

# Searching for Food or Hosts: The Influence of Parasitoids Behavior on Host–Parasitoid Dynamics

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**A host–parasitoid system with overlapping generations is considered. The dynamics of the system is described by differential equations with a control parameter describing the behavior of the parasitoids. The control parameter models how the parasitoids split their time between searching for hosts and searching for non-host food. The choice of the control parameter is based on the assumption that each parasitoid maximizes the instantaneous growth rate of the number of copies of its genotype. It is shown that optimal individual behavior of parasitoids, with respect to time sharing between hosts and food searching, may have a stabilizing effect on the host–parasitoid dynamics.** © 1997 Academic Press

## INTRODUCTION

Most studies of host–parasitoid interactions at the population level assume that the number of hosts parasitized per unit of time depends on host and parasitoid densities and on a species specific searching efficiency (Hassell and May, 1973). It is often assumed that the time a parasitoid devotes to host searching during its life is fixed, whereas in reality animals have to share their time between different activities. One of these activities which is important in most parasitoids species is feeding. Many species of parasitoids need food resources other than host tissues: mainly plant materials (Jervis *et al.*, 1993). Whether they encounter these non-host food sources within their host habitat (van Emden, 1990), or in plants which grow outside this habitat (Powell, 1986), the adult

parasitoids must share their time between consumption of these resources, and eventual searching for them, and activities linked to parasitism. The problem of time allocation between these two kinds of activities is very important for two reasons. First, several biological control studies (Leius, 1960; Leius, 1967; Powell, 1986; van Emden, 1990; Jervis *et al.*, 1993) revealed that the presence of non-host food is necessary to the maintenance of parasitoid populations. Second, experiments conducted at the individual level (Takasu and Hirose, 1991; Takasu and Lewis, 1995) clearly showed that parasitoids share their time between searching for non-host food and searching for hosts. The importance of non-host food sources in host–parasitoid models was stressed by Jervis and Kidd (1995): “...A valuable step in the development of foraging models and of population

models would be also to take account of the quality and spatial distribution of non-host food sources. There will, of course, be the added complication of incorporating the relative costs and benefits of searching for host and non-host food sources, but at least models explicitly incorporating non-host foods are likely to approximate more closely the natural situation in which parasitoids live....”

The choice between searching for hosts and searching for, and consuming, non-host food will influence the reproductive success of each parasitoid in two ways. First, it will affect the instantaneous reproductive rate of the parasitoid, because the effective time spent searching for hosts will be reduced if the parasitoid spends some time searching for food and feeding. Second, it will determine the lifespan of the parasitoid, which depends strongly on the consumption of non-host food (Jervis and Kidd, 1986; Jervis *et al.*, 1993). Therefore, the choice between searching for hosts and searching for food represents a trade-off: parasitoids that spend most of their time searching for hosts will have a high instantaneous reproductive rate, but also suffer a high mortality risk, caused by starvation. Parasitoids that invest in feeding will live and reproduce longer, but will have a lower instantaneous reproductive rate. As it influences the reproductive success of each parasitoid, the decision to search for hosts or for food will influence parasitoid-host dynamics.

A recent paper (Sirot and Bernstein, 1996) addresses the question of the optimal strategy with respect to that trade-off from the individual point of view. In the present paper we will incorporate the optimal strategy into a population dynamical model, to investigate how the host–parasitoid dynamics is influenced by the adaptive decision-making.

The host–parasitoid dynamics will be described by a controlled system of differential equations where the control parameter models the behavior of parasitoids with respect to searching for food and searching for hosts. With this dynamics we consider an optimality criterion, expressed through the maximization of a measure of *fitness* for each parasitoid. The fitness measure we use is 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). Assuming that each parasitoid is instantaneously maximizing its fitness allows us to determine the *optimal strategy* among all possible values for the control parameter.

Following Colombo and Křivan (1993), Křivan (1995), Křivan (1996) we show that this model is well defined, i.e., for each initial density of parasitoids and

hosts there exists exactly one solution starting from these initial densities, and we analyze the model. We will be mainly interested in the effect of the optimal choice between searching for hosts and for food on the persistence of the model. In Sirot and Bernstein (1996) it was suggested that optimal behavior of parasitoids may have a stabilizing effect on the population dynamics. In the present paper we show that the individual behavior of parasitoids on its own leads to persistence of the otherwise non-persistent host–parasitoid population dynamics.

