Three Comments on the Sex Ratio
in Arrhenotokous Animals

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THREE COMMENTS ON THE SEX RATIO IN ARRHENOTOKOUS ANIMALS

Arrhenotoky is a system of sex determination in which unfertilized eggs become males and fertilized eggs (usually) become females. Arrhenotoky is found in a few groups of animals, the most important of which are the Hymenoptera, which include social species such as some bees and ants, as well as solitary species, such as parasitic wasps. The number of arrhenotokous species is immense.

There has been some debate, both theoretical and empirical, over the sex ratios in social Hymenoptera (Trivers and Hare 1976 and Alexander and Sherman 1977). In this paper I will consider the sex ratios of solitary species, which may or may not show strong inbreeding. The issues I will consider were raised by Hamilton (1967) in his paper on "extraordinary sex ratios," and discussed by Hartl and Brown (1970) and Hartl (1971).

The first point I will comment on is the fact that in arrhenotokous species all females have mothers and fathers, but males have only mothers. The basis of Fisher's argument that the sex ratio should be 1:1 (if young of each sex cost the parents the same) was that all individuals have a mother and a father. If one sex were rarer its individual members would have proportionately more offspring and pass on more of their genes than individuals of the more common sex and selection would favor a change that would result in producing more individuals of the rarer sex.

In arrhenotokous species with random mating the sex ratio should still be 1:1. This is because while females produce more offspring than males any genes put into males get through to their offspring if they have

any. Genes put into females are passed on to only·half of their offspring. This point is made explicitly with the help of a mathematical model.

Inbreeding is a mechanism that may produce a sex ratio that favors females. Hamilton (1967) has considered this from a number of points of view. One of the examples he considered is the case of local competition for mates. All the eggs laid in a host develop into adults there and the adults mate randomly within the host. The mated females then disperse to look for other hosts in which to lay their own eggs. Hamilton gives a model that shows that if the females disperse randomly and each host has eggs from exactly n females and sex is determined by an autosomal gene, then the proportion of males should be $(n-1)/2n$. (Hereafter I shall refer to the proportion of males rather than the sex ratio.)

My second comment is about Hamilton's example. Consideration of his model shows the interesting fact that while a .5 proportion of males loses to the optimal $(n-1)/2n$ proportion overall, within each host females that produce eggs with proportion .5 males are fitter than those that produce eggs with the optimal proportion of males. This is an example of what is known in statistics as Simpson's paradox (Simpson 1951, Blyth 1972).

An explicitly genetic model is constructed to examine the example considered by Hamilton and numerical calculations show that the optimal sex ratios are not exactly what Hamilton's approximation shows them to be.

The final comment concerns the extreme case of inbreeding considered by Hamilton where most hosts contain the young of only one mother and they have to mate with each other. If one male is sufficient to insemi-nate all his sisters then extra males are a waste and the best number of

males is exactly one. Hartl (1971) considered this case and discussed the possibility of mortality of young within a host. If females must be fertilized before leaving a host and if there is a substantial chance of mortality of young then it would be risky to produce only one male. Hartl considered several models and found the proportion of males that would maximize the number of their inseminated sisters leaving a host (a measure of absolute fitness). Unfortunately, Hartl confused sex ratio of young with survival of young. He thus assumed that the actual number of males produced would be random, having a binomial distribution. I show that if the female can lay and leave unfertilized a precise number of (male) eggs she can do substantially better than if she lays a random number of unfertilized eggs, even if the probability of a given egg being unfertilized in the random case is best. The suggestion is made that the advantage of arrhenotoky is not that it permits a skewed sex ratio (as Hamilton suggested) but that it permits a precise sex ratio.

