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SEX-RATIO SELECTION IN EUSOCIAL HYMENOPTERA*

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FISHER'S SEX-RATIO THEORY

In 1930, R. A. Fisher proposed the first explanation of how natural selection should operate on the sex ratio. This theory, tersely developed in Fisher's book, has since been treated by a number of authors for both discrete and overlapping generations (Bodmer and Edwards 1960; Cavalli-Sforza and Bodmer 1971; Charnov 1975; Crow and Kimura 1970; Eshel 1975; Kolman 1960; Leigh 1970; Leigh et al. 1976; Shaw 1958; Shaw and Mohler 1953; Verner 1965; Willson and Pianka 1963). The theory is most easily developed for the following example: Consider a species where the parent lays eggs and then feeds the offspring for a period of time, putting b_2 units of some limiting resource into a son, and b_1 into a daughter. Thus for every son raised to the end of the period of parental care, b_2/b_1 daughters could have been raised. For simplicity, mortality during the parental care period is assumed to be zero and mortality after is assumed to be sex dependent but independent of family composition. Fisher's theory applied to this situation states that in evolutionary equilibrium, the population should be devoting one-half of the supply of limiting resource to each sex. The primary sex ratio is $b_2/(b_2 + b_1)$ proportion sons under this allocation. Note that this allocation is independent of any mortality after the parental care period, even if this mortality differs between the sexes (so long as the mortality is not itself dependent upon the sex ratio). The theory has been tested by Trivers and Hare (1976) for slave-making ants (and some solitary Hymenoptera) and by Smith (1968; see also Emlen [1973]) for the tropical bird group known as Oropendolas. In both cases the results supported the theory.

Several extensions of the basic theory have been made, altering various of its implicit assumptions (MacArthur 1965; Spieth 1974; Hamilton 1967; Trivers and Willard 1973; Charnov and Bull 1977; Shaw 1958). This paper will focus on one particular assumption, the alteration of which has far-reaching implications for the social Hymenoptera (Trivers and Hare 1976).

* This paper is dedicated to Dr. Richard F. Shaw for his pioneering work on evolution of the sex ratio.

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HAPLODIPLOIDY

Fisher (1930) developed the theory for diploids by first noting that, in terms of autosomal genes, half of the genome of an individual is contributed by its father and half by its mother. If we consider the viewpoint of a gene in the mother, it is clear that this gene has equal probability (one-half) of being present in a son or a daughter. Thus it follows that a son is as valuable as a daughter, and from this follow Fisher's results.

Suppose now that sex determination is by haplodiploidy, with males haploid and developing from unfertilized eggs (as in most Hymenoptera). If the mother controls whether or not an egg is fertilized (and thus controls the sex ratio), it is fairly easy to show that the equilibrium ratio of investment here also follows Fisher's theory. This is true under outbreeding in a uniform environment (Charnov 1978; Hamilton 1972).

The statement that Fisher's theory holds from the mother's viewpoint under haplodiploidy assumes that the mother controls the input of resources to offspring. While this is probably true for solitary species, it may not be for eusocial species. The workers in a Hymenoptera society are sisters; the reproductives they rear are sisters and some combination of brothers and worker-laid males. If the workers control the input of resources to reproductives, Fisher's theory does not necessarily hold. This follows from the simple fact that the workers are not equally related to the male and female reproductives they rear (Hamilton 1964, 1972; Wilson 1971; Trivers and Hare 1976).

With a single insemination of the queen, workers have a coefficient of relatedness of three-fourths to their sisters but only one-fourth to their brothers. Hamilton (1964, 1972) made this asymmetry the basis for his classic theory of the bias inherent in haplodiploidy for the evolution of eusocial societies. Trivers and Hare (1976) were the first to realize that this asymmetry also had far-reaching implications for sex-ratio evolution in eusocial species. They built a model very similar to Fisher's except that the workers were assumed to be the investors; the queen produced the ova, but the ratio of female to male reproductives was controlled by the workers. The Trivers-Hare theory predicts that in evolutionary equilibrium three-fourths of the colonies' resource should be devoted to female reproductives. Notice that, assuming a single insemination for the queen, this is also the ratio: $(\text{coefficient of relationship of worker to sister})/(\text{coefficient of relationship of worker to sister} + \text{coefficient of relationship of worker to brother}) = 3/4/(3/4 + 1/4) = 3/4$.