## POPULATION DYNAMICS

Here we derive the host–parasitoid model. Let us consider a parasitoid during  $T$  units of time. We assume that the parasitoid is only concerned with searching for food and feeding, and searching for and handling hosts during this time interval. We consider these two activities to be distinct, i.e.,

$$T = T_f + T_p,$$

where  $T_f$  is the time devoted to activities connected with feeding and  $T_p$  with parasitizing. Each of these two activities consists of searching and handling respectively food sources and hosts. We set

$$u = \frac{T_f}{T},$$

which means that  $u$  is the proportion of the time  $T$  that is devoted to feeding activities ( $0 \leq u \leq 1$ ). In what follows we will consider  $u$  as a control parameter that represents the strategy of the parasitoid. We have

$$\begin{aligned} T_f &= uT, \\ T_p &= (1 - u)T. \end{aligned} \tag{1}$$

$T_p$  splits into two parts

$$T_p = T_p^s + T_p^h$$

where  $T_p^s$  is time devoted to searching for hosts and  $T_p^h$  is time devoted to “handling” hosts, i.e., to lay eggs. If  $\lambda$  denotes the search rate of a parasitoid,  $h$  the time to lay one egg once a host is found, and  $x$  the host density, we get

$$T_p^h = h\lambda x T_p^s.$$

Thus

$$T_p = T_p^s(1 + h\lambda x)$$

and

$$T_p^s = \frac{T_p}{1 + h\lambda x}. \quad (2)$$

To derive the dynamics of the host–parasitoid system we make two assumptions. First, we assume that the population of hosts grows exponentially in the absence of parasitoids, with the rate of increase  $r$ . Second, it is assumed that the instantaneous mortality rate of parasitoids depends linearly on the proportion of time devoted to feeding activities. We will assume that the mortality rate is  $m$  if the parasitoid devotes all the time  $T$  to feeding activities ( $u = 1$ ) while it is  $M + m$  if it devotes all the time  $T$  to reproduction ( $u = 0$ ). For intermediate values of  $u$ , the mortality rate is  $m + M(1 - u)$ . This mortality is independent of time, so we assume that food abundance is constant. With the above stated assumptions we may write the difference equations describing the dynamics of the host–parasitoid system. By  $y$  we denote the parasitoid density. Then we have

$$\begin{aligned} x(t + T) - x(t) &= rx(t)T - \lambda x(t)y(t)T_p^s, \\ y(t + T) - y(t) &= \lambda x(t)y(t)T_p^s - (m + M(1 - u))y(t)T. \end{aligned}$$

Using (1) and (2) we get

$$\begin{aligned} x(t + T) - x(t) &= rx(t)T - \frac{\lambda x(t)y(t)(1 - u(t))T}{1 + h\lambda x(t)}, \\ y(t + T) - y(t) &= \frac{\lambda x(t)y(t)(1 - u(t))T}{1 + h\lambda x(t)} \\ &\quad - (m + M(1 - u(t)))y(t)T. \end{aligned}$$

Assuming  $T$  to be infinitesimally small, we get a continuous approximation of the above discrete system:

$$\begin{aligned} x'(t) &= rx(t) - \frac{\lambda x(t)y(t)}{1 + \lambda hx(t)}(1 - u(t)), \\ y'(t) &= \frac{\lambda x(t)y(t)}{1 + \lambda hx(t)}(1 - u(t)) - (m + M(1 - u(t)))y(t). \end{aligned} \quad (3)$$

## OPTIMALITY RULES

It is assumed that the fitness of each parasitoid is maximized when the rate of increase of the number of copies

of its genotype is maximum (Sibly, 1991; Stearns, 1992). This leads to the maximization of the instantaneous growth rate of the parasitoid population, represented by

$$R(u) = \frac{1}{y} \frac{dy}{dt} = \left( \frac{\lambda x}{1 + \lambda hx} - M \right) (1 - u) - m.$$

For each host density  $x$  we define the *strategy map*  $S(x)$  for every parasitoid as the set of those  $u$ 's that maximize  $R(u)$ , i.e., the set of optimal strategies when host density is  $x$ . We note that the basic mortality rate  $m$  has no influence on the optimal strategy, because it represents the part of mortality which does not depend on the parasitoid behavior. From Appendix A it follows that the strategy map  $S$  has following values:

(a) If  $Mh > 1$  then  $S(x) = \{1\}$  for any  $x > 0$ . Here the optimal strategy is to search for food exclusively since under this condition, the per capita growth rate of parasitoids is negative for any density of  $x$ . Thus, the population of parasitoids will always decline and if parasitoids devote some time to reproduction the rate of decrease will increase. Thus  $Mh > 1$  is a biologically unrealistic assumption since parasitoids do not reproduce under this condition. There is also experimental evidence that  $Mh \ll 1$ , see Hassell and May (1973).

