$

for any host abundance and any host-feeding strategy (we recall that we assume  $e_D > e_N$ ). This implies that

$$F_{\rm ND}(x) \ge F_{\rm NN}(x), F_{\rm CN}(x) \ge F_{\rm NN}(x);$$

see Fig. 1. Assume

$$o < \frac{e_N e_D}{e_D - e_N},\tag{11}$$

and denote

$$x^* = \frac{se_D}{\lambda (e_N e_D - o(e_D - e_N))}.$$

We note that for  $o < e_N$ , inequality (11) is satisfied. We get that  $F_{CN}(x) > F_{ND}(x)$  if  $x > x^*$ , and  $F_{CN}(x) \leq F_{ND}(x)$  otherwise; see Fig. 1A. Thus, if hosts are abundant, concurrent and non-destructive host feeding should be selected, while if the host abundance is below  $x^*$ , non-concurrent and destructive host feeding should prevail. The optimal parasitoids behavior leads to switching between the concurrent and non-destructive, and non-concurrent and destructive host feeding with respect to changing host abundance.

If  $o > e_N e_D / (e_D - e_N)$ , then  $F_{ND}(x) > F_{CN}(x)$  for all parasitoid densities above  $x_D^1$ ; see Fig. 1B, i.e. the non-concurrent and destructive strategy is always the best host-feeding pattern.

Thus, the two best possible host-feeding patterns are non-concurrent and destructive, and concurrent and non-destructive host feeding, which qualitatively agrees with observations (Jervis and Kidd, 1986).

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Now, we will consider the host-parasitoid dynamics in the case in which switching between concurrent and non-destructive, and non-concurrent and destructive host feeding occurs, i.e. (11) holds. Let  $v_i$  (here i = ND, CN and  $v_{CN} + v_{ND} = 1$ ) be the probability that host-feeding pattern i is chosen by a parasitoid. The corresponding population dynamics is described by

$$x' = ax - v_{\rm ND}\lambda xy - v_{\rm CN}F_{\rm CN}(x)y,$$
  

$$y' = -my + v_{\rm ND}F_{\rm ND}(x)y + v_{\rm CN}F_{\rm CN}(x)y,$$
(12)

and the average fitness per parasitoid is

$$F(x) = v_{\rm ND}F_{\rm ND}(x) + v_{\rm CN}F_{\rm CN}(x).$$

The optimal strategy is the vector  $(v_{ND}(x), v_{CN}(x))$  which maximizes F(x):

- If  $x > x^*$ , then the best host-feeding pattern is concurrent and non-destructive host-feeding, i.e.  $v_{CN}(x) = 1$ ,  $v_{ND}(x) = 0$ .
- If  $x = x^*$ , then the optimal strategy is not uniquely given,  $v_{ND}(x) + v_{CN}(x) = 1$ .
- If  $x_D^1 < x < x^*$ , then the best host-feeding pattern is non-concurrent and destructive host feeding, i.e.  $v_{ND}(x) = 1$ ,  $v_{CN}(x) = 0$ .
- If  $x < x_D^1$ , then the optimal strategy is not uniquely defined,  $v_{ND}(x) + v_{CN}(x) = 1$ .

The reason that, for host densities below  $x_D^1$ , the host-feeding strategy is not uniquely determined is due to the fact that, for all possible host-feeding scenarios, the energy obtained from host feeding is lower than the maintenance energy and, consequently, no eggs are produced. We will assume that, for low host abundances, destructive host feeding will prevail since it provides more energy for parasitoids to satisfy their energy requirements than non-destructive host feeding. Thus, for a host abundance below  $x_D^1$ , the dynamics is described by (3).

In what follows, we will assume that  $e_N e_D / (e_D - e_N) > e_N > o$ , and we note that

$$x_D^1 < x_N^1 < x^* < x_N^2$$
.