The Trivers-Hare theory goes much beyond this basic three-fourths prediction (but the data they presented were related to this prediction). They also considered the equilibrium investment when some or all of the male reproductives are from worker-laid eggs (since males are haploid, a worker need not be inseminated to produce them). Trivers and Hare distinguish between the laying workers' viewpoint and that of a nonlaying worker. If a single worker lays all of the worker-laid eggs, the male reproductives are its sons, and this worker differs from those not laying eggs in that from their viewpoint the male reproductives are nephews. In the first case, the coefficient of relation is one-half, in the second it is three-eighths. Thus laying and nonlaying workers are expected to

differ in their equilibrium ratio of investment, and both differ from the queen. The theory works out the respective equilibria from the two worker viewpoints and the queen. If the queen lays all the male eggs, the worker viewpoints do not differ and a three-fourths investment of resources in new queens is expected if the workers control the investment.

Finally, the theory deals with the case of multiple inseminations of the queen (common in eusocial species). If the queen is mated with more than one male, the relatedness between sisters depends upon the extent to which the sperm from different fathers are mixed (Hamilton 1964). If the sperm from different fathers do not mix, then at any point in time the workers and the female reproductives they are raising share the same father, provided the workers do not live long enough to overlap with the sisters produced by a different father. At any point in time the coefficient of relation is three-fourths between sisters. Trivers and Hare argue that, provided the sperm from different fathers do not mix, the results of their theory should hold under multiple inseminations of the queen.

Thus the theory predicts: (1) a conflict exists between the workers and the queen (each has a different equilibrium-investment ratio in reproductives) and between the two types of workers; (2) depending upon who is in control, the respective equilibria are affected by the fraction of males derived from worker-laid eggs (but not by multiple inseminations of the queen, if sperm clump).

The purpose of this paper is to give a genetical derivation of the major results in the Trivers-Hare theory. This will be done using the concept of "evolutionarily stable strategy" (or ESS) that Maynard Smith (1976) defined as follows: Consider a population made up of nests where the workers invest r of their resources in female reproductives. If a rare mutant colony (where the workers invest \hat{r}) is always selected against, we say that r is an ESS. It is stable to invasion from any new genotype which does something different and thus is maintained by selection. Using this basic idea (which seems implicit in the original Fisher theory), I shall derive the ESS ratios of investment for the eusocial hymenoptera, assuming overlapping generations, multiple insemination of the queen, and looking at the viewpoints of both workers and queen. The resulting formulas differ little from those derived by Trivers and Hare (1976) and are identical to those found by Benford (unpublished paper) using quite a different approach for a discrete-generation model. It is hoped that this derivation is a useful exercise in that it provides a genetical translation of the more intuitive arguments given in the previously cited papers. I also briefly consider the implications of sperm mixing and will introduce an idea termed "worker-worker conflict."

THE MODEL—A VERBAL DESCRIPTION

Consider a eusocial species with perennial colonies. Colonies reproduce once a year, and the workers rear male and female reproductives which they release into the environment. The reproductives mate at random, each female mating with n males. These new queens found colonies which become reproductive the

next year. Finally, all colonies are assumed to be the same size and themselves have a yearly survival rate of p . We introduce into this population a mutant (A) which alters some aspect of the resource allocation to male versus female reproductives (assuming control by workers or queen). The dynamics of this rare gene is the problem of interest. Interestingly, while the mutant is rare, we need only consider three colony types. These are colonies resulting from aa females mating with only a males or $(n - 1)a$ and one A , and the matings of Aa with only a males. All other colony types are too rare to matter (they occur with frequency of order ε^2) and may be ignored.

To develop the formal genetics, consider the following model (developed for the case where the genes controlling the behavior are located in the workers).