(b) If  $Mh < 1$  then

$$S(x) = \begin{cases} \{0\} & \text{if } x > x^*, \\ \{1\} & \text{if } x < x^*, \\ \{0 \leq u \leq 1\} & \text{if } x = x^*, \end{cases} \quad (4)$$

where

$$x^* = \frac{M}{\lambda(1 - Mh)}.$$

Thus the optimal control  $u$  is uniquely defined if  $x \neq x^*$ . If  $x = x^*$  then  $R(u)$  has a zero slope and any value of  $u$  between 0 and 1 leads to maximization of fitness.

If hosts are abundant, i.e.,  $x > x^*$ , the optimal strategy is to search for hosts only, since the reproductive rate will be high with respect to the mortality rate. If  $x < x^*$  then the optimal behavior is to search for food only. If  $x = x^*$  then the strategy cannot be uniquely derived from maximization of the fitness function. Nevertheless, we want to stress here that this does not mean that the strategy cannot be uniquely derived at all, since when deriving the optimal strategy we did not consider the dynamics of (3). In fact, as we will see later, the control parameter is also uniquely derived for  $x = x^*$ .

The dynamics is described by (3) with  $u$  belonging to the strategy map, i.e.,

$$\begin{aligned} x' &= rx - \frac{\lambda xy}{1 + \lambda hx} (1 - u), \\ y' &= \frac{\lambda xy}{1 + \lambda hx} (1 - u) - (m + M(1 - u)) y, \\ u &\in S(x). \end{aligned} \quad (5)$$

Despite the non-uniqueness in dynamics (5) it is proved in Appendix B that the above system has for every initial condition a solution that is uniquely defined. Thus, our model is well posed.

## QUALITATIVE BEHAVIOR OF THE SYSTEM

First we consider the case when  $Mh > 1$ . The optimal control  $u = 1$  does not depend on the density of the host population and (5) reduces to the differential equation

$$\begin{aligned} x' &= rx, \\ y' &= -my. \end{aligned} \quad (6)$$

The trajectory of this system that corresponds to the initial condition  $(x_0, y_0)$  is

$$(x(t), y(t)) = (e^{rt}x_0, e^{-mt}y_0).$$

Thus, we see that the population of parasitoids will go extinct, since they never parasitize, while the host population is growing exponentially. This is another reason why this combination of parameters cannot be considered as a reasonable representation of reality.

For the second case ( $Mh < 1$ ) the qualitative behavior is more complex. This is because (5) depends now on the control, which in turn, depends on the state of the system. Thus, the system is now governed by (6) only if  $x < x^*$ . If  $x > x^*$  we have to set according to (4) the optimal control  $u = 0$  and the resulting differential equation is

$$\begin{aligned} x' &= rx - \frac{\lambda xy}{1 + \lambda hx}, \\ y' &= \frac{\lambda xy}{1 + \lambda hx} - (M + m) y. \end{aligned} \quad (7)$$

System (7) is a predator-prey model with Holling type II response function. It has one non-trivial equilibrium  $E$  which is positive provided

$$m < \frac{1}{h} - M,$$

see Appendix C. Trajectories spiral away from this equilibrium with increasing amplitude and, consequently, the dynamics is not persistent. If  $E$  is positive then it is in the part of the space where  $x > x^*$ .

Consider a trajectory which starts in the part of the space where  $x < x^*$ . This trajectory is governed by (6) and it reaches in a finite time the line  $x = x^*$ . When it reaches the line  $x = x^*$  it may either cross this line and continue in the part of the space where  $x > x^*$  or it may start to move along the line  $x = x^*$ . In Appendix C it is shown that if the trajectory approaches the line  $x = x^*$  from the right, it cannot cross this line. Thus it can either move along this line or leave the line and move back to the part of the space where  $x > x^*$ . This means that a parasitoid can switch from pure feeding to pure parasitizing, but not from pure parasitizing to pure feeding.

