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A general approach to oviposition strategies in solitary parasitoids

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Abstract. Foraging theory has largely concentrated on oviposition rate as the currency parasitoids use to maximize reproductive success. Female parasitoids foraging in a patchy environment face a variety of mortality risks that influence the survival of both themselves and their offspring. A foraging model is developed to suggest that patch residence times in parasitoids should be based on the trade-off between female and offspring mortality risks.

The fitness gain of parasitoids that include all mortality risks in their calculation of optimal patch residence time is then compared to the fitness gain of rate-maximizing females, and to the fitness gain of females that ignore offspring mortality. It is shown that rate-maximizing foragers and foragers ignoring offspring mortality may suffer from substantial losses in fitness. The long-term average rate of eclosing adults produced and the lifetime number of eggs laid are therefore fitness currencies that are likely not to be selected for in insect parasitoids.

INTRODUCTION

Since foraging theory was introduced into ecology by the seminal works of Schoener (1971), Charnov (1976) and others, biologists have been interested in analysing the patch use, e.g. the question of how long a parasitic female should stay in a patch of hosts. To answer this question, foraging wasps are often assumed to maximize the long-term rate of ovipositions (Charnov & Skinner, 1984; Parker & Courtney 1984). The optimal solution for a rate-maximizing animal is given by the so-called Marginal Value Theorem (Charnov, 1976): A female should stay in a patch as long as the rate at which eggs are laid is higher than the maximum rate it can achieve in the rest of the habitat (Charnov, 1976).

There are, however, some problems with using long-term rate as a currency. Iwasa et al. (1984) and Houston & McNamara (1986) have shown that maximizing rate will not necessarily maximize total reproductive success when the female forages under mortality risks. In insect parasitoids, searching for and ovipositing in hosts is associated with a number of mortality risks, within and between patches. Within a patch, a female may be under attack from predators. Between patches, the probability of a wasp surviving the journey depends on the risks of predation while searching for a patch, and on the travel time. Since parasitoids are normally short-lived and spend a major part of their life foraging, death by physiological causes is a further mortality source that may interupt the accumulation of life-time reproductive success.

The parasitic larvae that develop in or on the host tissues as a result of their mother's oviposition behaviour also faces several mortality risks. Death of the host through predation invariably results in the death of the parasitoid. Furthermore, many insect parasitoids are attacked by a wide range of hyperparasitoids. Thus the number of surviving larvae in a patch is likely to be smaller than the number of eggs laid in the patch. Because hyperparasitoids have been shown to aggregate in patches with higher parasitoid larval density (e.g. Horn, 1988), the number of eclosing offspring may depend on the number of eggs a female lays in a patch in a density-dependent manner.

There is a potential conflict between the mortality risks of the female and offspring mortality. For example, high travel risks may suggest a higher number of eggs should be laid in a single patch, but this may decrease the per capita survival probability of the eggs, due to the density-dependent actions of hyperparasitoids.

This paper shows how the trade-off between female and offspring mortality can be analysed by using the life-time production of eclosing adults as a measure of total reproductive success. The mathematical details needed for the derivation of the model are given elsewhere (Weisser, Houston & Völkl, in prep.). The model is then used to investigate the fitness loss of females that do not consider all mortality risks in their calculation of optimal patch residence times, i.e. females ignoring offspring mortality, and rate-maximizing females.

THE MODEL

Figure 1 shows how the model is constructed. Because the main concern is the influence of mortality we assume that the animal forages in an environment of identical patches. Suppose the female has just arrived at a new patch and has to decide how much time it will spend on the current patch given her behaviour is optimal on all future patches. The relationship between the time spent in the patch and the female's total reproductive success can then be described as follows (Weisser et al., in prep.): The female is assumed to lay eggs on a patch at an instantaneous rate $r(t)$ after a time t has been spent on the patch, where $r(t)$ is a smooth decreasing function of t. In other words the patch depletes as a result of the action of the ovipositing female. While on the patch the female incurs several sources of mortality. Let $z(t)$ denote the probability of surviving t units of time on a patch. The function $z(t)$ accounts for both death by physiological causes and for additional environmental risks like predation.

