

**HOW MUCH DOES IT COST A PARASITOID  
TO BE UNMATED?**

by

Richard F. Green

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Department of Mathematics and Statistics  
University of Minnesota Duluth  
Duluth, Minnesota 55812

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Department of Mathematics and Statistics  
University of Minnesota Duluth  
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### ABSTRACT

Parasitic wasps (parasitoids) have the ability to determine the sex of their offspring. Some solitary wasps are known to produce daughters in high quality (large) hosts and sons in low quality (small) hosts. A theoretical explanation of this sex allocation pattern is possible if we assume that female offspring are affected more by host quality than are males. If we know how the fitness of each sex depends on host size, and if we know how the size of hosts is distributed, then we can determine which sex offspring should be assigned to which hosts. The optimal sex allocation strategy is known for the case in which it is assumed that all the wasps are mated. But what happens if some of the wasps are unmated and are only able to produce sons? Then mated wasps should produce more daughters, but even if most wasps are unmated, mated wasps should sometimes produce sons.

The method used to determine optimal sex allocation can also be used to measure the cost of being unmated. I do this by making comparable the fitness functions for the two sexes and then comparing the average fitness of an offspring produced by a mated mother with the average fitness of a son produced by an unmated mother. The difference between these averages provides a measure of the cost of being unmated. This cost, which can be substantial even when almost all mothers are mated, becomes greater as the proportion of unmated mothers increases.

The same sort of calculation that is used to measure the cost of being unmated can also be used to measure the cost to a mated female of producing a suboptimal sex ratio. It is seen that the cost of producing the wrong sex ratio is not great unless the sex ratio is quite far from the best.

**Key words:** parasitoid, optimal sex allocation, host quality effect, MacArthur's "product rule," constrained oviposition

## INTRODUCTION

In this paper I examine the cost to a parasitoid of being unmated and only able to produce sons. I do this by modifying a method that I used to study problems faced by solitary parasitoids (Green 1982). A mated female, which can produce either sons or daughters, must decide which sex to produce on each host. An unmated female can produce only sons. If many females are unmated and produce sons, this affects the decision of mated females about whether to produce sons or daughters. I am interested in the optimal sex allocation decision and how it depends on host size distribution, on the fitnesses of sons and daughters in hosts of various sizes and on the proportion of females that are unmated. I am also interested in the cost of being unmated, not only the loss of fitness to an individual female that is unmated, but also the force of selection against behavioral and physiological mechanisms that lead to females being unmated.

I will begin by sketching the historical background of thought about sex ratios, starting with sex ratios in general, then turning to sex ratios in parasitoids in particular, then finally and even more particularly, considering the effect of host quality on sex ratios in solitary parasitoids. The point of all the work that I discuss is to understand and explain observed sex ratios. Historically, observations came first, then simple models and explanations, followed by more observations and modifications of the models.

### **Historical background: sex ratios in general**

Sex ratios, particularly sex ratios of humans and of their domestic animals, are of great practical importance. Sex ratios are also noticeable and interesting theoretically. Once people started keeping records of vital statistics, an interesting pattern in human sex ratios became apparent. The human sex ratio is close to 1:1, but it is slightly male-biased, and it does not change much from year to year. In 1710, John Arbuthnott proposed a simple chance model of sex determination. The sex of each child might be determined by tossing a fair coin. Arbuthnott calculated the chance of equal numbers of males and females in his model and observed that the chance that there would be more male than female births in any year would be less than a half. He reported records for 82 years of births (christenings, actually) in London. In every year, there were more male than female births. Under the coin-tossing model, the probability of such an observation is infinitesimally small, and therefore not due to chance. Arbuthnott pointed out that males are subject to greater mortality than females (because males “must seek their Food with danger”). Therefore, “provident Nature” brings forth more males than females to make up the excess loss of males due to mortality.

Arbuthnott’s paper is important historically as a very early example of a hypothesis test and it has been reprinted in a collection of papers on the history of statistics (Kendall and Plackett 1977). Arbuthnott devised a mathematical model of sex determination, and he compared observed data with what would have been expected from his binomial model. He rejected his chance model and concluded that the (slightly) male-biased sex ratios observed in his London data was due to Divine Providence. People today do

similar kinds of work, comparing observations with theory, but they no longer use Divine Providence as an explanation.

Charles Darwin observed that sex ratios are often 1:1, but not always. Darwin (1874) is often quoted as saying in the *Descent of Man* that: “I formerly thought that when a tendency to produce the two sexes in equal numbers was advantageous to the species, it would follow from natural selection, but I now see that the whole problem is so intricate that it is safer to leave its solution for the future.” The solution was given by R. A. Fisher (1930) sixty years later, but Michal Bulmer (1994) noticed that the often-quoted statement appeared in the second edition of the *Descent of Man*, and that it replaced an explanation in the first edition (Darwin 1871) that was essentially the same as that given by Fisher (see Martin J. Osborne 1996).

Fisher’s (1930) well-known argument was that if one sex is rarer than the other in the next generation, then individuals in the present generation will do better to produce offspring of the rarer sex. That is, any deviation from a 1:1 sex ratio would be selected against. The result is more general, however. It is not the sex ratio itself that should be equalized but the effort exerted in producing each sex. So, for example, if females are twice as costly to produce as males, then twice as many males should be produced.

Fisher’s argument was generalized even further by Robert MacArthur (1965), who showed that if parents can produce various combinations of sons and daughters, the optimal choice is that which maximizes the product of the number of males and the number of females. The analysis that I offer in this paper is based on MacArthur’s “product rule.”

A systematic treatment of the theory of sex allocation (including sex ratios and the allocation of time and effort to reproducing as males or females in sequential hermaphrodites) was offered by Eric Charnov (1982). Charnov probably did the most to popularize the study of sex allocation by behavioral ecologists.

### **Sex ratios in parasitic wasps**

Parasitic wasps are convenient subjects for the study of sex ratios because, like other Hymenoptera, they are haplo-diploid and can determine the sex of their offspring. In most species, fertilized eggs become females while unfertilized eggs become males. Mated females carry sperm, and they can determine the sex of their offspring by fertilizing them or not. Parasitic wasps are of practical importance because the hosts of many species are agricultural pests.

I will generally use the term “parasitoid” to refer to the animals that I am talking about, but I have wasps in mind. The term “parasitoid” refers to animals that are like parasites in that they (generally) spend their whole lives on individual hosts, but they are unlike many parasites (and like predators) in that they (generally) kill their hosts in the end. Parasitoids may be flies as well as wasps (and rarely, they may be insects of other

orders), but I confine myself to wasps, because, being haplo-diploid, they have a convenient sex-determining mechanism.

Entomologists have long known that parasitoids often show strongly biased sex ratios, but a theoretical understanding of this was slow in coming. W. D. Hamilton (1967) offered an explanation of the female-biased sex ratio seen in gregarious parasitoids. If parasitoids mate on the natal host, some, perhaps all, matings will be between sibs. In particular, if all the young developing on one host mate with each other, it is only necessary to produce enough males to mate with all of their sisters. [There were quite a number of unrealistic assumptions made in this first model: (1) not all matings take place on the natal host; not every host would have been attacked (2) simultaneously, (3) by the same number of parasitoids; (4) not all parasitoid would lay the same number of eggs per host; (5) both sexes in parasitoids are not diploid, and (6) clutch sizes are not infinite. However, each of these problems was treated in subsequent work.]

Besides proposing a model for parasitoid sex ratio, Hamilton's paper was important because it introduced the issue of "extraordinary sex ratios," including sex ratios in parasitoids, to a wide audience of evolutionary biologists. Hamilton's explanation of female-biased sex ratios for gregarious parasitoids, known as "local mate competition," is one of the two best known ideas in the theory of parasitoid sex ratios. The other well-studied problem is the allocation of different sexes to different quality hosts by solitary parasitoids, a problem treated in an influential paper by Eric Charnov (1979). This is the particular problem that I will treat in this paper. However, I will also show how to measure the cost of being unmated in gregarious or quasi-gregarious parasitoids.

In a more general work, Charnov (1982) reviewed a great deal of empirical and theoretical work on sex allocation. Charnov inspired many students of sex ratios, including me, by his work and his enthusiasm. Parasitoids figure prominently in work on sex ratio theory, as is seen in Charnov's book, and in the collection of papers edited by Wrensch and Ebbert (1993). Works on the behavioral ecology of parasitoids (Godfray 1994; Wajnberg, Bernstein and van Alphen 2008) devote chapters to sex ratio theory.

### **One particular problem: the effect of host size on parasitoid sex allocation**

It had been observed for years that solitary parasitoids tend to produce sons on smaller hosts, or smaller instars, and daughters on larger hosts, or instars. Bethia King (1987) reviewed empirical work on this and other problems. One early paper cited by King was by Stan Flanders (1939), who discussed work done between the wars on parasitoid sex ratios and the anatomy of sex determination in Hymenoptera. Flanders also mentioned a paper written before the First World War by Chewyreu (1913), which described the sex ratios produced by a single parasitoid species on host species of three different sizes.

Charnov (1979) presented a genetic model of sex allocation in hosts of two different sizes. Assuming that sons and daughters would be equally fit on small hosts, that sons would be at least as fit on large as on small hosts, and that females would be more fit than males on large hosts, Charnov showed that if there were relatively few small hosts, then

all the small hosts should be used to produce sons, and that the large hosts should be used to produce both sons and daughters. If there were relatively few large hosts, all of these should be used to produce daughters, and small hosts should be used to produce both sons and daughters. If the ratio of small to large hosts lies in an intermediate range, then only sons should be produced in small hosts and only daughters in large hosts. It is interesting to note that if both sexes have higher fitness in large than in small hosts—the case illustrated in Charnov's (1979) Figure 2, then his model parasitoids would have male-biased sex ratio in all three cases (for host size distribution) that he considered. In this paper I will give an illustration that should make clear why a male-biased sex ratio should be expected whenever the ratio of female to male fitness increases as host size increases.

In 1982 I used an ecological model to extend the ideas about the effect of host size in Charnov's (1979) paper to the case in which host size varies continuously. I considered two critical values: (1) the host size below which eggs are not laid and (2) the host size such that sons are produced for smaller hosts and daughters are produced for larger hosts. These two critical values of host size were interpreted in terms of Charnov's (1976) "marginal value theorem" and MacArthur's (1965) "product rule," respectively. Here I ignore the possibility that some hosts will not be used for oviposition. It could be that some hosts are ignored, or are used for host feeding instead of oviposition, but if this happens, then the hosts that I consider could be understood to be only those that will be used for oviposition, even if they do not include all hosts.

In 1993 Godfray and Hardy considered the effect of virginity on sex allocation strategies. They pointed out that if parasitoid sex ratio is at equilibrium then there is no loss to a parasitoid that produces offspring of only one sex. If a substantial proportion of ovipositing females are virgins and can only produce males, then the mated parasitoids should produce a female-biased sex ratio. In their discussion, Godfray and Hardy did not consider the possibility that the fitness of offspring depends on host size and that females gain more from larger hosts than do males. I intend to include the effect of host size and look again at the effect on the optimal sex ratio of having unmated females, the issue that Godfray and Hardy raised. I also intend to look at the cost to parasitoids of being unmated.

## **METHOD**

As is seen in the papers and reviews that I have mentioned above, much work has been done on parasitoid sex ratios, both empirical and theoretical. This paper is theoretical. It uses a method appropriate for treating one of the main problems in parasitoid sex ratio theory, the allocation of sons and daughters to hosts of different sizes.

This paper uses ideas from four sources. (1) It is based on ideas about the varying fitness of the sexes in hosts of different sizes that are found in Charnov's (1979) seminal paper. (2) It relies on MacArthur's (1965) "product rule" for sex ratios. (3) It uses and modifies a method used by Green (1982) to extend the treatment given by Charnov. (4) It addresses a problem discussed by Godfray and Hardy (1993), the role of unmated females on the sex ratio of parasitoids. Godfray (1990) introduced the term "constrained

oviposition” to refer to the production of males by females that were unmated or were otherwise unable to fertilize their eggs.

In this paper I use a method that I used earlier (Green 1982) to study sex allocation in solitary parasitoids. I modify my earlier method in two ways, one that makes the earlier result easier to visualize by considering offspring fitness as a function of host size quantile instead of host size itself, and another that permits me to compare the fitnesses of sons and daughters.

### Notation

The problem under consideration is how a mated female parasitoid that lays one egg per host should decide whether to produce a son or a daughter in a particular host. I use the following notation:

$X$  = the size of a randomly chosen host,

$x$  = host size for a particular host,

$f(x)$  = the distribution of host size,  $f(x)$  is the density function of this distribution,

$F(x) = P(X \leq x)$  = the cumulative distribution of host size; I will refer to

$y = F(x)$  as “host size quantile;” that is, if  $x$  is the host size such that 40% of the hosts are smaller, then  $y = 0.40$ .

$W_s(x)$  = the fitness of a son produced in a host of size  $x$ ,

$W_d(x)$  = the fitness of a daughter produced in a host of size  $x$ .

[Note:  $W_s(x)$  measures the relative fitness of a male produced in a host of one size compared with a male in a host of a different size, and  $W_d(x)$  measures the relative fitness of a daughter produced in a host of one size compared with a daughter produced in a host of a different size. The fitnesses for sons and daughters are not, in general, comparable, but in this paper I show how to make them comparable in particular cases.]

$c$  = a particular host size that determines a sex allocation strategy: sons are produced in hosts of size  $x < c$ , daughters are produced in hosts of size  $x > c$ .

$c^*$  = the optimal value of  $c$ ,

$w_s(y)$  = the fitness of a son produced in a host whose size quantile is  $y$ ,

$w_d(y)$  = the fitness of a daughter produced in a host whose size quantile is  $y$ .

$k$  = a particular host size quantile, corresponding to host size  $c$ ; that is, where  $y = F(c) = k$ . Notice that  $k$  is equivalent to the sex ratio; that is,  $k$  is the proportion of sons produced by females using the strategy: produce sons in hosts of size  $x < c$  and produce daughters in hosts of size  $x > c$ .

$k^*$  = the host size quantile corresponding to the optimal choice of host size,  $c$ , namely  $c^*$ .

For a certain host, the fitnesses of son (or of a daughter) will be the same, whether specified by  $W$  or  $w$ , but the values of the arguments will be different.

$S$  = the total fitness of sons,

$D$  = the total fitness of daughters.

$T = S + D$  = total fitness.

In principle,  $S$  and  $D$  refer to all the sons and daughters in the whole population (the entire next generation). In practice,  $S$  and  $D$  refer to the expected fitness due to sons (one son at most) and the expected fitness in daughters (one daughter at most) produced in a single host whose size is chosen at random.

$p$  = the proportion of unmated females in the breeding population.