1. WHEN MATING IS RANDOM THE BEST SEX RATIO IS 1:1 FOR ARRHENOTOKOUS SPECIES*

In arrhenotokous animals unfertilized eggs become males, fertilized eggs (usually -- but I ignore the exceptions) become females. Thus, each male has only a mother, while each female has both a mother and a father. Thus, males have one female parent, one male and one female grandparent,

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*For the sake of the model I assume that the costs of the two sexes are the same, that the total number of eggs a female lays is fixed, regardless of their sex, and that all males have the same fitness and all females have the same fitness except in the sex ratio of the offspring they will produce.

one male and two female great-grandparents, two male and three female great-great-grandparents, and so on. If in one ancestral generation there were m male ancestors and f female ancestors, in the preceding ancestral generation there must have been f males (one father for each female) and m+f females (one mother for each of the males and females). The number of ancestors of each sex may be seen in the following table, starting with one male in the present generation (or one female in the preceding generation) and looking backward:

Table 1

Ancestral generation (0 is present, 1 is parental generation, 2 is grandparental, etc.)

	0	1	2	3	4	5	6	7
Number of male ancestors	1	0	1	1	2	3	5	8
Number of female ancestors	0	1	1	2	3	5	8	13
Total number of ancestors (Fibonacci)		1	2	3	5	8	13	21

In diploid animals each individual has two parents, four grandparents, eight great-grandparents, etc., the number of ancestors doubling each generation. In arrhenotokous animals the number of ancestors increases more slowly, in the well-known Fibonacci series: 1,2,3,5,8,13,21,..., seen in the table above, where each successive number is equal to the sum of the preceding two. We can see that the number of female ancestors leads the number of male ancestors by one step. Thus the number of female ancestors in the 10th generation would be equal to the number of male ancestors in the 11th generation. The ratio of the number of female to male ancestors

in distant ancestral generations will be simply the limit of the ratio of successive terms of the Fibonacci series: $(1 + \sqrt{5})/2 \doteq 1.618$. Thus the proportion of remote female ancestors will be $\doteq .618$ while the proportion of remote male ancestors will be .382.

The fact that all individuals have more female than male ancestors suggests that the sex ratio should favor females. Imagine a female who has the capacity to produce a certain fixed number of young and she can determine the sex of each. She has to "decide" how to "invest" her genes so as to pass on as many as possible to future generations. She "knows" two things.

1. All the females together produce more young than all the males together, which suggests that it might be best to produce an excess of females.

2. A son may not produce offspring, but if he does, any genes that he has will be surely passed on, while genes in a daughter may not be passed on, even if she has offspring.

It is not immediately clear what the effects of the conflicting advantages of producing offspring of the two sexes mentioned in 1 and 2 are. It is possible to construct a genetic model to determine the optimal sex ratio for randomly mating arrhenotokous species. The ideas will be used and expanded upon in the next section and so are given here, even though Hartl and Brown (1970) have given an argument that the sex ratio should be 1:1.

Assume that the sex ratio is determined by an autosomal gene with two alleles A and B. Using the notation of Hartl and Brown (1970) assume

that females with genotypes AA, AB and BB produce proportions u, v and w
males, respectively. Males are haploid, having genotypes A or B. Mating
is assumed to be random. Starting with given numbers of males and females
of each genotype it is easy to find the proportions of the sexes and geno-
types in succeeding generations. Hartl and Brown give the results of some
such runs in Table II (p. 186) of their paper. While a 50% proportion of
males is theoretically best, it may take a very long time for the best sex
ratio to eliminate a sub-optimal sex ratio if the sub-optimal sex ratio
is recessive.

2. A GENETICAL VERSION OF HAMILTON'S NON-SEX-LINKED CONTROL
OF SEX RATIO WITH LOCAL COMPETITION FOR MATES

Hamilton (1967) has considered a case where in every generation eggs
are laid in hosts where they develop to maturity and where the adults mate
randomly. The mated females emerge and disperse randomly to lay the next
generation's eggs in new hosts. Hamilton assumes that exactly n females
lay eggs in each patch. It is implicitly assumed that each female lays
the same large number of eggs. Hamilton concludes that the optimal pro-
portion of males produced will be $(n-1)/2n$. This result is obtained by a
fitness argument using a model that is not explicitly genetic. Further,
the assumption that parasite and host densities are constant in space and
time is not realistic biologically, but this assumption does permit a
simple mathematical conclusion.

