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ADAPTIVE SUPERPARASITISM AND HOST–PARASITOID DYNAMICS

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We consider a host–solitary parasitoid system with three categories of individuals: parasitoids, healthy hosts and parasitized hosts. Parasitoids are assumed to discriminate perfectly between the two kinds of hosts and they can reject those which are already parasitized. If parasitoids systematically accept or reject superparasitism or behave randomly, the system is always unstable. Using an optimal foraging model, we determine the behavior of parasitoids which leads to maximization of the instantaneous reproductive rate. When following this adaptive decision rule, parasitoids accept or refuse superparasitism according to the densities of both healthy and parasitized hosts. We study the dynamics of the system when parasitoids follow the optimal rule and show that under certain conditions it possesses a locally stable equilibrium point. In addition, our model predicts that at equilibrium parasitoids show partial preferences for superparasitism. © *1997 Society for Mathematical Biology*

Introduction. In solitary parasitoids, the number of offspring that emerge from a particular host is never greater than 1, regardless of the number of eggs laid in that host (Godfray, 1994). When a host is superparasitized, i.e. parasitized several times, the parasitoid larvae compete until, at most, one survives (Salt, 1961). Although many parasitoid species are able to distinguish healthy from parasitized hosts, and to reject the parasitized hosts (van Lenteren, 1981; Bakker *et al.*, 1985), superparasitism is a common phenomenon (van Alphen and Visser, 1990).

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In many cases, there is a non-negligible probability that the winning parasitoid larva is originated, not from the female that oviposited first in the host, but from a female that superparasitized. Hence, superparasitism has a non-zero payoff (e.g. Salt, 1961; Visser *et al.*, 1992b; van Baaren *et al.*, 1995). The choice between acceptance or rejection of already parasitized hosts affects the reproductive success of each individual for two reasons. First, it influences the mean number of offspring produced per oviposition, since ovipositions in healthy hosts have a higher payoff than ovipositions in parasitized hosts (Visser *et al.*, 1992b; Mangel, 1989a). Second, it influences the total number of ovipositions realized during the whole life span of parasitoids, since superparasitism is egg and time consuming, whereas rejection of parasitized hosts is only time consuming (Iwasa *et al.*, 1984; Mangel, 1989a; Speirs *et al.*, 1991; Weisser and Houston, 1993). The payoff from superparasitism is under certain circumstances large enough to make superparasitism adaptive (e.g. Mangel, 1989a; Weisser and Houston, 1993). Numerous theoretical studies explored these circumstances; for a review, see Speirs *et al.* (1991). The occurrence of superparasitism in solitary parasitoids can thus be caused by the selection of that particular behavior, rather than by imperfect discrimination between healthy and parasitized hosts (van Lenteren, 1981).

In this paper, we investigate the influence of individual adaptive behavior of parasitoids toward superparasitism on the host–parasitoid dynamics. We build a general model describing the dynamics of a host–parasitoid system with a control parameter which represents the tendency of parasitoids to superparasitize. When parasitoids behave randomly, i.e. they superparasitize with certain fixed probability, the dynamics is unstable. This also covers the cases when parasitoids always accept or always reject superparasitism. However, we assume in the model that due to natural selection the behavioral strategy adopted by parasitoids maximizes the individual fitness. This adaptive rule predicts that parasitoids will adopt different strategies toward superparasitism when the densities of healthy and parasitized hosts vary. We show that adaptive superparasitism stabilizes the host–parasitoid dynamics, and partial preferences toward superparasitism occur.

Model.   First we derive host–parasitoid population dynamics. Let us consider a single parasitoid during a short time interval T. We consider the following three activities of parasitoids during this time interval: searching for hosts, detecting upon an encounter whether the host is already parasitized and ovipositing. We denote by T_s the time spent searching for hosts (searching time) while the time spent detecting whether the encountered hosts are already parasitized and ovipositing is denoted by T_h (handling

time), i.e. $T = T_s + T_h$. The density of healthy hosts is denoted by x_1 while the density of already parasitized hosts is x_2. The parasitoid density is denoted by x_3. Parameter h_1 denotes the time a parasitoid needs to find out if the host encountered is already parasitized or not, and h_2 denotes the time to lay one egg. The expected encounter rate of a parasitoid with hosts is assumed to be linearly related to host density. Thus, a given parasitoid encounters on average λx_1 healthy and λx_2 parasitized hosts per unit of searching time. Whereas parasitoids always accept unparasitized hosts, they may or may not reject parasitized ones. We assume perfect host discrimination by parasitoids (van Lenteren, 1981). The control parameter $0 \le u \le 1$ describes the probability that upon an encounter with an already parasitized host, parasitoids will superparasitize. If $u = 0$, then parasitoids never superparasitize, while if $u = 1$, they always superparasitize. We assume (see below) that all parasitoids adopt the same decision rule. Following derivation of the Holling disc equation (Holling, 1959) we get

$$T_h = \lambda \big(x_1(h_1 + h_2) + x_2(h_1 + uh_2) \big) T_s$$

and

$$T_s = \frac{T}{1 + \lambda \big(x_1(h_1 + h_2) + x_2(h_1 + uh_2) \big)}. \tag{1}$$

