Host-feeding strategies of parasitoid wasps

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Summary

Three models of the evolution of host-feeding behaviour in parasitoid wasps are developed. The first assumes that the wasp host feeds purely to obtain resources to mature eggs (limited resource model) while the second assumes that host feeding provides energy for maintenance (pro-ovigenic model). The third model assumes that host feeding provides resources for both maintenance and egg maturation (resource pool model). Two variants of the third model are examined: the first assumes that the risk of mortality is constant and state-independent, the second that resource-depleted individuals suffer a higher risk of mortality. The models are analysed using a combination of stochastic dynamic programming and analytical techniques. The models make different predictions about the relationships between the probability of host feeding and egg load and host density. The available experimental evidence best supports the resource pool model.

Keywords: host feeding; parasitoids; dynamic programming

Introduction

Parasitoid wasps lay their eggs on or in the bodies of other insects which act as hosts for their developing larvae. The biology of these insects has attracted considerable attention because of their importance in controlling the populations of injurious pests. In recent years, parasitoid wasps have also proved themselves to be valuable experimental models with which to investigate the evolution of reproductive strategies (Godfray, 1993). During oviposition, the female wasp must make a series of well-defined decisions that have major consequences for the fitness of her offspring. On discovering a host, the wasp must decide whether it is of sufficient quality to be used as an oviposition site, a decision that has much in common with diet choice in foraging theory (van Alphen and Vet, 1986; Charnov and Stephens, 1988). If a host is accepted for oviposition, the female must decide how many eggs to lay (Charnov and Skinner, 1984, 1985, 1988; Godfray, 1987a,b; Godfray *et al.*, 1991) and the ratio of sons and daughters (Charnov, 1982; Waage, 1986; King, 1987; Werren, 1987). The female may also have to decide whether to lay eggs on a host that has previously been attacked by another parasitoid (van Alphen and Visser, 1990). Finally, where hosts have a patchy distribution in the environment, searching females must decide when to leave one patch and to search for another (van Alphen and Vet, 1986). These problems have stimulated much theoretical and empirical research using a variety of different species of parasitoid wasps (Godfray, 1993).

Many species of parasitoid wasps use hosts for food as well as for oviposition (Jervis and Kidd, 1986). Females of some species feed from and lay eggs on the same host individual while females of other species must decide whether to use a host for food or for oviposition. In using a host for food, the wasp is foregoing an immediate increment in her lifetime reproductive success. However, she may obtain limiting nutrients that can be used to mature more eggs or energy that

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may enable her to search for more hosts. There is thus a trade-off between the loss of an immediate opportunity to reproduce and greater future reproductive success. The form of the trade-off will be influenced by the parasitoid's metabolic physiology, by the dynamics of egg production, as well as by different aspects of the wasp's environment such as host availability and host quality.

Our aim in this paper is to analyse a series of simple models of host-feeding behaviour by parasitoid wasps based on different assumptions about egg dynamics and the value of food for the parasitoid. We concentrate on species that must chose whether to use a host for food or oviposition. We attempt to make simple predictions about the optimal host feeding strategy of different types of parasitoid and how the fraction of hosts used for food is influenced by host density.

Biological assumptions

Parasitoids might require to feed from hosts to keep themselves alive or to mature eggs that can be used in oviposition. Our first model, which we call the limiting resource model, assumes that parasitoids host feed only to obtain resources to mature eggs. We suppose that the parasitoid obtains energy from other sources such as flowers or honeydew or by metabolizing fat stores laid down while a larva. This situation can be compared with a model where we assume that the wasp is born with a fixed complement of eggs and uses food obtained from the host purely for daily maintenance. We call this the pro-ovigenic model, the term used to described parasitoids born with mature eggs (as opposed to synovigenic species that mature eggs throughout their life). As will be discussed below, there is quite good evidence that pro-ovigenic parasitoids seldom host feed. However, this model is useful because it provides a stark comparison with the limiting resource model and because it is a limiting case of our third model. In the resource pool model we assume that the wasp draws upon a common pool of resources for its daily requirement of energy and for the production of eggs. Here, the wasp's physiological state is described by a single variable and we assume that there are no constraints to the rate of egg maturation. We explore two submodels of the resource pool model: constant mortality and state-dependent mortality. In the first case we assume that the risks of mortality are not affected by the energy reserves of the insect, while in the second case wasps with low energy reserves are at greater risk of mortality.