In this section a numerical example of Hamilton's model is given that
compares the reproductive output during one generation of two types of
females, one producing 50% males and the other producing proportion
$(n-1)/2n$ males. The interesting fact is seen that within each host the

relative output of the females producing 50% males is greater than those producing proportion (n-1)/2n males, while overall production is higher for the females producing (n-1)/2n males. This is an example of what is known in statistics as Simpson's paradox (Simpson 1951, Blyth 1972), which is a relatively recent version of the idea that one can lose all the battles and still win the war.

In the example it is assumed that exactly n = 4 females lay their eggs in each host. There are two types of females: A and B. Type A produces 50% males while Type B produces (n-1)/2n = 37.5% males.

The number of Type A females laying eggs in a host has a binomial distribution with parameters n = 4 and p (I consider the case p = .5 here). Each female lays the same number of eggs in a host. All that varies is the sex ratio of the offspring. Mating between offspring within the host, is random. The absolute fitness of each genotype (which may be thought of as the number of the genes A or B carried by mature females emerging from the hosts) is proportional to the number of females of that type plus the number of matings by males of that type.

There are five possible values for the number of Type A females in a host: 0,1,2,3,4. I assume for definiteness that each female lays exactly 8 eggs. Type A females lay 4 unfertilized (male) eggs (all Type A) and 4 fertilized (female) eggs (also Type A). Type B females lay 3 unfertilized and 5 fertilized eggs (all eggs of Type B). The eggs develop and mate at random and the mated females leave the host. (Since females are assumed to be either of Type A or Type B this corresponds to having Type A females mated to Type B males remain Type A with probability .5 and

change to Type B with probability .5. Hamilton's model does not correspond to any reasonable genetic model as far as I can see.)

Table 2 shows the 5 different possible arrangements of the two types of females laying eggs in a host. The numbers of male and female eggs of each type are given for each case, as are the expected number (actually twice the number) of each type of female (or gene) emerging after random mating. The binomial probabilities are given for each possible number of Type A female laying in a host, call it X. The final row gives the expected number of females of each type emerging from hosts of each starting number of Type A females when the probabilities of each starting number (the binomial probabilities) are taken into account.

SEE TABLE 2 ON NEXT PAGE

Notice that while the total number of genes emerging from a host is greater for Type B than for Type A, in each host the proportion of Type A's among the emerging females is greater than among the females that lay their eggs in the host.

While this model does not realistically describe any genetic system it does provide an argument that inbreeding may result in a biased sex ratio. That is, selection would favor Type B over Type A. For a fixed number n of females laying eggs in each host and a binomial distribution of the number, X, of a particular type of female laying eggs in each host Hamilton finds that the best proportion of males is $(n-1)/2n$.

Hamilton also considered the case where X is not binomially distributed and found that the best proportion of males depends on the distribution. Another result, not mentioned by Hamilton, is that if n is random and has mean μ the best proportion of males need not be $(\mu-1)/2\mu$. That is,

Table 2

Number of Type A females in host = x	x =	0 Types		1 Types		2 Types		3 Types		4 Types	
		A	B	A	B	A	B	A	B	A	B
Young in host: Males		0	12	4	9	8	6	12	3	16	0
Females		0	20	4	15	8	10	12	5	16	0
Total		$\overline{0}$	$\overline{32}$	$\overline{8}$	$\overline{24}$	$\overline{16}$	$\overline{16}$	$\overline{24}$	$\overline{8}$	$\overline{32}$	$\overline{0}$
Number of females (genes) of each type emerging:		0	40	9.846	28.154	18.286	17.714	25.600	8.400	32	0
Binomial Probability, P(x=x):		.0625		.25		.375		.25		.0625	
(Weighted) numbers of females emerging:		0	2.5	2.462	7.038	6.857	6.643	6.400	2.100	2	0

(Weighted) Totals in: Type A: 2   Type B: 2

Totals out: Type A: 17.719   Type B: 18.281

σ

Hamilton's result does not hold if the number of females laying eggs in a host is random, with mean μ, rather than having the fixed value n.

