

Time sharing between host searching and food searching in parasitoids: state-dependent optimal strategies

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By varying the time spent searching for food, parasitoids modify their expected lifespan, and therefore their total lifetime reproductive success. Using a stochastic dynamic approach, we define the best choice between searching for food and searching for hosts as a function of the state of the parasitoid and the availability of food when hosts and food are found in different parts of the environment. A first model deals with the influence of food availability and survivorship conditions on the behavior of a single parasitoid. Our results suggest that under conditions of very low food availability, parasitoids should never search for food. When food availability is moderate, parasitoids should not wait until their reserves are low before searching for food. When food is abundant and survivorship is independent of food consumption, parasitoids should search for food only when their reserves are almost exhausted. They should not wait so long if survivorship depends on the energy reserves. By finding the state-dependent ideal free distribution for a population of parasitoids, we are able to predict their distribution between the feeding area and the host living area at equilibrium. The proportion of parasitoids in each area is altered by the number of competitors and interference. Finally, the model predicts that optimal time sharing between food searching and host searching may promote the stability of the host-parasitoid system. *Key words*: dynamic programming, ideal free distribution, parasitoids, population stability, state-dependent foraging decisions. [*Behav Ecol* 7:189–194 (1996)]

Numerous adult parasitoids use other food resources than hosts (Jervis et al., 1993; Leius, 1960). In many cases, hosts are not found at the same location as food (Jervis and Kidd, 1995). For example, Jervis et al. (1993) recorded 249 species of hymenopteran parasitoids feeding in inflorescences. For these animals, oviposition and feeding are two behavioral alternatives: searching for hosts, in order to obtain immediate fitness rewards, and searching for food, in order to gain additional expected lifetime. This choice between direct and indirect fitness rewards affects the overall efficiency of the parasitoids, and may therefore influence the population processes (Jervis and Kidd, 1995). Leius (1960) suggested that ignoring the feeding behavior of parasitoids may have been responsible for the failure of some parasitoid introductions.

Much theoretical work has attempted to explain different aspects of the foraging behavior of parasitoids from an adaptive point of view (e.g., Hubbard et al., 1987; Iwasa et al., 1984; Mangel, 1989; van der Hoeven and Hemerik, 1990; Visser et al., 1992; Weisser and Houston, 1993), but this work has been concerned only with parasitoids on their hosts' patches. The problem of the choice between searching for food or searching for hosts has been described in theoretical papers (Mangel, 1987; Mangel and Clark, 1986; Roitberg et al., 1992); however, none of these studies explored the effect of differences in food availability, which is, in fact, a common pattern in natural environments.

Lifespan is an important component of reproductive success and strongly depends on food consumption in parasitoids [for a review see Jervis and Kidd (1986) and van Lenteren et al. (1987)]. The parasitoid *Venturia canescens* can live approximately 20 days when it has access to honey, and only 4 days when starved (E. Sirot, unpublished results). It is therefore

reasonable that searching for food should be included in optimal foraging models for parasitoids, as suggested by Mangel (1987). In this case, expected lifetime will not just be represented by a fixed mortality rate (Iwasa et al., 1984; Mangel, 1992), or a fixed time of death (Mangel and Clark, 1986), but will be a consequence of the decisions made by the animal. Wäckers (1994) showed that the nutritional state of the parasitoid *Cotesia rubecula* strongly influences its choice between hosts and food, emphasizing the need of a state-dependent approach when analyzing this behavioral choice.

In this article, we develop an optimization model to explore the behavioral choice between food and host searching, taking into account the stochastic nature of the environment. We consider all parasitoid species that switch between feeding areas and host sites, regardless of the actual distance between these two locations. Hence, host-feeding parasitoids (Kidd and Jervis, 1989) and parasitoids feeding on host sites are beyond the scope of our work. To tackle the problem we employ dynamic state-variable models (Houston et al., 1988; Mangel and Clark, 1988). This method enables us to study the influence of the state of the parasitoid (energy reserves) and the environmental conditions on the parasitoid's optimal decision.