There are a number of factors that might influence host feeding strategy that we do not consider. The first very important assumption is that all hosts are of equal quality as oviposition sites for the wasp. This will very often be untrue and an obvious extension of the work described here is to relax this assumption (Chan, 1991, in preparation; Kidd and Jervis, 1991a; Rosenheim and Rosen, 1992). A second simplification is that we assume wasps encounter hosts at a constant rate. In other words we assume parasitoids search randomly for hosts that are themselves distributed randomly in the environment. This assumption will be violated if hosts tend to be distributed in patches (Houston *et al.*, 1991). Finally, we assume that handling time is relatively short compared with the time required to locate hosts and, hence, can be ignored and that egg maturation occurs sufficiently fast that it can be treated as instantaneous.

Modelling strategy

We seek the strategy that maximizes the wasp's lifetime reproductive success subject to the constraints embodied in the different models. In the majority of cases the optimal decision taken by the wasp depends on the values of its state variables: its energy reserves or egg load. To obtain the optimal decision it is usually necessary to employ a dynamic optimization technique and here

Table 1. Glossary of symbols used in this paper

Parameter	Symbol
Time	t, τ
End of the season (time horizon)	T
Energy reserves	x
Critical energy threshold below which wasp host feeds	x_c
Energy reserves at birth	x_i
Daily energy requirements (defined as 1 unit)	$\delta = 1$
Energy obtained from host feeding	α
Energy required to mature an egg	β
Encounter rate with hosts	λ
Mortality rate (from causes other than starvation)	μ
Mortality rate (when assuming state-dependent mortality) where m is a constant and μ and x are defined as above	$\mu (1+m/x)$
Probability of surviving one time unit (1−integrated mortality)	$p(x)$
Number of eggs (two-state models)	y
Future fitness at time t with energy reserves x (one-state model)	$W(t,x)$
Future fitness at time t with energy reserves x and egg load y (two-state model)	$W(t,x,y)$
Fitness at birth	W_i
Fitness when energy reserves $= x_c$ (deterministic model)	W_c

we use stochastic dynamic programming (Houston *et al.*, 1988; Mangel and Clark, 1988; see Iwasa *et al.*, 1984; Mangel, 1987, 1989a,b for applications to invertebrate reproductive strategies). The models predict that the wasp host feeds when its energy reserves fall below a certain threshold value. The value of this threshold is fixed – providing the wasp is neither close to death nor near to running out of eggs. We refer to this fixed value as the stationary threshold. In some cases it is possible to calculate analytically the value of this threshold using relatively simple deterministic models. These models often allow greater insight into the processes influencing fitness than dynamic programming.

The parameters used in the models are summarized and defined in Table 1. Stochastic dynamic programming requires that a time horizon is defined beyond which the animal can obtain no further increase in fitness. Here we suppose there is a finite end to the season when either all parasitoids die or there are no longer hosts available for parasitism. This is a less restrictive assumption than first appears as the time horizon can be placed so far in the future that the probability of a parasitoid surviving until the end of the season is very low. A brief introduction to stochastic dynamic programming and a summary of the recursion equations used in this study are given in Appendix 1.

Results and discussion

Limiting resource model

This model is by far the simplest to analyse and the optimal strategy can be written down without algebraic modelling. The wasp should use hosts for oviposition until it runs out of fertile eggs when it should host feed to mature new eggs. There is no advantage in maturing extra eggs until they are required by the wasp.

This model predicts that the proportion of hosts used for feeding should be constant over most

rates of host encounter (Fig. 1) and equal to $1/(1+\alpha/\beta)$ where α/β is the number of eggs that can be matured after feeding on one host (α/β are the resources obtained from feeding on a host (α) divided by the resources required to mature an egg (β)). If hosts are rare and some wasps fail to encounter enough hosts before death to require host feeding, then a greater proportion of hosts are used for oviposition.

