

A SHORT NOTE SUMMARIZING THE PROBLEMS INVOLVING LOCAL MATE COMPETITION, THE HOST QUALITY EFFECT AND CONSTRAINED OVIPOSITION IN PARASITIC WASPS

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ABSTRACT

Because of their arrhenotokous sex-determining system, Hymenoptera have the ability to adjust their sex ratios depending on conditions. While this fact has been known to entomologists for a century, it did not receive much theoretical consideration until the emergence of behavioral ecology, which began in the 1950s and emerged as a prominent approach to the study of animal behavior in the 1970s. In this paper, problems faced by ovipositing parasitic wasps are classified in terms of three conditions: (1) local mate competition, (2) host quality effect, and (3) constrained oviposition. A model for optimal sex allocation of parasitic wasps can be categorized in terms of the presence or absence in each of these three conditions. That is, there are eight categories of problems. For each of these problems one might ask the question: What is the optimal sex allocation strategy? This would make eight questions. One might also ask: How much does it cost to be unmated? This would make eight more questions. Overall there would be sixteen questions.

In fact, there are different versions of the problems, but since this is a short note, I will not include all possibilities. Not all of the sixteen possible questions have been asked, but I will try to mention one answer (or, rather, I will cite one author who has offered an answer) that has been proposed for each of the questions that has been asked.

INTRODUCTION

In his 1990 paper, Charles Godfray showed how to calculate the optimal sex ratio for unconstrained female wasps when confronted with some proportion of ovipositing females that are constrained to produce only sons, perhaps because they are unmated. Godfray considered two cases, one in which there is no local mate competition and no host-size effects, the other in which there is no host-size effect but there is local mate competition as described by Hamilton's (1967) with $n = 2$. If there is no local mate competition and no host-size effect, and if the mated females produce the optimal sex ratio, then there is no cost of being unmated unless the proportion of constrained females exceeds one-half. However, there is a cost of being unmated if there is local mate competition. Godfray (1990) mentioned, but did not treat the possibility of a host-size effect. In a 2008 technical report I showed how to find the optimal sex ratio for unmated females when there is a host-size effect. When there is a host-size effect there is a cost of being unmated, and I showed how to calculate it.

In this paper I consider all eight possible cases that can be characterized by the presence of absence of each of the three factors: (1) local mate competition, (2) the host quality effect (which I refer to as the "host-size effect"), and (3) constrained oviposition (which I refer to as having "unmated females"). In Table 1 I list authors who answer the question: What is the optimal sex-allocation strategy for this case? In Table 2 I list authors who answer (at least implicitly) the question: How much does it cost to be unmated in this case? Most of the answers to this second question are given either in my technical report, or in this note. In most cases the answers are implicit, they are found by solving an equation or by following some procedure. In some cases the answers can be visualized by looking at a picture. The main point of my 2008 technical report was to show how to visualize the optimal sex allocation strategy and the cost of being unmated when there is a host-size effect.

SUMMARY OF EIGHT PROBLEMS

The following tables illustrate the eight problems and the two questions for each. For each case I cite a piece of work that treats some version of the problem for that case. In a sense there is a $2 \times 2 \times 2 \times 2$ array of problems \times questions. Table 1 gives a $2 \times 2 \times 2$ array for the question: What is the optimal sex allocation strategy? Table 2 gives a $2 \times 2 \times 2$ array for the question: How much does it cost a parasitoid to be unmated? It can be seen that there is much more work on the question of optimal sex allocation than there is on the question about the cost of being unmated. This difference may be due to the fact that the question has only recently been asked in this way, even though the idea behind the question is an old one.

[Put Table 1 here.]

It is seen that six of the eight possible problems had been treated in one way or another before my 2008 technical report, of which this note is intended to be a companion. That technical report added a treatment of the problem with no local mate competition, but with a host-size effect. The Charnov (1979) paper treated that problem for the case in which there are two host sizes and in which there were no unmated females. My technical report treated that problem assuming a continuous host-size distribution and it included cases with and without unmated females. I do not know how to treat the eighth case.