First we build a model for the behavior of an isolated parasitoid, which defines the optimal choice between searching for hosts and searching for food for different food availabilities. With this model we can determine the proportion of the parasitoid's lifetime devoted to reproduction.

Next, to study the influence of the presence of conspecifics, we develop a state-dependent ideal free distribution model (McNamara and Houston, 1990). This model assumes that a large number of parasitoids forage together, each of them following the optimal strategy, and predicts the equilibrium distribution of the population between the egg-laying area and the feeding area.

The dynamics of the host-parasitoid system can be perceived as a succession of generations in which the distribution of parasitoids follows the state-dependent ideal free distribu-

tion. This allows us to explore the possible influence of optimal time sharing between searching for hosts and searching for food on the stability of the system.

THE MODELS

The individual level

Here we describe the model for the optimal decisions by a single parasitoid.

The energy reserves of the parasitoid are represented by a "state variable," e . Depending on the feeding behavior of the parasitoid, this variable ranges between its maximum value, E , and its minimum value, 0, which corresponds to starvation and death of the individual.

The parasitoid is confronted with the choice between two habitats: a host patch and a food patch. Each patch represents an area where resources (host and food, respectively) are randomly distributed.

Time is divided into discrete units, and at the beginning of each of these periods the parasitoid can move between patches. Movements between patches take one period and imply a metabolic cost α . For each period, regardless of the patch type, each nonstarving parasitoid has a mortality risk, $\mu(e)$, which takes into account all risks of dying except starvation. So the parasitoid's expected lifespan will be determined both by the time it has left before its energy reserves, e , are exhausted and the mortality risk $\mu(e)$. We studied two mortality conditions: constant $\mu(e)$ (two different values), or variable $\mu(e)$ (represented by a decreasing sigmoidal function).

When on the host patch, the parasitoid searches for hosts and lays eggs. The fitness reward of oviposition, f , is the expected (mean value) number of offspring from oviposition on the host patch; f is a function of host abundance and of the expected number of offspring of each oviposition. In each period spent on the host patch, the energy reserves decrease by a single unit.

In each period spent searching on the food patch, the parasitoid has a probability, λ , of finding a food source. If it finds food, the energy reserves of a parasitoid that stays j periods on a food source will increase from e to $e + \beta j$, β being the consumption rate. The food sources provide an unlimited supply, but the energy reserves of the parasitoid can never exceed their maximum value, E . When feeding is chosen, the optimal behavior incorporates the number of periods that the parasitoid will spend on the food source. When the parasitoid does not find food, its energy reserves decrease by one unit.

We assume that both patches are rich enough not to be depleted by a single parasitoid individual, so all environmental parameters are constant. Surviving parasitoids die at time T , that is, when the end of the season is reached.

The model is employed to find the behavior that results in the maximum lifetime number of offspring (Mangel, 1989). This quantity, $F(e, t, i)$, depends on the energy reserves of the parasitoid, e , the current time period, t , and the location of the parasitoid, i ($i = 0$ if the parasitoid is on a food source, $i = 1$ if it is on the host patch, but not on a food source, and $i = 2$ if it is on the host patch).

A parasitoid that is on a food source can either stay and feed, or leave the food patch for the host patch. In the former case, its maximum expected lifetime fitness is $(1 - \mu(e))F(\text{Min}(e + \beta, E), t + 1, 0)$, in the latter it is $(1 - \mu(e))F(\text{Max}(e - \alpha, 0), t + 1, 2)$. The parasitoid is assumed to choose the option that maximizes the overall fitness gain, so

$$F(e, t, 0) = (1 - \mu(e))\text{Max}\{F(\text{Min}(e + \beta, E), t + 1, 0); F(\text{Max}(e - \alpha, 0), t + 1, 2)\}, \quad (1)$$

where Max stands for the maximum between two alternatives,

and Min for the minimum. A parasitoid that is on the food patch, but not on a food source, has the choice between searching for food or leaving the food patch for the host patch. In the first case, it may or may not find a food source. The dynamic programming equation corresponding to that situation is built in the same way as for the preceding one:

$$F(e, t, 1) = (1 - \mu(e))\text{Max}\{\lambda F(\text{Min}(e + \beta, E), t + 1, 0) + (1 - \lambda)F(e - 1, t + 1, 1)\}; F(\text{Max}(e - \alpha, 0), t + 1, 2)\}. \quad (2)$$