Now we may derive the population dynamics. We assume that the host population is growing exponentially in the absence of parasitoids, with the growth parameter r. Parameter c denotes the emergence rate of parasitoids. This allows us to write the following difference equations (remember that T is a short time interval):

$$x_1(t + T) = x_1(t) + rx_1(t)T - \lambda x_1(t)x_3(t)T_s,$$

$$x_2(t + T) = x_2(t) + \lambda x_1(t)x_3(t)T_s - cx_2(t)T,$$

$$x_3(t + T) = x_3(t) + cx_2(t)T - mx_3(t)T.$$

Using (1) and taking the limit for T tending to zero, we get the following continuous dynamics:

$$x_1' = rx_1 - \frac{\lambda x_1 x_3}{1 + \lambda \big(x_1(h_1 + h_2) + x_2(h_1 + uh_2) \big)},$$

$$x_2' = \frac{\lambda x_1 x_3}{1 + \lambda \big(x_1(h_1 + h_2) + x_2(h_1 + uh_2) \big)} - cx_2,$$

$$x_3' = cx_2 - mx_3. \tag{2}$$

Parasitoids superparasitize randomly. Here we assume that the control parameter u is fixed, i.e. it does not depend on the state of the system. This is the case when parasitoids behave randomly when they encounter parasitized hosts. For example, if parasitoids accept superparasitism as often as they reject it, then $u = 0.5$; if they always superparasitize, then $u = 1$; if they never superparasitize, $u = 0$. Then (2) has the trivial equilibrium and one non-trivial ecological equilibrium

$$E^* = \frac{1}{\lambda(c - ch_1 m - ch_2 m - h_1 mr - h_2 mru)}(cm, mr, cr).$$

This equilibrium is positive provided

$$m < \frac{c}{ch_1 + ch_2 + h_1 r + h_2 ru}.$$

Stability analysis shows that this equilibrium is unstable for all values of u between 0 and 1 (see Appendix 1). Numerical simulations show that trajectories spiral outward from the equilibrium with increasing amplitude. Thus, this case resembles the Nicholson–Bailey discrete-time model which has also an unstable equilibrium with unbounded trajectories.

Parasitoids superparasitize in order to maximize fitness. Now we assume that the control parameter u changes in time in such a way that the fitness of each parasitoid is maximized. Let e_1 and e_2 denote the expected number of offspring from an oviposition in a healthy host and in an already parasitized host, respectively, with $e_2 < e_1$ (Mangel, 1989a). The average payoff during the time interval T is

$$R = \frac{E}{T},$$

where E denotes the number of offspring expected over the time interval T. Since

$$E = \lambda(x_1 e_1 + x_2 e_2 u)T_s,$$

using (1) we get

$$R(u) = \frac{\lambda(x_1 e_1 + x_2 e_2 u)}{1 + \lambda(x_1(h_1 + h_2) + x_2(h_1 + uh_2))}. \tag{3}$$

We assume that, as a result of natural selection, each parasitoid behaves in such a way that the rate of fitness gain R is maximized at every moment. The value of the control parameter u which maximizes R corresponds to the optimal strategy. In Appendix 2 the optimal strategy is derived. It is shown there that the optimal strategy is as follows:

(I) If

$$\frac{e_1}{h_1 + h_2} \le \frac{e_2}{h_2},$$

the optimal strategy is always to superparasitize ($u = 1$), because parasitized hosts provide a large payoff and/or require a long time to be recognized.

(II) If

$$\frac{e_1}{h_1 + h_2} > \frac{e_2}{h_2},$$

the following three cases must be distinguished:

(a) If

$$x_2 < \frac{\lambda x_1 \big(e_1 h_2 - e_2 (h_1 + h_2)\big) - e_2}{e_2 \lambda h_1},$$

the optimal strategy is to never superparasitize, i.e. $u = 0$. This is due to the fact that unparasitized hosts are abundant and it pays off to parasitoids to search only for healthy hosts. Let us note that the above inequality can be satisfied only if

$$x_1 > x_1^* = \frac{e_2}{\lambda\big(e_1 h_2 - e_2 (h_1 + h_2)\big)}.$$

Thus, if $x_1 \le x_1^*$, parasitoids will always superparasitize.

(b) If

$$x_2 > \frac{\lambda x_1 \big(e_1 h_2 - e_2 (h_1 + h_2)\big) - e_2}{e_2 \lambda h_1},$$

the optimal strategy is to always superparasitize, i.e. $u = 1$. This is due to the fact that healthy hosts are scarce, compared to already parasitized ones.