The most unrealistic aspect of this model is the assumption that egg maturation is essentially instantaneous. If this assumption is relaxed (a technically difficult problem), we conjecture that the wasp will host feed in advance of running out of eggs in order to ensure a continuing supply of eggs for oviposition. Another factor that may lead to host feeding before the complete exhaustion of egg reserves is variation in host quality. A wasp encountering a host that is of poor quality as an oviposition site may use it for host feeding to avoid the risk of wasting a good quality host when it runs out of eggs and is forced to host feed.

Pro-ovigenic model

This model requires two state variables, egg load and energy reserves. We explore the model by defining a canonical parameter set and calculating the optimal strategy. We then vary different parameters to see how they affect optimal host feeding behaviour.

Consider a wasp that uses one unit of energy for every unit of time ($\delta=1$). To investigate the factors that influence host feeding we begin by assuming that it is born with an energy level of 30 units (x_i) and that it obtains 30 units of energy every time it host feeds (α). If the wasp runs out of energy reserves ($x=0$), it dies. We further assume that it suffers an instantaneous risk of mortality of 0.0125 (μ) and that its instantaneous rate of host encounter is 0.2 (λ). If the wasp never host fed it could not survive beyond 30 time units and its maximum achievable fitness (number of hosts attacked) is $0.2(30)=6$ (the mean attained fitness, taking into account wasps that die before running out of reserves, can be calculated using the methods in Appendix 2 and is 5.00). If parasitoid starvation never occurs, the wasp would on average live $(1/0.015)=80$ time units during
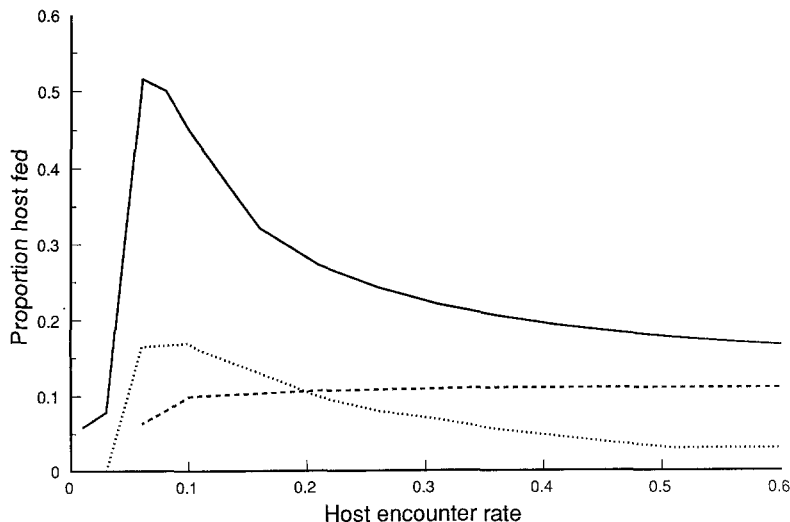

Figure 1. The proportion of hosts used for food as a function of host encounter rate (λ). (a) Dashed line, limiting resource model; (b) dotted line, pro-ovigenic model; (c) solid line, resource pool model with constant mortality. The parameters are those of the canonical parameter set described in the text except in (a) $\alpha = 8$ and $\beta = 1$ and in (b) $\alpha = 30$ and $\beta = 4$.

which time it would expect to parasitise 16 hosts. Host feeding increases the wasps expected fitness beyond 5 and a measure of its success in offsetting starvation is the degree to which it approaches 16.

