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Evolution of Eusocial Behavior: Offspring Choice or Parental Parasitism?

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Assuming the subsocial route towards eusociality, I show that selection favors worker habits (under haplodiploidy) provided the mutant workers are able to bias the sex ratio towards sisters and/or selectively substitute their sons for brothers. If the *original* workers are not able to do this, selection does not favor the habit. However, under these conditions, selection is indifferent as to whether an individual rears offspring or sibs. This makes it easy for a mother to enlist her daughter's services in rearing other offspring, since the daughter cannot evolve to stop the parental parisitism. These results deal with the origin of eusocial behavior. I also look at selection acting on genes (to invest in offspring rather than sibs) in existing eusocial societies. It is shown that selection for laying workers is very strong, even if such workers give up rearing a seemingly advantageous combination of brothers and sisters. This poses distinct problems for the maintenance of eusocial societies.

1. Kin-Selection—Introduction

In 1964 W. D. Hamilton proposed an important extension of the genetical theory of natural selection by showing that genes could be favored which reduced the personal fitness of their bearers to increase the fitness of relatives. This theory, now termed *kin-selection* (Maynard Smith, 1964) or *kinship theory* (Trivers & Hare, 1976), had been anticipated much earlier (see discussions in Williams, 1971; Williams & Williams, 1957; Hamilton, 1972; Ghiselin, 1974), but it was Hamilton who showed how very *basic* it was to the evolution of social behavior. The core idea is that if a gene causes its bearers to act as to decrease personal fitness by an amount c at the same time increasing the fitness of a relative by amount b, the gene is selected for if $c/b < r$ where r is the "coefficient of relationship" between donor and recipient. r measures the probability that the gene of interest in the donor is found as a copy in the recipient. Various procedures exist for calculating r, but the core idea remains the same even when inbreeding complicates the picture

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(Hamilton, 1964, 1970, 1972). For recent discussions of the population genetics of kin-selection, see Charnov (1977); Charlesworth (1978); Harpending (1978); Scudo & Ghiselin (1975), or Orlove (1975).

There are other aspects of kin-selection which have potentially useful implications. "Hamilton's Rule" ($c/b<r$) can be turned around—we may ask how much personal fitness an individual must gain, to make up for a decrement in fitness imposed upon a relative. In this case, the cost (c) is really a positive gain, while the benefit (b) (to the relative) is a decrement. This alteration simply reverses the inequality, and the "selfish" gene spreads if $c/b>r$. This asymmetry sets up what Trivers (1974) has discussed under the general title "parent-offspring conflict." For example, in full sibs $r=\frac{1}{2}$; thus sib A is selected to "demand" help from sib B whenever A's fitness is incremented by half the cost to B's fitness. However B is selected to provide A with help *only* when the benefit to A exceeds twice the cost to B.

As one final aspect of kin-selection, consider what has been termed *parental manipulation* (Alexander, 1974; West-Eberhard, 1975; Michener & Brothers, 1974). The above rules for offspring behavior are derived under the assumption that the genes controlling the behavior are *located in the offspring*. If the genes controlling the behavior are located in the parent, a wholly new rule applies (at least under the Hamilton model). A gene present in the parent has equal chance of being passed to an offspring. Thus from the *parent's viewpoint* full sibs are not related to each other by half but by one. An offspring operating in the interest of the mother should aid a sib when $c/b<1$. Thus the parent and offspring differ with respect to desired offspring behavior (Trivers, 1974). The above factors have been much discussed in the recent literature (Alexander, 1974; West-Eberhard, 1975; Trivers, 1974; Trivers & Hare, 1976). Hamilton (1964) based his theory on a particular genetic model, and applied suitable caution in its use. The most important aspect of "Hamilton's Rule" is the revolution in thinking it brought about.

The most novel use of the theory is in relation to the social Hymenoptera. Because males are haploid and develop from unfertilized eggs (while females are diploid and develop from fertilized eggs), there exist asymmetries in the way individuals in a family are related to each other. In particular, sisters share three-quarters of their genes in common (if mom mates once) but share only a quarter of their genes with their brothers. Since a parent is related by half to its own offspring, Hamilton (1964, 1972) suggested that females should prefer to raise sisters (as reproductives) and should be inclined to replace brothers (as reproductives) with sons. The basis of eusocial behavior in Hymenoptera is for female workers to raise sisters as female reproductives and some combination of sons (or nephews) and brothers as male reproductives. These accord with Hamilton's theory.