(c) If

$$x_2 = \frac{\lambda x_1 \big(e_1 h_2 - e_2(h_1 + h_2)\big) - e_2}{e_2 \lambda h_1},$$

the strategy of the parasitoids cannot be determined from the optimality criterion only, because all values of u between 0 and 1 lead to the same value of the fitness measure. In this case we say that the strategy of the parasitoids is partial superparasitism.

For the density $x = (x_1, x_2, x_3)$ we define the strategy map $S(x)$ as the set of values of the control parameter u which maximize the fitness measure R.

The dynamics which is governed by optimal strategy is described by (2) with $u \in S(x)$. Note that the optimal strategy is not uniquely given provided the case (c) occurs. Despite this non-uniqueness in the dynamics of (2), it is proved in Appendix 3 that (2) has for every initial condition an unique solution. Thus, our model is well posed.

Qualitative behavior of the system under optimality condition.   First, let us assume the case (I) holds, i.e.

$$\frac{e_1}{h_1 + h_2} \le \frac{e_2}{h_2}.$$

Then the optimal strategy for parasitoids is to superparasitize systematically ($u = 1$). The corresponding system (2) possesses one non-trivial equilibrium

$$E^2 = \frac{1}{\lambda(c - ch_1 m - ch_2 m - h_1 mr - h_2 mr)}(cm, mr, cr), \qquad (4)$$

which is unstable (see Appendix 1). If

$$\frac{e_1}{h_1 + h_2} > \frac{e_2}{h_2},$$

then there are three different optimal strategies depending on the values of x_1 and x_2. We denote by G^1 the part of the space where the optimal strategy is to always reject superparasitism, by G^2 the part of the space where the optimal strategy is to always superparasitize and by G^0 the part of the space where the optimal strategy is partial superparasitism; see Fig. 1.
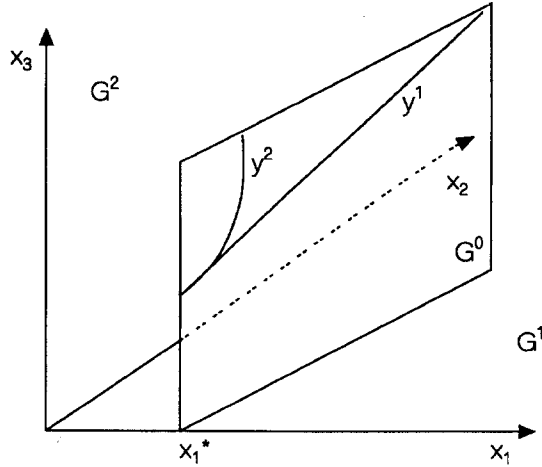
Figure 1. Division of the space into three parts G^0, G^1 and G^2. In G^1 parasitoids never superparasitize, while in G^2 they always superparasitize. The region in G^0 bounded by curves y^1 and y^2 is the sliding region where partial preferences of parasitoids for superparasitism do occur.

Let us consider dynamics (2) in the three regions G^1, G^2 and G^0 separately. In G^1 parasitoids always reject superparasitism and the corresponding dynamics has one non-trivial equilibrium

$$E^1 = \frac{1}{\lambda(c - ch_1m - ch_2m - h_1mr)}(cm, mr, cr).$$

Similarly, in G^2 parasitoids always accept superparasitism and there exists one non-trivial equilibrium E^2 given by (4). The equilibria E^1 and E^2 are unstable (see Appendix 1). We are interested in the case when parasitoids follow the optimal strategy. This means that the parasitoids choose the optimal strategy according to the density of healthy and already parasitized hosts. If, for example, we start with a system consisting only of healthy hosts with density higher than x_1^*, parasitoids according to the optimal strategy will never superparasitize. This means that the trajectory of the system moves in G^1. Since the number of parasitized host will increase, at a certain time the system may reach the set G^0 where both pure strategies (i.e. never to superparasitize or always to superparasitize) give the same fitness. Now there are two possibilities:

(i) The trajectory will start to move along G^0, i.e. partial superparasitism will occur. After some time the trajectory may leave G^0 and move either to G^1 or to G^2.

(ii) The trajectory will cross G^0 in a direction toward G^2, i.e. there is a switching in the behavior of parasitoids from systematic rejection to systematic acceptance of superparasitism.