THE MODEL—A MATHEMATICAL DESCRIPTION

Begin with the following definitions:

- $N_1(t)$ = number of nests at time t , where queen is aa and her mates were $(a)_n$
(n = number of mating for a queen, a constant in the model);
- $N_2(t)$ = number of nests at time t , where queen is aa and her mates were $(a)_{n-1}$,
(A) (i.e., she mated with one $A \delta$, $n - 1 a \delta$);
- $N_3(t)$ = number of nests at time t , where queen is Aa and her mates were $(a)_n$;
- R = resources available to each worker to be divided among δ and ♀
reproductives in any given year;
- r = proportion of R which aa workers invest in ♀ reproductives;
- \hat{r} = proportion of R which Aa workers invest in ♀ reproductives;
- q = proportion of the resources invested in δ reproductives which is
directed toward males produced by workers;
- c = number of workers in a colony;
- b_1, b_2 = cost of one $\text{♀}, \delta$ reproductive;
- s_1 = probability that a ♀ reproductive survives to found a new nest;
- s_2 = probability that a δ reproductive survives to the time of mating (all
new queens are assumed to be inseminated);
- p = nest survival rate (yearly).

Consider a population made up mostly of aa, a . If the A gene is introduced into this population, its dynamics when rare are given by a set of linear difference equations. To derive these equations, first note that while A is rare, we need only consider the three colony types introduced above. Their output in terms of reproductives is as follows:

1. $aa \times (a)_n$: There are $N_1(t)$ such colonies, each with c workers. Each worker is of genotype aa and produces $R \cdot r \cdot s_1/b_1$ female reproductives. Since the queen and workers are of the same genotype, all the males are the same ($= a$) regardless of who produces them. Each worker will raise $R(1 - r)s_2/b_2$ males. The output of this colony type is (i) $N_1(t) \cdot c \cdot R \cdot r \cdot s_1/b_1$ aa , (ii) $N_1(t) \cdot c \cdot R \cdot (1 - r) \cdot s_2/b_2$ a .

2. $Aa \times (a)_n$: There are $N_3(t)$ such colonies, each with c workers. Half of the workers are Aa , half are aa . The average worker in this colony will devote $(r + \hat{r})/2 = \bar{r}$ of its resources (R) to female reproductives. One-half of these will

be Aa . The average worker will devote $1 - \bar{r}$ of its resources to males, with q proportion devoted to worker-produced males. If each worker is equally likely to contribute a male to be raised, half of these are from the Aa workers and half of these are A . Since the queen is Aa , half of her males are A . The output of this colony type, in terms of Aa and A reproductives, is (i) $N_3(t) \cdot c \cdot R \cdot \bar{r} \cdot s_1 / (2 \cdot b_1) Aa$, (ii) $N_3(t) \cdot c \cdot R \cdot (1 - \bar{r}) \cdot (1 - q) \cdot s_2 / (2 \cdot b_2) A$ (queen produced), (iii) $N_3(t) \cdot c \cdot R \cdot (1 - \bar{r}) \cdot q \cdot s_2 / (4 \cdot b_2) A$ (worker produced).

The assumption that all workers are equally likely to contribute males needs further comment. What it means is that even though Aa workers allocate $1 - \hat{r}$ proportion of their resources to males, they still only lay one-half of the male-producing eggs themselves. Another possible assumption is that each worker individual raises only queen-produced males and males produced by its own genotype. Under this model an aa worker would devote $(1 - r)q$ of its resources to males produced by aa workers, while an Aa worker would devote $(1 - \hat{r})q$ to males produced by Aa workers. Under this second model, equation (iii) above would be altered by replacing \bar{r} with \hat{r} . The first model corresponds to a nonlaying worker, while the second is for a laying worker (Trivers and Hare 1976). If a genotype alters its investment in males versus females and produces extra males itself, such a genotype is a laying-worker genotype. If the genotype alters the investment without altering the proportion of worker-laid males contributed by it, the genotype is a nonlaying-worker genotype. The model developed in this section is for the nonlaying worker.