Finally, a parasitoid that is on the host patch may search for hosts or leave for the food patch. Thus,

$$F(e, t, 2) = (1 - \mu(e))\text{Max}\{[F(e - 1, t + 1, 2) + f]; F(\text{Max}(e - \alpha, 0), t + 1, 1)\}. \quad (3)$$

Stochasticity in food searching is reflected in Equation 2. Stochasticity in host searching is also taken into account in the model, but needs not be represented explicitly in Equation 3. This is so because, for one period on the host patch, the state of the parasitoid will evolve in the same way whether it encounters a host and oviposits, or not. If λ_h is the probability to encounter a host during one period on the host patch, and f_o is the fitness gain for an oviposition, then the maximum lifetime expected fitness for one period spent searching for hosts is $\lambda_h[F(e - 1, t + 1, 2) + f_o] + (1 - \lambda_h)F(e - 1, t + 1, 2)$, a quantity that is equal to $F(e - 1, t + 1, 2) + \lambda_h f_o$. So only the product $\lambda_h f_o$, which represents the expected number of offspring for one period on the host patch, is important. We represented it by the single parameter $f = \lambda_h f_o$.

The fitness for the final period T , $F(e, T, i) = 0$, because at the end of the season, the parasitoid can expect no future offspring. Here we are concerned with the stationary solutions of this process (i.e., solutions concerning a parasitoid far from the end of the season; Mangel and Clark, 1988; Weisser and Houston, 1993). The final result of the model is the optimal choice between searching for hosts or searching for food, for each state of the animal and for each set of environmental parameters, and the time devoted to a food source.

The only variable under the control of the parasitoid is the level of energy reserves at which it will switch between patches. The parasitoid is assumed to choose this level in order to maximize its overall fitness gain. This gain is obtained only in the host patch and is equal to the total number of time intervals in that patch over the entire lifespan, times the mean fitness gain per unit of time (f). As this gain is assumed to be constant, maximizing fitness gain is equivalent to maximizing the total number of time intervals in the host patch. For this reason, host availability, which is reflected in the actual value of f , has no influence on the predictions of the model.

A state-dependent ideal free distribution model

Using both the concept of ideal free distribution (Fretwell and Lucas, 1970) and dynamic programming, it is possible to find the equilibrium spatial distribution of an optimally foraging population (McNamara and Houston, 1990). Such a distribution is called the state-dependent ideal free distribution (SDIFD). Here we ask how N parasitoids should distribute themselves between their feeding area and their area of reproduction.

In our model, each individual adopts the optimal strategy (visiting the host or the food patch, as determined by dynamic programming) and stays on a food source as long as the optimal strategy dictates. On the food patch, the probability that

a given parasitoid finds food, λ , depends on the total number of food sources and the number of competitors also searching for food, because parasitoids interfere with one another (Hassell and Varley, 1969; see Appendix A). For the representation of parasitoid interference we have adopted the classical Hassell and Varley (1969) model, $a = QN^{-m}$, where a is a measure of the parasitoids' search rate for food, Q is the "quest constant," and m is the interference coefficient for food searching. In this model, interference accounts not only for physical interactions between parasitoids, but for all the factors that lead to a decrease in searching efficiency as parasitoid density increases. For instance, recent work (Bernstein and Driessen, in press) shows that parasitoids are less active in host searching if the patch has been marked by conspecifics. Similar processes could influence food search. Additionally, Arditì and Akçakaya (1990) demonstrate that mutual interference is often underestimated in parasitoids. As interference and parasitoid number alter the probability to find food, λ , which is a parameter of the dynamic programming equations, they also influence the predicted behavior.