One thing that a close examination of Hamilton's model does show is that while a biased sex ratio is best overall, in each host it is out-competed by an even sex ratio.

I have considered an explicitly genetic model to more realistically describe this local competition for mates situation considered by Hamilton. As in Section 1 I assume that sex ratio is determined by the female and that the sex ratio is controlled by an autosomal gene having two alleles, which I will now call A and B. There are three female genotypes: AA, AB and BB. The haploid males have genotypes A and B. The model can best be described by considering what happens at different stages.

A. <u>The dispersal stage.</u> Inseminated females search for hosts on which they lay their eggs. I assume

1. Females choose hosts randomly and independently of each other, except perhaps that the number of females laying eggs in a host may be limited.

2. Each female has been fertilized by one male.

3. Thus there are 6 "types" of females dispersing, corresponding to their genotypes and the genotype of the sperm they carry. The types are AA:A, AA:B, AB:A, AB:B, BB:A and BB:B (where AB:A means a female with genotype AB carrying sperm of type A).

B. <u>The settling stage.</u> Females find their host and lay their eggs. I assume

1. All females lay the same large number of eggs. The number of females laying eggs on a host does not influence the number of eggs laid by each female or the eggs' survival.

2. The sex ratio of the eggs laid by a female depends on her genotype, with AA, AB and BB producing proportion u, v and w males.

3. The number of females settling in a patch is a random variable N (I will consider only the case N = constant).

4. The genotypes of the eggs laid are determined at random: AB:A females produce females that are half AA and half AB and males that are half A and half B.

C. The stage of mating within the host, and female dispersal. I assume

1. All females are mated exactly once (see A. 2.).

2. Mating is random within a host. Of course, sib-mating will be common when the eggs in each host are laid by a small number of females.

I have written and run a computer program embodying the assumptions of this model. Two conclusions have been reached. The (n-1)/2n proportion of males that Hamilton found is not borne out. For n = 4 I found a best sex ratio of .35 rather than .375 and for n = 2 I found a best sex ratio of .21 rather than .25. In both cases I assumed simple dominance and the results were the same whether the dominant gene produced the higher or the lower sex ratio.

Second, the approach to a homozygous population was very slow. In fact, what I did was watch how the gene frequencies changed and assumed that the population would continue to change in the direction it was headed after the rates of change of the type frequencies became monotone and consistent.

The difference between the model considered here and that of Hamilton is that while Hamilton only considered genes I have considered genotypes;

and in the case of dispersing mated females, I have considered the type
of sperm they carry as well. In fact, Hamilton (1967, p. 481) said that
his was only an approximate analysis. As an approximation it is very
good.

3. A COMMENT ON THE EVOLUTION OF ARRHENOTOKY

In his paper on natural selection in arrhenotokous populations Hartl
(1971) discussed the number of unfertilized (male) eggs that should be
laid in a single host when sib-mating is complete and the number of eggs
laid in the host is finite. Hamilton (1967) produced a model that showed
that with complete sib-mating the optimum proportion of males per host was
near zero. If it is necessary to have at least some males this would be
possible only if the number of eggs per host were infinite, which Hamilton
implicitly assumed was the case. Hartl was interested in what happens
when there are a finite number of eggs laid in each host. Data summarized
by Hamilton showed many cases where the "typical" number of males per host
was one. Hartl was interested in developing a theory to see what number
of males per host was actually best, that is, would maximize the number
of fertilized females leaving the host.

Hartl considered a series of models where the number of eggs laid per
host has various distributions and the distribution of the number of un-
fertilized eggs in a host has a binomial distribution with r the prob-
ability that a given egg is unfertilized and n the number of eggs in the
host. Thus the distribution of the number of unfertilized eggs, given

the number of eggs in the host, has a binomial distribution. Hartl mistakenly refers to this as binomial survival (p. 318).