Trivers and Hare (1976) greatly extended Hamilton's analysis by linking it with Fisher's (1930) sex ratio theory. Actually, they proposed two rather different theories related to eusocial behavior. Firstly, they developed a model for the evolution of the sex ratio in eusocial species. Under outbreeding, with *worker control* of the allocation of resources to be put into male as opposed to female reproductives (and no laying workers), the equilibrium or ESS (Maynard Smith, 1976) allocation is for three-quarters of the resources to be put into female reproductives. For a discussion of this theory, see Charnov, 1978 and Oster *et al.*, 1977. For a critique of the data and alternative hypotheses, see Alexander and Sherman, 1977. Note that this sex ratio question is different from the question of when natural selection favors genes for *eusocial behavior itself.* Trivers and Hare (1976) are quite explicit on this point—they state that selection favors eusocial behavior provided the workers are able to bias the ratio of investment towards sisters (away from 1 : 1) or produce some of the male reproductives themselves (selectively substituting sons or nephews for brothers). It seems clear that what Trivers & Hare mean by this is that selection favors the continuation or maintenance of existing eusocial societies if some combination of these conditions are met. But this problem may not be the same as the *origin* of eusocial behavior. Consider a non-social wasp species. Suppose a mutant arises where the female bearers remain with their mother and help her to raise their sisters and brothers (as opposed to rearing their own progeny). Natural selection on such a mutant defines the problem of the *origin* of eusocial behavior. Trivers & Hare's discussion of this is somewhat difficult to follow. In one place they state that the above conditions are a basis for the origin of eusocial behavior, elsewhere they say that it is not necessary for the "original" workers (our mutant individuals) to bias the sex ratio or substitute sons for brothers. They suggest that this may have evolved after eusocial behavior arose (and thus helps maintain it).

I am keeping the two aspects of eusocial behavior, *origin* and *maintenance*, distinct because this turns out to be rather important. In the first case, we look at selection on genes affecting eusocial behavior, where the bearers are rare in a population of individuals, most of which do not have eusocial behavior. In the second case, the mutant gene is for investing in one's own progeny, where most workers invest in sibs.

While the fact that maintenance is different from origin seems widely known (Hamilton, 1964, 1972; Wilson, 1971; Trivers & Hare, 1976; Alexander, 1974; West-Eberhard, 1975), some aspects of it seem less widely appreciated. As an example, multiple inseminations of the queen lower the relatedness among daughters (although maybe not, if sperm clumps in a perennial colony—Trivers & Hare, 1976; Charnov, 1978) and has been posited as a major difficulty for the kin-selection hypothesis (a worker may become more related to its own offspring than the prevailing combination of sisters and brothers). As noted by Trivers & Hare (1976) (and others), multiple inseminations may well have evolved as a *result* of existing eusocial behavior. We can probably ignore multiple inseminations in discussions on the *origin* of the habit as most *solitary* Hymenoptera do not show it. It may, however, play a major role in the maintenance of eusocial societies or their continued evolution.

In this introduction, I have attempted briefly to discuss kin-selection and introduce two aspects of the problem of the evolution of eusocial behavior. The rest of this paper considers some specific biological situations. In particular, I will ask the following questions: (1) How does selection act on a rare gene whose bearers (♂ or ♀) remain with the parent and help raise sibs as reproductives? How is this altered if the genetic system is diploidy as opposed to haplodiploidy? (2) Under haplodiploidy, how does the ♀ worker's ability to produce sons affect the outcome? (3) How does selection act on a rare gene which, when present in a female, causes her to "manipulate" some of her offspring to act as sterile workers (Alexander, 1974; Michener & Brothers, 1974)? (Of course, this model assigns mom the necessary ability.) (4) How does selection act on rare genes (in already existing eusocial societies) whose bearers invest in their own offspring, rather than sibs? How is this altered with multiple inseminations of the queen?

Notice that each of these questions is phrased in terms of the initial spread of the genes of interest. This approach has two virtues, absent from more complete descriptions of the evolutionary dynamics. The first is that we are free to consider models which look at males and females separately—the mathematics involved is simple while the gene is rare (while a more complete description rapidly becomes mathematically intractible). In rare gene models we are free to vary parameters of biological interest with some hope of getting specific answers. The second reason for restricting attention to rare genes is that it is reasonable to suppose that: "all traits are at first rare"; that for a trait to be of selective advantage at all it must be of selective advantage when rare. I also assume outbreeding, and leave it to the more mathematically adept to extend the results to local mate competition and inbreeding (Hamilton, 1964, 1967, 1972).

