

A COMMENT ON SEX RATIOS IN PARTIALLY INBRED PARASITIC WASPS

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INTRODUCTION

Because parasitic wasps are able to choose the sex of their offspring they are a popular subject for the study of sex allocation. There are two distinct situations that require different theories. (1) Solitary wasps lay one egg per host. Their adult offspring leave their natal hosts and search for mates. After they are mated, females search for hosts. According to traditional sex ratio theory (Fisher 1930) the sex ratio, or reproductive effort to producing the sexes should satisfy MacArthur's (1965) product rule. It is frequently observed that female parasitoids emerge from larger hosts and males from smaller hosts. This is what would be expected if larger hosts result in larger wasps, and if large size were more important for females than for males (Charnov 1982). (2) Gregarious wasps lay more than one egg per host. If mating takes place in or on the natal host, sex ratios should be female-biased. Hamilton (1967) developed a theory for the optimal sex ratio for the case in which exactly n females lay eggs in each host. Of particular interest, both because it is an extreme case, and because it is probably the most likely to occur in nature, is the case in which $n = 1$. In this case, Green, Gordh and Hawkins (1982) showed that not only is the optimal sex ratio extremely female-biased, but it should be precise. That is, the variance in the number of males produced in a clutch of a particular size should be lower than it would be if the number had a binomial distribution. In their treatment, Green et al. assumed that all mating takes place on the natal host.

In this note a different situation is considered: parasitoids are, or may be, gregarious, but not all the mating takes place on the natal host. This is not an uncommon situation, as may be inferred by the fact that many gregarious parasitoids have winged males and females. Two theoretical questions should be asked about this case of partially inbred parasitic wasps. First, is there an advantage in producing a precise sex ratio in clutches larger than one? Second, what is the optimal overall sex ratio for such wasps?

1. THE SIMPLEST MODEL TO INVESTIGATE THE POSSIBLE ADVANTAGE OF PRECISE SEX RATIOS IN PARTIALLY INBRED PARASITIC WASPS

Let N = the number of eggs laid on a single host

F = the number of unmated females off the host

M = the number of males off the host

$R = F/M$

s = the number of unfertilized eggs (sons) on a single host

d = the number of fertilized eggs (daughters) on a single host; $d = N - s$

$W(s)$ = the fitness of a clutch consisting of s sons and d daughters

Note: $W(s)$ refers to the contribution to total fitness resulting from one clutch of size N laid by a mated female in the present generation. The other variables, F , M , s and d refer to the next generation (offspring).

Assumptions:

1. All females are mated on the natal host if there are males on the host.
2. The entire clutch survives to maturity.
3. All males compete equally off the host.
4. If females are not mated on the natal host they are all mated off the host.

Then we have

$$\begin{aligned} W(s) &= 2d + sR \text{ if } s > 0 \\ &= d \text{ if } s = 0. \end{aligned} \tag{1}$$

Fitness is measured as the number of alleles from the clutch that make it to the next generation. Therefore, if there are no sons in a clutch, one allele makes it through each daughter. If there is at least one son, then two alleles make it through each daughter—one from each daughter and one from the son who mates with the daughter. Then, when the sons leave the natal host, each son has a share of unmated females equal to R .

Table 1. Fitnesses of clutches of size N for various numbers of sons (s) and daughters (d)

Numerical examples:

$N = 3, R = 0$			$N = 3, R = 0.5$			$N = 3, R = 1.0$			$N = 3, R = 2.0$		
s	d	$W(s)$	s	d	$W(s)$	s	d	$W(s)$	s	d	$W(s)$
0	3	3.0	0	3	3.0	0	3	3.0	0	3	3.0
1	2	4.0	1	2	4.5	1	2	5.0	1	2	6.0
2	1	2.0	2	1	3.0	2	1	4.0	2	1	6.0
3	0	0	3	0	1.5	3	0	3.0	3	0	6.0

$N = 4, R = 0$			$N = 4, R = 0.5$			$N = 4, R = 1.0$			$N = 4, R = 2.0$		
s	d	$W(s)$	s	d	$W(s)$	s	d	$W(s)$	s	d	$W(s)$
0	4	4.0	0	4	4.0	0	4	4.0	0	4	4.0
1	3	6.0	1	3	6.5	1	3	7.0	1	3	8.0
2	2	4.0	2	2	5.0	2	2	6.0	2	2	8.0
3	1	2.0	3	1	3.5	3	1	5.0	3	1	8.0
4	0	0	4	0	2.0	4	0	4.0	4	0	8.0

$W(s)$ is the fitness—that is, the number of genes in the next generation produced by a clutch of size N when the number of sons is s and the number of daughters is $d = N - s$. $R = F/M$ is the ratio of the number of unmated females off their natal hosts (F) the total number of males (M).