Population dynamics which corresponds to the optimal choice of a host-feeding pattern is described by (2) for  $x_D^1 \le x \le x^*$ , by (6) for  $x^* < x < x_N^2$ , and by (5) for  $x_N^2 < x$ . If

$$m < \frac{s(e_D - e_N)}{e_D e_N - o(e_D - e_N)}$$
(13)

we show that adaptive host feeding may destabilize the host-parasitoid dynamics. Let us consider a segment of the line  $x = x^*$  which is between the points

$$y^{1} = \frac{a}{\lambda},$$
$$y^{2} = \frac{ae_{D}}{\lambda(e_{D} - e_{N})}.$$

Trajectories starting from a point which is close to this segment move away from this segment; see Appendix D. For this reason, trajectories which start from the segment are not uniquely defined since they may move either to the left or to the right. Consider initial densities of host and parasitoids which are close to  $E^2$ . Since, due to (13),  $E^2$  is to the left of the line  $x = x^*$ , the corresponding dynamics is described by (2) and follows a Lotka–Volterra cycle; see Fig. 4A. Thus,  $E^2$  is neutrally stable. If the initial densities are such that the corresponding trajectory intersects with the line  $x = x^*$ , then it cannot return to the region where  $x < x^*$  below the point  $y^2$ ; see Appendix D. This results in destabilization of the dynamics, and trajectories spiral away from the equilibria  $E^2$ ; see Appendix E and Fig. 4A. We note that, in this case, the parasitoid will switch the host-feeding pattern between non-concurrent and destructive, and concurrent and non-destructive periodically with respect to changing host abundance.

If the opposite inequality to (13) holds and  $m < s/(e_N - o)$ , then  $E^2$ ,  $E^6$  are to the right of the discontinuity line  $x = x^*$ , and  $E^6$  is to the left of the line  $x = x_N^2$ . In this case,  $E^6$  is locally stable, but numerical simulations such as those given in Fig. 4B suggest that  $E^6$  is not globally stable.

If  $m > s/(e_N - o)$ , then all trajectories do converge to the global attractor given by the largest Lotka-Volterra cycle of (5), which is to the right of the line  $x = x_N^2$ ; see Appendix E.

The case for which  $e_N e_D / (e_N - e_D) > o > e_N$  leads to similar results; see Appendix E. In this case, we note that  $x_N^2 < 0$ , and the dynamics (12) is described by (2) for  $x_D^1 \le x \le x^*$  and by (6) for  $x^* < x$ . If (13) holds, then the dynamics is destabilized in a similar way as in Fig. 4A.

**Discussion.** In this paper, we studied the effects of various host-feeding patterns on host-parasitoid population dynamics described by the Lotka-Volterra model assuming that parasitoids maximize their fitness. We showed that, while the destructive type of host feeding does not qualitatively influence host-parasitoid population dynamics, non-destructive type of host feeding has a strong effect on population dynamics since it leads either to a stable equilibrium, or it reduces the amplitude of maximal fluctuations in population densities. Since we did not include in our models



Figure 4. This figure shows the possible destabilization of the host-parasitoid dynamics when host-feeding pattern is chosen in an adaptive way. In A, equilibrium  $E^2$ , which is to the left of the line  $x = x^*$ , is neutrally stable (since it is surrounded by a family of closed curves), but trajectories which move to the region where  $x > x^*$  do spiral away from the equilibrium. Parameters are as follows: a = 1.5,  $\lambda = 1$ ,  $e_D = 6$ ,  $e_N = 2$ , o = 1.3, m = 0.3, s = 1.5. In B, equilibrium  $E^6$ , which is to the right of the line  $x = x^*$ , is locally, but not globally asymptotically stable. In this plot, m = 1, and other parameters are the same as those given in A.

any density dependence or other mechanism which could itself lead to a stable equilibrium, our model predicts that non-destructive host feeding per se may stabilize neutrally stable Lotka-Volterra dynamics. Earlier work (Briggs *et al.*, 1995) considered the effect of the egg load on host feeding and host-parasitoid dynamics for non-concurrent and destructive host

feeding. They assumed that per-capita parasitoid mortality rate is an exponentially decreasing function of egg load. Without the use of eggs for maintenance, host feeding does not qualitatively change the behavior of the underlying Lotka–Volterra continuous-time model, which agrees with the prediction from our model. However, when maintenance was included in the previous model (Briggs *et al.*, 1995), the result switched from no result on stability to a destabilizing effect. Instead, in our model, we assumed that per-capita parasitoid mortality rate is constant because maintenance requirements can be met by other non-host resources like pollen, honeydew, nectar, etc. and the stability (for destructive type of host feeding) is achieved through non-zero maintenance cost *s*. We note that if parasitoids may obtain energy for maintenance from other sources, or if there are no maintenance requirements, i.e. when s = 0, the stabilizing effect of non-destructive host feeding is lost, and population densities would fluctuate around an equilibrium following the Lotka–Volterra model.