2. On the Origin of Eusocial Behavior: a Simple Life History

The following description is oriented towards Hymenoptera—it is extracted from recent literature (Wilson, 1971; Evans, 1956; Evans & West-Eberhard, 1970). It captures the biological essentials (at least as presented by the above authors) and provides a base line—if an alternative life history is more appropriate for a particular situation, the methods employed for the analysis of the present one are easily modified.

Consider a female wasp (of a solitary species) who emerges in the spring from a winter hideout and begins constructing cells. She lays eggs in these cells and when the offspring hatch, she brings them food on a regular basis (*progressive provisioning*). Some of her offspring emerge while she is still caring for others (*overlap of offspring—parental generations*). These offspring may be considered to have two options. They can either mate and (for the daughters) rear their own sons and daughters, *or* they can remain with mom and help her raise their sibs. A likely combination of these (when the habit first arose) is to remain with mom and raise some combination of sibs and offspring. The essential features of the model are the overlap in generations (with progressive provisioning) and the "point of choice" by the first raised offspring.

In order to translate the biology into a formal genetic model, I will assume as follows. At time T (late summer), a newly emerged population of wasps mate among themselves. The females overwinter and in the spring begin the business of rearing offspring. Because Fisher's sex ratio theory applies to solitary Hymenoptera, this brood consists of half daughters (sons and daughters are assumed of equal cost). Let the mother rear to adulthood X offspring. These offspring (all assumed to emerge at once) then do one of two things. They (i) stay with mom and raise some combination of sibs and offspring *or* (ii) they go off, mate, and the females raise their own offspring. Each *worker* will raise Y offspring, while each female who goes off will raise Y offspring. This second brood we will count as the reproductive population of late summer (i.e. $T+1$). Again, the females who leave mom would be expected to produce a sex ratio of a half. While the process of rearing is actually continuous throughout the summer, this discrete approximation should be an adequate description.

From this description, several different models may be built (e.g. are the workers ♂ or ♀?, do the workers impose a sex ratio of other than a half?, does diploidy differ from haplodiploidy?). As an example, consider a solitary species, homozygous at a locus of interest (♀*aa*, ♂*a*). Introduce into this population a rare dominant mutant (A) where its female bearers remain with mom and act as workers, rearing sisters and brothers (as reproductives), with a sex ratio of r proportion sisters.

The condition for this gene to be selected for is shown in Appendix A. As noted by Hamilton, Trivers & Hare, the condition is that $r > \frac{1}{2}$. If $r = \frac{1}{2}$, the gene is selectively neutral—it is neither selected for or against. If $r < \frac{1}{2}$, it is selected against.

If we complicate the model by allowing the workers to produce some of the males, a similar argument (see Appendix A) shows that the worker gene spreads provided

$$r > \frac{1-P}{2-P}$$

(P = proportion of males from workers). This condition is that the workers be able selectively to substitute sons for brothers as reproductives. If they substitute sons for brothers and sisters, chosen at random,

$$r = \frac{1-P}{2-P}$$

and again the eusocial gene is not selected for.

Thus, the *origin* of eusocial behavior via this pathway requires that the original workers either bias the sex ratio or selectively substitute sons for brothers (see also Crozier, 1977). In solitary bees and wasps, in which the males are smaller than the females, it is common for the female to prepare cells of two sizes; large cells containing much food and a fertilized egg (♀) and small cells containing less food and an unfertilized egg (♂) (Evans, 1917; Krombein, 1967). In progressive provisioners, it is to the mother's advantage to gauge the amount of prey in accordance with the sex of the offspring. This argument is from Evans (1977): with it he suggested that there may have already existed, in non-social wasps, the ability to distinguish the sex of the offspring. Thus, it seems possible that the original workers be able to play the complex games required for selection to favor their worker habit.

I note here that if males are allowed to be the workers (as efficient at rearing offspring as their sisters would be) or if haplodiploidy is altered to diploidy, the eusocial gene is again selectively neutral.

In 1974 R. D. Alexander proposed an alternative to the *offspring choice* model for the origin of eusocial behavior (also see Michener & Brothers, 1974). He suggested that offspring remain with mom and aid her to raise their sibs because *she manipulates them to do so.* He applied Hamilton's basic model, with the rule that, operating in the parent's interest, an offspring should aid a sib whenever $c/b < 1$. He used the term manipulation since under this model the offspring should be selected to aid a full sib only when $c/b < \frac{1}{2}$. Thus parent and offspring disagree over offspring behavior when $\frac{1}{2} < c/b < 1$.