Our initial assumption is that there is also interference in the host patch. The optimal behavior is the one predicted by the individual model, and as before, the optimal decision is independent of the actual rate of fitness gain on the host patch. For this reason the optimal decision and hence the SDIFD are independent of the value of the interference coefficient on that patch. We can then consider that m is the interference coefficient on both patches.

The equilibrium distribution is found by iteration. In the first iteration, and as a consequence of the parasitoids' movements, the population is divided between the two patches. This distribution leads to a new probability to find food, and thus to a new optimal behavior, which in its turn will lead to a new distribution of the parasitoids. We assume that possible casualties of starvation or instantaneous mortality are replaced by newcomers, so N is a constant. The SDIFD is achieved when, starting from a randomly chosen initial position, the equilibrium is reached (McNamara and Houston, 1990). This equilibrium provides both the distribution of individuals among the patches and the distribution of the state variable among the individuals (McNamara and Houston, 1990).

Population stability

In our SDIFD model, for a population of N parasitoids, if x is the proportion of parasitoids on the host patch, only xN parasitoids will be foraging on that patch at any time. Hence, time sharing between food searching and host searching should modify the overall host capture rate and therefore might alter the stability of this host-parasitoid system.

If we assume that, in a system with discrete generations, the distribution of parasitoids among the two patches follows the SDIFD for each generation, we can compare the results of our model with those of classical host-parasitoid theory (Comins and Hassell, 1979; Hassell and May, 1973).

Our model assumes that, for every parasitoid, the payoff of one period on the host patch and the number of parasitoids are constant across generations. These hypotheses are not in contradiction with the classical host-parasitoid models which do not take into account any changes in host or parasitoid numbers within a generation.

Hassell and May (1973) showed that in the Hassell and Varley (1969) model, and provided $0 < m < 1$, larger values of m promote stability. Comins and Hassell (1979) used this result to study the stabilizing influence of pseudointerference (Free et al., 1977) resulting from the distribution among patches of optimally foraging parasitoids. Following their lead we have estimated the joint influence of interference on the

food patch and parasitoid number on the overall interference coefficient as it would be measured in a field situation, from the regression of searching efficiency on parasitoid number (Appendix B shows that the prediction of stabilization or destabilization is not affected by the interference coefficient on the host patch).

RESULTS

The individual level

The first model yields the optimal behavior for the simple alternative of searching for food or searching for hosts and the answer to the question "How long to stay feeding?," as a function of the state of the parasitoid (e), the instantaneous mortality risk (μ), and the probability of finding food (λ). The plots in Figure 1 show the optimal behavior for a foraging parasitoid, for all values of λ , and for the different forms of μ [constant, with two different values (Figures 1a,b) or variable (Figure 1c)]. We have explained before that host abundance has no influence on the optimal behavior because what is actually maximized is the time spent on the host patch. In Figure 1, two curves divide the (λ , e) plane into three sections corresponding to the optimal choices. A parasitoid with energy reserves e , living in an environment where the probability of finding food is λ , is represented by a point (λ , e). For any given value of λ , if its energy reserves are so high that the point is above both curves, the parasitoid should search for hosts. It should keep on laying eggs, and spending energy, until e reaches the lower curve. From this moment on, it should search for food. If it finds it, it should feed until its energy reserves climb to the upper curve, and then resume searching for hosts. In what follows, the lower curve is called the "switching curve for food searching" and the upper one is the "switching curve for host searching." If the parasitoid does not encounter a food source before its energy reserves are exhausted, it dies.