$C = C(p)$  = the cost of being unmated, which is a function of  $p$ .

An example of fitness function and an example of host size distribution are illustrated in **Figs. 1** and **2**. These and **Figs. 3** through **9** (are based on a particular numerical example, which is chosen to exemplify the assumptions listed below. This is **Example 1**.

[Put Figure 1 here.]

[Put Figure 2 here.]

### General assumptions of the model

1. The fitnesses,  $W_s(x)$  and  $W_d(x)$  are both non-decreasing functions of host size,  $x$ .
2. The ratio  $W_d(x)/W_s(x)$  is an increasing function of host size. That is, as host size increases, the fitness of daughters relative to sons increases.
3. Mating is random.
4. That sex allocation strategy is best which maximizes the product,  $SD$ , where

$$S = \int_0^c W_s(x) f(x) dx, \text{ and} \quad (1)$$

$$D = \int_c^\infty W_d(x) f(x) dx, \quad (2)$$

The integral for S is taken over the host sizes for which sons are produced and the integral for D is taken over the host sized for which daughters are produced. Notice that sons are produced in hosts of size less than some critical size,  $c$ , and daughters are produced in hosts of size greater than  $c$ .

### Applying MacArthur's "product rule"

Assumption 4 is basically MacArthur's (1965) "product rule," which says that animals should use the sex ratio that maximizes the product of fitnesses through sons and daughters.

In order to maximize a product, the simplest way to do the calculation is to take logarithms, take the derivative of the logarithms, set the result equal to zero and solve. The value of each of the terms, S and D, depends on the critical value of host size,  $c$ , so the derivative is taken with respect to  $c$ . Using the fundamental theorem of calculus to obtain the derivative of an integral, we have

$$d \log(SD)/dc = W_s(c) f(c) / S - W_d(c) f(c) / D = 0.$$

Canceling the factor,  $f(c)$  in each term yields

$$W_s(c) / S = W_d(c) / D, \quad (3)$$

or, equivalently,

$$W_s(c) : W_d(c) = S : D. \quad (3)$$

The value of  $c$  that satisfies (3) is the critical host size,  $c^*$ .

Expression (3) is the key algebraic idea in this paper. If I have explicit expressions for the relative fitnesses,  $W_s(x)$  and  $W_d(x)$ , and host size distribution,  $f(x)$ , I can find S and D for any value of  $c$  numerically using equations (2) and (3), and I can solve for  $c$ . What I really want to do is compare the fitnesses for sons and daughters so that I can measure the cost of being unmated—and also so that I can calculate the cost of choosing the wrong critical value,  $c$ .

### Making the fitnesses comparable for the two sexes

There are two ideas that are useful in visualizing and comparing the fitnesses of sons and daughters. First, I consider fitness as a function of host size quantile, not host size. Second, I make fitnesses comparable algebraically.

First, consider fitness as a function of host size quantile, not host size. For a host of a given size,  $x$ , the fitness of a son is given by  $W_s(x)$  and the fitness of a daughter is given by  $W_d(x)$ . However, for each host size  $x$ , there is some proportion of hosts,  $y$ , which are smaller. That is, a host of size  $x$  is a *host of quantile*  $y$ , where  $y = F(x) = P(X \leq x)$ , the probability that a randomly chosen host will have size  $X \leq x$ . The quantile  $y$  is a function of  $x$ . That is, I can write  $y = y(x)$ . If host distribution is continuous over the set of

possible host sizes, then host size is a function of quantile, and I can write  $x = x(y)$ . Further, I can write fitness as a function of  $y$ . For example, the fitness of sons can be written as  $w_s(y) = W_s[x(y)]$  and the fitness of daughters can be written as  $w_d(y) = W_d[x(y)]$ .

The advantage of considering fitness as a function of host size quantile rather than host size is that when one plots fitness against host size quantile, the area under the fitness curve represents total fitness. This will be illustrated in **Fig. 3** and subsequent figures. Algebraically, we can rewrite total fitness through sons and daughters as

$$S = \int_0^k w_s(y) dy, \text{ and} \quad (4)$$

$$D = \int_k^1 w_d(y) dy. \quad (5)$$

[Put Figure 3 here.]

Second, make the fitnesses comparable algebraically. When ovipositing females use the optimal sex allocation strategy, they produce sons in hosts smaller than size  $c^*$  and daughters in hosts larger than size  $c^*$ . For hosts of size  $c^*$ , males and females are equally valuable. Therefore, to make the fitness functions for the two sexes comparable, I fix one function [I fix the function for sons,  $W_s(x)$ ], and then standardize the other function,  $W_d(x)$ , by multiplying it by a constant such that  $W_s(c^*) = W_d(c^*)$ .

### Three ways to understand the sex allocation problem

Notice that there are three ways of thinking about and visualizing this problem of sex allocation. The first approach is **algebraic**. It treats fitness as a function of host size and considering host size,  $x$ , in terms of a probability density function,  $f(x)$ . The total fitness through sons and daughters,  $S$  and  $D$ , respectively, are understood intuitively as averages defined by equations (1) and (2), and the optimal sex ratio is specified by equation (3). For people with a certain kind of intuition, these expressions provide a good understanding of how MacArthur's "product rule" is used to understand how sexes should be allocated to hosts of different sizes. The algebraic approach is also used to get numerical results and to draw curves, including those using host size quantile.

The second approach is **visual**. If fitnesses for sons and daughters are plotted against host size quantile, the areas under the curves represent total fitness due the production of sons and daughters, respectively. This is seen in **Fig.3** for unstandardized fitnesses. When fitnesses are standardized by equating the fitnesses for sons and daughters at the critical host size,  $c^*$ , then the fitnesses and areas under the curves for the two sexes are comparable. This visual approach is useful in understanding the cost of being unmated (this cost corresponds, roughly, to a triangular-shaped region, labeled with a 3 in **Fig. 4**), and it is also useful in understanding the cost of producing a sub-optimal sex ratio.

[Put Figure 4 here.]

The third approach is **numerical**. The optimal sex ratio can be calculated for a variety of cases, the actual cost of being unmated can be calculated, and so can the cost of

producing a sub-optimal sex ratio. These calculated values are not very interesting in themselves, because they depend on the particular examples that I have chosen and the parameters that I have used. However, it is interesting to see how the numerical values change with parameter changes. For example, the cost of being unmated increases with the proportion of females that are unmated, and for a given pair of fitness functions for sons and daughters, the cost of being unmated can change when the distribution of available host sizes changes. These things are shown in Tables 1-4 and **Figs. 14, 15 and 16**.

### **The effect of differences in host-size distribution**

Even if the fitness functions for sons and daughters are the same, the optimal sex ratio and the cost of being unmated are different when host-size distributions are different. This can be seen by plotting fitnesses and standardized fitnesses against host size quantile for different host size distributions. **Figs. 3 and 4** were drawn for the fitness functions illustrated in **Fig. 1** and the host-size distribution shown in **Fig. 2**. I think of the host-size distribution illustrated in **Fig. 2**, which has an average host size of  $\mu = 2$ , as a *small* host-size distribution. **Figs. 5 and 6** are similar to **Figs. 3 and 4**, except that they are based on a *medium-sized* host distribution, having the same shape as the distribution illustrated in **Fig. 2**, but having an average host size of  $\mu = 4$ . **Figs. 7 and 8** are similar to **Figs. 3 and 4**, and to **Figs. 5 and 6**, except that they are based on a *large* host distribution, which has an average host size of  $\mu = 8$ .

[Put Figures 5-8 here.]

### **Finding the cost of being unmated**

There are two natural cases to consider in trying to measure the cost to a female parasitoid of being unmated. First, what is the cost to one parasitoid of being unmated if all others are mated? Second, and more generally, what is the cost of being unmated if some proportion,  $p$ , of all females are unmated, and the remaining proportion,  $1 - p$ , are mated?

For the first case I find the critical host size,  $c^*$ , assuming that everyone is mated. Then I standardize the fitnesses, so that  $W_s(c^*) = W_d(c^*)$ , and  $w_s(k^*) = w_d(k^*)$ . Then I plot  $w_s(y)$  and  $w_d(y)$  against host size quantile,  $y$ . The result is illustrated in **Figs. 4, 6 and 8**. The curves in Figure 4, and a vertical line drawn at the optimal sex ratio, break the potential contributions to fitness into four parts, which I have numbered. [Here I denote the area indicated by the number 1 as (1).] A mated female using optimal sex allocation will produce sons to the left of the vertical line and daughters to the right. That is,  $S = (1) + (2)$ , while  $D = (3) + (4)$ . A mated female can produce both sons and daughters, so her total fitness from sons and daughters would be  $T_m = (1) + (2) + (3) + (4)$ . An unmated female could only produce sons. She would produce sons on the same small hosts as a mated female, that is, in areas (1) and (2), but she would also produce sons on large hosts, where her yield would only be (4). Thus, an unmated female would have total fitness from sons equal to  $T_u = (1) + (2) + (4)$ . The difference between the fitness of mated and unmated females is (3). The “cost of being unmated” could be written as  $(3)/[(1) + (2) +$

(3) + (4)], which is the proportion of fitness that a mated female would lose if she were unmated. Equivalently, we could talk about (3)/[(1) + (2) + (4)] as the “advantage of being mated,” because it would be the proportion of fitness that an unmated female would gain by being mated. This latter way of talking might be misleading, however, especially in the case in which all but one females are mated.

In the general case, in which proportion  $p$  of females are unmated, it is necessary to use a slightly different formula for total fitnesses through sons and daughters,  $S$  and  $D$ , respectively. This is because sons can be produced by either mated or unmated mothers, while daughters can only be produced by mated mothers. Thus, equations (1) and (2) are modified as follows:

$$S = p \int_0^{\infty} W_s(x) f(x) dx + (1 - p) \int_0^c W_d(x) f(x) dx , \quad (6)$$

$$D = (1 - p) \int_c^{\infty} W_d(x) f(x) dx . \quad (7)$$

The results are illustrated in **Fig. 9**. Unlike in **Fig. 4**, the area representing the production of males has parts due to mated mothers—areas (1) and (2) in **Fig. 9a** are as in **Fig. 4**—but it also has a part due to unmated mothers—area (5) in **Fig. 9b**. The production of daughters is seen in **Fig. 9a**. The areas in parts **a** and **b** of **Fig. 9** are weighted according to the proportions of mated ( $1 - p = 0.8$  in this illustration) and unmated ( $p = 0.2$  in this illustration). The fitnesses illustrated in **Fig. 9** have been standardized so that the area for males, [(1) + (2) + (5)], equals that for daughters, [(3) + (4)].

[Put Figure 9 here.]

It is important to understand that I calculate the critical host size to maximize the fitness of mated females, subject to the condition that a certain proportion of females are unmated.

### **Example 2. Calculations for a simpler example**

The calculations illustrated in the figures above had to be done numerically using a computer. However, it is possible to find an example for which the calculations are transparent.

Fitness of sons is assumed to be constant, and without loss of generality I can set

$$W_s(x) = 1 \text{ for all } x.$$

In fact, I want to treat fitness as a function of host size quantile,  $y$ , not host size,  $x$ , so I will have

$$w_s(y) = 1 \text{ for } 0 < y < 1. \quad (9)$$

I want the fitness of daughters to be an increasing function of host size, and the simplest such function of host size quantile would be

$$w_d(y) = y \text{ for } 0 < y < 1. \quad (10)$$

I will refer to this part of the example, using equations (9) and (10) as **Example 2a**. I will break the treatment of Example 2a into two cases: (i) All females but one are mated, and (ii) Proportion  $p$  of the females are unmated.

**Case (i): all females but one are mated**

Since male fitness is 1, fitness through the production of sons is equal to the proportion of sons produced,

$$S = k, \quad (12)$$

and fitness through the production of daughters is the integral

$$D = \int_k^1 w_d(y) dy = \int_k^1 y dy = (1 - k^2)/2. \quad (13)$$

Taking the derivative of the product,  $SD$ , with respect to the sex ratio,  $k$ , and setting it equal to zero yields the equation

$$3k^2 - 1 = 0, \quad (14)$$

from which we see that the optimal sex ratio is

$$k^* = \sqrt{3}/3 \approx 0.577.$$

The cost of being the only unmated female is found by calculating the triangular area (3) illustrated in **Fig. 10**. The area of (3) is  $(1 - k^*)^2 / (2k^*) = 0.1547$ , which means that the cost of being unmated is  $(3) / [1 + (3)] \approx 13.3\%$ .

[Put Figure 10 here.]

**Case (ii): Proportion  $p$  of females are unmated**

In this case, fitness produced through sons is

$$S = p + (1 - p)k, \quad (15)$$

While fitness produced through daughters is

$$D = (1 - p) (1 - k^2)/2. \quad (16)$$

Now take the derivative of the product,  $SD$ , with respect to  $k$  and set equal to zero. A quadratic equation results:

$$3(p - 1)k^2 - 2pk + (1 - p) = 0. \quad (17)$$

From this it follows that the optimal sex ratio is

$$k^* = \{\sqrt{[p^2 + 3(1 - p)^2]} - p\} / 3(1 - p). \quad (18)$$

This reduces to  $k^* = \sqrt{3}/3$  if  $p = 0$ , which is **Case (i)**.

For Example 2a, once the optimal sex ratio for mated females,  $k^*$ , has been found, the cost of being unmated,  $C$ , can be calculated using the fact the formula

$$C = (1 - k^*)^2 / (1 + k^{*2}), \quad (19)$$

which can be seen from **Fig. 11**, using plane geometry and a little algebra to rearrange fractions.

[Put Figure 11 here.]

Example 2a is simple, and total male and female fitnesses can be expressed in simple forms: (12) and (13) or (15) and (16). However, it is unrealistic to have such a steep fitness function for daughters as expression (10). Perhaps it would be better to have the lowest possible fitness for daughters to be greater than zero, but still consider the fitness of daughters to be a linearly increasing function of host size quantile. Such a possible female function for daughters is shown in an illustration given by King (1993, Figure 12.1B), except that King's fitness function plots fitness against host size instead of host size quantile.

### The cost of producing the wrong sex ratio

The cost of producing the wrong sex ratio is analogous to the cost of being unmated. If a female is unmated, she can only produce sons, so her proportion of sons is 1. The cost of being unmated is seen in terms of an area [area (3)] in **Fig. 4** and other figures. The cost of producing the wrong sex ratio may be visualized with a picture very much like **Fig. 4**. Consider a particularly nice example, that illustrated in **Fig. 11a** for Example 2a, where proportion  $p = 0.2$  females are unmated. In this case, the optimal proportion of sons for mated females to produce is 0.5, and the cost of being unmated in  $C = 0.2$ .