[Put Table 2 here.]

The question of how much it costs to be unmated is quite new, although it is analogous to the question of whether there is selection against a sub-optimal sex ratio. That question was answered by Fisher (1930). If the population sex ratio deviates from 1:1 there is selection to return to 1:1, but if the population sex ratio is 1:1, then individuals, or pairs, that produce different sex ratios are not selected against. Godfray (1990) pointed out that unless there are too many females unmated there is no disadvantage of being unmated in his model, which assumed no local mate competition and no host-size effect. My 2008 technical report showed that if there is a host-size effect then there is cost of being unmated, whatever the proportion of females that are unmated. In the appendices of this note I show how to calculate the cost of being unmated for Hamilton's local mate competition model for any value of n if there are no other unmated females, and for Hamilton's model with $n = 2$ with a non-negligible proportion of unmated females (Godfray considered this case in 1990). For my continuous-time model, it is possible to find the optimal sex ratio when there is local mate competition and a host-size effect but when there are no unmated females by using a method similar to that used for the host-size effect alone (Green 2008). One simply requires that the ratio of overall fitnesses, $D:S = (n + 1)/(n - 1)$ when $W_s(c^*) = W_d(c^*)$. One needs to do a bit more in order to calculate the cost of being unmated. The cost to a single female of being unmated, when there is a host-size effect and local mate competition in the sense of Hamilton (1967) is given by

$$\text{Cost} = [(n + 1)S_1 - (n - 3)S_2] / \sqrt{2[nS_1 + S_2]} \quad (1)$$

where

$$S_1 = \int_0^c W_s(x) f(x) dx,$$

and

$$S_2 = \int_c^\infty W_s(x) f(x) dx.$$

Notice that if there is no host-size effect, then from Hamilton's local mate competition model we have $S_1 = (n - 1)/2n$ and $S_2 = (n + 1)/2n$ and (1) reduces to (A2). I do not know how to calculate the cost of being unmated when there is local

mate competition, a host-size effect and a non-negligible proportion of unmated females.

TABLE 1.

Treatment of the question: *What is the optimal sex allocation strategy for parasitoids in each of these eight conditions?*

Are there unmated females? No

Is there a host-size effect?	Yes	Charnov (1979)	Werren (1984)
	No	Fisher (1930)	Hamilton (1967)

No

Yes

Is there local mate competition?

Are there unmated females? Yes

Is there a host-size effect?	Yes	Green (2008)	?
	No	Godfray (1990)	Godfray (1990)

No

Yes

Is there local mate competition?

TABLE 2.

Treatment of the question: *How much does it cost to be unmated?*

Are there unmated females? No

Is there a host-size effect?	Yes	Green (2008)]Green (2008)]
	No	Fisher (1930)	This note

No	Yes
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Is there local mate competition?

Are there unmated females? Yes

Is there a host-size effect	Yes	Green (2008)	?
	No	Godfray (1990)	This note

No	Yes
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Is there local mate competition?

Appendix 1. The cost of being unmated when everyone else is mated for Hamilton's (1967) model.

In Hamilton's (1967) model, each host is attacked by exactly n female parasitoids. The optimal proportion of sons is $(n - 1)/2n$, which means that the optimal sex ratio is $n - 1$ sons : $n + 1$ daughters.

Without loss of generality, one may assume that each mated female lays $2n$ eggs, $n - 1$ of which are sons and $n + 1$ are daughters. Unmated females are assumed to lay $2n$ eggs, all of which become sons.

If all the females that attack a particular host are mated, each female on average gets $2(n + 1)$ genes out, $n + 1$ genes through her daughters, and $n + 1$ through daughters that are inseminated by her sons.

Now consider a single unmated female that shares a host with $n - 1$ mated females, each of which produces the optimal sex ratio. The unmated female can get her genes out only through her sons mating with the daughters of the mated females. There are $(n - 1)(n + 1)$ such daughters.