Let us denote

$$y^* = \frac{r}{\lambda(1 - Mh)}.$$

In Appendix C it is shown that trajectories that reach the line  $x = x^*$  will move along this line provided

$$y(t) > y^*. \quad (8)$$

Moreover, under this condition the  $u$ -value governing such a trajectory is uniquely given by

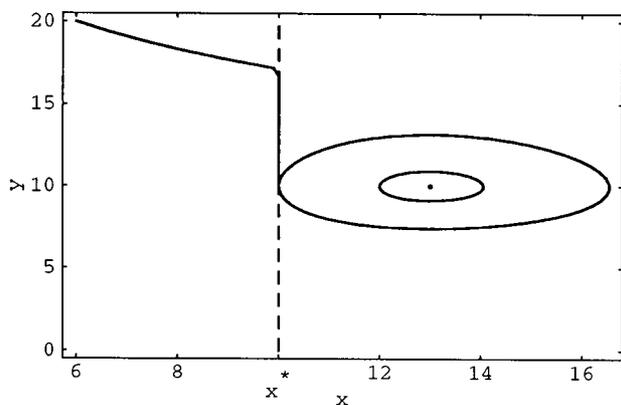
$$u(x^*, y) = \frac{r + \lambda y(hM - 1)}{\lambda y(hM - 1)}.$$

If a trajectory moves along the line  $x = x^*$  the optimal control is strictly between zero and one which leads to the emergence of *partial preferences* for food in the behavior of the parasitoids. We note that this formula specifies explicitly the optimal control  $u$  also for the case when the direct maximization of the function  $R(u)$  did not give a unique value of the optimal control. Thus, provided condition (8) holds, the dynamics along the line  $x = x^*$  is described by

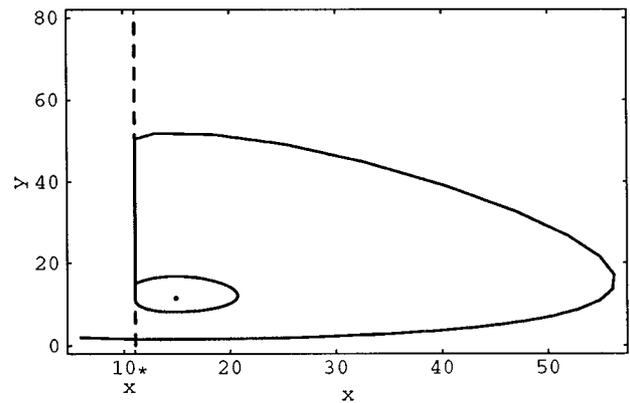
$$\begin{aligned} x' &= 0, \\ y' &= -my. \end{aligned}$$

This shows that the movement along the line  $x = x^*$  can only be downward.

To understand the behavior of (5) we start with a particularly simple case when the handling time is set to zero ( $h = 0$ ). Under this assumption (7) becomes the Lotka–Volterra equation. Let us consider a trajectory that starts at a point to the right of the line  $x = x^*$  (see Fig. 1). This trajectory follows a Lotka–Volterra cycle given by (7). There are two possibilities. Either the whole cycle is in the part of the space where  $x > x^*$ , or it reaches at certain time the line  $x = x^*$ . In this case it moves further on along this line until the point  $y^*$  is reached. At the moment of reaching  $y^*$  it leaves the line  $x = x^*$  and starts to move along the Lotka–Volterra cycle of (7) which passes through the point  $(x^*, y^*)$ . If the trajectory starts to the left of the line  $x = x^*$  then the dynamics is governed by (6) and the trajectory must necessarily reach the line  $x = x^*$ . There are two possibilities. Either it reaches this line at a point above  $y^*$  (see Fig. 1) and then it moves down to the point  $y^*$  where it starts to move along the Lotka–Volterra cycle that passes through the point  $(x^*, y^*)$ , or it reaches the line  $x = x^*$  below the point  $y^*$ . In this case it crosses this line and starts to follow a Lotka–Volterra cycle, which at a certain moment reaches the line  $x = x^*$ . In this way this trajectory reaches after a finite time again the Lotka–Volterra cycle that passes through the point  $(x^*, y^*)$ . Thus, all trajectories of (5) do converge to the set bounded by the Lotka–Volterra cycle which passes through the point  $(x^*, y^*)$ . This set is called global attractor. We note that for zero handling time no partial preferences do appear on the attractor, see Fig. 1.