It is shown in Appendix 4 that a trajectory which hits G^0 cannot leave G^0 as long as the inequality

$$y^1(x_1) < x_3 < y^2(x_1) \tag{5}$$

holds, with

$$y^1(x_1) = \frac{e_1 h_1}{e_1 - e_2} \left(\frac{(c+r)(e_1 h_2 - e_2(h_1 + h_2))}{e_2 h_1} x_1 - \frac{c}{\lambda h_1} \right)$$

and

$$y^2(x_1) = -y^1(x_1) \frac{e_2 + \lambda x_1(h_1 + h_2)(e_2 - e_1)}{\lambda e_1 h_1 x_1}.$$

It can easily be shown that we always have

$$0 < y^1(x_1) < y^2(x_1). \tag{6}$$

We define the sliding region as the part of G^0 where condition (5) is satisfied; see Fig. 1. We note that when the system moves in the sliding region, then the strategy of parasitoids is partial superparasitism.

Since G^0 is a two-dimensional plane, the system of equations which governs the dynamics of (2) in the sliding region is also two-dimensional:

$$x_1' = \frac{ce_2}{\lambda h_2(e_1 - e_2)} + \frac{c(e_1 h_2 - e_2(h_1 + h_2)) - e_2 h_1 r}{h_2(e_2 - e_1)} x_1,$$

$$x_3' = -\frac{c}{\lambda h_1} + \frac{c(e_1 h_2 - e_2(h_1 + h_2))}{e_2 h_1} x_1 - m x_3; \tag{7}$$

see Appendix 4. This system has a non-trivial equilibrium E^0 in G^0:

$$E^0 = \frac{1}{\lambda(-ce_2 h_1 + ce_1 h_2 - ce_2 h_2 - e_2 h_1 r)} \left(ce_2, \frac{ce_2 r}{m} \right).$$

The eigenvalues for this equilibrium are

$$\left(-m, \frac{ce_2h_1 - ce_1h_2 + ce_2h_2 + e_2h_1r}{(e_1 - e_2)h_2} \right).$$

Thus, we see that this equilibrium is locally stable in G^0 provided it is positive, i.e.

$$r < \frac{c(e_1h_2 - e_2(h_1 + h_2))}{e_2h_1}. \tag{8}$$

Since the dynamics in G^0 is described by a system of linear differential equations (7), equilibrium E^0 is also globally asymptotically stable in the sliding domain. This means that every trajectory of (2) which stays in the sliding domain converges to E^0.

We will study the behavior of trajectories of (2) when they hit the set G^0. It is shown in Appendix 4 that trajectories of (2) will pass through G^0 in direction from G^1 to G^2 if $x_3 > y^2(x_1)$ and in direction from G^2 to G^1 if $x_3 < y^1(x_1)$. This means that if the density of parasitoids is high when the system reaches G^0, then parasitoids will switch from systematic rejection to systematic acceptance of superparasitism, and vice versa if the density of parasitoids is low. However, if (5) holds when the system reaches G^0, then partial superparasitism will occur and the system will move for some time along G^0. If E^0 belongs to the sliding domain of G^0, then the system may tend to this equilibrium. Assuming that E^0 is positive, we get that E^0 belongs to the sliding domain for those mortality rates of parasitoids m which satisfy

$$\frac{ce_2}{ce_1h_2 + e_2h_2r} < m < \frac{e_2}{e_1h_2}. \tag{9}$$

Thus, if (8) together with (9) are satisfied, the system (2) has a locally stable equilibrium E^0. The mechanism which leads to stability is the following. Assume that a trajectory of (2) falls at a certain time into the sliding domain. Then this trajectory will move toward E^0 and, provided the whole trajectory is in the sliding domain, the trajectory will converge to E^0 (see Fig. 2). However, it may also happen that the trajectory of (2) does not fall into the sliding domain and then it will tend to infinity (see Fig. 3). We note that for this reason E^0 is not globally stable.

We may compute directly the probability u^0 that parasitoids will superparasitize at ecological equilibrium E^0 (see Appendix 4):

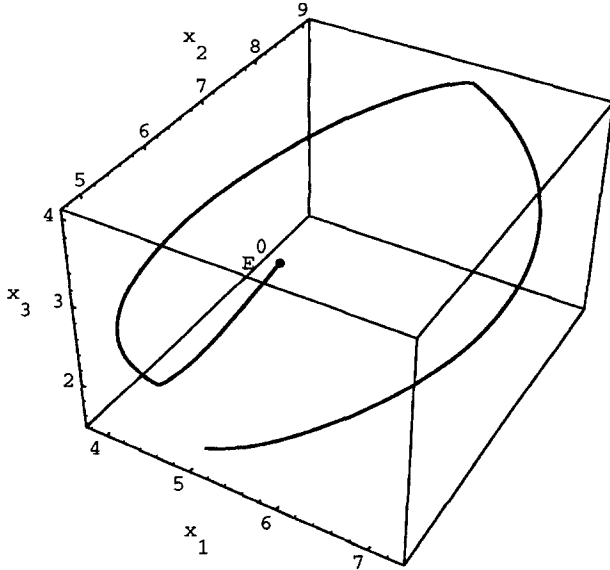$$u^0 = \frac{c(e_2 - e_1h_2m)}{e_2h_2mr}. \tag{10}$$

Figure 2. The trajectory of (2) converges to the locally stable equilibrium which is inside the sliding region. Thus, at the equilibrium, partial preferences do appear. Parameters: $x_1(0) = 5$, $x_2(0) = 5$, $x_3(0) = 1.5$, $r = 1$, $m = 1.7$, $e_1 = 1$, $e_2 = 0.2$, $h_1 = 0.09$, $h_2 = 0.1$, $\lambda = 1$, $c = 0.8$.