The unmated female produces $2n$ sons, while all of the mated females on the host produce a total of $(n - 1)(n - 1)$ sons. Thus, the proportion of all the sons on the host that are the sons of the unmated female is $2n/[2n + (n - 1)(n - 1)] = 2n/(n^2 + 1)$.

If sons of mated and of unmated females compete equally for daughters with which to mate, the number of genes that the average unmated female would get out is $[2n / (n^2 + 1)](n - 1)(n + 1)$. If this number is divided by the number of genes that the average mated female would get out, $2(n + 1)$, one obtains the (relative) fitness of an unmated female

$$W = (n^2 - n) / (n^2 + 1). \quad (\text{A1})$$

The cost of being unmated for Hamilton's (1967) model is

$$\text{Cost} = 1 - W = (n + 1) / (n^2 + 1). \quad (\text{A2})$$

Appendix 2. The cost of being unmated when proportion p of female parasitoids are unmated for Hamilton's (1967) model with $n = 2$.

I formulate this problem like Godfray (1990) did. Given that some fixed proportion, p , of all ovipositing females are unmated and can produce only sons, assume that the mated females produce some optimal proportion, r , of sons.

Godfray (1990) assumed that a rare mutant female produces a proportion, r^* , of sons, and he calculated the number of genes that such a mutant gets out.

Consider the mutant female. Since the total number of individuals ovipositing in the host is two, we need consider only three possible cases. Case 1: the mutant is mated and the other female (a non-mutant) is also mated—the probability of this is $(1 - p)^2$; Case 2: the mutant is mated and the other female is unmated—the probability of this is $p(1 - p)$. Case 3: the mutant is unmated and the other female is mated—the probability of this is $p(1 - p)$. There is a fourth case, in which both mutant and the other female are unmated, but this case can be ignored because the two unmated females can only produce sons, which have no one to mate with.

In principle, I will find the expected number of genes that a mutant would get out if she produced N offspring—all sons if she is unmated, but r^*N sons and $(1 - r^*)N$ daughters if she is mated. The expected number of genes per mutant in the three cases will be N times the following:

$$\text{Case 1. } (1 - r^*) + [r^*/(r^* + r)] (2 - r^* - r)$$

$$\text{Case 2. } (1 - r^*) + [r^*/(r^* + 1)](1 - r^*)$$

$$\text{Case 3. } [1/(1 + r)] (1 - r)$$

Note: The first terms for Cases 1 and 2 represent fitness through daughters, while the second terms in Cases 1 and 2 and the only term in Case 3 represent fitness through sons.

If we suppress the constant N we can write the fitness of the mutant as a function of the proportion of sons, r^* , which she produces:

$$\begin{aligned} W(r^*) = (1 - p)^2 \{ & (1 - r^*) + [r^*/(r^* + r)] (2 - r^* - r) \} & \text{(A3)} \\ & + p(1 - p) \{ (1 - r^*) + [r^*/(r^* + 1)] (1 - r^*) \} \\ & + p(1 - p) [1/(1 + r)] (1 - r) \end{aligned}$$

In order to find the cost of being unmated I will calculate the number of genes gotten out per mutant female for two different values of r^* , namely: $r^* = r$ (mutant is optimal) and $r^* = 1$ (mutant is unmated).

For $r^* = r$, (A3) becomes

$$W(r) = 2 (1 - p) (1 - r) \quad (\text{A4})$$

while, for $r^* = 1$, (A3) becomes

$$W(1) = (1 - p) [1/(1 + r)] (1 - r) \quad (\text{A5})$$

Thus, the fitness of an unmated female, relative to a mated female producing the optimal proportion of sons, r , will be $W = W(1) / W(r)$, or

$$W = 1/[2(1 + r)]. \quad (\text{A6})$$

Therefore, and finally, the cost of being unmated is

$$\text{Cost} = 1 - W = (1 + 2r) / (2 + 2r). \quad (\text{A7})$$

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