Now, consider a mated female that produces sons in small hosts and daughters in large hosts (that is, she does roughly the right thing), but she chooses the wrong critical host size,  $c$ , and this results in her producing a proportion sons equal to  $k = 0.75$ , instead of the optimal  $k^* = 0.5$ , which all the other mated females use. Her loss is illustrated in area (3a) in **Fig. 12**. The size of her "mistake" is half the size of the "mistake" of being unmated  $(0.75 - 0.50) = (1/2) \times (1.00 - 0.50)$ , and the area representing her loss is 1/4 of the loss incurred by being unmated (the triangles representing the losses are similar and the side of one is half the side of the other). Therefore, her cost for producing the wrong proportion of sons would be  $(1/4) \times 0.20 = 0.05$ . If the proportion of sons produced by a mated female is not so far from the optimal, say it is 0.4 or 0.6 for this example, the loss is represented by a smaller triangle, in this case with a side of length equal to 0.1 instead of the 0.5 which it would have for an unmated female, and the cost of an error of this size would be  $(0.1/0.5)^2 \times 0.20 = 0.008$ , or 0.8%, which is a pretty small cost. The general

conclusion is that if other mated females use the optimal sex ratio, a mated female that produce a sex ratio that is a moderate amount away from the optimal will not lose much.

[Put Figure 12 here.]

In practice, the allocation of offspring sex to hosts of various sizes is not exact. But my calculations suggest that this may not matter. For example, what if in the above example a female produces sons in the smallest quarter of hosts and daughters in the largest quarter of hosts, and for the half of hosts that are in the middle, she produces sons and daughters at random. How much does she lose? For hosts in the third quartile of size, she would lose half the amount she would if she produced sons rather than daughters, since she should produce daughters and does so half the time. On the other hand, for hosts in the second quartile, she should produce sons, and does so half the time. Therefore she would lose half as much as she would if she produced daughters for all hosts in the second size quartile. Overall, the cost of her choosing the sex of her offspring correctly in the most extreme cases, and randomly in the remaining half of the cases would be  $C = 0.05$ .

### **Example 2b—female fitness is a linear function of host quantile**

Again, as for Example 2a, I break this example into two cases, according to whether all females are mated except one [**case (i)**], or some proportion,  $p$ , of females are unmated [**case (ii)**].

#### **Case (i): All females are mated except one**

Assume that the fitness of sons is constant, and again, without loss of generality, I can assume that

$$W_s(x) = 1 \text{ for all } x.$$

For practical purposes, I want to consider the fitness of sons as a function of host size quantile, so, of course, I have

$$w_s(y) = 1 \text{ for } 0 < y < 1.$$

Now, I want female fitness to be a linear function of host size quantile, but instead of starting with fitness 0 for the smallest host size that is attacked [that is,  $w_d(0) = 0$ ], I want to start with fitness  $a$  for the smallest host size that is attacked [that is,  $w_d(0) = a$ ]. If the maximum fitness of daughters is to equal 1, then we must have

$$w_d(y) = a + (1 - a)y \text{ for } 0 < y < 1.$$

We might begin by thinking of the fitness of daughters as having a uniform distribution on the interval  $(a,1)$ . I will treat Example 2b exactly the same way as I treated Example 2a, that is, I will treat female fitness as if it were proportional to host

quantile:  $w_d(y) = y$  for  $0 < y < 1$ , but I calculate overall fitness through the production of daughters by considering only host size quantiles greater than  $a$ .

I think of a critical host size quantile in terms of a value  $k$ , the fitness of a daughter produced in a host of that size quantile, which must be in the interval  $(a,1)$ . Then, total fitness through the production of sons will be

$$S = (k - a)/(1 - a), \quad (20)$$

and the fitness through the production of daughters would be

$$D = (1 - k^2) / [2(1 - a)]. \quad (21)$$

I want to find the value of  $k$  that maximizes the product  $SD$ , and to do this I can ignore the numerators in (20) and (21). Taking the derivative of the product  $SD$  with respect to  $k$  and setting the derivative equal to zero yields the following quadratic equation:

$$3k^2 - 2ak - 1 = 0, \quad (22)$$

for which we have the solution

$$k^* = [a + \sqrt{(a^2 + 3)}] / 3. \quad (24)$$

However, I am not interested in  $k$  itself, but rather the optimal sex ratio and the cost of being unmated. The optimal sex ratio that  $k$  would specify is

$$S. R. = (k^* - a) / (1 - a), \quad (25)$$

which would be

$$S. R. = [\sqrt{(a^2 + 3)} - 2a] / [3(1 - a)], \quad (26)$$

Equation (26) produces the familiar answer,  $S. R. = \sqrt{3}/3$ , for the case  $a = 0$ .

A little bit of geometry and a little bit of algebra yields a formula analogous to (19),

$$C = (1 - k)^2 / (1 + k^2 - 2ak). \quad (27)$$

[Put Figure 13 here.]

**Fig. 13**, which is comparable to **Figs. 4, 6 and 8**, shows the standardized fitnesses of sons and daughters for example 2b with  $a = 0.5$ . Notice that in this case, however, the sex ratio is not equal to  $k^*$ , but to  $(k^* - a)/(1 - a)$ .

**Case (ii): Proportion  $p$  of females are unmated**

In Example 2b, if proportion  $p$  of females are unmated and must produce only sons, then the total production through sons is

$$S = p + (1 - p) (k - a) / (1 - a), \quad (28)$$

and the total production through daughters is

$$D = (1 - p) (1 - k^2) / [2(1 - a)]. \quad (29)$$

Taking the derivative of the product,  $SD$ , with respect to  $k$  and setting the derivative to zero yields the quadratic equation:

$$3(1 - p)k^2 + 2(p - a)k - (1 - p) = 0. \quad (30)$$

Solving for  $k^*$  yields

$$k^* = \{a - p + \sqrt{[(a - p)^2 + 3(1 - p)^2]}\} / [3(1 - p)]. \quad (31)$$

Unfortunately, this  $k$  is not the desired sex ratio. Rather, the optimal sex ratio is

$$S. R. = (k^* - a) / (1 - a).$$

The cost of being unmated can be calculated plugging the value for  $k$  given in expression (31) into the formula for  $C$  given in expression (27).

Some results for Examples 2a and 2b will be given, along with some results for Example 1, in the Results section.

### **The cost of being unmated in gregarious parasitoids.**

The cost to gregarious parasitoids of being unmated seems to be greater than the cost to solitary parasitoids. Here I will look at only one example in one way. The example is Hamilton's (1976) diploid model for local mate competition. The way I will look at this example is to assume that almost all parasitoids are mated ( $p = 0$  in my solitary parasitoid example).

In Hamilton's (1976) diploid model, each brood is produced by  $n$  foundresses and the optimal proportion of sons is

$$r = (n - 1)/2n. \quad (32)$$

Without loss of generality, I can assume that each foundress lays a clutch of size  $2n$ , which for mated females using the optimal sex ratio will consist of  $n - 1$  sons and  $n + 1$  daughters. If all clutches within each brood are the same, then, on average, each clutch results in

$$2(n + 1) \tag{33}$$

genes,  $n + 1$  through daughters and  $n + 1$  through sons. However, if there is a rare unmated female, who lays a clutch of  $2n$  unfertilized eggs among  $n - 1$  clutches, each with  $n - 1$  unfertilized eggs and  $n + 1$  fertilized eggs, the unmated female will produce proportion

$$2n/[2n + (n - 1)^2] = 2n/[n^2 + 1] \tag{34}$$

of the sons. Then, assuming random mating on the host between sons and daughters, where there are

$$(n - 1)(n + 1) = n^2 - 1 \tag{35}$$

daughters, the number of genes that the unmated female gets out is the product of (34) and (35), namely

$$2n(n^2 - 1)/(n^2 + 1). \tag{36}$$

The cost of being unmated is the difference between the number of genes gotten into the next generation by mated and unmated females, divided by the number of genes gotten into the next generation by mated females, that is,  $C = [(33) - (36)]/(33)$ , which is

$$C = (n + 1)/(n^2 + 1). \tag{37}$$

If, using formula (32), we infer values of  $n$  from commonly seen proportions of males between 0.30 and 0.40, we get values of  $n$  from slightly less than 3 to slightly more than 4. For  $n = 3$  we have  $C = 4/10 = 0.400$ , and for  $n = 4$  we have  $C = 5/17 \approx 0.294$ . These are substantial costs of being unmated.

I have not tried to investigate how the cost of being unmated depends on the proportion of females unmated. If almost all females are mated, no host is likely to be attacked by more than one unmated female and most hosts will be attacked by none, but if a substantial fraction of females are unmated, there hosts may be attacked by various numbers of unmated females and the calculation will be more difficult.

## RESULTS

I have described two particular examples of the host quality effect in parasitoids. In both examples the relative fitness of daughters increases faster than the relative fitness of sons as host size increases. The *optimal behavior* for a solitary parasitoid is to produce sons in smaller hosts and daughters in larger hosts, with smaller and larger hosts divided by some *critical size* such that sons and daughters are equally valuable if produced on hosts of that size. If all parasitoids allocate the sex of their offspring optimally, the overall sex ratio of offspring will equal some *equilibrium value*.

Example 1 embodies some reasonable assumptions about the fitness function of offspring. For the smallest hosts, fitness is zero. As host size increases, fitness increases for both sexes, but faster for sons at first. But for larger hosts, female fitness increases faster with host size. For large enough hosts, both sons and daughters achieve their maximum fitness. While this example is moderately realistic, it is relatively difficult to handle mathematically, and equations must be solved numerically.

Example 2 is simpler and easier to handle mathematically, but it makes the possibly unrealistic assumption that the fitness of sons is constant over all host sizes. Example 2 also is based on the assumption that the fitness of daughters is almost as simple, being a linearly increasing function of host size quantile.

### **Example 1.**

#### **The optimal sex ratio and the cost of being unmated**

Table 1 gives the optimal sex ratios and the cost of being unmated for three different host size distributions. In Example 1, the optimal proportion of sons decreases from 69% when host sizes tend to be small to 51% when they tend to be large. That is, the optimal sex ratio can change from strongly male-biased to almost unbiased when the host size distribution changes from small to large, and this can happen even if the fitness functions remain the same.

[Put Table 1 here.]

Similarly, the cost of being unmated can change radically when the host size distribution changes, as Table 1 also shows. For Example 1, the cost of being unmated decreases from about 14% to about 2% as the host size distribution changes from small to large. When a typical host is large enough to produce a fit daughter, then there is little loss to being unmated, at least if not too many other females are unmated.

The last column in Table 1 compares the fitness through daughters of females that produce the optimum proportions of sons and daughters under three different host size distributions. This is not of importance for understanding the nature or consequences of behavioral decisions. However, if competing species differ in how well adapted they are to hosts of various sizes, then these values suggest that if one parasitoid species was as well adapted to small hosts as another species was to large hosts, and if hosts tended to be small, then the species adapted to smaller hosts would be almost three times as fit as the one adapted to larger hosts.

### **Example 2.**

#### **The optimal sex ratio and the cost of being unmated**

In Example 2 it is assumed that the fitness of sons does not depend on host size and that the fitness of daughters increases linearly with host size quantile. For both Example 2a and 2b I assume that

$$w_s(y) = 1 \text{ for } 0 < y < 1.$$

### Example 2a.

For Example 2a I add a particular assumption about the fitness of daughters:

$$w_d(y) = y \text{ for } 0 < y < 1.$$

Proportion  $p$  of females are assumed to be mated. They produce only sons.

**Fig. 14** shows the changes in the optimal proportion of sons that a mated female should produce and the cost of being unmated as the proportion of unmated females changes. It is seen that the optimal proportion of sons for a mated female to produce decreases as the proportion of unmated females decreases, but the overall proportion of sons increases fairly rapidly. It should be noted that the optimal proportion of sons produced by mated females stays positive, even when most of the females are unmated and are all producing sons. Notice that **Fig. 14** is labeled as a case in which  $a = 0$ . That this means is that Example 2a can be thought of as special case of **Example 2b** in which the parameter  $a = 0$ .

[Put Figure 14 here.]

The cost of being unmated increases as the proportion of unmated females increases, and it is particularly large for when this proportion is large. This may be why large proportions of unmated females are not found in nature. The numbers on which Figure 14 are based are given in Table 2.

[Put Table 2 here.]

### Example 2b.

For **Example 2b** I again assume that the fitness of sons is constant and equals one. However, instead of ranging from 0 to 1, I want the fitness of daughters to vary from some constant value,  $a$ , to 1, where  $0 < a < 1$ . I want the fitness of daughters to be uniformly distributed on the interval  $(a,1)$ , which I could indicate by writing

$$w_d(y) = a + (1 - a)y \text{ for } 0 < y < 1.$$

[In fact, I find it convenient to use a little trick. I think of the fitness of daughters as varying from 0 to 1, which I would write as

$$W_d(x) = x,$$

where  $x$  is host size, and host size is uniformly distributed on the interval  $(a,1)$ . That is,  $f(x) = 1/(1 - a)$  for  $a < x < 1$ .]

I have done all my calculations for Example 2b using the value  $a = 0.5$ . It is possible to interpret the relationship between Examples 2a and 2b in terms of the host size

distribution. Example 2a may be thought of as involving hosts whose size ranges from small to medium, while Example 2b involves hosts whose size ranged from medium to large. In practice, what this means is that the fitness of daughters can be small (as small as 0) in Example 2a, while in Example 2b, the least fit daughters have a = 0.5 times the fitness of the fittest daughters.

**Fig. 15** plots sex ratio and fitness against the proportion of unmated females. It is seen that the optimal proportion of sons is greater than 0.5 (it is 0.535) when there are no unmated females, and that this proportion of sons decreases at an increasing rate to zero as the proportion of unmated females increases to a value of  $p = 0.6$ . The overall proportion of males increases slowly to a value of 0.6 as the proportion of unmated females increases to 0.6. For larger proportions of unmated females, mated females should produce no sons and the overall proportion of males equals the proportion of unmated females who produce them.

[Put Figure 15 here.]

The cost of being unmated begins with a fairly small value ( $C = 0.066$ ), and it increases slowly as the proportion of unmated females increases. If the proportion of unmated females is  $p = 0.2$  (a fairly large value in nature) the cost of being unmated is  $C = 0.10$ . More numbers are given in Table 3.

[Put Table 3 here.]

### **Example 2c.**

Example 2c is actually a limiting case of Example 2b with  $a = 1$ . If  $a = 1$  then the fitnesses of sons and daughters are the same and do not depend on host size. For this case, which was treated by Godfray (1990), the cost of being unmated is zero unless the proportion of unmated females exceeds  $p = 0.5$ . If the proportion of unmated females exceeds 0.5, then the cost of being unmated is given by the formula  $C = 2 - 1/p$ . The optimal proportion of sons for mated females follows a hyperbolic curve given by the equation  $k^* = (1 - 2p)/(2 - 2p)$  for  $0 \leq p \leq 0.5$  and is zero for  $p > 0.5$ . This optimal sex ratio for mated females results in an overall proportion of males equal to 0.5 as long as the proportion of unmated females is no larger than one-half. If the proportion of unmated females is greater than one-half, then the overall sex ratio equals the proportion of unmated females. Curves for the optimal proportion of sons for mated females, the overall proportion of sons and the cost of being unmated are shown in **Fig. 16**. The formula for the optimal proportion of sons for mated females was given and its form was illustrated by Godfray (1990, p. 4 and Figure 1).