We note that due to the assumption (9), u^0 is strictly between zero and one, which means that at equilibrium parasitoids do exhibit partial preferences for superparasitism.

Conclusion. In the present paper, we study how the dynamics of a host−solitary parasitoid system is affected when parasitoids accept or reject superparasitism according to an optimality criterion.
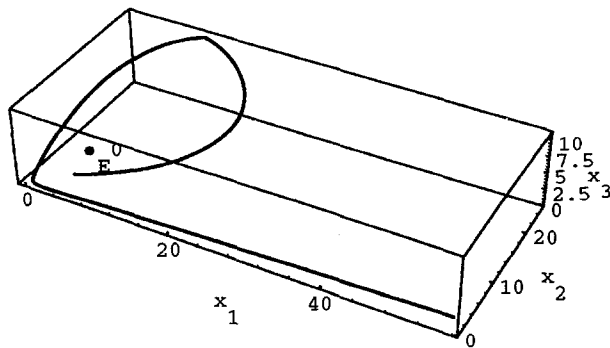

Figure 3. Simulation of (2) as in Fig. 2 but with different initial conditions. In this case the trajectory does not tend to the equilibrium; thus this equilibrium is not globally stable.

The question of mechanisms which stabilize host–parasitoid dynamics led to taking into account several aspects of parasitoid behavior. Obviously, interference (Hassell and Varley, 1969) is one mechanism which may lead to stability of the host–parasitoid dynamics. Another mechanism was proposed in Hassel and May (1973), where it was shown that strong aggregation of parasitoids in patches with high host density may also lead to stabilization of the otherwise unstable discrete-time Nicholson–Bailey model. More generally, heterogeneity in the risk of parasitism is a strong stabilizing factor (Chesson and Murdoch, 1986; Pacala *et al.*, 1990). For continuous Lotka–Volterra or Holling types of dynamics the effect of aggregation of parasitoids (or predators) on the stability of host–parasitoid (or predator–prey) systems was studied in Murdoch and Stewart-Oaten (1975, 1989), Godfray and Pacala (1992), Colombo and Křivan (1993), Křivan (1996, 1997). The implication of these studies on the stability of host–parasitoid systems depends on the meaning of aggregation. In Murdoch and Stewart-Oaten (1989) this term is defined in terms of the variance in parasitoid distribution and the covariance between the distributions of host and parasitoids, and then it was shown that aggregation typically has a destabilizing effect.

In order to study the impact of natural selection at the population level, several studies focused on optimal foraging rules for parasitoids and showed that they may stabilize host–parasitoid systems [response of parasitoids to host distribution: Comins and Hassell, 1979; optimal choice between hosts of different values: Mangel and Roitberg, 1992; optimal time sharing between searching for food and searching for hosts: Sirot and Bernstein, 1996) and Křivan and Sirot, (1996); host-feeding: Yamamura and Yano, 1988)]. Driessen and Visser (1993) suggested that optimality rules concerning patch time and superparasitism may have a stabilizing effect on population equilibrium, since they contribute to reduce the overall population efficiency. However, they did not consider the dynamics explicitly.

In our model, the population dynamics is described by a system of differential equations. This corresponds to populations with overlapping generations, which is a common situation in host–parasitoid systems (Murdoch *et al.*, 1987). When generations overlap and the assumption is made that each female transmits the integrality of her genotype to the next generation, the instantaneous growth rate of the number of copies of a given genotype is an appropriate measure of fitness for that genotype (Sibly, 1989; Nur, 1984; Stenseth, 1984). In order to get simple decision rules, we made the assumption that ovipositions could be counted in terms of immediate fitness gain. As a first step, this assumption is quite reasonable and should not lead to important discrepancies with reality. In that condition, the quantity to be maximized is the instantaneous reproductive rate of parasitoids. Thus, our optimality rule corresponds to the classical rate-maximizing theory (Stephens and Krebs, 1986). The optimal foraging part

of our model predicts that the response of parasitoids should be influenced by the abundance of both healthy and parasitized hosts. If the densities are the same, parasitoids should superparasitize if the density of healthy hosts is below a certain threshold and refuse to superparasitize if it is above. Qualitatively, this prediction is similar to more accurate optimality models, based on dynamic programming (Mangel, 1989a; Iwasa et al., 1984; Weisser and Houston, 1993). In fact, the individual part of our model is similar to other models for parasitoid diet, which take into account the recognition time (e.g. Visser et al., 1992a; Janssen, 1989). We make the simplifying assumption that the payoffs resulting from ovipositions in healthy and parasitized hosts, respectively, are constant. Normally, these two quantities depend on the probability that the host may be superparasitized in the future and on the number of eggs already present in that host. More complicated models have explored how parasitoids should adjust their behavior to the number of competitors and the number of eggs in parasitized hosts (van der Hoeven and Hemerik, 1990; Visser et al., 1992a), but this makes the link between individual behavior and population dynamics more complex (Driessen and Visser, 1993).