In previous work (Yamamura and Yano, 1988), the effects of host feeding on population dynamics were studied in the framework of the Lotka-Volterra model with intraspecific competition in host population. They showed that for a positive intraspecific competition, trajectories of the model converge to equilibrium, while for zero intraspecific competition, ecological equilibrium is neutrally stable. These results are qualitatively the same as in the case of the classical Lotka-Volterra equation without host feeding.

In the ecological literature, the decision whether to host feed or to oviposit is often interpreted as a tradeoff between future and current reproduction (Collier et al., 1994; Heimpel and Rosenheim, 1995). On the level of individuals, this tradeoff leads to dynamical programming which predicts the best feeding behavior of a parasitoid. The general prediction of these models is that there is a threshold in the egg load; if the egg load is below the threshold, host feeding appears (Collier et al., 1994). However, these models do not consider population dynamics. The main difference between the dynamic approach and our model is in the definition of fitness. The dynamic approach defines fitness as the overall number of eggs deposited over the lifespan of a parasitoid, while in our interpretation, fitness is measured through the instantaneous rate of egg laving. Our choice of fitness corresponds to the classical rate-maximizing theory (Stephens and Krebs, 1986; Abrams, 1983) where fitness is defined as the instantaneous rate of increase of the number of genotype copies, which is commonly used to measure the advantages of life history traits (Stearns, 1992). Although this approach is more coarse when compared with the dynamic programming approach, it allows the consideration of population dvnamics.

We found that the host-feeding pattern which maximizes parasitoid fitness is either non-concurrent and destructive, or concurrent and non-

destructive host feeding, depending on the host abundance and parameters of the model. If the amount of energy required to mature one egg is high, then non-concurrent and destructive host feeding is the host-feeding pattern which maximizes parasitoid fitness. If the amount of energy needed to mature one egg is low, then for low host abundances, the non-concurrent and destructive host-feeding pattern maximizes parasitoid fitness, while when hosts are abundant, concurrent and non-destructive host feeding is the best choice. These predictions correspond to an earlier survey (Jervis and Kidd. 1986), which found that the most common patterns of host feeding are, in descending order, non-concurrent and destructive, concurrent and non-destructive, and concurrent and non-destructive/non-concurrent and destructive. In view of these observations, our models suggest that either host abundance for most host-parasitoid systems is low, or the amount of energy needed to mature one egg is high since these are the conditions predicting the occurrence of the non-concurrent and destructive host-feeding pattern. We showed that when the host-feeding pattern is chosen in an adaptive way, this may destabilize host-parasitoid population dvnamics.

Traditionally, host-parasitoid interactions were modeled by the discretetime Nicholson-Bailey model, but continuous-time models based on the Lotka-Volterra like dynamics were also used (Briggs *et al.*, 1995; Yamamura and Yano, 1988; Murdoch *et al.*, 1992; Murdoch and Stewart-Oaten, 1989). Inclusion of optimal host-feeding behavior of parasitoids leads, in this paper, to non-smooth differential equations and differential inclusions. A theory for such types of problems has been recently developed (Filippov, 1988; Aubin and Cellina, 1984; Aubin, 1991; Deimling, 1992), and it seems that this methodology may prove to be useful when modelling the effects of behavioral tradeoffs on population dynamics (Křivan, 1996; Křivan, 1997; Sirot and Křivan, 1997; Křivan and Sirot, 1997). Although we used the simplest possible type of population dynamics in this paper, which allowed for a deeper mathematical analysis, the present methodology also may be used for more realistic models, including, for example, Holing second type functional response function, delays, etc.