[Put Figure 16 here.]

## **DISCUSSION**

The advantage of using mathematical models to help understand biological problems is that they show how to connect a set of assumptions about the world with conclusions about what would be observed if the assumptions were true. These conclusions may lead

to novel predictions, or, as is the case with this paper, they may lead to an understanding of some things that have already been observed. If the assumptions of the model and the argument made by the model are correct, then the conclusions should follow. However, if the conclusions are known to be false, then one can look at the assumptions and the argument to find a flaw. Thus, with a model one can work forward from assumptions to predictions, but one can also work backward from incorrect predictions to modify the assumptions or the argument.

In this paper I have used some assumptions which are interesting and suggestive in themselves. The optimal allocation of offspring sex in hosts of differing quality depends not only on host quality (I use size as a proxy for quality), but also on the distribution of host quality. This point is easily seen from the model, and is now understood by students of parasitoid ecology and behavior, but it was not always recognized by entomologists.

### **Assumptions and method**

MacArthur's (1965) "product rule" is a convenient idea to use in studying sex allocation, and writing the overall fitness from sons and from daughters as integrals, seen in equations (1) and (2), is intuitively understandable and provides a mathematically tractable formulation. Then, looking at the resulting equation (3) shows that the critical host size depends on the fitness of sons and daughters in hosts of various sizes, but it also depends on the overall effort dedicated to producing sons and daughters. That is, the decision of whether to produce a son or daughter on a host of a given size depends not just on the size of that host and the fitnesses that sons and daughters would have on that host, but it also depends on the decisions that other parasitoids make when faced with other hosts.

I have used two ideas to make the results of my calculations more tractable. One is to treat fitness as a function of host size quantile rather than host size. This permits the visualization of  $S$  and  $D$ , the overall fitnesses through the production of sons and daughters, as areas under the fitness curve. The second is to make the fitness functions comparable by equating the values of the fitness functions for sons and daughters for the critical host size (the host size at which it is equally valuable to produce a son or a daughter). These two ideas together permit one to visualize the cost of being unmated as an area between two curves in an illustration, such as **Fig. 4** or **6** or **8**. In fact, for Example 1, it is convenient to do the calculations using the definitions of  $S$  and  $D$  given in equations (1) and (2). However, it is easier to see what calculations to do after visualizing the problem considering host size quantile rather than host size. In Example 2 I described fitnesses directly in terms of host size quantile.

### **Numerical calculations**

Several numerical calculations are interesting, even if the exact form of the model and the parameters used are chosen arbitrarily, without reference to empirical observations. One can see what numbers arise from the calculations, but more important, one can see that the numbers depend on the parameters chosen, and one can see qualitatively how results change as conditions change. For example, the optimal sex ratio is more strongly

male-biased and the cost of being unmated is greater when hosts are smaller (and the relative fitnesses of the sexes are changing most rapidly as host size changes). The optimal sex ratio for mated females decreases, and the cost of being unmated increases, as the proportion of mated females increases. Even when I have looked at examples that exaggerate the cost of being unmated (Example 1 for small hosts, Example 2a), I find that the cost of being unmated is not huge, at least if the proportion of unmated females is not large.

Several general results arise from this model. One, which was observed before [Godfray 1994; (see also Ode and Hardy 2008) mentions some examples of writers who made the observation, beginning in the late 1980s], is that *sex ratios should always be male-biased*. In fact, solitary parasitoids do not always show male-biased sex ratios, a fact that I will discuss below. Another result is that *there is always a cost of being unmated*. This possibility was ignored in some early work, for example, that by Godfray (1990) and by Godfray and Hardy (1993), but, as my calculations show, this cost may be very small, in fact, small enough to be negligible. The cost of having the wrong sex ratio can be calculated in a similar way to that used to calculate the cost of being unmated. It is seen that for practical purposes, it may not matter much if parasitoids choose an imprecise rule to decide how to allocate offspring. What evidence there is indicates that parasitoids are far from precise in the rule they use to allocate the sexes to hosts of various sizes. It is possible that parasitoids do not measure host quality in exactly the same way that biologists do, but it is interesting that the cost of imprecision suggested by observations of sex allocation behavior seems to be what one might expect from theory.

### **The connection of the theory with reality**

The final question about any theory is what is its relation with reality. My calculations reveal a cost of being unmated, but this cost is large only under certain circumstances. When there is a cost of being unmated, theory says that this cost increases with the number of females unmated. That is, if some unmated females reproduce, there should not be too many of them. While it is difficult to measure the proportion of unmated females in a population, what evidence there is indicates proportions from 0 to about 0.20, with smaller values more common (Godfray and Hardy 1993).

The relative rarity of unmated females suggests that there might be some disadvantage to being unmated. The fact is that some parasitoids do tend to produce sons in smaller hosts, and females in larger hosts, but they do not do so by changing sex at some precise critical host size. The optimal strategy found in my model calls for such a precise critical value, but calculations suggest that being precise in this way does not matter very much to the animals. This is an advantage of a quantitative treatment of a theory, it does not just show what the best strategy is, but it can also show how much it matters to an animal what it does.

One of the more interesting results of my model, although not original with me, is that optimal sex allocation would always result in male-biased sex ratios. This bias may be small, but certainly, female-biased sex ratios are never favored in my model. However,

female-biased sex ratios are sometimes seen in solitary parasitoids. When this happens, does this invalidate my model? I would say that it does not. What is wrong with the model is the assumption of random mating.

### **Random mating: where does it take place?**

The assumption of random mating is common in evolutionary models, particularly in genetic models. In the paper in which he introduced the name “constrained oviposition” for the problem that I am treating in this paper, Charles Godfray (1990) referred to the assumption of “panmixia” or random mating throughout a population. This is probably the most common interpretation of the idea of random mating. However, for parasitoids, the local structure of mating is very important, and I think that one should distinguish among three different levels at which one might imagine “random mating” as taking place. Random mating might take place (1) globally, in the whole species population, or (2) regionally, in a regional population, or sub-population, small enough to be influenced by local conditions different from that in other parts of the species population, but large enough to make negligible the proportion of matings that are with sibs, or (3) locally, where some, perhaps much mating takes place within a colony of hosts, or a colony of colonies and the proportion of matings with sibs is non-negligible. At level (3), mating might be random with respect to degree of relatedness, but it would take place over a restricted area in which sibs are likely to be encountered.

#### Global random mating

What one would expect from a model of the host quality effect would depend on where mating takes place. Even if we assume random mating, we get different results, depending on exactly what we mean by that phrase. If random mating were to be global, then the sex allocation decisions of all females should be the same, independent of local or regional conditions. If, for example, in most regions, the host distribution is small, the critical host size would be small in all regions. But if in one region the host distribution is large, then since parasitoids in this region use the same small critical host size as parasitoids in other regions, they would find most of their hosts larger than the critical value and produce daughters. This would result regionally in a strongly female-biased sex ratio.

#### Regional random mating

Of course, random mating at a global level is unlikely in practice. It is more likely, but perhaps still not very likely, at a regional level. This would still be random mating in the important sense that sib-matings are unlikely, but female-biased sex ratios would not be expected at the regional level. The regional level is probably what Charnov had in mind in his early work on the host quality problem (Charnov 1979; Charnov et al. 1981). One idea of Charnov and his collaborators, especially van den Assem (1971), was that sex allocation decisions might depend on the experience of a parasitoid. That is, not only would her decision be based on the quality of host being attacked now, but on her experience of other hosts. While the evidence that parasitoids modify their oviposition strategies based on their previous experience was not particularly convincing—especially

the work of Chewyreu (1913)—the idea is intriguing. [In Appendix 2 I analyze the data of Chewyreu that van den Assem (1971) and Charnov (1979) offered as evidence of what I refer to here as random mating at the regional level.]

### Local random mating

If solitary parasitoids have female-biased sex ratios, this is probably because a substantial proportion of their matings are with sibs. The phenomenon of having some matings with some sibs on the natal host and some non-sibs off the natal host (and perhaps some on) has been referred to as “partial local mate competition” (Werren and Simbolotti 1989). One can conceive of a general treatment, possibly with some matings with sibs on the natal host and some off, and some matings with non-sibs on the natal host and some off. For a diploid model, if proportion  $r$  of all matings are with sibs, then the optimal sex ratio,  $\sigma:\varphi = (1 - r):(1 + r)$ .

If we combine the possibility of sib-matings with the question of the host quality effect, we might conjecture that an optimal sex allocation strategy would be to produce males in small hosts and daughters in large hosts, but to separate sons and daughters by using a critical host size determined by modifying equation (3) and solving

$$(1 - r) W_s(c^*) : W_d(c^*) = (1 + r) S : D$$

for the critical host size  $c^*$ . Werren (1984) treated this problem of combining consideration of the host size effect and local mate competition. However, he followed Charnov (1979) in assuming that hosts were of two sizes.

### How strong is selection against being unmated?

My measure,  $C$ , of the cost of being unmated measures the difference in fitness between a mated female that produces sons and daughters using the optimal sex allocation strategy and an unmated female that is only able to produce sons. My  $C$  is this fitness difference between mated and unmated females divided by the fitness of an mated female. That is, my measure of the cost of being unmated compares mated and unmated females. But natural selection does not operate on mated or unmated females, but on some anatomical or physiological or behavioral characteristics that affect the chance of being unmated.

For example, imagine a solitary parasitoid, which mates off (say far off) the natal host. Females produce and emit pheromones, which males detect and follow to find mates. Now, imagine that females produce a pheromone and males detect it in such a way that only 60% of females are mated. Imagine, further, that there is a mutation that improves the pheromone production and detection systems such that 80% of females are now mated, but this improvement comes with a metabolic cost. Is this mutation favored by natural selection? This question cannot be answered without knowing the costs, but I will show how to measure the strength of the force of selection against being unmated.

The cost of being unmated,  $C$ , is a fitness cost for an unmated individual, but not for a strategy or genotype. The value of  $C$  depends on the proportion of females unmated,  $p$ ,

so I can write it as a function of this proportion, namely,  $C(p)$ . If a certain strategy results in proportion  $p$  females being unmated, and each of the unmated females suffers cost  $C(p)$ , then the total cost due to this strategy due to producing unmated females is the product,  $pC(p)$ . In Example 2a, for which the costs of being unmated,  $C$ , are plotted in **Fig. 14** and given in Table 3, we have that if 20% of females are unmated, then  $C(0.2) = 0.2$ , which implies that  $pC(p) = 0.2 \times 0.2 = 0.040$ . However, if 40% of females are unmated, then  $C(0.4) = 0.315$ , which implies that  $pC(p) = 0.126$ . The difference between the total cost for  $p = 0.2$  and  $p = 0.4$  is  $0.126 - 0.040 = 0.086$ . This is how much of the total cost due to unmated females would change if the strategies change from one resulting in 40% of females being unmated to one resulting in 20% of females being unmated.

The total cost of being unmated can be visualized as a rectangular area whose dimensions are the proportion of females unmated,  $p$ , and the cost of being unmated  $C(p)$ . This is illustrated in **Fig. 17**. The force of selection against being unmated can be visualized as the difference between the areas of the two rectangles. If  $C(p)$  increases with  $p$ , then the force of selection against being unmated also increases with  $p$ . The fact that the proportion of unmated females is seldom observed to be large says something about the relative costs and benefits of producing efficient mate-finding strategies.

[Put Figure 17 here.]

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## APPENDIX 1: Ideas about the gamma distribution, which is used in Example 1 for the host size distribution and for the fitness functions for sons and daughters

The fitness functions for sons and daughters and the host size distribution used in Example 1 are all based on the gamma distribution. The family of gamma distributions is a rich family of distributions that is useful in fitting non-negative, continuous-time variables such as size and waiting time.

I parameterize gamma distributions using the form and notation of DeGroot (1970). If  $X$  is a random variable of interest, host size, for example, then the probability density function of  $X$  is given by the formula

$$f(x; \alpha, \beta) = K x^{\alpha-1} e^{-\beta x} \text{ for } x > 0, \quad (\text{A1})$$

where  $K = \beta^\alpha / \Gamma(\alpha)$  is the constant of integration. With this parameterization, the mean of the variable  $X$  is  $\mu = \alpha/\beta$  and the variance is  $\sigma^2 = \alpha/\beta^2$ .

In Example 1 I use a gamma distribution with shape parameter,  $\alpha = 8$  for all three host size distributions. For a small host distribution I use a scale parameter of  $\beta = 4$ , yielding a mean host size of two. For medium and large host distributions I use  $\beta = 2$  and  $\beta = 1$ , respectively, yielding mean host sizes of four and eight, respectively.

For all three distributions of host size I use the same fitness functions for sons and daughters. For sons, the fitness function is the cumulative distribution function of a gamma-distributed variable with parameters  $\alpha = 2$  and  $\beta = 1$ , while for daughters, the fitness function is the cumulative distribution function of a gamma-distributed variable with parameters  $\alpha = 4$  and  $\beta = 1$ . Notice that the maximum fitness for both sexes is one.

The cumulative distributions (fitness functions) could be calculated approximately using the density function (A1), but since I consider gamma distributions with integer parameters, the cumulative distributions can be calculated using the connection between the gamma distribution and the Poisson distribution through the Poisson process. Thus, the cumulative distribution of host size,  $X$ , is written as

$$F(x) = P(X \leq x) = P(N_x \geq \alpha) = 1 - P(N_x \leq \alpha - 1), \quad (\text{A2})$$

where  $N_x$  is a Poisson-distributed random variable with a mean of  $\mu = \beta x$ .

In my calculations, for each value of host size,  $x$ , there are values of the fitness of sons,  $W_s(x)$  and the fitness of daughters,  $W_d(x)$ , and the value of the host density function  $f(x)$ . In **Fig. 1** I plot the fitnesses for sons and daughters and in **Fig. 2** I plot the density function for host size,  $f(x)$  and also the cumulative distribution,  $F(x)$ . In **Fig. 3** I plot the fitness functions for sons and daughters against the cumulative distribution of host size,  $F(x)$ , which I denote as  $y$ . That is,  $y = F(x)$ . In **Fig. 4** I plot the standardized fitnesses of sons and daughters, both plotted as functions of the cumulative distribution of host size, which I refer to as host size quantile. **Fig. 4** differs from **Fig. 3** in one important way, the

scale of the fitness function for daughters is changed so that the fitnesses of sons and daughters will coincide when host size assumed its critical value,  $c^*$ . That is, I multiply the scale of the fitness of daughters shown in **Fig. 3** by an appropriate constant, which equals 3.37 for the case of a small host size distribution, which is illustrated in **Figs. 2**. For a medium host size distribution the appropriate constant is 1.53, which is used to pass from **Fig. 5** to **Fig. 6**, and for a large host size distribution, the appropriate constant is 1.047, which is used to pass from **Fig. 7** to **Fig. 8**.