Notice that fitness is highest when a clutch has precisely one son, except when $R = 2.0$ (or more). In this case, there are so many unmated females available off the natal host that the gain of producing another son matches (for $R = 2$) or exceeds (for $R > 2$) the value of producing a daughter who would leave the host with her own genes plus those of a brother already on the same host.

What is the average fitness of a clutch of size N if the number of sons in a clutch of size N is random, coming from a binomial distribution with p = the chance that an egg will be unfertilized (and thus becoming a male), and what is the value of p that maximizes the fitness of the average clutch of size N if the off-host female/male sex ratio is equal to R ? Values are given in the following table.

Table 2. Average fitness for clutches of size N , ratio R , and binomial sex determination

$N = 3$	Best p	W	$W(1)$	$W/W(1)$
$R = 0$	0.1835	3.2659864	4.0	0.8165
$R = 0.5$	0.2929	3.6213205	4.5	0.8047
$R = 0.75$	0.3545	3.8637431	4.75	0.8134
$R = 1.0$	0.4228	4.1547008	5.0	0.8309
$R = 2.0$	1.0000	6.0000000	6.0	1.0000
$N = 4$	Best p	W	$W(1)$	$W/W(1)$
$R = 0$	0.2062	4.7622032	6.0	0.7937
$R = 0.5$	0.2789	5.2460614	6.5	0.8071
$R = 0.75$	0.3215	5.447669	6.75	0.8071
$R = 1.0$	0.3701	5.8898816	7.0	0.8414
$R = 2.0$	1.0000	8.0000000	8.0	1.0000

N is the clutch size. $R = F/M$ is the ratio of unmated females off the natal host (F) to the total number of males (M). For each number of sons and daughters the clutch fitness is calculated using equation (1), the results of which are shown in Table 1. W is the weighted average of the fitnesses shown in table 1, where the weights are probabilities from a binomial distribution with parameters $n = N$ and $p = \text{Best } p$, the value of p that maximizes the fitness W . For each N and R the average fitness for binomial sex determination may be compared with $W(1)$, the fitness of a clutch with exactly one male. The advantage of a precise sex ratio over a binomial sex ratio may be seen by comparing the fitnesses, W , for binomial sex determination, and $W(1)$, the fitness when sex determination is precise. The relative efficiency of binomial sex determination is given as the ratio: $W/W(1)$.

Notice that for values of R from 0 to 1 the fitnesses of producing a binomially-distributed sex ratio are about 20% less than the fitness for a precise sex ratio with $s = 1$ son.

Special case:

The case in which $R = 0$ is special. Above it is assumed that if there are no sons the fitness of the clutch is equal to the number of daughters, where $d = N$. This follows from assumption 4. However, one might assume that there is no mating off the host, in which case equation (1) is replaced by:

$$W(s) = 2d \text{ if } s > 0 \text{ and} \quad (2)$$

$$W(s) = 0 \text{ if } s = 0.$$

In this case, we have the following table:

Table 3. Fitness of clutches of size N when all mating is on the natal host

$N = 3$				$N = 4$			
s	d	$W(s)$	$f(s)$	s	d	$W(s)$	$f(s)$
0	3	0	0.1925	0	4	0	0.1575
1	2	4	0.4227	1	3	6	0.3701
2	1	2	0.3094	2	2	4	0.3260
3	0	0	0.0755	3	1	2	0.1276
				4	0	0	0.0187

The $f(s)$ values are the binomial probabilities for the binomial parameters that maximize fitness ($p = 0.4226$ for $N = 3$ and $p = 0.3700$ for $N = 4$). Fitness equals $\sum f(s)W(s)$. For $N = 3$, fitness equals 2.3094, while for $N = 4$, fitness equals 3.7798. These values may be compared with $W(1)$, the fitness for a precise sex ratio ($s = 1$), which are $W(1) = 4$ for $n = 3$ and $W(1) = 6$ for $N = 4$. Thus, the relative fitnesses for a binomial sex ratio compared to precise sex ratios are: $W/W(1) = 2.3094/4 = 0.5574$ for $N = 3$ and $W/W(1) = 0.6300$ for $N = 4$.