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# APPENDIX A: COMPUTATION OF THE OPTIMAL STRATEGIES

First, we consider the non-concurrent and destructive host-feeding pattern. For  $x < x_D^1$  and for every  $u \in [0, 1]$ , we have  $(\lambda uxe_D - s)/o < 0$ ; thus,  $f_{ND}(x, u) = 0$ , and the corresponding optimal strategy u cannot be uniquely determined. If  $x > x_D^1$ , then  $(\lambda uxe_D - s)/o \ge 0$  for

 $u \in [u_D^1, 1]$ . Since  $(\lambda uxe_D - s)/o$  is an increasing function of u, while  $(1 - u)\lambda x$  is decreasing,  $f_{ND}(x, u)$  is maximized at the point  $u_{opt}$  where these two lines intersect, i.e.

$$u_{\rm opt} = \frac{o\lambda x + s}{\lambda x(e_D + o)}.$$

For the concurrent and non-destructive host-feeding pattern,  $(\lambda uxe_N - s)/o < 0$  for every  $u \in [0,1]$  if  $x < x_N^1$ . Therefore,  $f_{CN}(x,u) = 0$  if  $x < x_N^1$ , and optimal strategy  $u_{opt}$  cannot be uniquely defined. Let us assume that  $e_N > o$ . If  $x < x_N^2$ , then  $(\lambda uxe_N - s)/o < \lambda x$  for every  $u \in [0,1]$ . Thus,  $u_{opt} = 1$  and  $F_{CN}(x) = (\lambda xe_N - s)/o$ . If  $x_N^2 < x$ ,

$$f_{\rm CN}(x,u) = \begin{cases} \frac{\lambda u x e_N - s}{o} & \text{if } u < u_N^2 \\ \lambda x & \text{if } u \ge u_N^2. \end{cases}$$
(A1)

Thus, for  $x_N^2 < x$ ,  $f_{CN}$  is maximized at any  $u_{ont}$  which satisfies  $u_N^2 \le u_{ont} \le 1$  and  $F_{CN}(x) = \lambda x$ .

If  $e_N < o$ , then  $(\lambda u x e_N - s)/o < \lambda x$  for every  $u \in [0, 1]$ , i.e.  $f_{CN}(x, u) = \max\{(\lambda u x e_N - s)/o, 0\}$ . In this case,  $f_{CN}$  is maximized at  $u_{opt} = 1$  when  $x > x_N^1$ . If  $x \le x_N^1$ , then  $f_{CN}(x, u) = 0$  for every  $u \in [0, 1]$ .

#### **APPENDIX B: QUALITATIVE ANALYSIS OF (1)**

We construct a first integral for (1) driven by the optimal strategy. Let

$$V(x,y) = \begin{cases} \frac{\lambda e_D}{e_D + o} x - \frac{s + m(e_D + o)}{e_D + o} \ln x - a \ln y + \lambda y & \text{for } x > x_D^1 \\ -m \ln x - a \ln y + \lambda y - \frac{s}{e_D + o} \left( \ln \frac{s}{\lambda e_D} - 1 \right) & \text{for } x \le x_D^1. \end{cases}$$
(A2)

We note that the above function is continuous. Moreover, it is easy to see that the derivative of V along trajectories of (1) is zero almost everywhere, and consequently, solutions of (1) which are driven by the optimal strategy are closed curves centered at  $E^2$ .

#### APPENDIX C: QUALITATIVE ANALYSIS OF (4) AND (9)

The characteristic polynomial corresponding to  $E^6$  is

$$\sigma^2 + \frac{as}{mo}\sigma + ma + \frac{as}{o}.$$

Thus, due to the Routh-Hurwitz criterion,  $E^6$  is locally asymptotically stable for (6) since we assume that all parameters are positive. We will prove that  $E^6$  is globally stable using the Poincaré-Bendixon theorem (Hartman, 1964; Hofbauer and Sigmund, 1984). To this end, we have to exclude the existence of periodic orbits. This can be achieved by using the Dulac criterion (Hofbauer and Sigmund, 1984), which is usually stated only for smooth vector fields (Hofbauer and Sigmund, 1984), but it can easily be generalized for piecewise smooth vector