3. $aa \times (a)_{n-1} \times A$: A critical assumption for this colony type is that sperm clump—that in any season all the workers and reproductives are from the sperm of a single father. This is probably quite a reasonable assumption (Parker 1970; Trivers and Hare 1976). When it holds, $1/n$ proportion of these colonies are expected to have the A father contributing sperm in any given season. Thus $N_2(t)/n$ colonies are effectively of an $aa \times A$ mating. Only these colonies need be considered. Since all the workers here are Aa , the output of Aa and A reproductives is seen to be (i) $[N_2(t)]/n \cdot c \cdot \hat{r} \cdot s_1 \cdot R/b_1 Aa$, (ii) $[N_2(t)]/n \cdot c \cdot (1 - \hat{r}) \cdot q \cdot s_2 \cdot R/(b_2 \cdot 2)A$.

Note that in looking at the reproductive output of colony types 2 and 3, the aa and a are ignored (only Aa and A are listed). This is done because when the A gene is rare, the contribution of these colonies to the production of aa and a reproductives is negligible and may be ignored. With this in mind, the following equations describe the colony numbers at $t + 1$ (to a reasonable approximation):

$$\begin{aligned} N_1(t + 1) &\simeq N_1(t)(p + R \cdot c \cdot r \cdot s_1/b_1), \\ N_2(t + 1) &\simeq N_2(t) \cdot p + N_1(t) \cdot R \cdot c \cdot r \cdot s_1 \cdot \varepsilon/b_1, \\ N_3(t + 1) &\simeq N_3(t)(p + R \cdot c \cdot \bar{r} \cdot s_1/2b_1) + \frac{N_2(t) \cdot c \cdot \hat{r} \cdot s_1 \cdot R}{n \cdot b_1}, \end{aligned} \quad (1)$$

where ε is the fraction of the aa virgin queens which are mated with $(n - 1) a$ and 1 A . To calculate ε , we first need to know what fraction of the males are A . Call this ε^* . It is given by (number of A among reproductive δ)/(number of a

among reproductive ♂) (to a reasonable approximation). Adding up the A and a , it follows that:

$$\varepsilon^* \simeq \frac{1}{4} \frac{N_3(t)}{N_1(t)} \left(\frac{1-\bar{r}}{1-r} \right) (2-q) + \frac{1}{2} \frac{N_2(t) \cdot q}{N_1(t) \cdot n} \left(\frac{1-\hat{r}}{1-r} \right). \quad (2)$$

To get ε , note that under the assumption of random mating, the probability that a virgin queen who mates n times mates with k A males and $(n-k)$ a males is given by the binomial *pdf*. This is of course

$$\binom{n}{k} \cdot \varepsilon^{*k} \cdot (1-\varepsilon^*)^{n-k}.$$

Setting $k=1$ (since $\varepsilon^{*2} \ll \varepsilon^*$), we have $n \cdot \varepsilon^* \cdot (1-\varepsilon^*)^{n-1} \simeq n \cdot \varepsilon^*$. Thus $n \cdot \varepsilon^* = \varepsilon$, the proportion of the matings which are with one A . If this is substituted in equation (1), the following results:

$$\begin{aligned} N_1(t+1) &\simeq N_1(t) \cdot \lambda_1 \\ N_2(t+1) &\simeq N_2(t) \left[p + \left(\frac{R \cdot c \cdot r \cdot s_1 \cdot q}{b_1 \cdot 2} \right) \left(\frac{1-\hat{r}}{1-r} \right) \right] \\ &\quad + N_3(t) \left[\left(\frac{R \cdot c \cdot r \cdot s_1 \cdot n}{4 \cdot b_1} \right) \left(\frac{1-\bar{r}}{1-r} \right) (2-q) \right], \\ N_3(t+1) &\simeq \frac{N_2(t) \cdot c \cdot \hat{r} \cdot s_1 \cdot R}{n \cdot b_1} + N_3(t) \left(p + \frac{R \cdot c \cdot s_1 \cdot \bar{r}}{2 \cdot b_1} \right), \end{aligned} \quad (3)$$

where λ_1 is defined by correspondence to equation set (1). Equation set (3) is valid when colony types 2 and 3 are rare (i.e., when the A gene is rare). The equations for N_2 and N_3 form a set of linear difference equations. If the largest positive eigenvalue (λ) associated with this set is $> \lambda_1$, colony types 2 and 3 are increasing relative to type 1 and the A gene is being selected for. On the other hand, if we can find r such that $\lambda \leq \lambda_1$ for all \hat{r} , then the a , aa population is stable. This value of r is the evolutionarily stable strategy (ESS) (Maynard Smith 1976), since a population made up of it cannot be invaded by a rare genotype who does something different (i.e., the \hat{r} genotype).