Figure 2 shows the optimal host-feeding threshold as a function of egg load and time in the season. The model predicts a stationary threshold ($x_c = 21$) except when the animal is near to running out of eggs or near to the end of the season. In both these circumstances, the wasp host
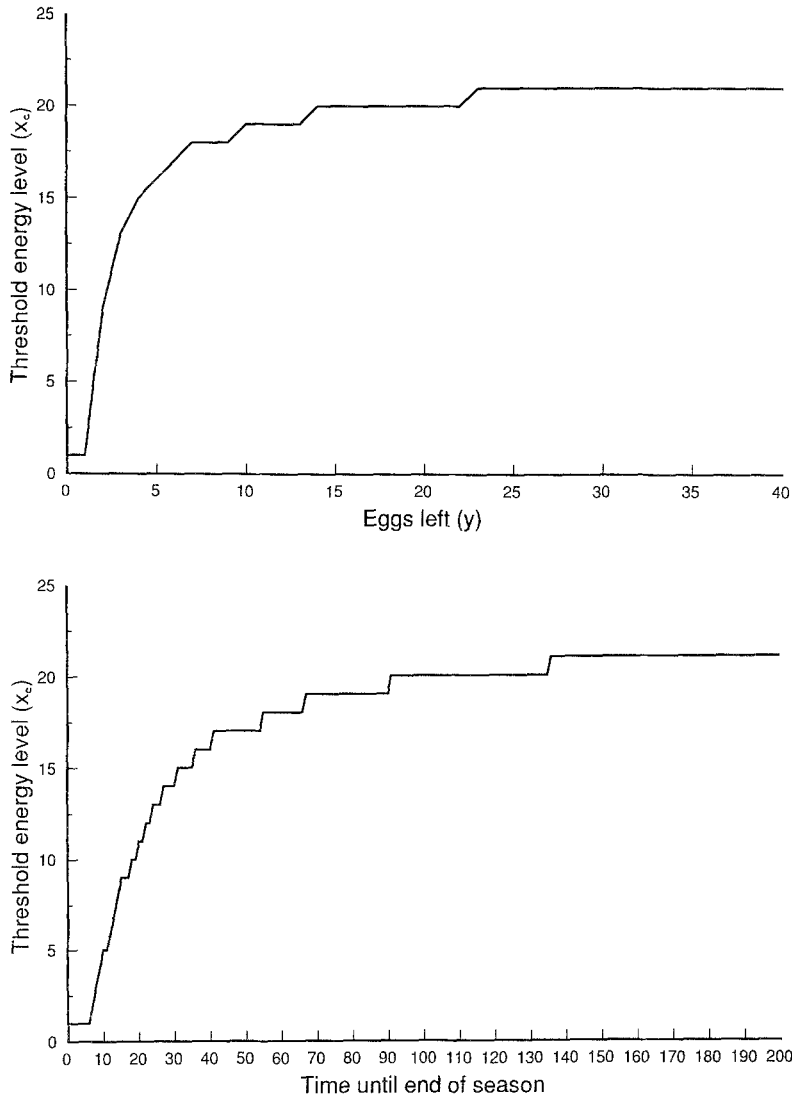

Figure 2. The threshold energy reserves at which the wasp switches from parasitism to host feeding predicted by the dynamic programming version of the pro-ovigenic model. The parameters used are those in the canonical parameter set described in the text. Wasps that have both large reserves of eggs and are not approaching the end of the season should host feed when their energy threshold drops below 21 (the stationary threshold). Wasps approaching the end of the season (a) and wasps with low egg reserves (b) switch to host feeding at lower threshold energy reserves.

feeds at a lower threshold. The function of host feeding it to prolong reproductive life and this is of less importance when the wasp is either close to certain death or near egg exhaustion.

The value of the stationary threshold can be calculated using a deterministic model developed in Appendix 2. For the canonical parameter set, the stationary threshold is $x_c = 25.0$ and the fitness of the wasp adopting this strategy is $W_i{=}13.0$ (compare this with the expected fitness of the wasp in the absence of any risk of starvation which is 16). By choosing a threshold x_c, the wasp is accepting a chance of dying from starvation of $e^{-\lambda x_c}{=}0.0067$, a very low probability. The relationship between fitness and the position of the threshold is shown in Fig. 3. The fitness curve is asymmetric about the optimum: there are greater penalties in adopting a lower threshold than there are in adopting a higher threshold. Note, the stationary threshold predicted by the deterministic model ($x_c{=}25$) is not identical to that predicted by the dynamic programming model ($x_c{=}21$). The reason for this discrepancy is that the dynamic programming model sums over discrete time steps (in our case of one time unit) while the deterministic model integrates over continuous time. The two models with the same parameter sets are thus only approximately comparable.