## APPENDIX 2. An analysis of some data in a paper by Chewyreuv

In an important paper in the history of sex allocation in wasps, Ivan Chewyreuv (1913) presented evidence that Ichneumonid wasps produce sons in small hosts and daughters in larger hosts. He also showed that unmated females produce sons only, and they produce smaller sons in smaller hosts and larger sons in larger hosts. When previously unmated females that had produced only sons were mated, they produced both sons and daughters. The only explanation that Chewyreuv could suggest for this latter pattern was that mated wasps produced daughters by fertilizing their eggs and they produced sons by leaving their eggs unfertilized.

For one particular *Pipla instigator* female (“female 66”), Chewyreuv offered either large or small host species, in an alternating pattern. Then he offered two species of small hosts, with one species larger than the other. One host species, *Pieris brassicae*, was the smaller host paired with larger hosts in the first part of the experiment, and was the relatively larger of two species in the second part of the experiment. As Chewyreuv put it, “[T]he *Pieris* nymphs were relatively small when they were alternating with the *Sphynx* and *Saturnia* nymphs, but they were relatively large when they were alternating with the *Vanessa* nymphs” (translation by Carl Green). All of the largest hosts produced only daughters and all of the smallest hosts produced only sons, but the *Pieris* nymphs produced both sons and daughters.

Charnov (1979) developed a model for the host size effect and referred to Chewyreuv’s (1913) result:

The model provides an answer to one somewhat puzzling aspect of Chewyreuv’s (1913) data. As discussed by Assem (1971): “A most interesting result was that it does not seem to be the absolute size of the host alone, but some relative measurements as well that play a role, though Chewyreuv does not conclude so explicitly. When he offered, again in an irregular order, (host) pupae of *Sphinx ligustri* (large) and those of *Pieris brassicae* (small), the former produced females and the latter males. If, however, the *Pieris* pupae were alternated with those of *Vanessa levana* (still smaller) the same wasps produced an offspring of females in the former and males in the latter.” This is exactly the outcome predicted under the present model. [Charnov 1979, p. 477]

I think that this comment is incorrect. Chewyreuv’s (1913) data do not provide evidence for any such relative host-size effect, and van den Assem’s description is inaccurate, as I will show below.

If my reading is correct, the sexes of the offspring produced on intermediate-sized (*Pieris*) hosts were no different when those hosts were relatively large from when the hosts were relatively small. The data show:

	Sons	Daughters
Hosts relatively small	6	2
Hosts relatively large	8	3

Note: These data are based on observations of one female (“female 66”), the only example given which is relevant to the idea that there is a relative host size effect.

To test whether there is a difference between the sex ratios for offspring in *Pieris* nymphs when the nymphs are relatively small or relatively large, we can use Fisher’s exact test. If we use the number of daughters produced in relatively small hosts ( $x = 2$  in this case) as a test statistic, we can calculate the p-value (the probability that the number of daughters is less than or equal to 2 if there is no effect of relative host size). We find a p-value of 0.664, which is nowhere near the common cutoff value of 0.05. In fact, two daughters is the most likely number to observe, given the other numbers and the assumption that there is no relative host-size effect. The distribution of the value of  $x$  under the null hypothesis of no effect is given in the following table:

x	f(x)	F(x)
0	0.0397	0.0397
1	0.2270	0.2668
2	0.3973	0.6641
3	0.2649	0.9290
4	0.0662	0.9952
5	0.0048	1.0000

Chewyreu (1913) offered no other evidence that is relevant to the idea that beyond the *host size effect*, which he demonstrated quite convincingly, there is also a *relative host-size effect*. Thus, I think that we can dismiss the claim made by van den Assem (1971) and quoted by Charnov (1979) that Chewyreu (1913) provided evidence in favor of a relative host-size effect. Charnov et al. (1981) did provide other evidence about a relative host-size effect. This evidence must be evaluated on its own, without reference to earlier work of Chewyreu, which seems to have shown that sons are produced on small hosts, daughters are produced on large hosts, and that both sons and daughters are produced on intermediate-sized hosts, but the frequencies of the sexes on intermediate-sized hosts does not depend on whether they are offered along with hosts of larger or of smaller species.

**Table 1.** Sex ratios and cost of being unmated for various host distributions

Host size distribution	Sex ratio (% males)	Cost of being unmated (%)	Expected fitness of daughters
Small	69.2	14.3	0.162
Medium	59.7	8.9	0.309
Large	50.7	2.3	0.467

The cases of small, medium and large host size distributions are illustrated in Figures 4, 7 and 9, respectively. The “expected fitness of a daughter” is the ratio of the average fitness through daughters [areas (3) and (4) in the figures], divided by the fitness of a daughter produced in the largest possible host.

**TABLE 2. COST OF BEING UNMATED—EXAMPLE 2a**

Proportion unmated, p	Optimal proportion of males, c	Proportion of males in population, r	Advantage of being mated, a	Cost of being unmated, $a/[1 + a]$
0.00	0.577	0.577	0.155	0.134
0.05	0.560	0.582	0.173	0.147
0.10	0.542	0.587	0.194	0.163
0.15	0.522	0.593	0.220	0.180
0.20	0.500	0.600	0.250	0.200
0.25	0.477	0.608	0.287	0.223
0.30	0.452	0.616	0.332	0.249
0.35	0.425	0.626	0.389	0.280
0.40	0.396	0.638	0.460	0.315
0.45	0.366	0.651	0.550	0.355
0.50	0.333	0.667	0.667	0.400
0.55	0.299	0.685	0.821	0.451
0.60	0.264	0.706	1.028	0.507
0.65	0.227	0.730	1.312	0.567
0.70	0.191	0.757	1.715	0.632
0.75	0.155	0.789	2.309	0.698
0.80	0.120	0.824	3.239	0.764
0.85	0.086	0.863	4.839	0.829
0.90	0.055	0.906	8.110	0.890
0.95	0.026	0.951	18.053	0.948

**Table 3.** Cost of being unmated—Example 2b

Proportion unmated, $p$	Optimal proportion of sons for mated females, $k^*$	Proportion of sons in population	Cost of being unmated, $C(p)$
0.00	0.5352	0.5352	0.0657
0.05	0.5129	0.5372	0.0727
0.10	0.4884	0.5396	0.0808
0.15	0.4614	0.5422	0.0903
0.20	0.4314	0.5452	0.1014
0.25	0.3981	0.5486	0.1147
0.30	0.3608	0.5526	0.1305
0.35	0.3188	0.5572	0.1496
0.40	0.2712	0.5627	0.1728
0.45	0.2169	0.5693	0.2013
0.50	0.1547	0.5774	0.2363
0.55	0.0830	0.5874	0.2797
0.60	0.0000	0.6000	0.3333

**Table A1. Data useful for Example 1**

	Host size distribution		
	Small	Medium	Large
$\mu$	2	4	8
$c^*$	2.28	4.132	7.736
$k^*$	0.692	0.596	0.507
$W_s(c^*)$	0.6657	0.9200	0.9955
$W_d(c^*)$	0.1976	0.6012	0.9510
S	0.3296	0.4729	0.4980
D	0.0979	0.3088	0.4757
S+	0.5651	0.8612	0.9864
D+	0.1619	0.5361	0.8896
Const.	3.37	1.530	1.047
Cost	0.143	0.089	0.023

In Table A1 the variables are:  $\mu$  = mean host size;  $c^*$  = critical host size;  $k^*$  = optimal proportion of males = critical host size quantile; S = expected fitness in sons for a mated parasitoid that produces sons in hosts whose size is less than  $c^*$ : S = areas (1) + (2) in **Fig. 4**;  $W_s(c^*)$  = fitness of son for critical host size,  $W_d(x^*)$  = fitness of daughter for critical host size, S = expected fitness in daughters for a mated parasitoid that produces daughters in hosts whose size is greater than  $c^*$ : If D is multiplied by the constant (“Const.”) then the product = areas (3) and (4) in **Fig. 4**; S+ = the expected fitness through sons of an unmated female that produces sons on all hosts. S+ = areas (1) + (2) + (4) in **Fig. 4**; D+ = the expected fitness through daughters for a parasitoid that produced daughters in all hosts: If D+ is multiplied by the constant (“Const.”) the product = areas (2) + (3) + (4) in **Fig. 4**; “Const.” is the constant that the fitness of daughters,  $W_d(x)$  must be multiplied by to make the fitnesses of sons and daughters comparable.; and “Cost” is the cost of being unmated.

## SEX RATIO ABSTRACT FIGURES

### FIGURE LEGENDS

**Fig. 1.** Fitness of sons,  $W_s(x)$ , and fitness of daughters,  $W_d(x)$ , plotted against host size,  $x$ . The same two fitness functions are used for all three cases of Example 1, that is, in Figures 3 through 9.

**Fig. 2.** Host size distribution illustrated in two ways. The probability density function,  $f(x)$ , for host size is shown with a solid line and the cumulative distribution,  $y = F(x)$ , is shown with a dotted line. This particular illustration is for a small host distribution, which is used in Figures 3 and 4. Illustrations for a medium-sized and large host distributions would look exactly the same except for scale. A host of size  $x = 2$  for a small host distribution corresponds to a host of size  $x = 4$  for a medium-sized host distribution (used in Figures 5, 6 and 9) and to a host of size  $x = 8$  for a large host distribution (used in Figures 7 and 8).

**Fig. 3.** Fitness of sons,  $w_s(y)$ , and fitness of daughters,  $w_d(y)$ , plotted against host quantile,  $y$ . Notice that the functions illustrated in Figures 1 and 3 are different, because the arguments are different. But, for corresponding values of the arguments, the values of  $W(x)$  and  $w(y)$  are the same. That is,  $W(x) = w(y)$  if  $y = F(x)$ .

**Fig. 4.** Standardized fitnesses of sons and daughters, plotted against host size quantile. The curves for the fitness of sons is exactly the same as in Figure 3, while the female fitness is adjusted (multiplied by the constant 3.37 in this case) so that the fitnesses of sons and daughters are equal at the critical host size quantile,  $k^* = 0.692$ . Notice two things. First, if sons are produced on smaller hosts (hosts whose quantile is smaller than  $k^*$ ), and daughters are produced on larger hosts (hosts whose quantile is larger than  $k^*$ ), then the area showing reproduction through sons [ $S = (1) + (2)$ ] equals the area showing reproduction through daughters [ $D = (3) + (4)$ ]. Second, reproduction through sons and daughters for mated females using optimal sex allocation is indicated by the sum:  $(1) + (2) + (3) + (4)$ , while reproduction through sons by unmated females is indicated by the sum:  $(1) + (2) + (4)$ . Therefore, area (3) represents the difference between the fitness of a mated female using optimal sex allocation and the fitness of an unmated female constrained to produce only sons.

**Fig. 5.** This is the same as Figure 3, except that this figure is for a medium-sized host distribution.

**Fig. 6.** This is the same as Figure 4, except that this figure is for a medium-sized host distribution.

**Fig. 7.** This is the same as Figures 3 and 5, except that this figure is for a large host distribution.

**Fig. 8.** This is the same as Figures 4 and 6, except that this figure is for a large host distribution.

**Fig. 9.** Standardized fitnesses of sons and daughters of mated females plus sons of unmated females. This figure, which is drawn for a medium-sized host distribution, resembles Figure 6, except that it includes sons from unmated females, and that the critical host size quantile is different. **Fig. 9a** is for sons and daughters of mated females, and **Fig. 9b** is for sons of unmated females. The curves in the two parts of the figure are drawn to scale, weighted by the proportion of reproduction due to unmated females,  $p = 0.2$ , and the proportion due to mated females,  $1 - p = 0.8$ . Notice that the sum of the areas representing reproduction due to production of sons,  $(1) + (2) + (5)$ , is equal to the sum of the areas representing reproduction due to the production of daughters,  $(3) + (4)$ . Again, area (3) represents the difference between the fitness of a mated female using the optimal sex allocation strategy and an unmated female constrained to produce only sons.

**Fig. 10.** Standardized fitnesses of sons and daughters for Example 2 with  $a = 0$ . In this picture, all but one female are assumed to be mated. This figure is comparable to **Figs. 4, 6 and 8**. The cost of being unmated is  $(3)/[(1) + (2) + (3) + (4)]$ .

**Fig. 11.** Standardized fitnesses of sons and daughters of mated females plus sons of unmated females. This figure resembles Figure 10, except that it includes sons from unmated females, and that the critical host size quantile is different. **Fig. 11a** is for sons and daughters of mated females and **Fig. 11b** is for sons of unmated females. The curves in the two parts of the figure are drawn to scale, weighted by the proportion of reproduction due to unmated females,  $p = 0.2$ , and the proportion due to mated females,  $1 - p = 0.8$ . The cost of being unmated is  $(3)/\{(1) + (2) + (3) + (4) + (4)\}$ .

**Fig. 12.** The cost of choosing the wrong sex ratio. This illustration is chosen assuming the same optimal sex allocation strategy as used for **Fig. 11a** (proportion of males = 0.5). However, in this example, the parasitoid is assumed to use a higher critical host size so that the actual proportion of males produced would equal 0.75. A mated female using the optimal sex allocation strategy would achieve a fitness indicated by the sum of all the areas,  $(1) + (2) + (3a) + (3b) + (4a) + (4b)$ . A mated female using the sub-optimal strategy would achieve the same fitness except for the bit represented by area (3a). Thus, the cost of using the wrong strategy would equal (3a) divided by the sum of all six areas. This example uses the assumption that all females are mated.