$W(s)$ is the fitness—that is, the number of genes in the next generation produced by a clutch of size N when the number of sons is s and the number of daughters is $d = N - s$. Here all mating is assumed to be on the natal host and all-female and all-male clutches have fitness zero.

Notice that the efficiency of binomial sex determination to precise sex determination is very low in the case in which there is no mating off the host. This case of no mating on the host (“highly inbred” parasitic wasps) was the case considered by Green, Gordh and Hawkins (1982). If there is mating off the host, there is still an advantage of a precise sex ratio (shown in Table 2), but the advantage of a precise sex ratio over a binomial sex ratio is not nearly as great as it is when there is no mating off the host.

Table 4. An empirical example: fitness of clutches averaged using empirical and theoretical distributions—data for *Metaphycus luteolus*

N = 3		R = 0.5			R = 0.75		R = 1.0	
<u>s</u>	<u>d</u>	<u>Observed</u>	<u>W(s)</u>	<u>f(s)</u>	<u>W(s)</u>	<u>f(s)</u>	<u>W(s)</u>	<u>f(s)</u>
0	3	0.1845	3.0	0.3535	3.0	0.2690	3.0	0.1923
1	2	0.7379	4.5	0.4393	4.75	0.4431	5.0	0.4226
2	1	0.0194	3.0	0.1820	3.5	0.2434	4.0	0.3095
3	0	0.0583	1.5	0.0251	2.25	0.0445	3.0	0.0756
Relative efficiency:		4.0197/4.5 =		4.3576/4.75 =		4.4955/5 =		
		0.8933		0.8963		0.8991		
N = 4		R = 0.5			R = 0.75		R = 1.0	
<u>S</u>	<u>d</u>	<u>Observed</u>	<u>W(s)</u>	<u>f(s)</u>	<u>W(s)</u>	<u>f(s)</u>	<u>W(s)</u>	<u>f(s)</u>
0	4	0.1667	4.0	0.2704	4.0	0.2119	4.0	0.1574
1	3	0.7000	6.5	0.4183	6.75	0.4017	7.0	0.3700
2	2	0.1000	5.0	0.2427	5.5	0.2855	6.0	0.3261
3	1	0.0000	3.5	0.0626	4.25	0.0902	5.0	0.1277
4	0	0.0333	2.0	0.0061	3.00	0.0107	4.0	0.0188
Relative efficiency:		5.7834/6.5 =		6.0417/6.75 =		6.3000/7 =		
		0.8898		0.8951		0.9000		

Observed number of sons and daughters from Kapranas (2007) for clutches of size $N = 3$ and $N = 4$. Fitness, $W(s)$, are based on equation (1) for each number of sons, s . The binomial distribution, $f(s)$, for the number of sons is based on the binomial probabilities shown in Table 3. The relative efficiency compares the weighted averages of fitnesses using the weights from the Observed column.

Notice that the fitnesses resulting from the observed distribution of sex ratios are about 10% less than the fitness for a precise sex ration with $s = 1$ son.

2. WHAT IS THE OPTIMAL OVERALL SEX RATIO IF SOME MATING TAKES PLACE ON THE NATAL HOST AND SOME OFF IT?

Consider a random individual. Use the following notation:

Proportion male = y

Proportion female = $x = 1 - y$

Proportion of matings on the natal host = p

Proportion of matings off the natal host = $1 - p$

1. Assume that all females on a host with males will be mated on the host.
2. Assume that all females will be mated, either on or off the natal host.

Start with a fixed sex ratio $y_0:x_0$. Then introduce a rare type with sex ratio $y_1:x_1$. Then compare the number of genes passed on through an individual of rare Type 1 with the number passed on through a typical individual of common Type 0.