Hartl found that the best proportion of males was generally larger than that observed in the data reported by Hamilton. (In fact, some of the "typical" numbers of males cited by Hamilton were merely averages.) This discrepancy may have resulted from Hartl's confusion of sex ratio and survival. Hartl's model implicitly assumes that whether an egg is fertilized or not is completely random and does not depend on the number of eggs in a host or the proportion of eggs already fertilized.

One of the evolutionary advantages suggested for arrhenotoky (Hamilton 1967, p. 482) is that it permits the production of biased sex ratios. Other mechanisms could produce biased sex ratios by having a fixed probability (other than .5) of producing a male. Arrhenotoky could provide a more precise mechanism for regulating sex ratios by permitting the fertilization (or non-fertilization) of a precise number of eggs.

I would like to suggest that an evolutionary advantage of arrhenotoky is not that it permits biased sex ratios, but that it permits precise sex ratios. This idea is explored in a model similar to that of Hartl's in that it seeks to maximize the number of inseminated females emerging from a host where all the eggs were laid by the same mother.

The difference between my model and Hartl's is that Hartl assumed that the female cannot determine whether the individual eggs it lays are fertilized but that there is a fixed probability, r, that a given egg will be fertilized. Hartl sought to find the optimal value, r, given some

distribution of the number of eggs laid in each host. I assume that the female is able to determine whether each of her eggs is fertilized or not and that what is optimized is the number of eggs fertilized given the number of eggs laid in the host. I assume that the individual eggs then survive to emergence or not independently of each other, with the same probability of survival for each egg, regardless of whether it is fertilized or not.

THE MODEL

The situation I consider is this: Each inseminated female (and only inseminated females) lays a batch of eggs in a host. Each host contains the eggs of only one female. Some of the eggs laid will be fertilized (female) and the others will be unfertilized (male). The problem is to find the number of unfertilized eggs that maximizes the expected number of females emerging from the host and inseminated by the males. I assume that one male will be able to inseminate all the females.

In describing the model four variables must be described:

1) N is the number of eggs laid in a patch. N may be random and have a specified distribution. Hartl successively assumed that N is: a) a constant; b) a Poisson random variable, and; c) a negative binomial random variable.

2) M is the number of unfertilized eggs laid. M will depend on N. Hartl assumed that M has a binomial distribution with parameters r (the probability that a given egg will be unfertilized) and N. The problem Hartl attacked was to find the optimal r, that is, the r that will result in the maximum possible expected number of eggs developing into mated adult females.

3) Z is the number of eggs that survive to emergence. It is a random variable and depends on N, the number of eggs originally laid. For mathematical convenience I only consider binomial survival. That is, Z will have a binomial distribution with parameters p (the survival probability for an individual egg) and N. Hartl refers to "binomial survival" but it is the sex ratio (or properly, the number of unfertilized eggs laid, M) that he really assigns a binomial distribution. It is possible to have binomial survival in my sense for his Poisson and negative binomial cases, but not for the first case (constant N) that he considers.

4) X is the number of males emerging (and Y = Z - X is the number of females emerging). This number will also be a random variable. I will assume that there is no differential mortality for the two sexes and that all deaths are independent with respect to sex. Under these assumptions X will have a hypergeometric distribution with parameters Z (the sample size) and M and N - M the number of males and females, respectively, from which the drawing is made. M unfertilized and N - M fertilized eggs are laid and Z of these survive. The eggs that survive are a random sample of the N eggs originally laid.

RESULTS

I will concentrate on the case where a) the number of eggs laid in a host is a constant N; b) survival of eggs to maturity is binomial, and c) survival chances are the same for males and females. That is, the number of eggs that reach maturity in a host, namely Z, is a binomial random variable with parameters p and N.