As the parameters are arbitrary, and no particular species of parasitoid is considered, the predictions of our model can only be of a qualitative nature. Nevertheless, repeated calculations changing the parameter values do not change the general shape of the switching curves. This shows that the predictions are robust (Houston et al., 1992). For this reason a set of basic parameters was used in all the computation of this work: $E = 20$, $T = 400$, $f = 1$, $\alpha = 1$, $\beta = 1$. The shape of the curves and alterations in their relative positions resulting from changes in the form of μ lead to the following predictions.

Constant mortality risk

Prediction 1. When food is very scarce, parasitoids will stay in the host patch for their entire life. When food is abundant parasitoids will leave the host patch with lower energy reserves than when its availability is moderate.

Searching for food is useless when it has a high probability of not being rewarded (low values of λ for which both switching curves coincide with $e = 0$, in Figures 1a,b), and so the parasitoid will devote all its lifetime to reproduction. A higher survivorship (Figure 1b) allows for longer searching for food before death, and thus a higher overall probability of finding food (the range of values of λ for which no food should be searched is narrower in Figure 1b).

When food is very abundant, the insect can afford foraging for hosts until its reserves are almost exhausted, since it would take it a short time to find food. For intermediate conditions, it is worth searching for food, in order to get a higher life expectancy, but since food is not easily found, the parasitoid must not wait until its reserves are almost exhausted.

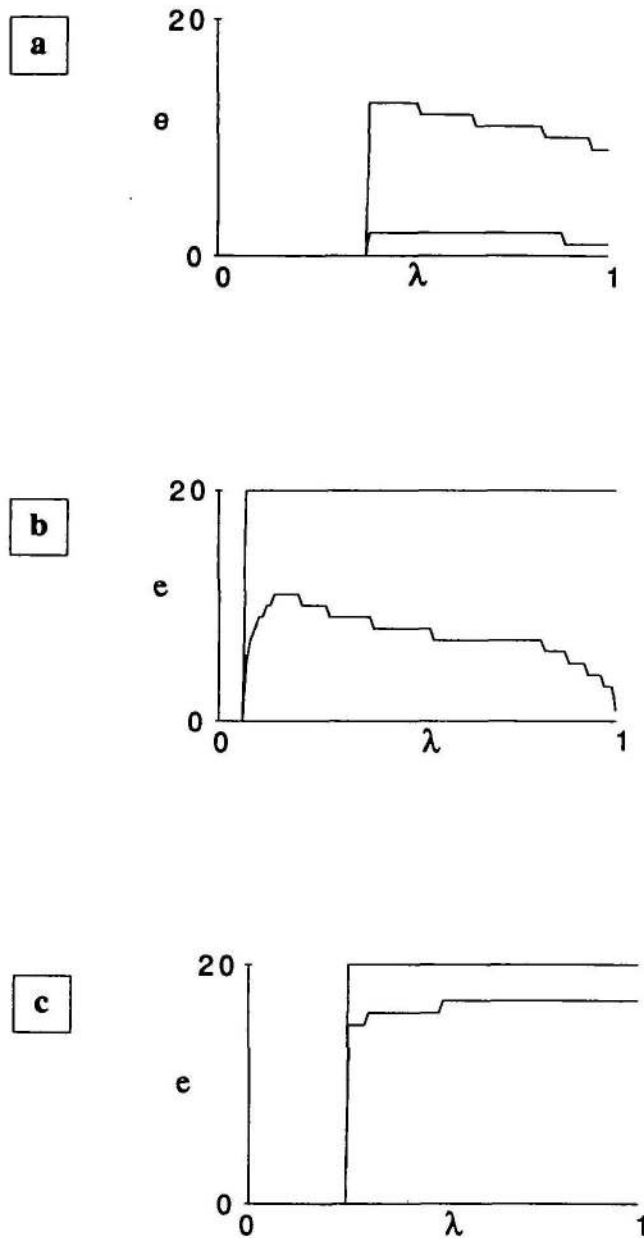


Figure 1
 Optimal behavior of a single parasitoid as a function of the probability to find a food source (λ) and energy reserves (e). For a given value of λ , if the parasitoid has an amount of e above both curves, it should search for hosts. If e is between the curves, it should search for hosts, unless it is already on a food source. In the latter case it should keep on feeding until e reaches the upper curve. Below both curves, the parasitoid should search for food, or keep on feeding if it is already on a food source. (a) Constant and high mortality risk: $\mu = 0.05$. (b) Constant and low mortality risk: $\mu = 0.00005$. (c) Mortality risk μ is dependent on energy reserves e (decreasing sigmoidal function).