For a random individual of Type 0 the number of genes passed on through male and female effort is given in the following table:

	Matings on the natal host	Matings off the natal host
Male	px_0	$(1 - p)x_0$
Female	px_0	$(1 - p)x_0$

Notice that the sum of the terms in this table is just $2x_0$, that is, twice the proportion of females. This is reasonable, since each female carries her own genes plus those of a male of her own type. [Here I ignore the fact that while female offspring receive genes from both the mother and father, her male offspring receive genes from the mother alone. That this does not matter must be argued separately.]

For a rare individual of Type 1 trying to invade a population of Type 0 the number of genes passed on through male and female effort is given in the following table:

	Matings on the natal host	Matings off the natal host
Male	px_1	$(1 - p)x_0y_1/y_0$
Female	px_1	$(1 - p)x_1$

Notice that the only difference between the entries in the table for Type 0 and Type 1, except for the subscripts, is in the term for reproduction through male effort off the natal host. The number of females available to be mated off the host is proportional to $(1 - p)x_0$, in either case. When all individuals are of Type 0, all of these females will be mated by Type 0 males. However, when there are rare Type 1 individuals, the number of females available off the natal host will still be proportional to $(1 - p)x_0$, but males of Type 1 will have an relative advantage (disadvantage) equal to y_1/y_0 .

Now consider the difference between the number of genes gotten out by individuals of Type 1 and Type 0. The point is to find a value of x_0 such that this difference is zero. The difference between the sum of the terms in the tables for Type 1 and Type 0 is

$$\begin{aligned} D &= 2p(x_1 - x_0) + (1 - p)(x_1 - x_0) + (1 - p) [x_0(y_1/y_0 - 1)] \\ &= (1 + p)(x_1 - x_0) + (1 - p)(x_1 - x_0)[(y_0 - 1)/y_0]. \end{aligned}$$

Setting $D = 0$ and cancelling the factor $(x_1 - x_0)$, yields

$$1 + p = (1 - p)(1 - y_0)/y_0, \text{ or}$$

$$(1 + p)y_0 = (1 - p)(1 - y_0), \text{ or}$$

$$y_0 + py_0 = 1 - p - y_0 + py_0, \text{ or}$$

$$2y_0 = 1 - p, \text{ or, finally}$$

$$y_0 = \frac{1}{2} - p/2. \tag{2}$$

Or, equivalently

$$x_0 = \frac{1}{2} + p/2. \tag{3}$$

Equations (2) and (3) give simple expressions for the optimal proportions of females and males, respectively, as functions of the proportion, p , of matings that take place on the natal hosts

Table 5. Data for *Metaphycus luteolus* (from Kapranas 2007)

375 males
 + 819 females

 1194 individuals

819 females
 - 278 females on hosts with no males

 571 females on hosts with males

p = fraction of matings on natal hosts (assumed to equal the number of females on hosts with males/number of females)

$$= 571/819 = 0.66056.$$

Theoretical optimal proportion of females in the population [Eqn. (3)]:

$$p/2 + 1/2 = 0.83028$$

Observed proportion of females in population:

$$819/1194 = 0.68593$$

$$R = F/M = \text{females on hosts with no males/number of males} = 278/375 = 0.74133.$$

Notice that the observed proportion of females in the population, 0.68593, is substantially smaller than the theoretical value 0.83028. There are a number of possible explanations for this. Most likely, the theory is completely wrong, possibly because it assumes that the numbers of males and females on hosts may be fractions rather than individuals. Another possibility is that the assumption that all females on a host with males will be mated while on their natal host. If this is not true, the value of p will be smaller than the value found above by assuming that it equals the number of females on hosts with males divided by the total number of females.

The observed value of R , 0.74133, is very close to the value $R = 0.75$ included in Tables 2 and 4. Table 2 shows that the fitness advantage of a precise sex ratio over a binomial sex ratio in this case is about 20% for clutches of size $N = 3$ and $N = 4$, while Table 4 shows that a sex ratio as precise as actually observed in *Metaphycus luteolus* is about 10% better than a binomial sex ratio for clutches of size $N = 3$ and $N = 4$.