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fields (see also Busenberg and van der Driessche (1993)), which is the case of the system (4). Let us assume that  $e_N > o$ . In the region  $x_N^1 < x < x_N^2$ , we have

$$\frac{\partial}{\partial x}\left(\frac{1}{xy}\left(ax-\frac{\lambda xe_N-s}{o}y\right)\right)+\frac{\partial}{\partial y}\left(\frac{1}{xy}\left(\frac{\lambda xe_N-s}{o}y-my\right)\right)=-\frac{s}{ox^2}<0$$
 (A3)

and in the region  $x_N^2 < x$ ,

$$\frac{\partial}{\partial x}\left(\frac{1}{xy}(ax-\lambda xy)\right)+\frac{\partial}{\partial y}\left(\frac{1}{xy}(\lambda xy-my)\right)=0.$$

Assume that there exists a periodic orbit of (4). If  $m < s/(e_N - o)$ , equilibria  $E^5$ ,  $E^6$  are to the left of the line  $x = x_N^2$ , and every periodic orbit must partly belong to the region  $x_N^1 < x < x_N^2$ . However, due to (A3), the Dulac criterion excludes existence of a periodic orbit, and the Poincaré-Bendixon theorem implies that  $E^6$  is globally asymptotically stable. If  $E^6$  is to the right of the line  $x = x_N^2$  (which happens if  $m > s/(e_N - o)$ ), we construct a

Lyapunov function for (4). Let

$$V(x, y) = \begin{cases} \lambda x - m \ln x - a \ln y + \lambda y \\ \text{for } x > x_N^2 \\ \frac{1}{o} \left( e_N \lambda x - (mo + s) \ln x + \lambda o y - a o \ln y + s \ln \left( \frac{s}{\lambda (e_N - o)} \right) - s \right) \\ \text{for } x_N^1 < x \leqslant x_N^2. \end{cases}$$

The above function is continuous. For  $x > x_N^2$ , it is the first integral for the Lotka-Volterra equation (5). For  $x_N^1 < x < x_N^2$ , we have  $(f^6$  denotes the right-hand side of (6))

$$\langle V', f^6 \rangle = \frac{y e_N \lambda^2(e_N - o)}{o^2 x} (x - x_N^2) \left( \frac{mo + s}{e_N \lambda} - x \right).$$

Assuming  $m > s/(e_N - o)$ , we note that  $(mo + s)/(e_N\lambda) > x_N^2$ . Thus, for  $x_N^1 < x < x_N^2$ , the derivative of V along trajectories of (4) is negative for  $e_N > o$ . Trajectories of (4) do converge to a global attractor bounded by the largest Lotka–Volterra cycle of (5) which is to

the right of the line  $x = x_N^2$ . If  $e_N < o$ , then the host-parasitoid dynamics is described by (6) for  $x > x_N^1$  and by (7) for  $x \le x_N^1$ . We see that the part of the (x, y) space for which  $x > x_N^1$  is invariant with respect to (4) and (A3) holds. The Dulac criterion and the Poincaré-Bendixon theory imply that  $E^6$  is globally asymptotically stable.

Now, we consider non-concurrent and non-destructive host feeding. The characteristic polynomial corresponding to  $E^{10}$  is

$$\sigma^2 + \frac{as}{m(e_N + o)}\sigma + \frac{a(e_N m + e_N o + s)}{e_N + o}.$$

Thus, due to the Routh-Hurwitz criterion,  $E^{10}$  is locally stable provided we assume that all parameters are positive. To prove that  $E^{10}$  is globally stable, we again use the Dulac

criterion to exclude closed orbits. We have

$$-\frac{\partial}{\partial x}\left(\frac{1}{xy}\left(ax-\frac{\lambda xe_N-s}{e_N+o}y\right)\right)+\frac{\partial}{\partial y}\left(\frac{1}{xy}\left(\frac{\lambda xe_N-s}{e_N+o}y-my\right)\right)=-\frac{s}{(e_N+o)x^2}<0.$$

Thus, there are no periodic orbits, and  $E^{10}$  is globally asymptotically stable.