We showed that the adaptive individual behavior of parasitoids may stabilize an unstable (and non-persistent) dynamics; see Fig. 2. In this case, condition (9) is satisfied and, despite the fact that for both $u = 1$ and $u = 0$ the trajectories of the system are moving outward from the corresponding unstable equilibria, the system in which parasitoids choose whether to superparasitize or not according to the criteria we introduced in this paper possesses a locally stable equilibrium point. However, we want to stress that E^0 need not be globally stable; see Fig. 3.

The effect of the optimal individual behavior on the population dynamics comes from the fact that the situation where all parasitoids maximize the rate of increase of the number of copies of their genotype does not correspond to the maximization of the instantaneous growth rate of the population of parasitoids. When parasitoids superparasitize, they may get a new offspring, but from the population point of view it is a waste of searching time, and the resort to superparasitism leads to a decrease of the population efficiency. Indeed, if parasitoids do not superparasitize (i.e. $u = 0$), then they will have more time to search for hosts. This would result in higher growth rate of the parasitized hosts and thus to the higher growth rate of parasitoids. However, from the point of view of an individual parasitoid it pays off to superparasitize if the number of hosts is low, since this will increase its fitness. This mechanism is responsible for the stabilization that we showed.

Though the part of our work which is dedicated to individual behavior is similar to classical theory, the population dynamics frame of our study led us to consider a particular case more precisely. Actually, we showed that

our system may have a locally stable equilibrium point in the region where the optimal criterion alone cannot be used to predict the strategy of parasitoids. However, this criterion, together with the host–parasitoid dynamics described by (2) leads to the unique description of the system trajectory and to the unique value of the parameter which controls the probability that a parasitoid will superparasitize at ecological equilibrium. We showed that our model predicts partial preferences for parasitized hosts, i.e. partial superparasitism.

Classical diet models (e.g. Stephens and Krebs, 1986) predict that, depending on circumstances, one particular type of prey should always be rejected or always be accepted (as in G^1 and G^2 in our model, parasitized hosts being considered as prey). Thus, these models lead to a "zero–one" rule, but they do not pay attention to the limit case where acceptance and rejection of the prey are equivalent for the predator (G^0 in our model; Stephens and Krebs, 1986, p. 23). Here we showed that a system in which parasitoids behave optimally may evolve toward an equilibrium where this limit case is met, which stresses the ecological importance of this particular situation.

Partial preferences are a common pattern in the behavior of both parasitoids (van Dijken *et al.*, 1986; Kraaijeveld and van Alphen, 1986; Sirot *et al.*, 1996) and predators (Rechten *et al.*, 1983; Krebs *et al.*, 1977; Lea, 1979). A few general kinds of explanations were given for the apparent discrepancy between this phenomenon and the failure of the classical diet model to predict them. One is that this deterministic model assumes that the animal has a perfect knowledge of the parameter values (McNamara and Houston, 1987), whereas "errors" may happen when the animal discriminates between different kinds of items (Krebs *et al.*, 1977; Rechten *et al.*, 1983; Krebs and McCleery, 1984) and when it estimates the densities of these kinds of items (Snyderman, 1983; Krebs and McCleery, 1984). Another explanation is that even if the zero–one rule is followed by each individual, the threshold determining the switching is not the same for all the animals and for all the states of the same animal (Stephens, 1985; Mangel, 1989b). These explanations are based on real processes and they are highly relevant. However, we have shown that a host–parasitoid system may reach a locally stable equilibrium point where the behavior of parasitoids toward superparasitism is strict partial preferences, even within the frame of the classical diet model. From the ecological point of view, we think that three aspects make our work relevant. The first one is that superparasitism is known to play an important role in population processes (Driessen and Visser, 1993). Second, although it is not possible analytically define the attraction area of the equilibrium point, numerical results suggest that it is wide; see Fig. 4. So, it is a strong prediction of our model that optimal strategy of parasitoids should tend to bring the system near the
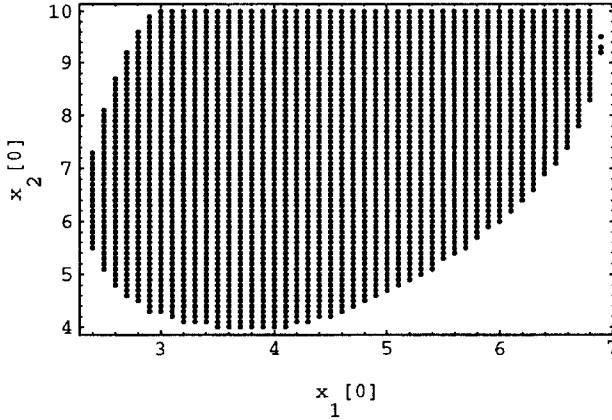
Figure 4. Approximation of the domain of attraction of the equilibrium. The points $x_1(0)$ and $x_2(0)$ are plotted from which the corresponding trajectory of (2) with $x_3(0) = 1.5$ converges to equilibrium.