I intend to compare two strategies. The first, implicit in Hartl's (1971) work, assumes that the female has a fixed probability, r, of leaving each egg unfertilized and the value of r is that which maximizes the expected number of inseminated females emerging from a host. It follows that the number of unfertilized eggs laid in a host will have a binomial distribution with parameters N and r and that the number of males maturing in a host, X, given that the total number of eggs reaching maturity is Z, will have a binomial distribution with parameters Z and r.

The second strategy is to produce the precise number of males that maximizes the expected number of inseminated females emerging from a host. If M unfertilized eggs are laid and if Z eggs survive to maturity, then the number of males that reach maturity will have a hypergeometric distribution with parameters Z, M and N - M. That is, the number of males maturing in a patch, X, has a distribution given by the formula

$$P(X=x) = \frac{\binom{M}{x}\binom{N-M}{Z-x}}{\binom{N}{Z}} \quad .$$

The important difference between the strategies is that the first results in a binomial distribution of the number of males surviving given a total of Z survivors, while the second results in a hypergeometric distribution of the number of males surviving given a total of Z survivors. The variance will be smaller for the hypergeometric and the expected number of fertilized females emerging will be greater for the second strategy.

For both strategies N eggs are laid, Z of which survive, where Z has a binomial distribution with parameters N and p. The probability that exactly z eggs survive is given by

$$P(Z = z) = \binom{N}{z}p^z(1-p)^{N-z} .$$

Strategy 1: A constant r is chosen and the number of eggs left unfertilized has a binomial distribution with parameters N and r. If r is the probability that a given egg is left unfertilized and if z is the number surviving to maturity then the expected number of fertilized females emerging from a host is

$$E(Y \cdot I_{(X \geq 1)}|z) = z(1-r) - z(1-r)^z$$

which is just expression (8) in Hartl (1971). Here $I_{(X \geq 1)}$ is the indicator function which takes value 1 if the statement $X \geq 1$ is true and 0 otherwise. The statement $X \geq 1$ means that there is at least one male in the patch to inseminate the females. It is assumed here that one male is sufficient to inseminate all the females. This assumption may be wrong in practice, but it is made by Hartl (1971) and my analysis is parallel to his. Thus, averaging over the possible values of z, the number of surviving adults, we have that the expected number of inseminated females emerging from a host is

$$E(Y \cdot I_{(X \geq 1)}) = \sum_{z=2}^{N} (z(1-r - (1-r)^z)\binom{N}{z}p^z(1-p)^{N-z} .$$

The best strategy is to choose the value of r that maximizes $E(Y \cdot I_{(X \geq 1)})$. Values of E (and the values of r) have been found for the best value of r for several sets of values of the parameters N and p. These values are given in Table 3 where they are compared with comparable values found for Strategy 2.

Strategy 2: If N eggs are laid, a fixed number of eggs, M, are left un-fertilized. M is chosen so as to maximize the expected number of insemi-nated adult females emerging from a host. Since each egg survives to maturity with probability p the expected number of inseminated females leaving a host is

$$E(Y \cdot I_{(X \geq 1)}) = (N - M) \, p(1 - (1 - p)^M) \ .$$

Here $(N - M)p$ is the expected number of females reaching maturity in a host and $(1 - (1 - p)^M)$ is the probability that there will be at least one male to inseminate them.

Table 3 gives the best proportion of unfertilized (male) eggs and the expected number EM (for Strategy 1) and the best number of males (for Strategy 2) and the expected number of inseminated females emerging from a patch using each strategy for several sets of values for the parameters N and p.

Table 3

Parameters		Strategy 1			Strategy 2		
N	p	Best r	EM	E_1	M	E_2	E_2/E_1
10	.25	.3904	3.904	.9192	4	1.0254	1.1155
10	.50	.3144	3.144	2.6925	3	3.0625	1.1374
10	.75	.2626	2.626	4.7623	2	5.6250	1.1812
10	1.00	.2257	2.257	6.9684	1	9.0000	1.2915
20	.25	.3072	6.144	2.7051	6	2.8771	1.0636
20	.50	.2216	4.433	6.9480	4	7.5000	1.0794
20	.75	.1751	3.502	11.5208	2	12.6562	1.0986
20	1.00	.1459	2.918	16.2285	1	19.0000	1.1708

Table 3: For various number of eggs laid, N, and survival probabilities, p, the best strategies are given. For Strategy 1 the value r is the probability that each egg is left unfertilized and EM is the expected

of eggs left unfertilized. For Strategy 2 M is the precise number of eggs that are left unfertilized. The payoff is E, the expected number of inseminated females emerging from a host when the best strategies are used. The final column gives the ratios of the expected numbers of fertilized females emerging from each host using Strategies 2 and 1.