The probability of surviving the τ units of travel time between two patches depends on the abundance and frequency of host patches and is given by the function $s(\tau)$. The fitness contribution that a single egg makes to the female depends on the survival probability of the larva within the host. The function $\varphi(t)$ is therefore defined as the probability that a single egg develops successfully within a host. Since hyperparasitoids may aggregate in patches with high larval density, it is assumed that $\varphi(t)$ decreases with t, i.e. with the number of eggs laid in a patch.

To find an expression for the expected total fitness for female, define $G(t)$ as the expected total fitness over the period from arriving on the new patch until the animal dies. It can be shown (Weisser et al., in prep.) that

$$G(t) = \frac{\varphi(t)g(t)}{1 - z(t)s(\tau)} \qquad (1)$$

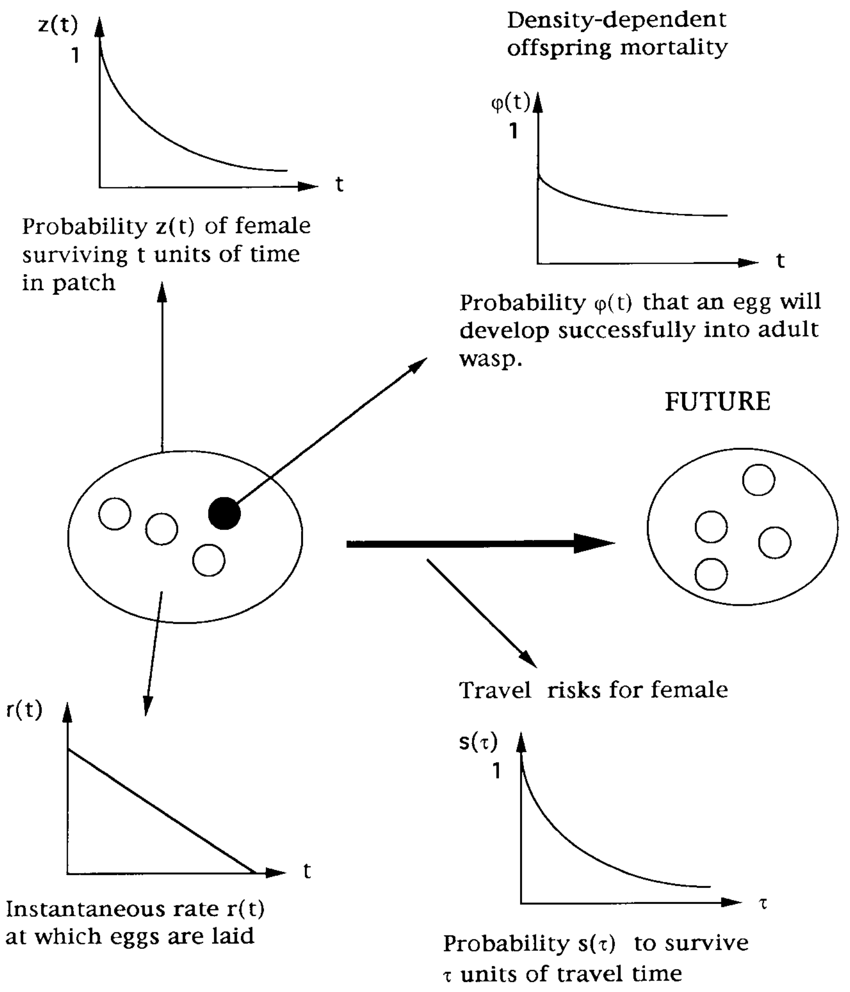

Fig. 1. Graphical illustration of the model. The female has to decide how long it will stay in the current patch (large circle), given she behaves optimally on all future patches.

where g(t) is the expected number of eggs laid on the current patch. The optimal patch residence time t^* is then found by differentiating equation (1) with respect to t and setting the derivative equal to zero.