equilibrium, where partial preferences are predicted. Third, the relationships upon which our predictions lie are simple enough to be tested in real systems. As a first step, the strategy of parasitoids toward superparasitism could be tested using different densities of healthy and parasitized hosts, two factors which are known to influence parasitoids decisions (for a review, see Godfray, 1994).

APPENDIX 1: INSTABILITY OF THE ECOLOGICAL EQUILIBRIUM OF (2)

For fixed u, the characteristic polynomial is

$$\sigma^3 + (c + m + h_2 mr(u-1))\sigma^2 + mr(-ch_1 - ch_2 - h_2 m - h_1 r + h_2 mu - h_2 ru)\sigma$$

$$+ mr(c - ch_1 m - ch_2 m - h_1 mr - h_2 mru).$$

Assuming that the equilibrium E^* is positive implies that $c - ch_1 m - ch_2 m - h_1 mr - h_2 mru > 0$. Since $0 \le u \le 1$, the coefficient of σ is negative, which means that there is an eigenvalue with a positive real part (Yodzis, 1989, p. 184).

APPENDIX 2: OPTIMAL STRATEGY

The derivative of R is

$$R'(u) = \frac{\lambda x_2(e_2 + \lambda x_1(e_2 h_1 - e_1 h_2 + e_2 h_2) + \lambda h_1 e_2 x_2)}{(1 + \lambda(x_1(h_1 + h_2) + x_2(h_1 + u h_2)))^2}.$$

If

$$\frac{e_1}{h_1 + h_2} \leq \frac{e_2}{h_2},$$

then $R'(u) > 0$ and the optimal control $u = 1$. If

$$\frac{e_1}{h_1 + h_2} > \frac{e_2}{h_2},$$

we get that $R(u)$ is maximized for

$$u \begin{cases} = 0, & \text{if } x_2 < \dfrac{\lambda x_1(e_1 h_2 - e_2(h_2 + h_1)) - e_2}{e_2 \lambda h_1}, \\[2ex] = 1, & \text{if } x_2 > \dfrac{\lambda x_1(e_1 h_2 - e_2(h_2 + h_1)) - e_2}{e_2 \lambda h_1}, \\[2ex] \in [0, 1], & \text{if } x_2 = \dfrac{\lambda x_1(e_1 h_2 - e_2(h_2 + h_1)) - e_2}{e_2 \lambda h_1}. \end{cases}$$

APPENDIX 3: EXISTENCE AND UNIQUENESS OF SOLUTIONS OF (2)

Let

$$G^1 := \left\{ (x_1, x_2, x_3) \in \mathbf{R}_+^3 \mid x_2 < \frac{\lambda x_1(e_1 h_2 - e_2(h_1 + h_2)) - e_2}{e_2 \lambda h_1} \right\},$$

$$G^2 := \left\{ (x_1, x_2, x_3) \in \mathbf{R}_+^3 \mid x_2 > \frac{\lambda x_1(e_1 h_2 - e_2(h_1 + h_2)) - e_2}{e_2 \lambda h_1} \right\},$$

$$G^0 := \left\{ (x_1, x_2, x_3) \in \mathbf{R}_+^3 \mid x_2 = \frac{\lambda x_1(e_1 h_2 - e_2(h_1 + h_2)) - e_2}{e_2 \lambda h_1} \right\},$$

and

$$n = \left(-\frac{e_1 h_2 - e_2(h_1 + h_2)}{e_2 h_1}, 1, 0 \right) \tag{A1}$$

is a perpendicular vector to G^0, oriented from G^1 toward G^2. Denoting by $f^1(x_1, x_2, x_3)$ the right-hand side of (2) for $u = 0$ and by $f^2(x_1, x_2, x_3)$ for $u = 1$, we get on G^0

$$\langle n, f^1(x_1, x_2, x_3) \rangle = \langle n, f^2(x_1, x_2, x_3) \rangle + \frac{(e_1 - e_2)(\lambda x_1(e_1 h_2 - e_2(h_1 + h_2)) - e_2)x_3}{e_1 h_1(-e_2 + \lambda x_1(h_1 + h_2)(e_1 - e_2))}.$$