I suggest here that the model Alexander (1974) applied is inappropriate for the problem of the origin of eusocial behavior. The reason is as follows: *there is no conflict between mother and offspring over whether the offspring should rear sibs or their own offspring as reproductives.* Whereas Trivers & Hare stated that selection *does not favor* workers behavior in daughters with a sex ratio of a half (with no substitution of sons for brothers), the proposition may just as well be turned around; with a sex ratio of a half, daughters are indifferent as to whether they rear sibs or their own offspring (the gene is selectively neutral). However, the perspective of the mother is quite different. Her options are as follows—"allow" her daughters to rear their own children, thus producing her grandchildren or "force" the daughters to rear their brothers and sisters (thus producing her children). On average mother is related by a half to her own children, a quarter to her grandchildren—thus selection strongly favors her to turn some daughters into workers. Consider the following scenario. A solitary wasp species nests in aggregations, the selective force being perhaps parasites or predators (Evans, 1977). In such a situation females might well attempt to take over or themselves parasitize the cells of other individuals of their species. If individual *C* tries to lay an egg in a cell of individual *B*, *B* would be selected to stop *C*, since the parasitism act as a decrement to *B*'s fitness. However, if *B* is the daughter of *C*, no such decrement is present. I suggest that the origin of eusocial behavior lies in the ecological conditions which allow females easily to parasitize the food-gathering efforts of their offspring. This requires a very small shift in behavior—it mostly requires daughters nesting close to their mother since that aids parasitism by mother.

It seems likely that the first attempts at parent→offspring parasitism would result in actions by the offspring to prevent it, actions similar to those directed towards any unrelated conspecific parasite. However, mother has a large advantage here. She is selected to pursue the parasitism even if she kills some of her daughters—while her daughters are not selected to continue stopping her. A daughter loses fitness by being killed by its mother; it does not gain by killing its mother.

If parent→offspring parasitism is indeed the first step towards eusocial behavior, this immediately provides "queen-like" behavior for the mother. Selection would favor her giving up the duties (which probably carry considerable mortality risk) of provisioning cells to remain at the nest site and parasitize her daughters' cells. Once the daughters are rearing mostly their sibs, selection *then* favors their efforts to alter the sex-ratio or substitute their sons for brothers.

3. Maintenance of Eusocial Societies

In this section, I consider the problem of the maintenance of an existing eusocial society. For present purposes, the basic question is: *Under what conditions does selection favor a worker who leaves the colony and raises its* *own offspring?* The Trivers-Hare theory suggests an answer to the above to be that selection favors staying within the colony when the workers (for example) control the ratio of investment, or produce sisters and sons (as reproductives). For the first case, a worker who leaves produces (for example) sons but forfeits what seems to be an advantageous combination of brothers and sisters. Here I reconsider this proposition by looking at the conditions for the spread of genes for workers to invest in their own offspring—under multiple inseminations of the queen and worker or queen control of the proportion of colonies resources put into female reproductives. Note that these workers will not simply produce sons instead of brothers; they will give up rearing *both brothers and sisters.*

Consider an annual species, where the workers control the sex ratio (ratio of investment) but produce no sons in the eusocial nest. Suppose a mutant arises where its bearers (workers) leave the nest and produce sons on their own (the argument similarly extends to the strength of selection for laying workers within the nest, however, there is one difference with respect to laying workers. Such a worker probably need only *produce* the son eggs, as they will mostly be reared by the other workers. A worker who leaves the nest must produce *and* rear the sons itself). The question becomes—what are the conditions for such a gene to spread? To answer this question we first need to know how the equilibrium ratio of investment (resources put into ♀ reproductives) changes under worker vs. queen control and multiple inseminations. The following discussion is from Charnov (1978) and Trivers & Hare (1976).

(1) If the queen controls the ratio of investment, the equilibrium is for half of the colonies' resources to go to female reproductives.

(2) If the workers control the ratio of investment, the equilibrium is for three-quarters of the colonies' resources to go into female reproductives. This is unaltered with multiple inseminations of the queen provided the sperm from different fathers clumps—(at any point in time the workers and the female reproductives they are rearing share the same father). The system acts as if the queen was only inseminated once.

(3) Suppose the sperm from different fathers is mixed; the equilibrium ratio of investment then depends upon the number of times the queen was inseminated. If the queen mates n times (with the sperm mixed at random), the worker's equilibrium is for $(n+2)/(2n+2)$ fraction of the colonies' resources to go into female reproductives (Charnov, 1978*a*).