The next section analyses how patch residence times and fitness given by equation (1) compare to patch residence times and fitness gains of females that do not include all mortality risks in their calculation of behaviour.

IGNORING OFFSPRING MORTALITY $\varphi(t)$

Table 1 gives the patch residence times for optimally foraging females [equation (1)], and for females that do not include offspring mortality, in their calculation of the optimal behaviour, for two levels of female travel mortality risk. Table 1 also shows the fitness gain of both types of females and gives the percentage fitness loss in females that ignore offspring mortality.

Patch residence times calculated by using equation (1) are always smaller than those calculated when $\varphi(t)$ is ignored. Offspring mortality of females ignoring this risk is therefore higher as in optimally foraging females which leads to the loss in total reproductive success (Table 1). The stronger the density-dependence in offspring mortality, the higher the loss in fitness. Even when density-dependence is weak, an increase in the mortality rate while travelling may force the female to stay longer in a patch so that offspring mortality becomes important for parasitoid fitness (Table 1).

RATE-MAXIMIZING

Parasitoid females are often considered to maximize the long-term average rate of ovipositions (e.g. Charnov & Skinner, 1984), or the rate of eclosing adults produced (e.g. Ayal & Green, 1993). In both cases, female mortality risks are ignored. In this section the fitness of optimally foraging females is compared to the fitness of females maximizing the long-term rate of eclosing adults, i.e. females maximizing

$$R(t) = \frac{\varphi(t)g(t)}{t+\tau} \qquad (2)$$

where g(t) does not include female mortality within a patch. Fig. 2 shows the difference in total fitness between females using the different methods for calculating their behaviour. Independent of travel time, τ, rate-maximizing females experience a loss in total reproductive success. The higher the ratio k of female mortality rate while travelling over female mortality rate within patches, the higher the loss in fitness for rate-maximizing females (cf. Houston & McNamara, 1986).

TABLE 1. The effect of ignoring offspring mortality.

1. $\beta = 0.004$						
μ	t_l	t^*	$G(t_l)$	$G(t^*)$	$-\Delta G(\%)$	$\varphi(t^*)$
0.001	168.54	126.61	213.44	218.58	2.35	0.881
0.003	168.54	90.44	152.36	176.85	13.85	0.762
0.005	168.54	72.36	108.76	150.52	27.74	0.696
0.007	168.54	61.01	77.64	131.83	41.10	0.652
0.009	168.54	53.07	55.42	117.66	52.90	0.620
2. $\beta = 0.01$						
0.001	264.22	180.72	152.82	160.57	4.84	0.835
0.003	264.22	121.57	90.09	119.83	24.82	0.694
0.005	264.22	94.21	53.11	96.83	45.15	0.624
0.007	264.22	77.65	31.31	81.63	61.65	0.581
0.009	264.22	66.34	18.46	70.73	73.90	0.550

t_l – patch residence times of females not considering offspring mortality in their calculation of behaviour; t^* – optimal patch residence time calculated by maximizing equation (1); G – expected total reproductive success; $\varphi(t^*)$ – offspring survival under optimal behaviour; β – female mortality rate while travelling; μ – parameter giving the strength of density-dependence in offspring mortality; α – female mortality rate within a patch. The functions used were: $s(\tau) = \exp(-\beta\ \tau)$. $\varphi(t) = \exp(-\mu\ t)$. $r(t) = K \exp(g\ t)$. $z(t) = \exp(-\alpha\ t)$. $\tau = 40$, $K = 1.0$, $g = 0.005$, $\alpha = 0.002$.