The position of the optimum threshold does not depend on the resources with which the wasp is born (x_i) and the amount of energy a wasp gains from host feeding has very little effect on the threshold (changing α from 10 to 1000 raises x_c from 21 to 26). The two other parameters, encounter rate (λ) and mortality (μ), have larger effects. The longer the wasp lives (the smaller μ), the greater the threshold at which the insect host feeds. A long-lived wasp has most to loose from succumbing to starvation and will be selected to raise its threshold to avoid this possibility. The effect of encounter rate is more complicated (Fig. 4): the highest thresholds are found at intermediate encounter rates. When encounter rate is low the wasp's future reproductive success is relatively small and, thus, the advantages of sacrificing a current opportunity to oviposit in order to offset a small risk of starvation is reduced. However, when encounter rate is high and expected future reproductive success also high, the wasp can afford to lower its threshold because of the much greater probability of locating hosts and consequent reduction in the risk of starvation.

The relationship between host density (as reflected by encounter rate) and the proportion of hosts used for host feeding is domed (Fig. 1). At very low densities no host feeding is predicted
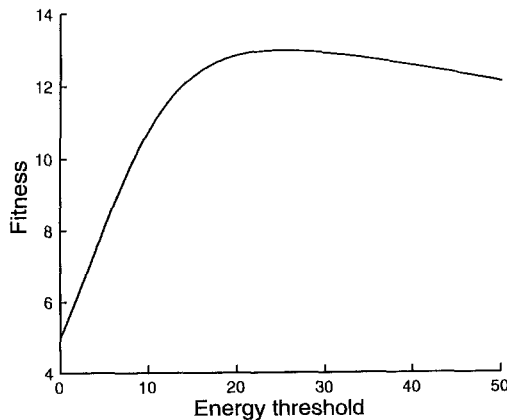

Figure 3. The fitness of a wasp as a function of the energy threshold at which the insect switches from parasitism to host feeding. Results from the deterministic version of the pro-ovigenic model using the canonical parameter set described in the text.

(see above) and all hosts are used for oviposition; above a threshold encounter rate, the wasp begins to host feed. Initially, a high proportion of hosts are used for maintenance as the wasp discovers hosts only infrequently but then as encounter rate rises the fraction required for food gradually decreases.

Resource pool model

Constant mortality. We now assume that the animal uses its energy reserves both for general maintenance and to mature eggs. Specifically we assume each egg requires the expenditure of β units of energy but that otherwise the same assumptions apply as in the last model. Dynamic programming models again show that the optimal strategy is to parasitize hosts as long as the energy reserves are greater than a critical threshold which remains nearly constant except towards the very end of the season when parasitism is favoured over host feeding even at low levels of the energy reserves. There is one other circumstance in which parasitism is always favoured: when host encounter rates are so low that even if the wasp host feeds there is a high probability of death before another host is encountered.

The position of the stationary threshold can be calculated using the deterministic model in Appendix 2. Consider again the canonical parameter set defined in the discussion of the pro-ovigenic model. With these parameter values the stationary threshold was $x_c=25.0$ and expected lifetime fitness $W_i=13$. Incorporating egg maturation costs leads to (1) an increase in the host feeding threshold (for example, $\beta=4$, $x_c=27.3$; $\beta=16$, $x_c=30$) and (2) a decrease in lifetime reproductive success ($\beta=4$, $W_i=11.4$; $\beta=16$, $W_i=8.5$). The response to changes in other parameters was qualitatively similar to those observed in the pro-ovigenic model and the relationship between host density (as reflected by encounter rate) and the proportion of hosts used for host feeding is again domed (Fig. 1).