In Appendix B I derive a result to answer the following question. If a worker who leaves the eusocial nest is α times as efficient at raising sons as a worker who stays is at raising brothers and sisters, what must α be for the "splitting" habit to be favored? If the queen is mated n times (with sperm mixing), the critical value of α is given as follows for worker control of the ratio of investment:

$$\alpha = \frac{n(2n+1)}{(n+1)(5n-2)}.$$

This result is interesting in that $\alpha = \frac{1}{2}$ with one insemination of the queen but only drops to 0·4 as n gets very large. Since a single insemination of the queen is the same as multiple inseminations with clumped sperm, it is clear that under worker control of the ratio of investment, selection is fairly strong for the workers to invest in sons (even if they give up the seemingly advantageous combination of sibs). The result is quite insensitive to multiple inseminations of the queen. Provided the workers control the ratio of investment, the above calculation seems to remove as a problem (to the maintenance of eusocial societies) multiple inseminations of the queen—only to replace it with the issue of why workers do not in general invest in sons (they need only be $\sim$0·5 as efficient at raising them).

If the queen controls the investment of resources in male and female reproductives, we can also calculate the critical α value here. It is seen to be as follows: (derivation in Appendix B)

$$\alpha = \frac{2n+1}{5n-2}.$$

This value is always above the critical α under worker control. It is one with a single insemination of the queen and approaches 0·4 as n gets large. Most of the decline is for the first few n (example: $\alpha = 0{\cdot}625$ if $n = 2$). Thus queen control of the investment ratio is more favorable to the maintenance of eusocial behavior but with multiple inseminations this advantage rapidly disappears (if sperm mixes).

Since multiple inseminations of the queen is common among eusocial species, it is useful to ask why the colonies stay together. In the above cases, selection would seem to favor a worker who invested in sons. So long as more than half of the colonies resources are going into female reproductives, selection favors a worker who cheats and invests in sons (all else equal), even if the worker gives up investing in the prevailing combination of sisters and brothers. The critical assumption is of course "*all else equal*". In long established eusocial societies, selection has probably *favored worker attributes which preclude the ability of a worker to "go it alone*". This would help explain why eusocial societies stay together, but it does not explain why laying workers are not much more common. In any event the above calculations clearly suggest that while the ability of the "workers" to overinvest in sisters as reproductives may have played an important role in the *origin* of eusocial behavior, the same control poses distinct problems for the maintenance of existing eusocial societies.

4. Discussion

A great deal has been made in recent literature of the bias implicit in haplodiploidy for the evolution of eusocial behavior (see Fig. 1 in the Appendix). However, Evans (1977) recently challenged the long accepted datum that eusocial behavior has arisen much more often associated with haplodiploidy than diploidy. The adult→offspring parasitism hypothesis advanced in this paper works just as well with diploidy. Also, if the mother is multiply inseminated (offspring less than full sibs), both diploidy and haplodiploidy make it more advantageous for offspring to rear their own offspring (rather than sibs), and thus to resist parental parasitism. A single father, plus nesting aggregations which make it simple for mother to parasitize the food-gathering behavior of her offspring, would seem to set the stage for the beginnings of eusocial behavior. Such conditions would seem to occur only rarely. It would be interesting to know if there is any link between such conditions and haplodiploidy itself.

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REFERENCES

ALEXANDER, R. D. (1974). *Ann. Rev. Ecol. Syst.* **5,** 325.
ALEXANDER, R. D. & SHERMAN, P. W. (1977). *Science* **196,** 494.
CHARLESWORTH, B. (1978). *J. theor. Biol.* (in press).
CHARNOV, E. L. (1977). *J. theor. Biol.* **66,** 541.
CHARNOV, E. L. (1978). Sex-ratio selection in eusocial hymenoptera. *Am. Nat.* **112,** 317.
CROZIER, R. H. (1977). *Ann. Rev. Entomol.* **22,** 263.
EVANS, H. E. (1956). *Proc. 10th Inter. Cong. Ent.* 449.
EVANS, H. E. (1977). *Bioscience* **27,** 613.
EVANS, H. E. & EBERHARD, M. J. W. (1970). *The Wasps.* Ann Arbor: University of Michigan Press.
FISHER, R. A. (1930). *The Genetical Theory of Natural Selection.* Oxford: Oxford University Press.
GHISELIN, M. T. (1974). *The Economy of Nature and the Evolution of Sex.* Berkeley: University of California Press.
HAMILTON, W. D. (1964). *J. theor. Biol.* **12,** 1.
HAMILTON, W. D. (1967). *Science* **156,** 477.
HAMILTON, W. D. (1970). *Nature* **228,** 1218.
HAMILTON, W. D. (1972). Altruism and related phenomena. *Ann. Rev. Ecol. Syst.* **3,** 193.
HARPENDING, H. (1978). *Am. Nat.* (in press).
LIN, N. & MICHENER, C. D. (1972). *Quart. Rev. Biol.* **47,** 131.