Prediction 2. When mortality is high, energy reserves when leaving the food patch will be higher at intermediate levels of food availability. When mortality is low, parasitoids will feed to saturation.

High but constant mortality risk (Figure 1a) will reduce the expected lifetime even of well-fed animals. Hence, a strategy leading to a high instantaneous reproductive rate provides higher fitness, and in consequence, parasitoids will spend only

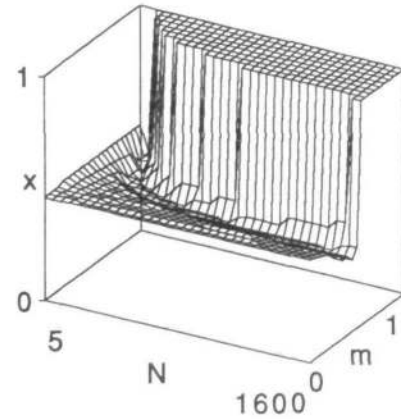


Figure 2
 Proportion x of parasitoids on the host patch at SDIFD, as a function of total number of parasitoids (N) and interference coefficient on both patches (m). Constant and low mortality risk: $\mu = 0.00005$.

short periods feeding. The mean level of the energy reserves of these parasitoids will be low (compare the upper curve of Figure 1a with that of Figure 1b). High probabilities of finding food will enhance this effect (the upper curve in Figure 1a is lower for high λ values) because the animals will easily find food when they need it.

When the instantaneous probability of dying is low (Figure 1b), animals can afford accumulating high energy reserves. These reserves are quite likely to be used later in the reproductive process. As a consequence, the parasitoid will stay longer on the host patch.

Variable mortality conditions

Prediction 3. As is the case for constant mortality conditions, when food is scarce parasitoids will devote their entire lifetime to reproduction. When food is more abundant parasitoids will leave the host patch when the energy reserves are still high and feed to saturation.

In variable mortality conditions, the parasitoid can afford searching for food only if it is abundant enough to allow the maintenance of a high energy level (values of λ to the right of the "cliff" of both switching level curves in Figure 1c). Therefore, when food is abundant, the parasitoid does not wait long on the host patch, and feeds to the maximum extent (high switching curves). Under other conditions, the probability of surviving a few periods quickly decreases, and the best strategy is to search for hosts exclusively.

In separate trials, with μ represented by other decreasing functions of e , we found very similar patterns. The only difference is observed when μ reaches low values and levels off at low values of e . In this case the lower curve slightly bends for high values of λ (see Prediction 1).

A state-dependent ideal free distribution model

The main purpose of this model is to determine the proportion of parasitoids on each patch at the SDIFD. Figure 2 shows the proportion of parasitoids on the host patch as a function of the total number of parasitoids, N , for different values of the interference coefficient, m . The results depicted correspond to constant and low mortality conditions (i.e., that of Figure 1b).

Prediction 4. When competition is strong (a high number of competitors or strong interference), all the parasitoids will be on the host patch. As a consequence of competition, the proba-