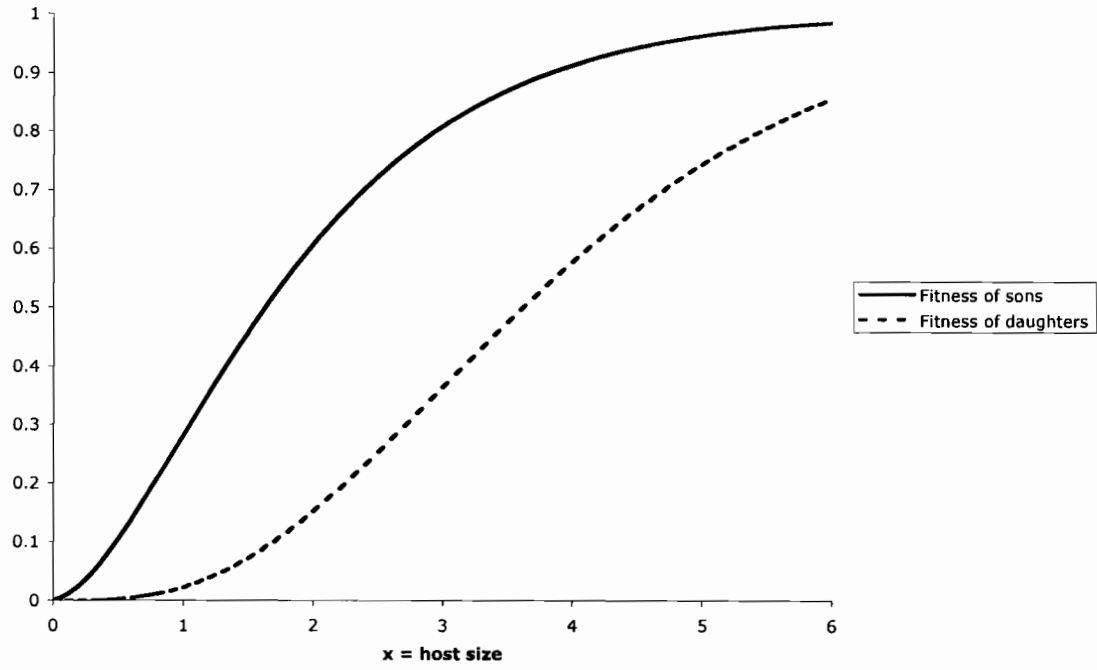
**Fig. 13.** Standardized fitnesses of sons and daughters for Example 2 with  $a = 0.5$ . In this example, all but one female are assumed to be mated. In this figure, which resembles **Fig. 10**, the argument is host size,  $x$ , rather than host quantile,  $y$ . The idea is that host size is uniformly distributed over the range:  $0.5 < x < 1$ .

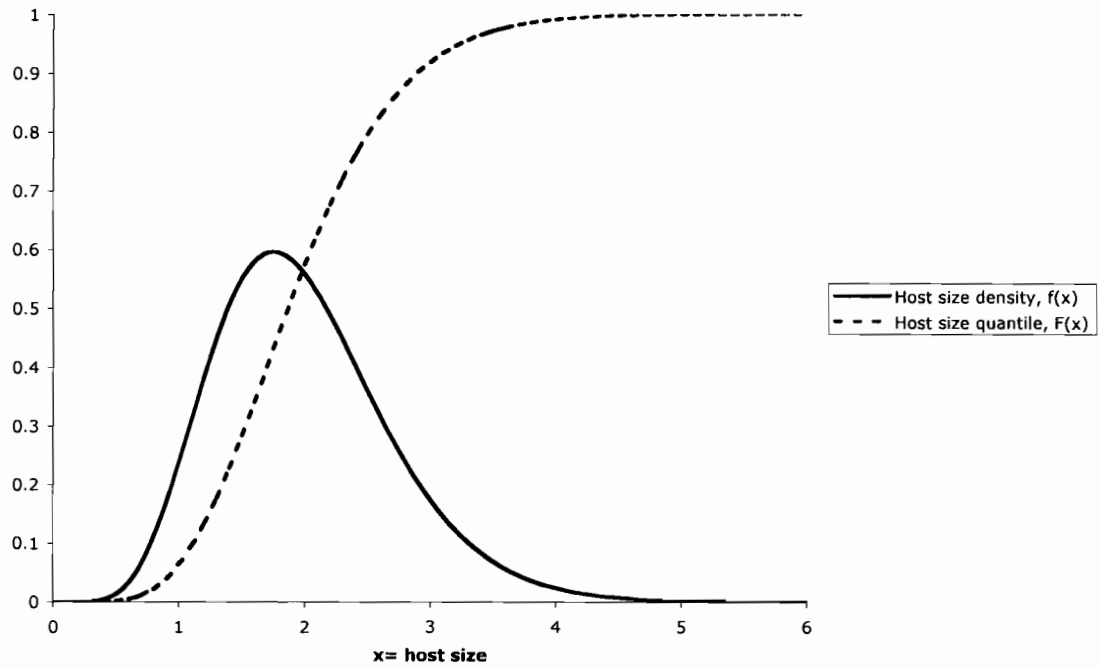
**Fig. 14.** Sex ratio and the cost of being unmated for Example 2 with  $a = 0$ . The optimal proportion of sons for mated females, the overall proportion of sons, and the cost of being unmated, are plotted against the proportion of females that are unmated,  $p$ . Two of the sets of values plotted here are the same as shown in **Fig. 10** ( $p = 0$ ) and **Fig. 11** ( $p = 0.2$ ).

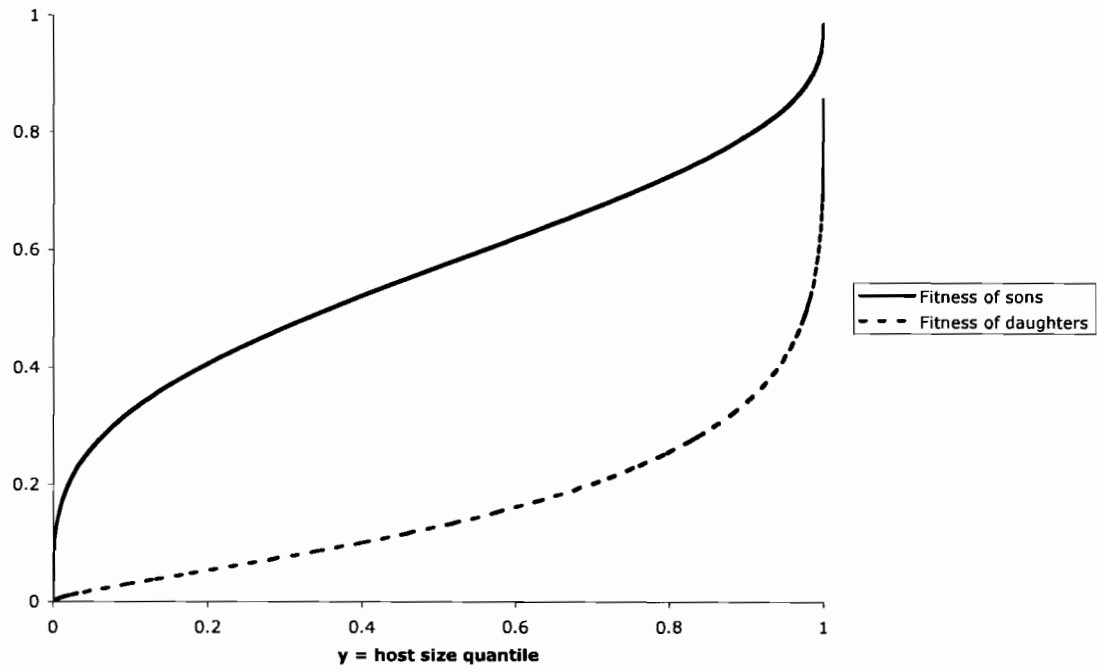
**Fig. 15.** Sex ratio and the cost of being unmated for Example 2 with  $a = 0.5$ . This figure is similar to **Fig. 14**, except that it does not include values of the proportion of females unmated beyond  $p = 0.6$ , at which point the optimal proportion of sons for a mated female to produce equals zero.

**Fig. 16.** Sex ratio and the cost of being unmated for Example 2 with  $a = 1$ . Actually, this is the limiting case in which the fitnesses of the two sexes are constant and there is no host quality effect. Notice that there is no cost of being unmated, unless more than half the females are unmated. The overall proportion of sons is one-half unless most of the females are unmated.

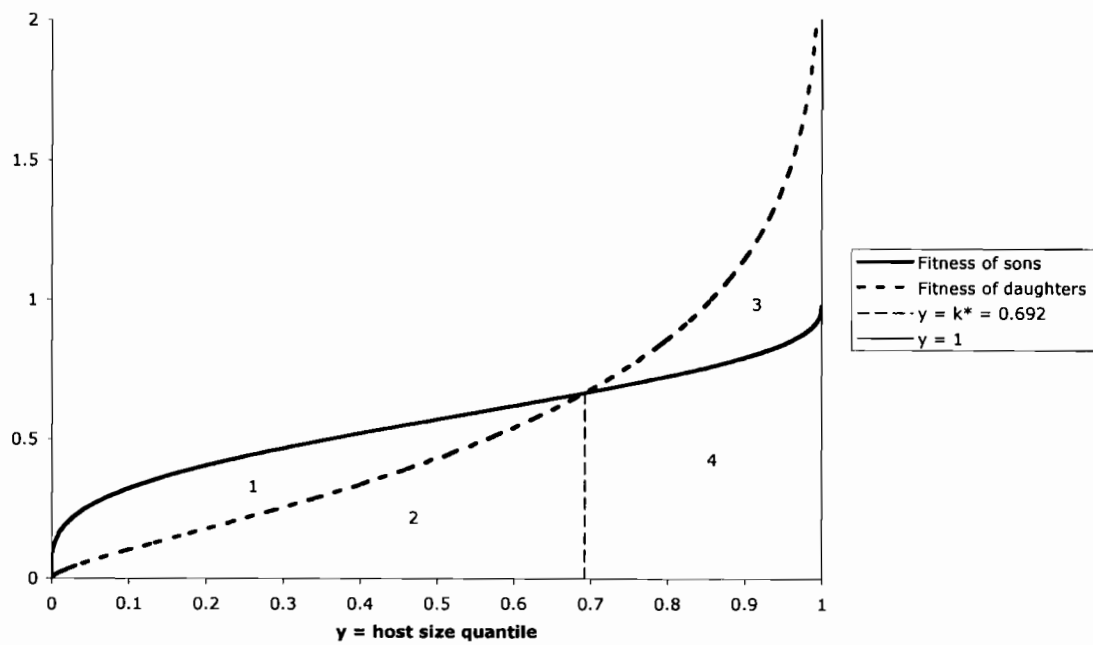
**Fig. 17.** The strength of the force of selection against being unmated. The curve for the cost,  $C(p)$ , of being unmated here is the same as that shown in **Fig. 14**. However, this cost refers to individuals. That is, it compares the reproductive success (measured in terms of the relative values of sons and daughters) for mated and unmated individuals. The cost of a *strategy* resulting in a certain proportion of unmated females,  $p$ , equals the product,  $pC(p)$ , because the strategy produces proportion  $p$  females, each of whom pay the cost,  $C(p)$ . This product is indicated by a rectangle formed by drawing vertical and horizontal lines from the axes to the point  $[p, C(p)]$  as shown. The figure shows the cost for two different values of  $p$ :  $p = 0.2$  and  $p = 0.4$ . The difference between these areas is a measure of the advantage of changing the mate-finding strategy from one resulting in  $p = 0.4$  to one resulting in  $p = 0.2$ .

**Figure 1. Fitnesses of sons and daughters**

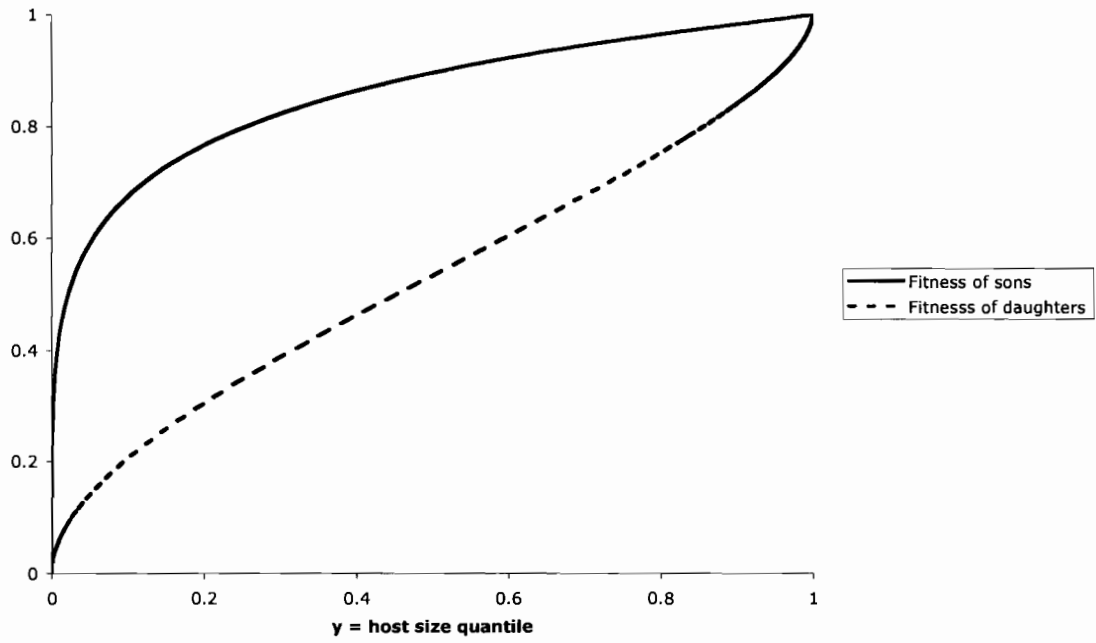
**Figure 2. Host size distribution**

**figure 3. Fitnesses plotted against host size quantile**

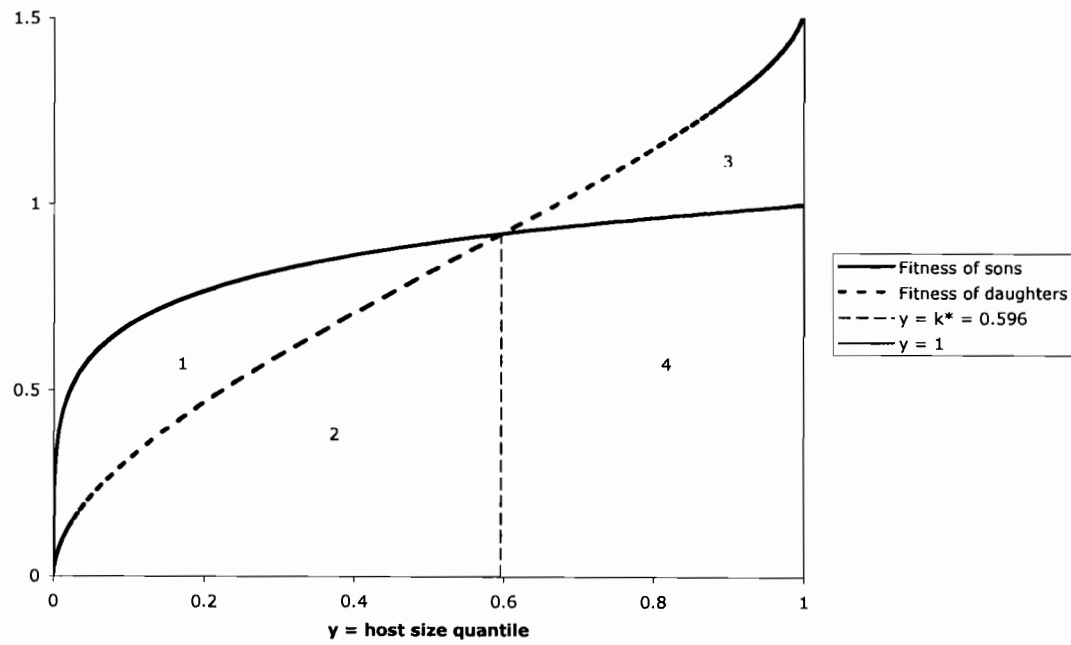
**Figure 4. Standardized fitnesses of sons and daughters for small hosts**