**FIG. 1.** A solution of (5) plotted in space domain. For  $x > x^*$ , trajectories follow Lotka–Volterra cycles since the handling time was set to zero. All trajectories of (5) which start outside the interior of the large Lotka–Volterra cycle do converge to this cycle in a finite time. Trajectories starting inside follow a Lotka–Volterra cycle given by (7). Parameters:  $r = 1, h = 0, \lambda = 0.1, m = 0.3, M = 1$ .



**FIG. 2.** A solution of (5) plotted in space domain. Handling time is non-zero. In this case the optimal behavior of parasitoids leads to the persistence of the host–parasitoid dynamics. Parameters:  $r = 1, h = 0.1, \lambda = 0.1, m = 0.3, M = 1$ .

The behavior of trajectories for the case  $h > 0$  is similar, see Fig. 2. We will assume that the equilibrium  $E$  is positive. Then for small  $h$  the trajectories are spiraling outwards around the unstable equilibrium  $E$  and they reach the line  $x = x^*$  (see Fig. 2). When a trajectory reaches this line it will move downward along it till it reaches the point  $y^*$ . At the moment of reaching  $y^*$  it will leave the line  $x = x^*$  and it will move along another orbit of (7) which reaches again the line  $x = x^*$ . Thus, a limit cycle appears. We note that for  $h > 0$  partial preferences do appear, see Fig. 2.

We may compare the case when parasitoids behave optimally with the case when they behave at random. This would correspond to fixed value of the control  $u$  in (3). It is well known that Holling second type functional response has a destabilizing effect on population dynamics. Solutions are unbounded and, consequently, the system where parasitoids behave at random is not persistent, see Appendix C.

## DISCUSSION

In this paper, we explored how optimal time sharing between searching for hosts and searching for food in parasitoids affects the dynamics of the host–parasitoid system. We chose to focus our study on the consumption of non-host food, thus addressing the necessity to incorporate an important part of parasitoid behavior in a population model (Jervis and Kidd, 1995). The behavioral choice we study is clearly different from the choice that face parasitoids that choose between host–feeding and egg-laying when they encounter a host (Jervis and Kidd, 1986; Heimpel and Rosenheim, 1995).

Indeed, the problem we studied concerns time allocation between nutrition and reproduction, whereas host–feeding parasitoids encounter a problem of resource allocation, the resource being the host (Houston *et al.*, 1992). Furthermore, as hosts play a different role in the two kinds of problems, the effect of these two behavioral choices on population dynamics is of a different nature (see Yamamura and Yano (1988), Kidd and Jervis (1991) and Briggs *et al.*, 1995 for studies on the influence of host–feeding strategies on population dynamics).

In classical theory, dynamics of host–parasitoid systems are represented by difference equations models (Hassell and May, 1973). This theory concerns hosts and parasitoids with discrete generations. Here we chose a continuous time approach that allows us to derive explicitly the control parameter corresponding to a mixed strategy when parasitoids both parasitize and feed. Therefore, our model addresses populations with overlapping generations. This situation, however, is widely spread in nature for hosts and parasitoids (Murdoch *et al.*, 1987).

When generations overlap, it pays not only to have many offspring, but also to have them early, because the sooner they hatch, the sooner they may reproduce and contribute to the spreading of their genotype (Giske *et al.*, 1993). Consequently, the instantaneous growth rate of the number of genotype copies is an appropriate measure of fitness (Sibly, 1991; Stearns, 1992).

We want to stress that the reason why maximization of the fitness function  $R(u)$  does not give a unique control is due the fact that the function  $R(u)$  is linear. This is the result of the linearity of the mortality rate of parasitoids. If we take another, nonlinear mortality rate we would get an optimal strategy that might be uniquely determined. However, our choice leads to a model that can be easily studied from the qualitative point of view, while another choice for the mortality rate could lead to a model that would be difficult, if possible, to analyze.