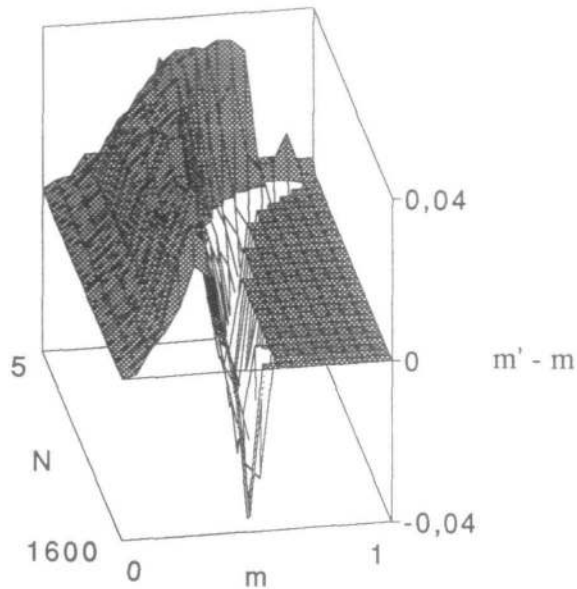


Figure 3
Effect of optimal time sharing between host and food searching on the stability of the host-parasitoid system. This effect is revealed by difference between the overall interference coefficient (m') and the interference coefficient on the host patch and food patch (m). Positive values of $m' - m$ indicate a stabilizing effect, negative values indicate a destabilizing effect. Constant and low mortality risk: $\mu = 0.00005$.

bility of finding food gets so low that all the parasitoids will prefer searching for hosts (see Prediction 1). There will be a certain proportion of parasitoids on the food patch only if both the total density of parasitoids and the interference coefficient are moderate or low. When the proportion of parasitoids on the host patch is not 1, this proportion is very little affected by changes in N or m . This is so because changes in the time spent feeding will result in similar changes in the time on the host patch that can be sustained by the energy reserves, and the proportion of time spent on each patch will be little affected. However, the “cliff” on the surface of the proportion of the parasitoids on the host patch is surrounded by a small depression. This corresponds to a situation where the combination of parasitoid density and the interference coefficient makes competition moderate. In these conditions parasitoids spend more time searching for food than when it is easily found (see Prediction 1).

As can be seen, the distribution of the parasitoids at the SDIFD can be easily deduced from the predictions for the behavior of isolated parasitoids. For this reason we present only one type of mortality condition.

Population stability

Classical host-parasitoid theory suggests that stability is promoted by the decrease in parasitoid efficiency as their number increases (Hassell and May, 1973). In our model two processes might contribute to decrease mean efficiency: classical interference and the fact that an increasing proportion of parasitoids may visit the food patch. Figure 3 shows the difference between the measured, overall interference coefficient (m' ; see Appendix B) and the actual value that controls food searching in the model (m). This difference shows the influence of the introduction of optimal time sharing between host and food searching on the stability of the system. Positive values indicate a stabilizing effect, negative ones indicate the opposite effect.

Figure 3 corresponds to the situation of Figure 2, and indicates that in almost all the situations where at the SDIFD there are some parasitoids on the food patch, there is a slight stabilizing effect. For a given m value, an increase in the number of parasitoids reduces the efficiency of each parasitoid not only because of the interference process, but also because it will affect the proportion of parasitoids on the host patch. This is especially pronounced for the conditions of intermediate competition, where an increase in the number of parasitoids leads to a decrease in the proportion of them on the host patch (Prediction 4). When all the parasitoids are on the host patch, the situation is similar to the classical one, and we have $m = m'$.

DISCUSSION

In this article, we study the optimal choice between searching for food and searching for hosts in a parasitoid. This choice determines the proportion of time spent on reproduction sites and the expected lifespan. Fitness results from the combination of these two factors.

Our results suggest that this behavioral choice should be strongly dependent on the state of the animal. They also suggest that there are conditions of relatively low food availability in which searching for food (even if it is present) could be a nonadaptive behavior. In the same way, in conditions of high food availability, parasitoids might seldom search for food. This counterintuitive prediction does not hold when instantaneous mortality is dependent on the nutritional status of the animal. In this case there is an additional payoff to being well fed, and animals should tend to maintain high energy reserves.

