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Parasitoids flip a coin before deciding to superparasitize

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Summary

1. Host acceptance decision in parasitic wasps depends strongly on the parasitism status of the encountered host. In solitary species, a host allows the development of only a single parasitic larva, and then any oviposition in an already parasitized host leads to larval competition and to potential loss of offspring. The ability of parasitoids to discriminate between parasitized and healthy hosts is well documented. Despite this, parasitized hosts are still accepted by the foraging wasps, an occurrence termed superparasitism.

2. In the last decades, theoretical studies have suggested that under certain circumstances superparasitism can be optimal. Generally, the superparasitism theory predicts that the optimal host acceptance decision should follow a zero-one rule: in response to both environmental and physiological state characteristics, a given female should switch from acceptance to rejection of parasitized hosts.

3. However, some experiments have shown that parasitoids may decide to accept parasitized hosts with an intermediate probability.

4. A model was developed in order to explain this partial preference in parasitoids.

5. More generally, the present study demonstrates that when the consequences of one decision cannot be predicted perfectly, the optimal decision rules could be stochastic rather than deterministic. Accordingly, behavioural stochasticity need not necessarily result from errors in decision-making or from an incapacity to assess the actual environmental state but could instead have evolved as the optimal response to the uncertainty of future environmental state.

Key words: host selection, partial preferences, solitary parasitoids, stochastic decision.

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Introduction

Host acceptance decisions in parasitic wasps depend strongly on the characteristics of the hosts (Visser, van Alphen & Hemerik 1992); in particular, whether or not the encountered host has already been parasitized (Ueno 1994). In solitary parasitoids, only one individual can develop in a host and supernumerary individuals are eliminated through intrahost competition (Hubbard *et al*. 1987). Generally, and particularly in endoparasitoids, the oldest parasite most frequently eliminates all the younger competitors (Mangel 1989). Thus, a parasitized host is of lower quality for solitary parasitic wasps (Nelson & Roitberg 1995). In a wide range of species, host-marking chemicals allow the foragers to recognize previously parasitized hosts and therefore avoid wasting eggs and time on hosts in which their progeny will have a low probability of survival. In spite of this host discrimination ability, superparasitism (i.e. oviposition in a host already parasitized by the same species) has often been observed, both in the field and in the laboratory (van Alphen & Visser 1990).

The study of superparasitism has occupied a central place in parasitoid biology throughout the last decades (Godfray 1994). First considered as a behavioural error (van Lenteren 1981), numerous theoretical studies have explored the conditions under which superparasitism

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would be an optimal strategy (Weisser & Houston 1993). Among these conditions both environmental characteristics, such as host availability (Weisser & Houston 1993), number of competitors (Visser *et al.* 1992), mortality risk (Iwasa, Susuki & Matsuda 1984) and the physiological state of the forager, such as egg load (Mangel 1989), energy reserves (Mangel 1987; Sirot & Bernstein 1997) and life expectancy (Sirot, Ploye & Bernstein 1997), have been shown to influence strongly the decision to superparasitize. Foraging models based on maximizing the instantaneous rate of fitness increase generally predict that it exists a critical environmental threshold beyond which wasps should always accept parasitized hosts and above which they should always reject them (Harvey, Marris & Hubbard 1987; Hubbard *et al.* 1987; Charnov & Stephens 1988; van Alphen & Visser 1990). Alternatively, models using dynamic programming predict that females will switch from rejection to acceptance after reaching a particular state (Mangel 1999). Thus, the superparasitism theory suggests that the optimal host acceptance decision should follow a zero-one rule depending on environmental context and physiological state of a female.