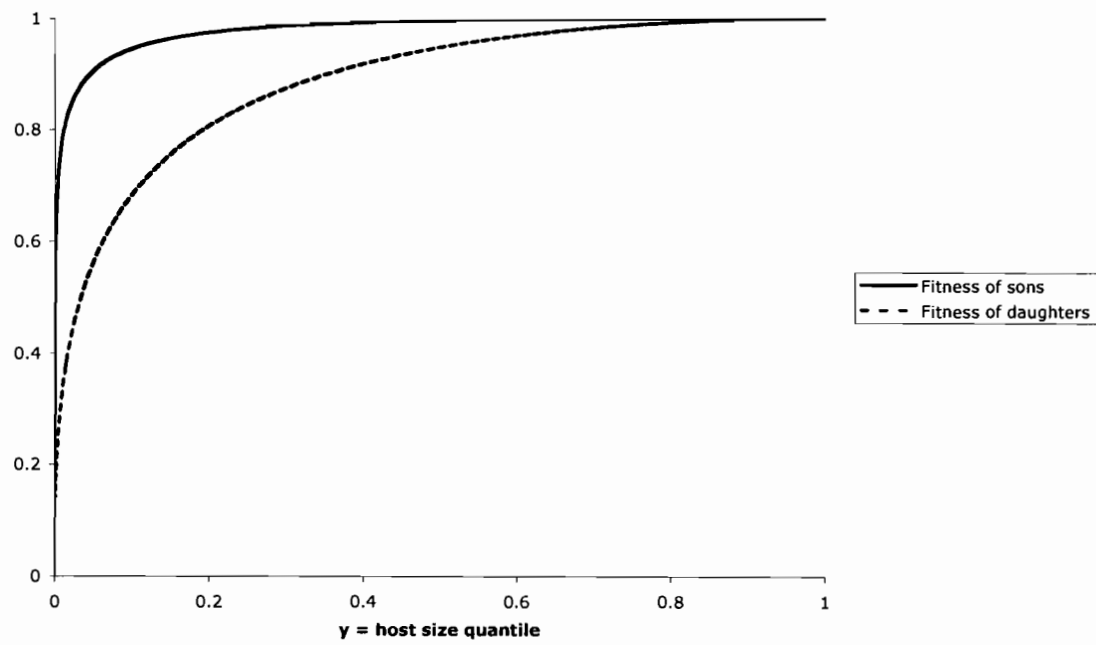
**Figure 5. Fitnesses plotted against host size quantile for medium-sized hosts**



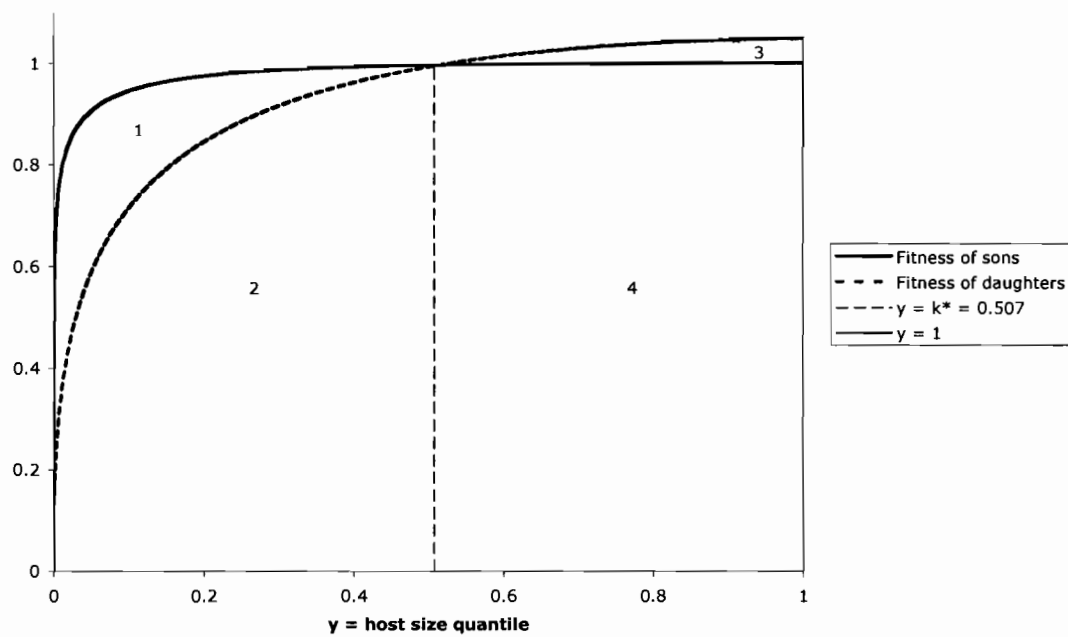
**Figure 6. Standardized fitnesses of sons and daughters for medium-sized hosts**



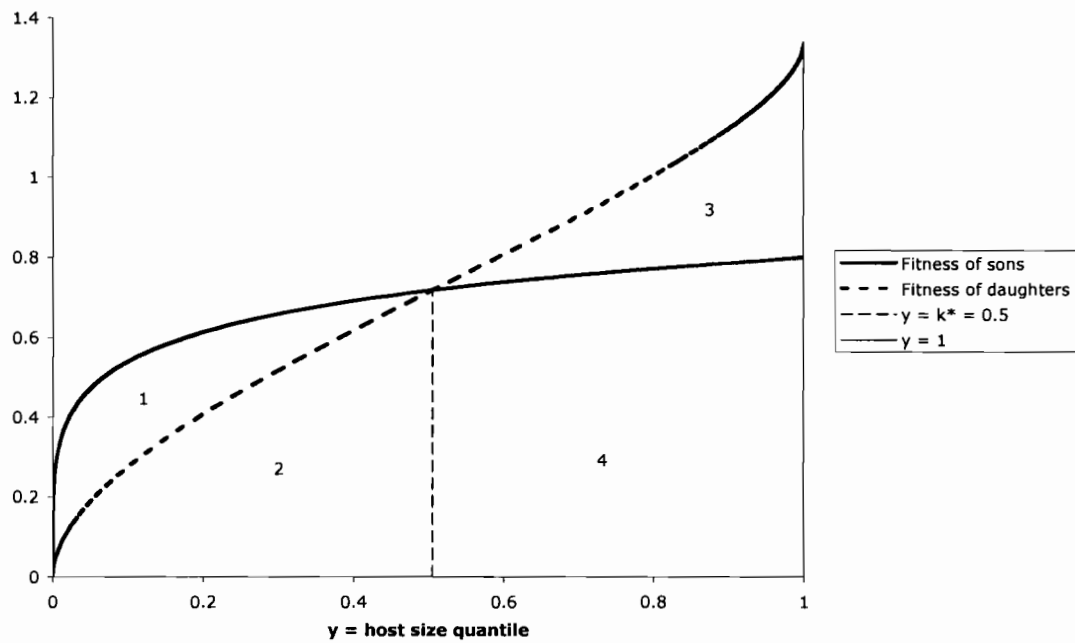
**Figure 7. Fitnesses plotted against host size quantile for large hosts**



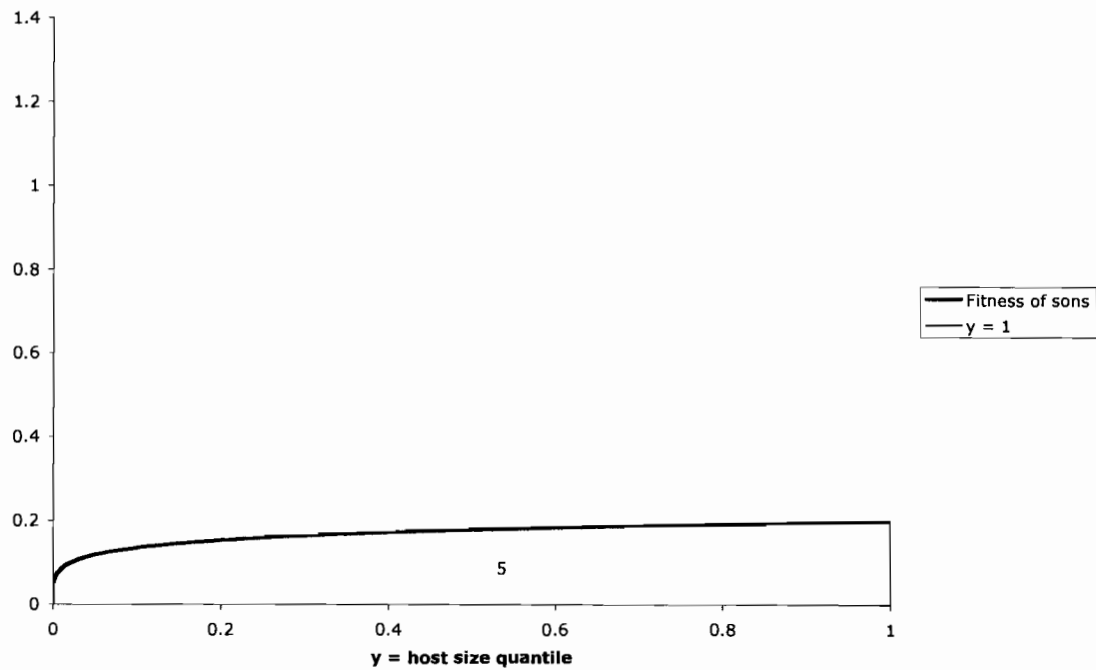
**Figure 8. Standardized fitnesses of sons and daughters for large hosts**



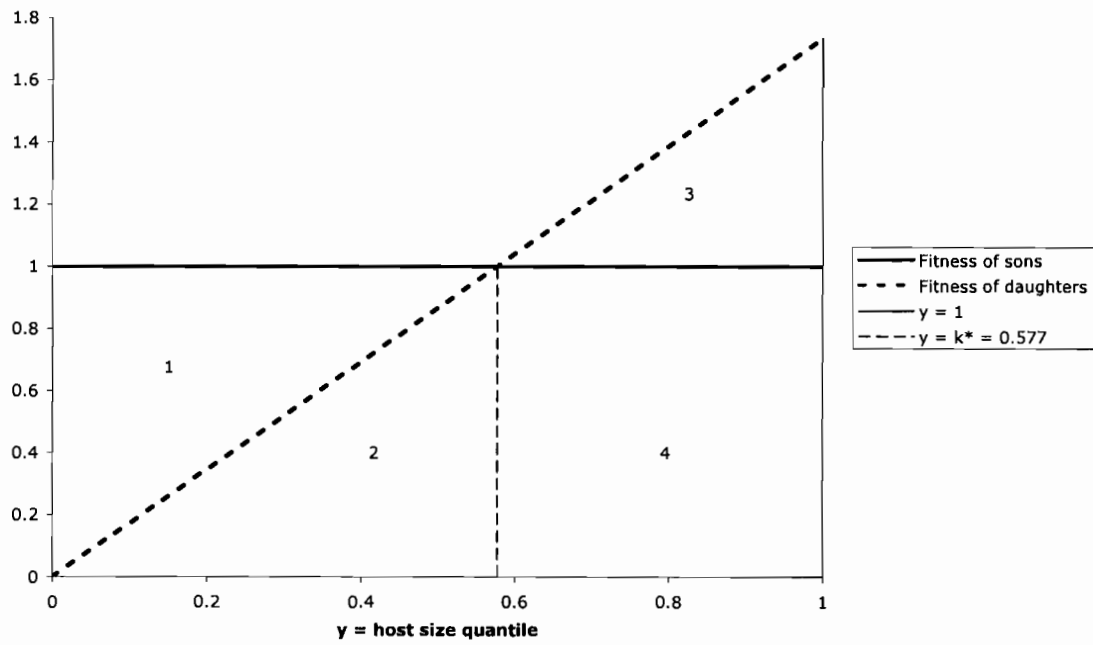
**Figure 9a. Standardized fitnesses of sons and daughters from mated females**



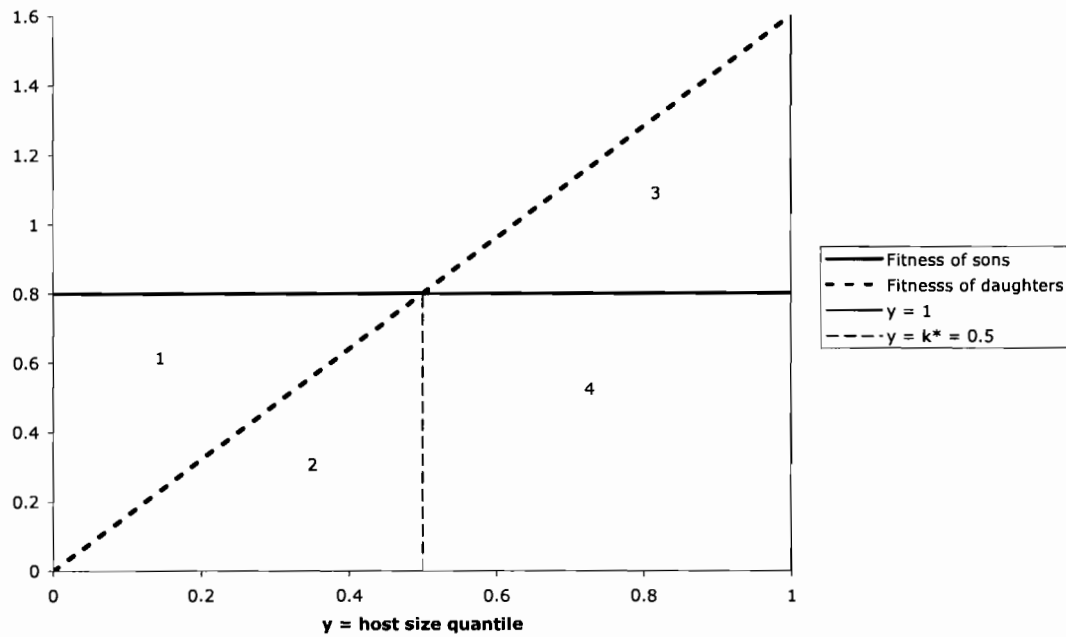
**Figure 9b. Standardized fitnesses of sons from unmated females**