The optimal strategy described here refers to the well-known trade-off between survival and reproduction (Sibly and Calow, 1983), which are the basic components of fitness (Stearns, 1992). Here the trade-off is expressed through the need for the animals to share their time between feeding and searching for hosts. We represented the trade-off by assuming that the mortality of the parasitoids is low when they devote a large proportion of their time to feeding. This assumption represents the fact that animals that feed a lot, maintain a high level of energy reserves and are healthier than animals that feed less (Sirot and Bernstein, 1996). Other work addresses this trade-off from the point of view of allocation of physiological resources between reproductive effort and

survivorship of an individual (Horn and Rubenstein, 1984).

The main result of this study is that introducing a rule of optimal behavior in the choice between host and food searching leads to persistence for a system which otherwise is non-persistent. The mechanism through which this is achieved is that the host depletion rate is maximum if hosts are abundant (when  $x > x^*$  then the parasitoids spend all their time searching for hosts), and it is zero if hosts are scarce (when  $x < x^*$  then the parasitoids search only for food). This avoids the collapsing of the host population. This effect is qualitatively similar to that of other equilibrating factors, such as parasitoids being less efficient as their density increases (interference, Hassell and Varley, 1969, Hassell and May, 1973), or parasitoids reacting optimally to the characteristics of the host population: parasitoids aggregating on rich patches (Comins and Hassell, 1979), super-parasitizing more in the presence of conspecifics (Driessen and Visser, 1993), or neglecting low ranking hosts when these are scarce (Mangel and Roitberg, 1992). The present work emphasizes the need to introduce in population models all aspects of animal behavior that can affect reproductive success, even if these activities do not interact directly with reproduction.

## APPENDIX A: OPTIMAL STRATEGY

We want to maximize

$$R(u) = \left( \frac{\lambda x}{1 + \lambda h x} - M \right) (1 - u) - m$$

over the interval  $[0, 1]$ . Since  $R$  is a linear function in  $u$  it achieves its maximum at the point 1 if it has a positive slope or at the point 0 if it has a negative slope. If the slope is zero, which happens when

$$x = x^* = \frac{M}{\lambda(1 - Mh)},$$

then  $R$  is a constant function and the optimal strategy is not uniquely given. We note that for  $Mh > 1$ ,  $x^*$  is negative and  $R$  is increasing for every density of hosts  $x$ . Thus, in this case the optimal strategy is always  $u = 1$ . If  $Mh < 1$  then, for  $x > x^*$ , the function  $R$  is decreasing and the optimal strategy is given by  $u = 0$  while for  $x < x^*$  the optimal strategy is  $u = 1$ . Thus we get the optimal strategy  $S(x)$ .

## APPENDIX B: EXISTENCE AND UNIQUENESS OF SOLUTIONS OF (5)

Existence of trajectories of (5) follows from Colombo and Křivan (1993). Let us denote

$$G^1 = \{(x, y) \in \mathbf{R}_+^2 \mid x < x^*\},$$

$$G^2 = \{(x, y) \in \mathbf{R}_+^2 \mid x > x^*\},$$

$$G^0 = \{(x, y) \in \mathbf{R}_+^2 \mid x = x^*\}.$$

Let  $n = (1, 0)$  denote the normal vector to  $G^0$ , oriented from  $G^1$  towards  $G^2$ . We denote by  $f^1(x, y)$  the right handside of (5) in  $G^1$  and by  $f^2(x, y)$  in  $G^2$ . We note that since  $f^i$ , ( $i = 1, 2$ ) are smooth functions, uniqueness of trajectories in  $G^1$  and  $G^2$  follows from standard theorems for differential equations. However, we have to prove uniqueness of trajectories when they fall on  $G^0$ . Denoting by  $\langle \cdot, \cdot \rangle$  the scalar product in  $\mathbf{R}^2$  we get

$$\langle n, f^1(x^*, y) \rangle = \langle n, f^2(x^*, y) \rangle + \frac{\lambda x^* y}{1 + x^* \lambda h}.$$

Thus, at every point  $(x^*, y)$  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 at each point of  $G^0$  at least one of the inequalities  $\langle n, f^1 \rangle > 0$  or  $\langle n, f^2 \rangle < 0$  holds. These are the conditions that ensure uniqueness of trajectories of (5), see Theorem 2, p. 110 in Filippov (1988) (see also Colombo and Křivan, 1993).