State-dependent mortality. We now assume that the risk of mortality is not independent of state but is greater when the wasp has low energy reserves. Specifically we assume that the instantaneous rate of mortality equals $\mu(1 +m/x)$ where μ is the background mortality independent of energy reserves (x) and m scales the increasing risk of death as energy reserves decline. We were unable to obtain any analytical results for this model. Dynamic programming
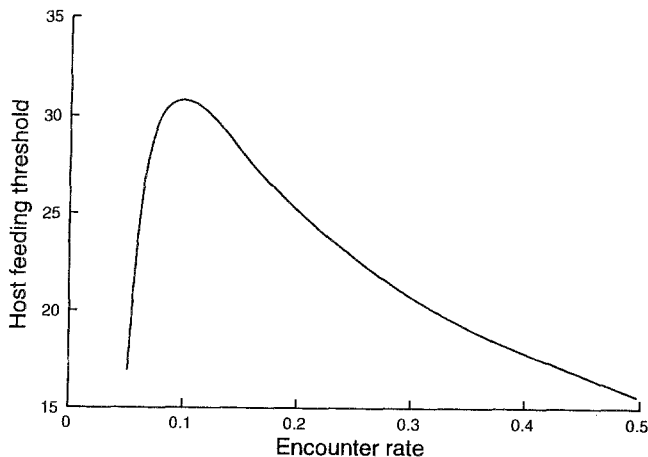

Figure 4. The relationship between the energy threshold at which the wasp switches from parasitism to host feeding and the encounter rate with hosts. Results from the deterministic version of the pro-ovigenic model using the canonical parameter set described in the text.

predicts qualitatively similar results to the constant mortality model with one major difference: there is a far greater tendency for wasps with low energy reserves to switch from host feeding to parasitism, an effect that increases as m gets greater. This occurs because when hosts are rare, wasps with low energy reserves (and, hence, an increased risk of mortality) are more likely to die without encountering another host in comparison with wasps which experience no increased mortality at low energy reserves. This effect can be ameliorated if host feeding provides a large increment in energy reserves (high α) so that the probability of death before the discovery of another host is low.

General discussion and conclusions

The evolution of host feeding strategies have been discussed by Jervis and Kidd (1986; Kidd and Jarvis, 1989, 1991a) and Houston *et al.* (1991). Jervis and Kidd assumed that the function of host feeding is to provide both limiting resources for egg maturation and energy for maintenance (as in our resource pool model). Their model also incorporates egg resorption under conditions of starvation. They do not explore state-dependent strategies or attempt to calculate the optimal strategy, but instead compare the performance of different fixed strategies by computer simulation. Their conclusions are thus strongly influenced by the strategies chosen for exploration. They conclude that the proportion of hosts parasitized should increase with host density, a prediction made by our models. A domed relationship between encounter rate and the energy threshold was not noted however. They have also used their modelling framework to explore the relative benefits of concurrent and non-current host feeding (that is whether to feed and oviposit on the same host) and to consider whether wasps should oviposit or feed on hosts of different size. Houston *et al.* (1991) studied a pro-ovigenic model using dynamic programming. Their interest was in exploring the influence of the variance in host encounter rate on the threshold energy reserves at which a wasp is predicted to switch from parasitism to host feeding. Increased variability selected for a higher threshold for host feeding in order to avoid the risk of starvation 'from a run of bad luck'. Houston *et al.* (1991) point out the parallels between this result and other studies of foraging and reproductive strategies in variable environments. Population dynamic consequences of host feeding have been studied by Jervis and Kidd (1986; Kidd and Jervis, 1989, 1991b), Yano (1987) and Murdoch *et al.* (1992).

The limiting resource model predicts that a constant fraction of hosts should be used for food at all but the lowest host densities while the pro-ovigenic model predicts that the probability of host feeding should be independent of egg load. The resource pool model predicts that a greater proportion of hosts should be used for oviposition at high host densities and that host feeding should occur most often when egg reserves are low. The limited amount of evidence about the physiological function of host feeding is reviewed by Jervis and Kidd (1986). Of 150 species of parasitoid in which host feeding had been described, all were either synovigenic (matured eggs throughout life) or had an unknown pattern of egg maturation – none were reported to be pro-ovigenic. Some wasps that are prevented from host feeding show a reduction in fecundity or an inability to oviposit (Leius, 1961; Sandlan, 1979; Jervis and Kidd, 1986; van Lenteren *et al.*, 1987; Wardle and Borden, 1990). There is thus little support for a pure pro-ovigenic model. Several studies have found that the fraction of hosts used for food decreases at high host densities (DeBach, 1943; Collins *et al.*, 1981; Löhr *et al.*, 1988). This pattern is predicted by the resource pool model, but not by the limited resource model. Recently, Rosenheim and Rosen (1992) have tested the hypothesis that when the assumptions of the limiting resource model are met, wasps should host feed when their egg supplies are low. Experiments with the aphelinid *Aphytis lingnanensis* did not support this hypothesis. We suggest that *A.lingnanensis* may also host feed to

obtain energy for its daily maintenance requirements (i.e. that the resource pool model is more appropriate) and that variation in the energy reserves of the wasps obscured the expected relationship with egg reserves.