To find this r , the following technique is useful. We write equation set (3) for $N_2(t+1)$ and $N_3(t+1)$ in matrix notation

$$\begin{pmatrix} a_{11} & a_{12} \\ a_{21} & a_{22} \end{pmatrix} \cdot \begin{bmatrix} N_2(t) \\ N_3(t) \end{bmatrix} = \begin{bmatrix} N_2(t+1) \\ N_3(t+1) \end{bmatrix}, \quad (4)$$

where a_{ij} , are functions of r and \hat{r} . The λ is given by the characteristic equation associated with (4):

$$\lambda^2 - \lambda \cdot (a_{11} + a_{22}) + a_{11} \cdot a_{22} - a_{21} \cdot a_{12} = 0. \quad (5)$$

When $\hat{r} = r$, $\lambda = \lambda_1$, since the worker genotypes are functionally the same. Therefore, if r is an ESS, the maximum value of λ must be λ_1 and must occur at $\hat{r} = r$. Hence, for some r to be an ESS it is necessary that $\partial\lambda/\partial\hat{r} = 0$ at $\hat{r} = r$. The

characteristic equation may be treated as follows: We implicitly differentiate with respect to \hat{r} , setting the partials equal to zero as we go (i.e., $\partial\lambda/\partial\hat{r} = 0$). What is left is an equation in λ , r , \hat{r} , q , and various life-history parameters. Set $\hat{r} = r$ and $\lambda = \lambda_1 = p + R \cdot c \cdot s_1/b_1$. The result may be solved for r . After a lot of algebra, everything except r and q cancels out. What is left is quite simple:

$$r = \frac{6 - 3q}{8 - 2q}. \quad (6)$$

To show that this critical point is in fact the ESS, (6) may be substituted back into (5); λ is seen to be $\leq \lambda_1$ with this value for r , regardless of the value of \hat{r} . This value of r is unique; with any other there exists some \hat{r} with $\lambda > \lambda_1$. In particular, if $r < (6 - 3q)/(8 - 2q)$, $\hat{r} > r$ will be selected for. If $r > (6 - 3q)/(8 - 2q)$, $\hat{r} < r$ is selected for.

There are two other sex-ratio problems to be considered. These are, of course, the equilibrium investment from (1) the queen's viewpoint and (2) the viewpoint of a "laying worker." Earlier we introduced the difference between a laying worker and a nonlaying worker genotype. Repeating the above argument for the laying worker genotype yields the unique ESS r to be

$$r = \frac{6 - 3q}{8 - q}. \quad (7)$$

From the queen's viewpoint, the ESS r is 1/2 regardless of the q value.

These three ESS values, laying and nonlaying workers and queen, differ very little from the formulas given in Trivers and Hare (1976). Somewhat surprisingly, they are the same as derived by Benford (unpublished paper) using quite different methods in a discrete generation model. In practice, it is probably not possible to distinguish between these and the Trivers-Hare formulas. Likewise, it is not obvious whether the laying or nonlaying worker model is more realistic, but the respective predictions are close enough to make little difference in practice. As stressed by Trivers and Hare (1976), the utility of these results is that ratios of investment can be measured with sufficient precision to test the relationship between the amount of laying workers and the expected ratio of investment. The degree to which the ratio approximates the workers' preferred ratio or the queen's is a measure of the relative power of the two parties (i.e., who wins the conflict?).

SOME EXTENSIONS

It will be useful here to review just what has been shown (and some generalizations).

1. The results hold for overlapping generations. They are unaltered if the colonies are allowed to grow with age and if nest survival rates are age specific. The constancy of size and survival were made to keep the mathematics relatively simple but in no way affect the final results. The results are also unaltered if the resource/worker (R) is a function of nest size, provided b_1 and b_2 are constants. It might be expected that the resource investment in a male or

a female reproductive would be fixed by selection independent of the total resources available to the nest. Theory developed for the optimal investment per offspring in a diploid makes this prediction (Smith and Fretwell 1974; Schaffer and Gadgil 1975), and it is easy to show that a similar relation holds in a two-sex model under haplodiploidy.