Strategy 2 is better than Strategy 1. Notice in Table 3 that the relative advantage of Strategy 2 (a precise sex ratio) over Strategy 1 is greater when brood size is smaller and when egg survival is greater. It is better to leave a precise number of eggs unfertilized than a random number. Hamilton (1967, p. 482) mentions that one of the properties of arrhenotoky is that it permits the production of biased sex ratios. But biased sex ratios are surely possible with other modes of reproduction as well. I would like to suggest that an advantage of arrhenotoky is not simply that it makes possible the production of biased sex ratios, but that it makes possible the production of precise sex ratios.

Hartl (1971, p. 320) says that the survival of one egg is not likely to be independent of survival of another and that families are likely to survive or die as a group. He gives this as a justification for assuming that the number of eggs laid, N, is a random variable having a negative binomial distribution. This argument reveals two mistakes. First, the distribution of brood size is confused with the distribution of the number of eggs that survive to maturity. Second, the negative binomial distribution is not likely to arise because broods survive or die together. More likely is that surviving broods may show good survival, with some mortality due to infertility of eggs or cannibalism. This mortality might well be binomial. For broods that die together the sex ratio

doesn't matter, so the best strategy would be to optimize the sex ratio
for all families as if they will survive.

I have assumed that the number of eggs laid, N, is a constant. If
N is variable then the best number of eggs M to leave unfertilized will
be a function of N. In all cases with binomial survival, laying the best
precise number of unfertilized eggs (which number may be a function of
the total number of eggs laid) will be better than leaving a binomial
number of eggs unfertilized even if the best binomial parameter r is used.

EVIDENCE OF PRECISE SEX RATIOS

The calculations in the previous section show that in theory it may
be better to produce a precise sex ratio than a binomial sex ratio. The
question is, what happens in practice? George C. Williams (1979) con-
sidered this in his paper, "The question of adaptive sex ratio in out-
crossed vertebrates." Williams considered the hypothesis that sex
determination is adaptive, with sex ratios showing either more or less
than random variation.

Williams concluded that for outcrossed vertebrates the evidence favors
the theory that sex is randomly determined. Williams admits that sex may
not be randomly determined for highly inbred animals such as those con-
sidered by Hamilton (1967). The studies cited by Hamilton do provide good
evidence of sex ratios biased in favor of females, but most of those
studies fail to provide evidence that sex ratios are not simply determined
binomially with the probability of a male being different from one half.
The studies Hamilton cited were generally done with sex ratio in mind, but
not the variation in the sex ratio. In some cases only the mean number of

males and females per host are given, in others where the actual numbers are given the sample sizes are too small. The sex ratios given are also for adults and the primary sex ratio is not known. In some cases the appearance of a precise sex ratio may have resulted from cannibalism among the males.

Good data that sex determination is sometimes precise has been given by Gordh (1976) in his study of the bethylid wasp *Goniozus gallicola*, which is a parasite of moth larvae. Gordh's study, conducted under careful laboratory conditions, showed very little juvenile mortality among the parasites. Therefore the sex distribution of emerging adult parasites quite accurately reflects the primary sex ratio.

Gordh gives data for 185 parasite broods and the data is repeated here in Table 4. Since the best number of males in a brood is one (at least for small broods, where one male is sufficient to inseminate all the females) the number of broods of a given size having exactly one male is given in the table.