To conclude, different assumptions about host feeding in parasitoids lead to structurally different models of the evolution of host feeding. The predictions of the different models are sufficiently distinct that they can be used to discriminate between the competing hypotheses. The data available to date point towards the resource pool model as the most accurate description of the selection pressures and constraints experienced by most host-feeding parasitoids. However, in interpreting experimental data, the simplified nature of our models and the many assumptions we make need to be borne in mind. Future theoretical work should examine the natural time delays in the conversion of food to utilizable energy and mature eggs, the whole resource budget of the insect including egg resorption and variance in the quality of hosts as feeding and oviposition sites. Theoretical and experimental studies of host feeding are of obvious interest to parasitoid behavioural ecologists; we also believe that parasitoid host feeding is an ideal model system with which to extend the classical behavioural ecological research programme to strategy sets that involve physiological as well as behavioural decisions.

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Appendix 1: stochastic dynamic programming

Dynamic programming is a means of calculating an optimal strategy that may be influenced by dynamic variables such as time or the internal state of the animal. It assumes that the future fitness of an animal in a particular state at any point in time is influenced by present and future decisions, but not by decisions made in the past (except in how they influence the current values of the state variables). The overall optimum set of behaviours is found by calculating the optimal decision at successively earlier time steps starting at a time horizon. In this study we assume the time horizon is the end of the season – a time when either all parasitoids die or there are no hosts remaining to be parasitized.

In the resource pool model, the state of the animal can be described by a single variable, energy reserves (x). At any time prior to the time horizon the optimal decision is found by choosing the reproductive strategy that maximizes fitness $W(t,x)$,

$$W(t,x) = (1 - \lambda)p(x)W(t + 1, x - 1) + \lambda \max \{1 + p(x)W(t + 1, x - 1 - \beta),$$
$$p(x)W(t + 1, x - 1 + \alpha)\}$$

where the symbols are defined in Table 1. The first term on the right-hand of the equation reflects what happens if the wasp fails to find a host in the next time unit (probability $1-\lambda$); the wasp survives with probability $p(x)$ and its future fitness is $W(t+1,x-1)$ because it is one time unit older and has expended one unit of energy for maintenance. The second term describes what happens when a host is encountered (probability λ). The wasp either host feeds or oviposits depending on which behaviour leads to the higher fitness. If it parasitizes the host its fitness immediately increases by one and, providing it survives (probability $p(x)$), its future fitness is $W(t+1, x-1-\beta)$ because it is one time unit older and has expended 1 unit of energy on maintenance and β units on the egg. If it host feeds it does not get an immediate increment in fitness but its future reproductive success if it survives until the next time unit is $W(t+1, x-1+\alpha)$ where α is the energy obtained from host feeding. The model is solved iteratively working back from the time horizon $(t=T)$ where $W(T,x)=0$.

In the pro-ovigenic model, fitness $(W(t,x,y))$ depends on two state variables, energy reserves (x) and egg load (y). The recursion equations can be constructed in a similar way to the single state models and are

$$W(t,x,y) = (1 - \lambda)e^{-\mu}W(t + 1, x - 1, y) + \lambda \max \{1 + e^{-\mu}W(t + 1, x - 1, y - 1),$$
$$e^{-\mu}W(t + 1, x - 1 + \alpha, y)\}$$

(In this model, the risk of mortality is constant and state independent so $p(x)$ is replaced by $e^{-\mu}$.)

Appendix 2: deterministic model

Here we develop a deterministic version of the pro-ovigenic model applicable to situations when the wasp is neither near to running out of eggs nor approaching the end of the season. We define the energy required for general maintenance to be 1 unit of energy per unit of time ($\delta = 1$) and scale other time and energy variables accordingly. Note, this scaling of energy requirements allows us to measure time and energy using the same units. Thus, an animal with x units of energy will starve, in the absence of host feeding, after x units of time.