2. The results hold for multiple inseminations provided that sperm clump so that at any point in time the workers and female reproductives share the same father. The assumption of a fixed number (n) of inseminations is also not critical. It is straightforward to show that if the new queens have a fixed probability distribution for the number of matings (e.g., probability a queen is mated i times is P_i), equation set (3) still holds, with n replaced by the average number of matings for a queen. While perhaps somewhat unrealistic, it is fairly simple to ask how the theoretical results are altered if this is violated, at least when sperm are completely mixed (with each father contributing the same amount). Where the queen produces all the male reproductives, the ESS ratio of investment from the workers' viewpoint becomes $(n + 2)/(2n + 2)$ proportion in new queens. That this formula is intuitive follows from its identity with the following:

$$r = \frac{\text{coefficient of relationship of worker to average sister}}{\text{coefficient of relationship of worker to average sister} + \text{coefficient of relationship of worker to brother}}. \quad (8)$$

If sperm completely mix, the coefficient of relation between sisters is a function of the number of times the queen is inseminated and is equal to $1/2(1/2 + 1/n)$ (Hamilton 1964). A worker is related to a brother by a coefficient of $1/4$ regardless of n . Putting these into (8) produces $(n + 2)/(2n + 2)$. Of course, the equilibrium ratio of investment for the queen is still $1/2$ —unchanged with multiple inseminations.

3. There is one other alteration of the basic model which may prove useful, even though only the hint of an answer can be provided here. Of the three nest types which must be considered in the ESS analysis, one [$Aa \times (a)_n$] contains both kinds of workers. In the original formulation, these workers were assumed to operate independent of each other with each Aa worker investing \hat{r} in ♀ and each aa worker investing r . This follows from the definition of $\bar{r} = (r + \hat{r})/2$. Another possible assumption is that the workers are able to "influence" each other, which sets up a sort of "worker-worker conflict." Suppose that when the two worker types are together in one nest, the aa workers are able to coerce the Aa workers into investing r instead of \hat{r} (thus $\bar{r} = r$). We can write a general function for this conflict as follows: $\bar{r} = m \cdot r + (1 - m)\hat{r}$.

If $m = 1$, the aa workers are in charge; if $m = 0$, the Aa are. The independent case is $m = 1/2$, with each worker behaving according to its own genotype. If the queen lays all the male eggs, it is fairly straightforward to show that an ESS ratio of investment, from the worker viewpoint, is given by

$$r = \frac{2 - m}{3 - 2m}. \quad (9)$$

With this relation: $m = 0$, $r = 2/3$; $m = 1/2$, $r = 3/4$; $m \rightarrow 1$, $r \rightarrow 1$.

This result is rather surprising, but it must be interpreted with some caution. The stability analysis is local; a global analysis would seem to be very difficult. For one thing, the other end point (AA) may also be locally stable; this depends on how the "conflict" is resolved in the other mixed nest (i.e., $Aa \times [A]_n$) (this colony type was of course not considered in our analyses). In order to get some idea how the system behaves, I constructed a simulation model which allowed me to vary m , \hat{r} , r and which assumed the AA genotype coded for an investment of \hat{r} (as did the Aa). The results are complicated, but one thing did emerge; using formula (9) to define r as a function of m showed that $r \geq .9$ were not very stable. Quite often the condition could be invaded by some $\hat{r} < r$ if the gene frequency of A , Aa got above some small level (e.g., .05). The closer r got to 1, the smaller was the stable zone around it. Usually the end result was a fixation of the A gene, but for some combinations a polymorphism resulted. It appears that a worker-worker conflict model can produce some fairly complex results.

SUMMARY

Trivers and Hare (1976) were the first to appreciate that the asymmetry in relatedness within a Hymenoptera society held far-reaching implications for sex-ratio evolution. This paper develops their theory for a very general model. The ESS results differ but little from their original treatment. I introduce one new factor (termed worker-worker conflict) and derive a new equilibrium ratio of investment by workers in new queens. The difficulties of interpreting this result are briefly discussed.

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