As in most studies, complete distributional data is not given. Nevertheless, using the data given it is a simple matter to test whether the number of males in a brood of a given size has a binomial distribution. Since the number of broods having exactly one male is given for each brood size, this number may be compared with the number of such one-male broods expected by chance if the number of males is, in fact, binomial.

Under the null hypothesis that the number of males in a brood of a given size is binomial, the probability of exactly one male in a brood is given by

$$P(X = 1) = \binom{N}{1} p (1 - p)^{N-1}$$

where X = the number of males in the brood, N is the brood size, and p is the probability that each egg will be unfertilized (male). This probability will be largest when p = 1/N. In this case $P(X=1) = (1-1/N)^{N-1}$; call this value $\hat{P}$.

The null hypothesis that X is binomially distributed is to be tested against the hypothesis that sex ratios are (more) precisely determined. Since the test will consist of seeing whether the number of broods with exactly one male is significantly larger than expected, using the value of p that maximizes $P(X=1)$ will make the test conservative.

Let N be the brood size and let n be its frequency (the number of broods of that size). Let k be the number of broods of size N having exactly one male. Then k will be a random variable having a binomial distribution with parameters n and P where P is no larger than $\hat{P}$. Under the null hypothesis the probability of observing as many as k (or more) broods with exactly one male will be no larger than

$$X = \sum_{x=k}^{n} \binom{n}{x} \hat{P}^x (1-\hat{P})^{n-x} \ .$$

For example, there are 20 cases where the brood size is 4. For N=4 the sex ratio value that maximizes the probability of exactly one male is 1/4 and the resulting maximum possible probability of exactly one male is

$$\hat{P} = (1 - 1/N)^{N-1} = (1 - 1/4)^3$$
$$= 0.421875 \ .$$

Of the 20 broods of size 4 there were 17 with exactly one male. We have

$$\alpha = \sum_{x=17}^{20} \binom{20}{x} \hat{P}^x (1 - \hat{P})^{20-x}$$
$$= 1.058 \times 10^{-4} \ .$$

Thus, using the binomial test, we see that there are significantly too many single male broods among broods of size four.

Gordh's data is given in Table 4, along with α, an upper bound on the probability that the number of broods of a given size would have exactly one male as often as (or more often than) observed if sex is randomly (binomially) determined.

Table 4

Distribution of brood size for 185 broods of *Goniozus gallicola*. Here K is the number of broods of a given size having exactly one male and α is an upper bound on the probability of observing that many one-male broods or more. Data from Gordh (1976).

Brood size	Frequency	One-male broods	
$\underline{N}$	$\underline{n}$	$\underline{K}$	$\underline{\alpha}$
1	10	8	--
2	14	13	9.155×10^{-4}
3	24	22	1.631×10^{-6}
4	20	17	1.058×10^{-4}
5	21	16	1.135×10^{-3}
6	17	15	6.094×10^{-5}
7	15	13	2.519×10^{-4}
8	10	8	1.082×10^{-2}
9	21	15	2.633×10^{-3}
10	4	3	.165
11	10	5	.331
12	5	2	.635
13	5	1	.910
14	6	1	.944
15	3	1	.762

Notice that for all brood sizes from N=2 to N=9 there are significantly too many one-male broods. This is strong evidence that *Goniozus gallicola* produces a much more precise ratio than it would if the sex of eggs were determined at random and the number of males had a binomial distribution. For larger brood sizes (with N > 10) the parasites tend to lay more than one unfertilized (male) egg. This might be a useful strategy if the capacity of an individual male to inseminate females is limited.

Theoretically, there is an advantage for certain highly inbred animals to produce not only a brood whose sex ratio is biased in favor of females, but also to produce a precise sex ratio. Data on a highly inbred species of parasitic wasp give evidence of just such precise sex determination. Such precision is made possible by the wasps' arrhenotokous mode of sex determination. Thus, it is suggested that an advantage of arrhenotoky is not simply that it permits the production of a biased sex ratio, but that is permits the production of precise sex ratios as well.

Acknowledgments

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