Table 6. Data for *Metaphycus angustifrons* (from Kapranas 2007)

523 males
 + 1861 females

 2384 individuals

1861 females
 - 939 females on hosts with no males

 922 females on hosts with males

p = fraction of matings on natal hosts (assumed to equal the number of females on hosts with males/number of females)

$$= 922/1861 = 0.49543.$$

Theoretical optimal proportion of females in the population [Eqn. (3)]:

$$p/2 + 1/2 = 0.74772.$$

Observed proportion of females in the population:

$$1861/2384 = 0.78062.$$

$$R = F/M = \text{females on hosts with no males/number of males} = 939/523 = 1.79541.$$

Notice that the observed and theoretical sex ratios, 0.78062 and 0.74772, respectively, are quite close in this case. This may well be a fluke. If there is no other explanation of the difference between this case and the previous one, perhaps *Metaphycus angustifrons*, whose data are shown in this Table 6, are more likely to mate on their natal host than *Mataphycus luteolus*, whose data are shown in Table 5. I have not included a case with an R very close to 1.79541 in Tables 2 and 4, but it is not terribly far from the extreme case, $R = 2.0$, above which value the best thing to do is produce all males. This conclusion is paradoxical: if there are very many females available for mating off the natal host, the best sex allocation is all males. But if all males are produced (to mate with all those females), then there would not be all those females.

DISCUSSION

This paper is a crude sketch of two ideas about sex ratios in partially inbred parasitic wasps. The first point is to show that there is an advantage of precise sex ratios when males mate with their sisters on the natal host and then emigrate and mate with dispersing females that were not mated on their natal hosts. The second point is to determine the optimal sex ratio if a certain proportion of matings occur on the natal host and the rest occur off it. The second part treats the proportions of the sexes as continuous variables and ignores the fact that the numbers of parasitoids on individual hosts must be integers.

Calculations show that there is an advantage in precise sex ratios for partially inbred parasitic wasps. This advantage (as much as 20%) may be large enough that it would be selected for. The overall optimal proportion of males ranges from 0% (or $\epsilon\%$), when all mating is on the natal host, to 50% when all mating is off the natal host.

These results are for the simplest, crudest models. These are simple models which popped into my mind. I have not looked carefully at any of the theoretical literature on sex ratios. My impression from the most casual inspection of some important work (Hamilton 1967, Nunnery and Luck 1988) is that the emphasis of other workers is on the source of the wasps on a host. Are the offspring from one, or from more than one mother? and, if they are from more than one mother, were the eggs laid simultaneously or sequentially? Are there males from other hosts waiting to mate with the emerging females? I am more interested in the careers of the wasps from a given host, both on and off that host.

Even though this work is crude, there are advantages to it. One advantage is that it suggests different ways to look at data. The sex ratio is an important fact, but my crude models require knowledge of how many matings take place on the natal host and how many take place off the natal host. It also requires knowledge of the effective sex ratio off the natal host (determined by the total number of males and the number of females not mated on the natal host). This knowledge can be obtained by looking at the distribution of the numbers of males and females deposited on each host. Another advantage of theory, not specific to this theory, is that it may stimulate scientists to look longer and harder at their data.

This theory lacks biological realism. For example, it is assumed that if there are males and females on a host, all the females are mated before they emerge. But, what happens if some females leave their natal host unmated? Most important for the theory, if some females leave the hosts unmated, how does the number of departing unmated females depend on the number of males and females on the natal host? This is a question that a modeler must ask, but it is a question that an experimenter is more likely to answer when he or she has theory in mind.

REFERENCES

Charnov, E. L. 1982. The Theory of sex allocation. Princeton University Press, Princeton, New Jersey.

Green, R. F., Gordh, G. and Hawkins, B. A. 1982. Precise sex ratios in highly inbred parasitic wasps. *American Naturalist* 120:653-665.

Hamilton, W. D. 1967. Extraordinary sex ratios. *Science* 156:477-488.

Kapranas, A. 2007. Precise sex allocation by several encyrtid parasitoid species exploiting brown soft scale, *Coccus hesperidum* L. (Coccidae: Hemiptera) in southern California citrus. Chapter 3 of a Ph. thesis written at the University of California, Riverside.

Nunney, L. and Luck, R. F. 1988. Factors influencing the optimum sex ratio in a structured population. *Theoretical Population Biology* 33:1-30.

MacArthur, R. H. 1965. Ecological consequences of natural selection. In: *Theoretical and Mathematical Biology* (T. H. Waterman and H. J. Morowitz, eds.) Blaisdell, New York.