Moreover, we see that  $\langle n, f^1 \rangle < 0$  and  $\langle n, f^2 \rangle > 0$  cannot hold simultaneously. We use this result in Appendix C.

## APPENDIX C: QUALITATIVE BEHAVIOR OF THE HOST-PARASITOID SYSTEM

We use the notation introduced in Appendix B. We will study the behavior of a solution of (5) when it falls on  $G^0$ . This behavior is given by projections of vector

fields  $f^1$  and  $f^2$  on the normal vector  $n$ . We have to distinguish four possible cases:

(i)  $\langle n, f^1 \rangle > 0$ ,  $\langle n, f^2 \rangle < 0$  which means that trajectories of (5) will stay in  $G^0$

(ii)  $\langle n, f^1 \rangle > 0$ ,  $\langle n, f^2 \rangle > 0$  which means that trajectories of (5) will pass through  $G^0$  from  $G^1$  to  $G^2$

(iii)  $\langle n, f^1 \rangle < 0$ ,  $\langle n, f^2 \rangle < 0$  which means that trajectories of (5) will pass through  $G^0$  from  $G^2$  to  $G^1$

(iv)  $\langle n, f^1 \rangle < 0$ ,  $\langle n, f^2 \rangle > 0$  which means that trajectories of (5) which start on  $G^0$  will move either to  $G^1$  or to  $G^2$ ,

see Křivan (1996). From Appendix B it follows that the case (iv) cannot happen. Under the condition (i) a trajectory which hits  $G^0$  stays there as long as (i) holds. If condition (i) holds we may compute directly the value of  $u$ . In what follows we will assume  $Mh < 1$ . Let us assume that a solution of (5) is in the part of  $G^0$  where (i) holds. Since in this case it cannot leave  $G^0$  it must hold

$$x'(t) = 0.$$

This allows to compute explicitly  $u$ . We get

$$u(x^*, y) = \frac{r + \lambda y(hM - 1)}{\lambda y(hM - 1)}.$$

For our model (5) we get on  $G^0$

$$\langle n, f^1 \rangle > 0 \quad \text{always} \tag{9}$$

$$\langle n, f^2 \rangle > 0 \quad \text{if } y < \frac{r}{\lambda(1 - Mh)} = y^*.$$

We may describe the movement of trajectories of (5) when they fall on  $G^0$  with respect to the  $y$  coordinate. Due to (9) we see that cases (iii) and (iv) cannot hold. Thus there are only two possibilities:

(i) if  $y^* < y$  then trajectories of (5) stay on  $G^0$

(ii) if  $y < y^*$  then trajectories of (5) cross  $G^0$  from  $G^1$  towards  $G^2$ .

In  $G^2$  the dynamics of (5) is given by (7). This system has the trivial equilibrium and one non-zero equilibrium

$$E = (E_1, E_2) = \left( \frac{M + m}{\lambda - h\lambda(M + m)}, \frac{r}{\lambda - h\lambda(M + m)} \right).$$

The eigenvalues corresponding to the trivial equilibrium are  $(-(m+M), r)$  and the eigenvalues corresponding to the non-trivial equilibrium are

$$\begin{aligned} & 1/2(hr(M+m) \\ & + \sqrt{-4r(m+M)(1-h(m+M)) + h^2(m+M)^2 r^2}), \\ & 1/2(hr(M+m) \\ & - \sqrt{-4r(m+M)(1-h(m+M)) + h^2(m+M)^2 r^2}). \end{aligned}$$

Thus we see that none of these two equilibria is locally stable.

The equilibrium  $E$  is positive if

$$m < \frac{1}{h} - M.$$

Using Bendixon–Dulac criterion, see (Hofbauer and Sigmund, 1984), it is possible to see that there are no limit cycles in dynamics of (7). Let

$$B(x, y) = \frac{1}{xy}.$$

Then we get

$$\frac{\partial}{\partial x}(B(x, y) x') + \frac{\partial}{\partial y}(B(x, y) y') = \frac{h\lambda^2}{(1+h\lambda x)^2} > 0.$$

It follows that (7) does not have a limit cycle, see Hofbauer and Sigmund (1984). Thus the  $\omega$ -limit sets are unbounded and consequently trajectories of (7) are not bounded. Moreover, we note that  $E_1 > x^*$  if  $E$  is positive.

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