# **APPENDIX D: BEHAVIOR OF THE HOST-PARASITOID MODEL ALONG THE LINE** $x = x^*$

By n = (1,0), we denote the normal vector to the line  $x = x^*$ . Denoting the right-hand side of (2) by  $f^2$  and similarly for (6), we get  $(\langle \cdot, \cdot \rangle$  stands for the scalar product)

$$\langle f^2, n \rangle < 0$$
 if  $y > \frac{a}{\lambda}$   
 $\langle f^6, n \rangle > 0$  if  $y < \frac{ae_D}{\lambda(e_D - e_N)}$ .

It follows that trajectories of (12) driven by the optimal strategy cross the line  $x = x^*$  in the direction from left to right if  $y < y^1$  and from right to left if  $y > y^2$ . In the segment with end points  $y^1$  and  $y^2$ , trajectories are not uniquely determined by the initial condition, and they may move either to the left or to the right.

# **APPENDIX E: QUALITATIVE ANALYSIS OF (12)**

First, we assume  $e_N e_D / (e_D - e_N) > e_N > o$ , and we define

$$V(x,y) = \begin{cases} \lambda x - m \ln x - a \ln y + \lambda y \\ \text{for } x > x_N^2 \\ \frac{1}{o} \left( e_N \lambda x - (mo+s) \ln x + \lambda oy - ao \ln y + s \ln \left( \frac{s}{\lambda(e_N - o)} \right) - s \right) \\ \text{for } x^* \le x \le x_N^2 \\ - \left( m + \frac{s}{e_D + o} \right) \ln x + \frac{\lambda e_D}{e_D + o} x - a \ln y + \lambda y + C_1 \\ \text{for } x_D^1 \le x \le x^* \\ - m \ln x - a \ln y + \lambda y + C_2 \\ \text{for } x \le x_D^1 \end{cases}$$

where constants  $C_1, C_2$  are chosen in such a way that V is a continuous function. Function V is the first integral for (2), (3) and (5). Assume

$$m < \frac{s(e_D - e_N)}{e_D e_N - o(e_D - e_N)}$$
(A4)

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which implies that  $E^6$  is to the left of the line  $x = x^*$ , i.e.

$$\frac{mo+s}{e_N\lambda} < x^*.$$

We get that, for  $x^* < x < x_N^2$ ,

$$\langle V', f^6 \rangle = \frac{y e_N \lambda^2(e_N - o)}{o^2 x} (x - x_N^2) \left( \frac{mo + s}{e_N \lambda} - x \right) > 0.$$

Therefore, V is increasing along trajectories of (12) provided they are to the right of the line  $x = x^*$ , which leads to destabilization of the dynamics.

Now, we consider the case  $m > s/(e_N - o)$ . In this case, for  $x^* < x < x_N^2$ , we have  $\langle V', f^6 \rangle < 0$  since

$$\frac{mo+s}{e_N\lambda} > x_N^2 > x^*$$

and all trajectories of (12) do converge to a global attractor given by the largest Lotka-Volterra cycle of (12) which is to the right of the line  $x = x_N^2$ . Second, we assume  $e_N e_D / (e_D - e_N) > o > e_N$ , and we define

$$V_{1}(x,y) = \begin{cases} \frac{1}{o}(e_{N}\lambda x - (mo+s)\ln x + \lambda oy - ao\ln y) & \text{for } x^{*} \leq x \\ -\left(m + \frac{s}{e_{D} + o}\right)\ln x + \frac{\lambda e_{D}}{e_{D} + o}x - a\ln y + \lambda y + C_{3} & \text{for } x_{D}^{1} < x < x^{*} \\ -m\ln x - a\ln y + \lambda y + C_{4} & \text{for } x < x_{D}^{1} \end{cases}$$

where constants  $C_3, C_4$  are chosen in such a way that V is a continuous function. The stability analysis can be carried along the same lines as for the case  $e_N > o$ , replacing function V by V<sub>1</sub>. If (A4) holds, we get that, for  $x^* < x$ ,

$$\langle V_1', f^6 \rangle = \frac{y e_N \lambda^2 (e_N - o)}{o^2 x} (x - x_N^2) \left( \frac{mo + s}{e_N \lambda} - x \right) > 0$$

since  $x_N^2 < 0$ , which leads to destabilization of those trajectories of (12) which enter the region  $x > x^*$ .

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