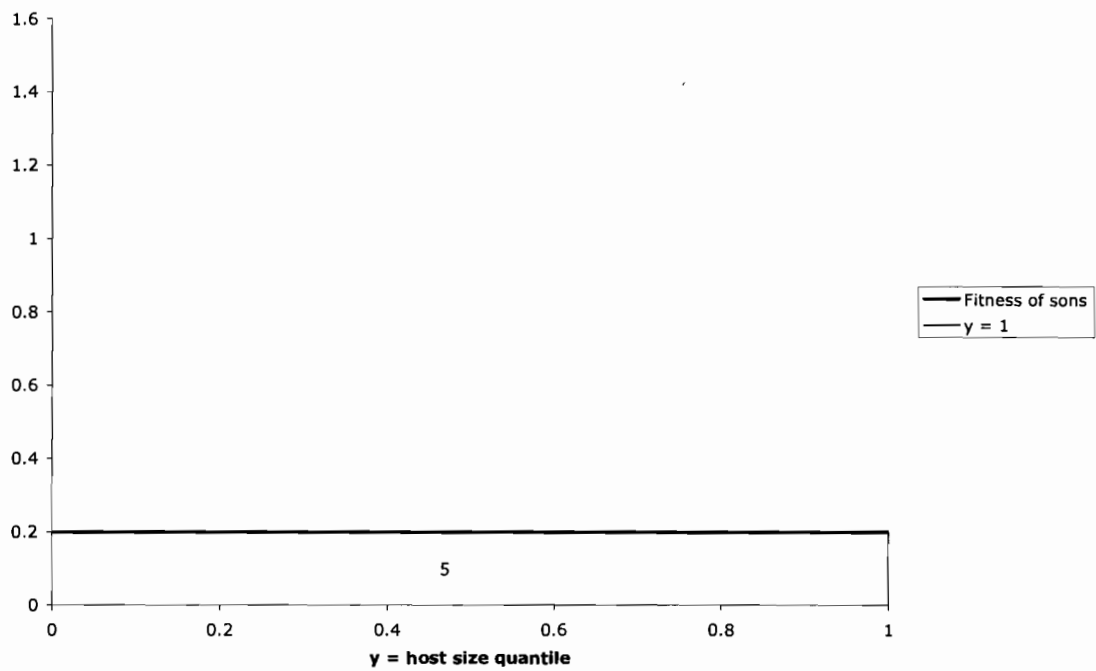
**Figure 10. Standardized fitnesses of sons and daughters for Example 2 with  $a = 0$**



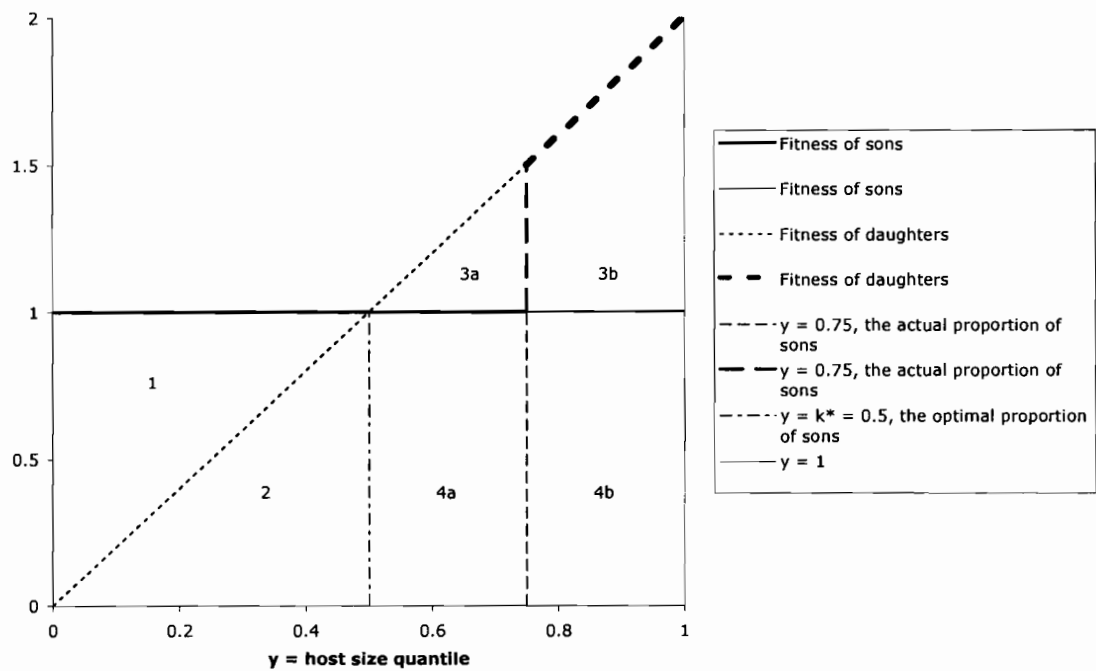
**Figure 11a. Standardized fitnesses of sons and daughters from mated females**



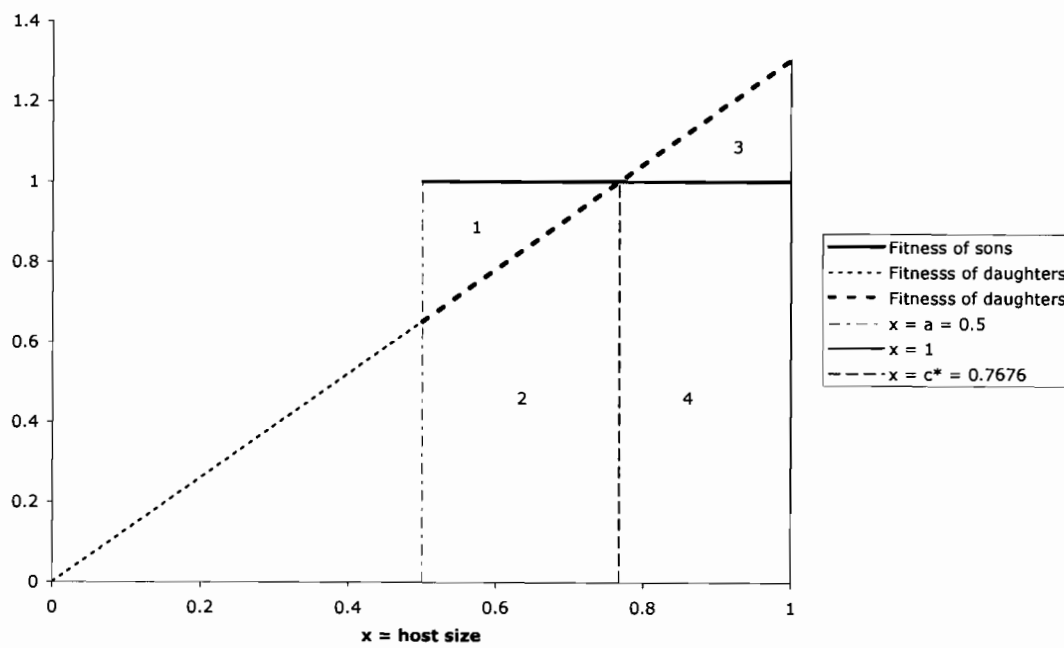
**Figure 11b. Standardized fitnesses of sons from unmated females**



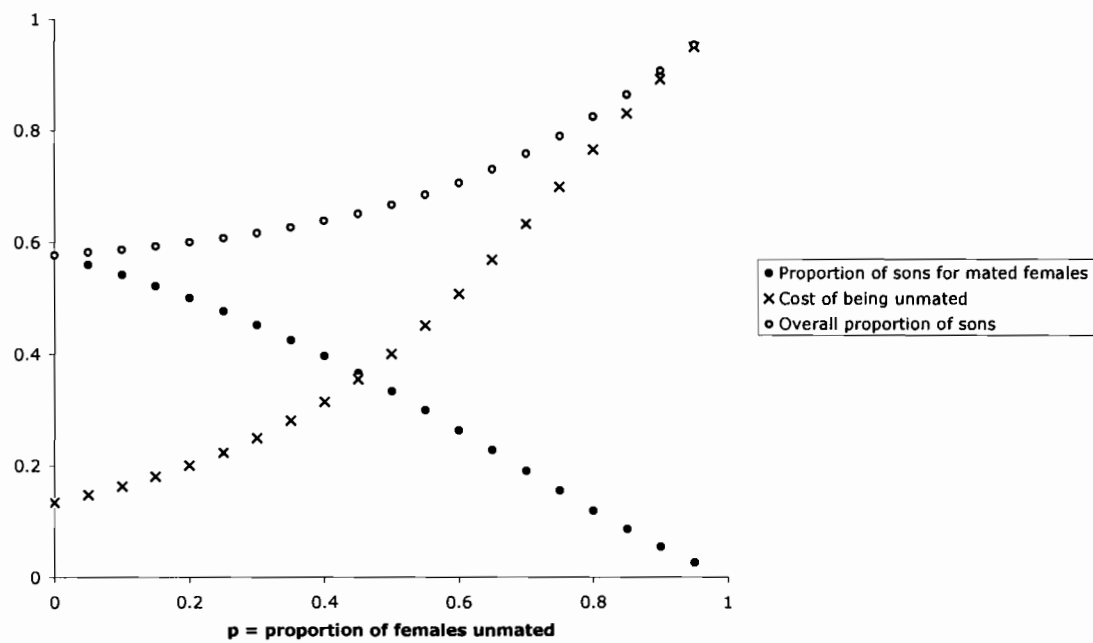
**Figure 12. The cost of choosing the wrong sex ratio**



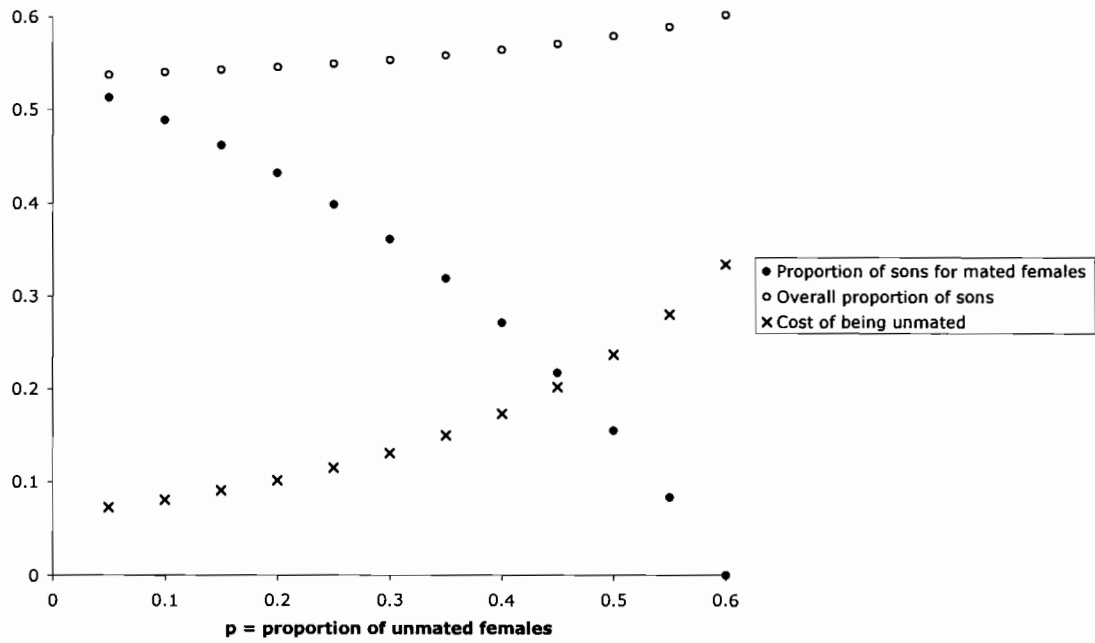
**Figure 13. Standardized fitnesses of sons and daughters for Example 2 with  $a = 0.5$**



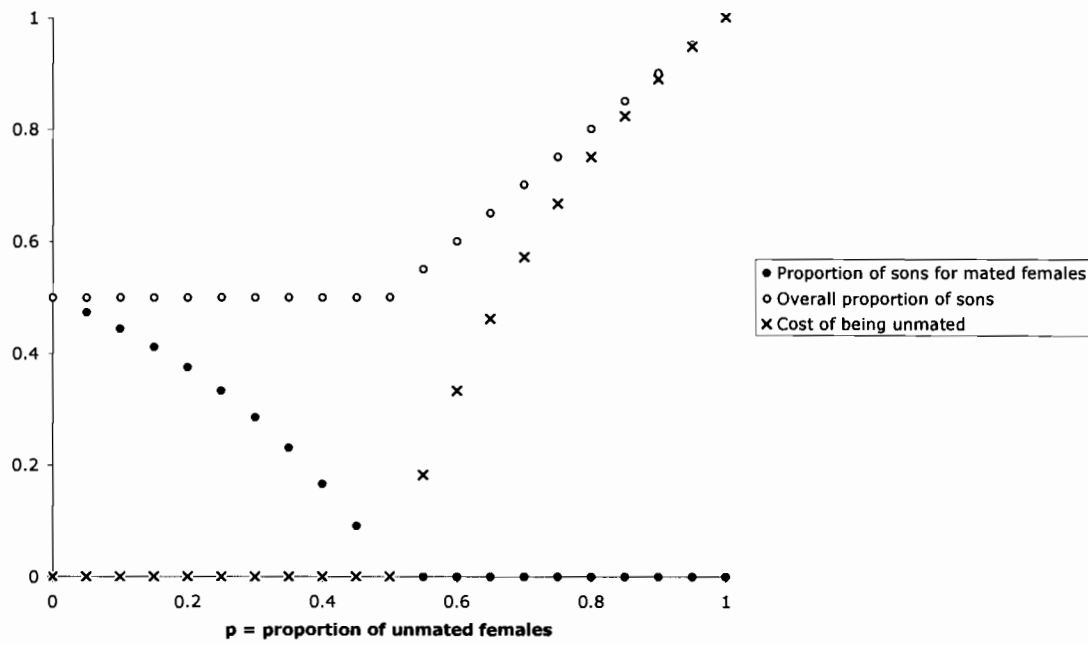
**Figure 14. Sex ratio and the cost of being unmated for Example 2 with  $a = 0$**



**Figure 15. Sex ratio and the cost of being unmated for Example 2 with  $a = 0.5$**



**Figure 16. Sex ratio and the cost of being unmated for Example 2 with  $a = 1$**



**Figure 17. The strength of the force against being unmated**