The fitness of a wasp at birth, W_i is

$$W_i = \text{(number of hosts parasitized by wasps dying before energy reserves fall to } x_c) +$$
$$\text{(probability of surviving to } x_c) \text{ (Hosts attacked before reaching } x_c + W_c)$$

where W_c is the future fitness of a wasp with energy reserves at the critical level x_c. The first term in this equation can be decomposed into

$$\int_{t=0}^{x_i-x_c} \text{(probability dying at time } t \text{ with energy reserves } x: x>x_c)$$
$$\text{(Hosts attacked before death) d}t$$
$$\rightarrow \int_{t=0}^{x_i-x_c} [\mu e^{-\mu t}][\lambda t]\text{d}t$$

The probability of surviving to x_c is $e^{-\mu(x_i-x_c)}$ during which time the wasp will have on average attacked $(x_i-x_c)\lambda$ hosts. Thus,

$$W_i = \int_{t=0}^{x_i-x_c} [\mu e^{-\mu t}][\lambda t]\text{d}t + e^{-\mu(x_i-x_c)}(\lambda(x_i - x_c) + W_c) \tag{1}$$

Consider now the fitness of a wasp with energy reserves x_c. The wasp will die unless it finds a

host in the next x_c time units. If it finds a host after τ time units, its energy reserves increase to $x_c + \alpha - \tau$. Thus,

$$W_c = \int_{\tau=0}^{x_c} \text{(probability of finding a host at time } \tau) \times$$

{(number of hosts discovered by wasps who die before energy reserves again reach x_c)

+ (probability of surviving to x_c)(hosts attacked before reaching x_c + $\mathbf{W_c}$)} dτ

Proceeding as before

$$W_c = \int_{\tau=0}^{x_c} \lambda e^{-\tau(\mu+\lambda)} \left\{ \int_{t=0}^{\alpha-\tau} \mu e^{-\mu t}\lambda t \, dt + e^{-\mu(\alpha-\tau)}(\lambda(\alpha - \tau) + W_c) \right\} d\tau \qquad (2)$$

This equation can be solved and an explicit (although not particularly transparent) expression for W_c obtained. If this is substituted in Equation 1, the optimal threshold x_c can be found by finding x_c that satisfies $\partial W_i/\partial x_c = 0$. We performed these calculation using a symbolic algebra programme (*Mathematica*) and obtained values of x_c from the resultant transcendental expression using a numerical method.

A deterministic version of the resource pool model with constant mortality can also be constructed. Recall that in the last model, time and the wasp's energy reserves could be measured in the same units. If energy is required for eggs as well as daily maintenance then the wasp will use up its energy reserves at a greater rate. More specifically, the time taken for an animals energy reserves to drop by x units is $x/(1+\lambda\beta)$ where $\lambda\beta$ is the amount of energy required per unit time to mature the eggs required for oviposition (see Charnov and Skinner (1988) and Charnov and Stephens (1988) for similar approaches in other contexts). Equations 1 and 2 now become

$$W_i = \int_{t=0}^{(x_i-x_c)/(1+\lambda\beta)} [\mu e^{-\mu t}][\lambda t]dt + e^{-\mu(x_i-x_c)/(1+\lambda\beta)} \left(\frac{\lambda(x_i - x_c)}{1 + \lambda\beta} + W_c \right) \qquad (3)$$

$$W_c = \int_{\tau=0}^{x_c} \lambda e^{-\tau(\mu+\lambda)} \left\{ \int_{t=0}^{(\alpha-\tau)/(1+\lambda\beta)} \mu e^{-\mu t}\lambda t \, dt + e^{-\mu(\alpha-\tau)/(1+\lambda\beta)} \left(\frac{\lambda(\alpha - \tau)}{1 + \lambda\beta} + W_c \right) \right\} d\tau \qquad (4)$$

which were solved in the same way as Equations 1 and 2. Extension of this approach to state-dependent mortality gives rise to non-integrateable functions.