Since in G^0,

$$x_1 \geq \frac{e_2}{\lambda(e_1 h_2 - e_2(h_1 + h_2))},$$

it follows that

$$\frac{(e_1 - e_2)(\lambda x_1(e_1 h_2 - e_2(h_1 + h_2)) - e_2)x_3}{e_1 h_1(-e_2 + \lambda x_1(h_1 + h_2)(e_1 - e_2))} > 0.$$

Thus, either

$$\langle n, f^2 \rangle \geq 0$$

and consequently $\langle n, f^1 \rangle > 0$ or

$$\langle n, f^2 \rangle < 0.$$

We see that either $\langle n, f^1 \rangle > 0$ or $\langle n, f^2 \rangle < 0$. Let f denote the right-hand side of (2). Then for every $u \in S(x)$,

$$\frac{d}{du} \langle n, f(x) \rangle = \frac{(e_2 - e_1)h_2^2 \lambda^2 x_1 x_2 x_3}{e_2 h_1(1 + \lambda(h_1 + h_2)(x_1 + x_2))^2} < 0$$

in $\mathbf{R}_+^3$. These are the conditions that ensure existence and uniqueness of trajectories of (2); see Theorem 3, p. 113 in Filippov (1988).

APPENDIX 4: BEHAVIOR OF TRAJECTORIES ON G^0

We assume that

$$\frac{e_1}{h_1 + h_2} > \frac{e_2}{h_2}.$$

For $u = 1$ we denote the right-hand side of (2) by f^2 and for $u = 0$ by f^1. We will study the behavior of a solution when it falls on G^0. This behavior is given by projections of vector fields f^1 and f^2 on the vector n given by (A1). We get

$$\langle n, f^1 \rangle = \frac{c}{\lambda h_1} + \frac{(c + r)(e_2(h_1 + h_2) - e_1 h_2)x_1}{e_2 h_1} + \frac{e_1 - e_2}{e_1 h_1}x_3$$

and

$$\langle n, f^2 \rangle = \frac{c}{\lambda h_1} + \frac{(c+r)(e_2(h_1+h_2)-e_1h_2)x_1}{e_2 h_1} + \frac{e_2-e_1}{e_2+\lambda x_1(h_1+h_2)(e_2-e_1)}\lambda x_1 x_3.$$

Let

$$y^1(x_1) = \frac{e_1 h_1}{e_1 - e_2}\left(\frac{(c+r)(e_1 h_2 - e_2(h_1+h_2))}{e_2 h_1}x_1 - \frac{c}{\lambda h_1} \right)$$

and

$$y^2(x_1) = -y^1(x_1)\frac{(e_2 + \lambda x_1(h_1+h_2)(e_2-e_1))}{\lambda e_1 h_1 x_1}.$$

We get that $\langle n, f^1 \rangle > 0$ if $x_3 > y^1(x_1)$ and $\langle n, f^2 \rangle > 0$ if $x_3 > y^2(x_1)$. We note that the curves y^1 and y^2 intersect at x_1^* and

$$x_1^{**} = \frac{ce_2}{\lambda(c+r)(e_1 h_2 - e_2(h_1+h_2))},$$

i.e., $x_1^{**} < x_1^*$. When a trajectory of (2) falls on G^0, we have to distinguish four possible cases (see Fig. 1):

(i) $\langle n, f^1 \rangle > 0$, $\langle n, f^2 \rangle < 0$, which means that trajectories of (2) will stay in G^0. This occurs for $y^1(x_1) < x_3 < y^2(x_1)$.

(ii) $\langle n, f^1 \rangle > 0$, $\langle n, f^2 \rangle > 0$, which means that trajectories of (2) will pass through G^0 from G^1 to G^2. This occurs for $x_3 > y^2(x_1)$.

(iii) $\langle n, f^1 \rangle < 0$, $\langle n, f^2 \rangle < 0$, which means that trajectories of (2) will pass through G^0 from G^2 to G^1. This occurs for $x_3 < y^1(x_1)$.

(iv) $\langle n, f^1 \rangle < 0$, $\langle n, f^2 \rangle > 0$, which means that trajectories of (2) which start on G^0 will move either to G^1 or to G^2. This case cannot occur; see Appendix 3.

Under the condition (i), a trajectory which hits G^0 stays there as long as (i) holds. This allows us to derive uniquely a value of u along G^0. Let us assume that a solution of (2) is in the part of G^0 where (i) holds. Since in this case it cannot leave G^0, it must hold that

$$x_2' = x_1' \frac{e_1 h_2 - e_2(h_1+h_2)}{e_2 h_1}.$$

This allows us to compute explicitly $u(x_1, x_3)$. Substituting this u into the dynamics (2) gives (7).

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