However, some experimental works have shown that parasitic wasps are probably not using this deterministic decision rule but may decide to accept parasitized hosts with an intermediate probability (van Dijken *et al.* 1986; Sirot *et al.* 1997). Different explanations have been proposed for the existence of this partial preference in parasitoids. First, partial superparasitism may arise if females have an imperfect ability to discriminate between healthy and parasitized hosts (Outreman *et al.* 2001). In this case, females could make some discriminating errors, leading to partial low-quality host acceptance. Secondly, partial superparasitism could be an average artefact at the population level. Individuals would use a zero-one rule, but due to some variability in their internal state or in their environmental characteristics only a part of them might be superparasitizing while the other part would not, resulting in an apparent partial preferences in the population (Mangel 1989). Finally, Sirot & Krivan (1997) have shown that a host–parasitoid dynamic system reaches a locally stable equilibrium point when parasitoids perform partial preferences. However, their explanation requires that selection acts at both the individual and the species level, favouring an individual behaviour that results in a stable equilibrium at the population level, for the system to persist in the long term.

Until now the superparasitism theory has, however, ignored the possibility that optimal host acceptance decisions might result from a trade-off between offspring production and the uncertainty of the oviposition opportunities. The stochastic component of the parasitoid's foraging activity has received little attention (see van Baalen 2000). Life expectancy and host availability could be random variables: wasps may die before they have depleted all their eggs or may encounter fewer hosts than they are able to attack during their lifetime (these effects being analogous). Cooper & Kaplan (1982) and Kaplan & Cooper (1984) predict that stochastic decision rules could be favoured by natural selection when the future is uncertain. We would therefore expect that the uncertainty associated with future oviposition opportunities will be a critical factor influencing partial preferences in parasitoids. We have addressed this issue by developing a theoretical approach that considers the frequency of encounters with healthy hosts (vs. parasitized) as a random variable and then determines to what extent partial preferences may be adaptive.

Description of the model

Parasitoids are considered to forage in an environment containing both healthy and parasitized hosts, the proportion of which are h and $(1 - h)$, respectively, and considered constant. Once a host is encountered, the oviposition decision depends on the host's parasitism status. Since attacking a healthy host returns the maximal pay-off, it is obvious that such a host should always be accepted by the foraging female. Accordingly, the acceptance rate of healthy hosts is assumed to be 1 and when the wasp oviposits in such a host, it gains a fitness increment of r_0. Let p be the acceptance rate of parasitized hosts. In previously parasitized hosts the fitness increment is r $(r_0, r \leq 1)$. As a consequence of the low probability of superparasitism success, it is assumed that $r \leq r_0$. The value of r depends on the time elapsed since the first parasitization (Visser *et al.* 1992) and on the species involved (Weisser & Houston 1993). For the sake of simplicity, it is assumed that all already-parasitized hosts are parasitized by the same species and that r is constant. It is also assumed (with no loss of generality) that parasitoid return pay-off is 1 when it oviposits in a healthy host (i.e. $r_0 = 1$). Thus, r can be interpreted as a measure of the relative value of already parasitized hosts to healthy ones. Finally, it is assumed that accepting or rejecting hosts has no associated time costs.

Upon encountering a host, the ovipositing probability is:

$$P = h + p \cdot (1 - h) \qquad \text{(eqn 1)}$$

and each oviposition in a host leads to the average fitness return

$$R = \frac{h + p \cdot (1 - h) \cdot r}{h + p \cdot (1 - h)} \qquad \text{(eqn 2)}$$

Considering that a female encounters N hosts during its life and its initial egg load is n, the frequency distribution of the number of eggs C the female will lay during its entire life span can be deduced from the binomial distribution:

$$\text{if } n \geq N, \begin{cases} \Pr(C = c) = \binom{N}{c} P^C (1 - P)^{N-c}, \text{ for } c \leq N \\ \Pr(C = c) = 0, \text{ for } c > N \end{cases} \qquad \text{(eqn 3)}$$

$$\text{if } n < N, \begin{cases} \begin{cases} \Pr(C = c) = \binom{N}{c} P^{C}(1 - P)^{N-c} \\ \Pr(C = n) = 1 - \sum_{c=1}^{n-1} \Pr(C = c) \end{cases}, \text{ for } c \leq n \\ \Pr(C = c) = 0, \text{ for } c > n \end{cases} \qquad \text{(eqn 4)}$$