The SDIFD model has shown that the choice between searching for hosts and searching for food might have a stabilizing influence on the dynamics of the host-parasitoid system, because it affects the number of parasitoids that is at any time searching for hosts. This is so because, in our model, the proportion of animals on each patch depends on the total density. A similar situation was studied theoretically by Moody and Houston (1995) and in the field by Gillis and Kramer (1987).

Under natural conditions, parasitoid and host numbers fluctuate within each generation, as does food abundance. Our model assumes that parasitoid and host numbers, and food availability, are constant. The results most probably are applicable for small variations in these values, but it is not clear yet how they would be affected by severe fluctuations. Including host depletion is one of the first extensions we plan to include in our models. Another limitation of our approach is that it does not include the effect of optimal food consumption on parasitoid death rates.

We have shown that when a single behavioral alternative to reproduction is introduced, optimal foraging can stabilize the system. Other activities, such as preening, resting, or information acquisition, should be incorporated when modeling parasitoid behavior because they compete for time with reproduction. Optimal decisions on these activities could play a role in the stability that classical models fail to explain.

Some experimental work supports our results on the behavior of isolated parasitoids. Roitberg et al. (1992) showed that the *Drosophila* parasitoid *Leptopilina heterotoma* spends much more time on host patches when expected lifespan is short. This observation coincides with the predictions of both their model and ours (Prediction 2), but food consumption has not been included in their experiments. Wäckers (1994) showed that the parasitoid *Cotesia rubecula* can choose between the scents of its host and that of its food, and that it prefers the latter when starving. This result supports our pre-

diction that the energy reserves of the parasitoid should strongly influence its decisions.

Our predictions should lead to other experiments studying behavioral choices, incorporating both the hunger state of the parasitoids and the food abundance in the environment, and if possible, the influence of competition among parasitoids.

APPENDIX A

On the food patch of surface S , A discrete food sources are randomly distributed. These food sources provide an unlimited food supply, and any number of parasitoids can feed on them. Food sources are not immediately found.

The probability of finding a food source in a given time period is a function of food abundance, A , the number of competitors searching for food, N_1 , and the interference coefficient, m (Hassell and Varley 1969).

When searching for food, each parasitoid covers an area $a = QN_1^{-m}$ per time unit (Hassell and Varley, 1969; Royama, 1971). To find food the parasitoid must visit an area that contains at least a food source. The probability that, during a unit of time, the parasitoid will not find a given food source is $(1 - a/S)$. For a given parasitoid, the probability of not finding any food source is $(1 - a/S)^A$. The probability that a parasitoid will find at least one food source during a time unit on the patch is then: $\lambda = 1 - (1 - a/S)^A$.

APPENDIX B

In the Hassell and Varley (1969) model, the survival probability of each host during a foraging period is $s = \exp(-QN^{-m})$, where m is the interference coefficient and N is the number of parasitoids. In our model,

$$s = \exp(-Q(Nx)^{1-m_h}) \quad (\text{B1})$$

because there are only Nx parasitoids on the host patch, and m_h is the interference coefficient on this patch.

In discrete time models for host-parasitoid systems the overall area of discovery, a' , can be estimated as

$$a' = -N^{-1} \ln(s) \quad (\text{B2})$$

(Hassell and Varley, 1969), and m' (the observed interference coefficient) is estimated as

$$m' = -d \ln a' / d \ln N \quad (\text{B3})$$

(Comins and Hassell, 1979).

Provided $0 < m' < 1$, optimal time sharing between host searching and food searching would have a stabilizing effect if $m' - m_h > 0$, and a destabilizing effect otherwise (Hassell and May, 1973). We have shown that the proportion x of parasitoids on the host patch is independent of m_h . For this reason (from Equations B1, B2, and B3):

$$m' - m_h = -(1 - m_h) d \ln x / d \ln N.$$

Since $0 < m_h < 1$, this shows that the sign of the difference $m' - m_h$ is independent of the value of m_h . For simplicity we have still assumed in Figure 3 the same value for both interference coefficients. Relaxing this assumption does not change the qualitative behavior of the model.

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