Increasing travel time, τ, has two effects. First, it decreases the amount of reproductive success both rate-maximizing and optimally foraging females can gain in their environment. Second, patch residence times in both types of females decreases (cf. Weisser & Houston, 1993). The net effect is that the difference in fitness loss first increases up to a critical value of travel time, and then decreases. Fig. 2 shows that as k ratio increases, the turning point decreases. Thus, rate-maximizing females may experience a substantial loss in fitness depending on their mortality rate and the distribution and abundance of host patches in their environment.

DISCUSSION

Foraging theory has often considered reward rate as the currency animals use to determine their optimal strategy. Mortality risks clearly influence the reproductive success of foraging females, yet mortality has often been neglected as a possible explanation for oviposition strategies in parasitoids. Furthermore, foraging models tend to concentrate on the female's performance rather than on the consequences of her decisions on offspring survival.

Ignoring offspring mortality leads to longer than optimal patch residence times which results in a decrease in offspring survival. This decrease in offspring survival leads to a decrease in total reproductive success.

Ayal & Green (1993) used the long-term average rate of eclosing adults as a fitness currency. The analysis presented here shows that rate-maximizing females may suffer from a great reduction in fitness. The reason is that eggs not laid on the current patch may

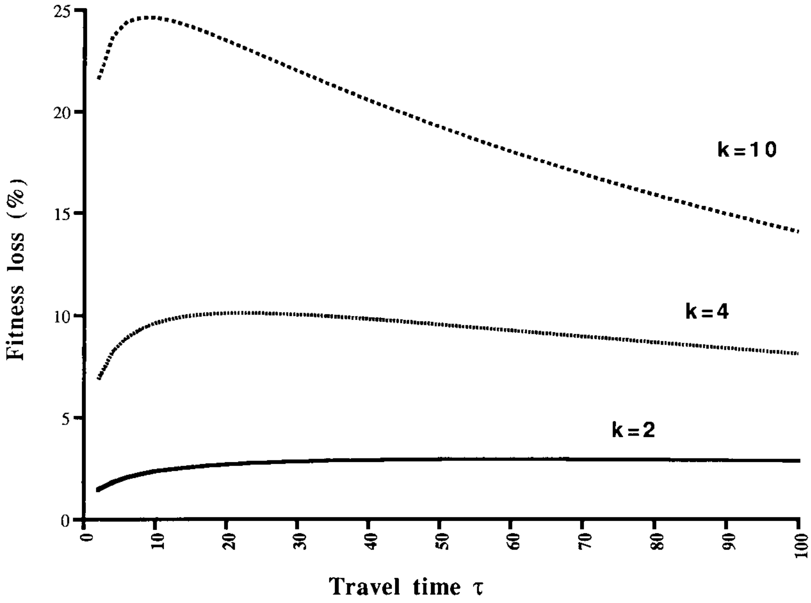

Fig. 2. Fitness loss in rate-maximizing females (in percent of fitness of optimally foraging females). $k = \beta/\alpha$ = female mortality rate while travelling/female mortality rate within a patch.

not necessarily be laid on future patches when there is a risk that the female dies before reaching the next patch.

The results presented in this paper suggest that when determining the behaviour that maximizes total reproductive success, it is important to consider the trade-off between female and offspring mortality rather than treating these factors separately. For example, when offspring mortality is high, long patch residence times of females can only be understood if female travel mortality is considered (Table 1).

Whatever mortality risk is neglected in the determination of optimal patch residence times, a suboptimal behaviour may result in a substantial loss in fitness. The loss in fitness for a rate-maximizing female has been shown to depend on the ratio of the mortality rate while travelling over mortality rate while in patches. In insect parasitoids, searching for patches is likely to be much more dangerous for the female than foraging within a patch. Thus, in the real world, rate-maximizing females can be expected to do much worse than females using a fitness currency that considers their mortality risks. It is therefore unlikely that fitness currencies not accounting for mortality risks have been selected for by natural selection.

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