In the present study, the measure of the lifetime reproductive success (i.e. fitness) is the expected number of fitness increments accumulated by the insect through ovipositions over the course of its life and is noted G. From eqn 3 and eqn 4, G can be computed as:

$$\text{if } n \geq N, G = \sum_{c=1}^{N} cR\Pr(C = c) \qquad \text{(eqn 5)}$$

$$\text{if } n < N, G = nR\Pr(C = n) + \sum_{c=1}^{n-1} cR\Pr(C = c) \qquad \text{(eqn 6)}$$

An optimal strategy is then defined by the value of p that maximizes G. Maximization of G can be analytically treated by differentiating it with respect to p. This expression is complicated and cannot be simplified in any useful way. We thus decided to present here some numerical results only. The function Solver of Microsoft® Excel 97 SR-2 was used to maximize G.

Results

Figure 1 shows how the optimal superparasitism acceptance rate depends on the total number of hosts that the wasps have encountered during their whole life. If wasps are unable to locate enough suitable hosts in their lifetime to deposit all their eggs (i.e. $n > N$), then the optimal strategy is to always accept superparasitism. Under these circumstances females are time-limited, and they should oviposit whatever the quality of the hosts they encountered. Conversely, when host availability is high, the risk of becoming egg-limited (i.e. depletion of the egg supply prior to running out of oviposition opportunities) rises (i.e. $N >> n$). Under these conditions, females are egg-limited and are expected to be increasingly selective with respect to oviposition and should wait for the best opportunity to lay all their eggs. In this case, they should accept only the healthy hosts. Finally, when the total number of hosts encountered is slightly greater than the initial egg-load, an intermediate rate of superparasitism acceptance should be selected for. In these circumstances, if the wasp rejects all parasitized hosts encountered during its life then time-limitation prevails. Conversely, if the female decides to always accept parasitized hosts, then she might waste eggs in low-quality hosts. The probabilistic feature of the model leads the wasp to be alternatively egg-limited or time-limited and to adopt an intermediate rate of poor quality hosts acceptance, leading to a partial superparasitism. The optimal strategy is then a kind of 'bet-hedging'. Figure 1 shows how the extent of the area in which partial superparasitism is an optimal strategy depends on the superparasitism fitness return. The higher the superparasitism pay-off, the more likely is partial superparasitism to evolve.

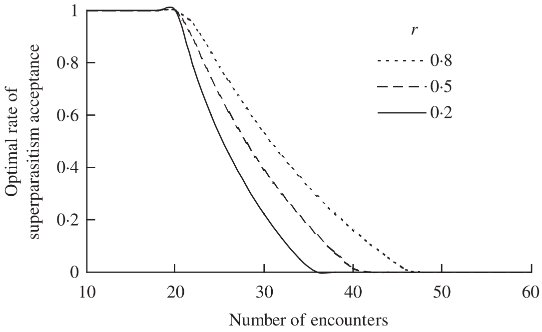

Fig. 1. Influence of the total number of encountered hosts on the optimal rate of superparasitism acceptance. Different curves represent three different levels of the fitness gained through ovipositions in parasitized hosts, r. Parameters used in the computation are $n = 20$ and $h = 0{\cdot}5$.

In Fig. 2, all state variables and environmental parameters but the wasp's initial egg-load n and the number of host encountered during its life N are fixed to particular values. Changing these values do not alter the qualitative predictions of the model. Figure 2 shows conditions that promote superparasitism. If wasps can lay more eggs than the number of oviposition opportunities (i.e. $n \geq N$, time-limitation), they should always superparasitize. If females are strongly egg-limited (i.e. $N >> n$), they should never superparasitize. Finally, for some moderated level of egg-limitation, the optimal strategy is to perform a stochastic host acceptance decision, leading to partial superparasitism.

Discussion

Some experimental work suggests that partial superparasitism should be the rule and not the exception

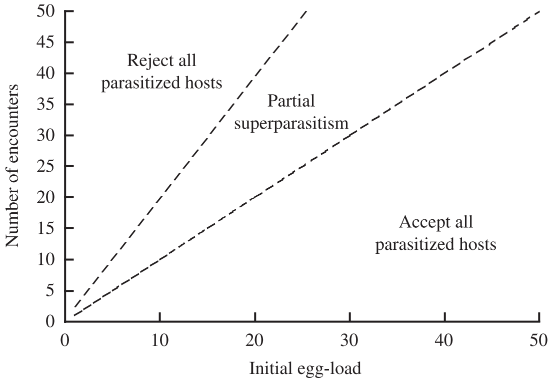

Fig. 2. Predicted optimal behaviour of a foraging solitary parasitoid as a function of its initial egg-load and the total number of encountered hosts during its life span. In the partial superparasitism area, the optimal strategy for a female is to decide randomly to oviposit in a parasitized host with a probability dependent on its initial egg-load and on the total number of encountered hosts during its life span. Parameters used in the computation are $r = 0{\cdot}4$ and $h = 0{\cdot}5$.

(van Dijken *et al*. 1986; Sirot *et al*. 1997). Here we show that an intermediate rate of superparasitism acceptance can be an optimal strategy when the initial egg-load of the forager is slightly lower than the potential number of hosts encountered. Is such a situation be observed frequently under natural conditions?

Females must trade-off investment in egg production (increasing *n*) with investment in searching for a suitable host (increasing *N*) (Rosenheim 1998, 1999). If the number of hosts encountered remains lower than the total number of eggs a female can lay, she will die without having laid all her eggs and waste the energy invested in egg production. In this case, it would be better to invest more energy in host searching. Conversely, if the total number of hosts encountered is far greater than the number of eggs the female can lay, she would do better to invest more in egg production. Therefore, it is very likely that selection has favoured females that optimize investment in egg production and searching activity in such a way that egg supply approximately matches the expected number of suitable hosts encountered. In this case, female parasitoids would be neither egg- nor time-limited. However, the number of suitable hosts encountered may fluctuate in a stochastic manner, hence females may switch between being egg-limited or time-limited. The optimal strategy they should then adopt is a compromise between always and never superparasitizing hosts, leading to partial superparasitism. The likelihood for such an intermediate level of superparasitism will be higher if the fitness return from attacking a parasitized host is not too low (Fig. 1) and if the frequency of previously attacked hosts is high.

Partial superparasitism has previously been considered as a byproduct of long-term dynamic persistence of host–parasitoid system (Sirot & Krivan 1997), of discrimination errors (Outreman *et al*. 2001) or of individual variability in the decision rules (Mangel 1989). These explanations are realistic and could explain patterns observed in natural systems. The model proposed here is conceptually different. It suggests that partial superparasitism could be selected for without being a byproduct of some other mechanisms. This implies that, even with a perfect knowledge of their environment, parasitic wasps could adopt a stochastic behaviour as the optimal response to the uncertainty of future host availability. Our model complements the study of Sirot *et al*. (1997), but uses a very different modelling framework as it provides quantitative predictions that could be tested against real data. Our approach was drawn from very simplified assumptions. The model could be rendered more realistic by including state dependence and/or by considering the egg supply and the ovipositions opportunities as random variables. Despite this, the model exhibited a new and very interesting feature: that randomness in behaviour could be an intrinsic feature of parasitoids favoured by natural selection rather than a byproduct of some other causal process. Further work from both empirical and theoretical viewpoints are now needed to assess the effects of the uncertainty of the future on the evolution of behaviour in foraging parasitic wasps.

Common sense suggests that even when the possible consequences of a decision are not known perfectly there should exist a ‘best decision’. Therefore, an organism behaving optimally is expected to adopt deterministic rules in decision-making. Accordingly, stochasticity in behaviour should necessarily result either from errors in decision-making or from some incapacity of the organism to correctly assess the actual current environmental state. Conversely, our model demonstrated that stochastic decision-making is likely to evolve as the best response to the uncertainty of the future.

In the general problem of diet choice in consumers, partial preferences are also found frequently. Such behaviours could also be explained by the optimality of stochastic decision rules. More generally, in any situation when animals face behavioural alternatives whose consequences are uncertain, stochastic decision rules may have been selected for. We suggest, therefore, that stochastic decision rules may be a very general feature in behavioural ecology when the uncertainty of the future has a significant influence on the fitness return associated with a decision.

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