MAYNARD SMITH, J. (1964). *Nature* **201,** 1145.
MAYNARD SMITH, J. (1976). *Am. Sci.* **64,** 41.
MICHENER, C. D. & BROTHERS, D. J. (1974). *Proc. natn. Acad. Sci. U.S.A.* **71,** 671.
ORLOVE, M. J. (1975). *J. theor. Biol.* **48,** 557.
OSTER, G., ESHEL, I. & COHEN, D. (1977). *Theor. Pop. Biol.*
SCUDO, F. M. & GHISELIN, M. T. (1975). *J. Genetics* **62,** 1.
TRIVERS, R. L. (1974). *Am. Zool.* **14,** 249.
TRIVERS, R. L. & HARE, H. (1975). *Science* **191,** 249.
WEST-EBERHARD, M. J. (1975). *Quart. Rev. Biol.* **50,** 1.
WILLIAMS, G. C. (1975). *Sex and Evolution.* Princeton: Princeton University Press.
WILLIAMS, G. C. (ed.). (1970). *Group Selection.* 210 pp. Chicago: Aldine-Atherton.
WILLIAMS, G. C. & WILLIAMS, D. C. (1957). *Evolution* **11,** 32.
WILSON, E. O. (1971). *The Insect Societies.* 548 pp. Cambridge: Harvard.
WILSON, E. O. (1975). *Sociobiology: The New Synthesis.* Cambridge: Harvard.

APPENDIX A

Daughters as Workers

At time T (late summer), a newly emerged population of wasps mate among themselves. The females overwinter and in the spring begin the business of rearing offspring. Because Fisher's sex ratio theory applies to solitary Hymenoptera, this brood consists of half daughters (sons and daughters are of equal cost). Let the mother rear to adulthood X offspring. These offspring (all assumed to emerge at once) then do one of two things. They (i) stay with mom and raise some combination of sibs and offspring (act as workers) *or* (ii) they mate, and the females raise their own offspring. Each *worker* will raise Y offspring, while each female who goes off will also raise Y offspring. This second brood we will count as the reproductive population of late summer (i.e. $T+1$). Again, the females who leave mom would be expected to produce a sex ratio of a half. The question is: when does selection favor the worker habit?

Consider a solitary species, homozygous at a locus of interest (♀aa, ♂a). Introduce into this population a rare dominant mutant (A) where its female bearers remain with mom and act as workers, rearing sisters and brothers (as reproductives), with a sex ratio of r proportion sisters. While the gene is rare, we may ignore the homozygote (AA). Let the frequency of A among the males at time T be ε_1, and the frequency of Aa among the females ε_2. Finally, let each female mate once (a reasonable assumption for solitary Hymenoptera). Ignoring all matings which take place with frequency of order ε^2, there are three mating types of interest.

(1) $aa\times a$. This takes place with frequency ~ 1. Each of these yields $X/2$ a, $X/2$ aa offspring.

(2) $aa \times A$. This mating takes place with frequency $\sim \varepsilon_1$ and these yield $\varepsilon_1 X/2$ Aa.

(3) $Aa \times a$. This mating takes place with frequency $\sim \varepsilon_2$ and yields $\varepsilon_2 X/4$ Aa, $\varepsilon_2 X/4$ A.

All offspring except Aa go off and mate. The frequency of A among these new males is $\sim \varepsilon_2/2$. This calculation is $\# A/\# a$ where $\# a$ ignores the a contributed via $Aa \times a$ or $aa \times A$ matings (their contribution is negligible compared to $aa \times a$ matings). Of course, all the females in this new mating are aa (the Aa having remained with mom). There are $X/2$ aa; $\varepsilon_2/2$ proportion of them mate with A; $1-\varepsilon_2/2 \sim 1$ proportion mate with a. Thus we have,

(1) $aa \times A$—there are $X\varepsilon_2/4$ such matings and each produces $Y/2$ Aa offspring.

(2) $aa \times a$—there are $X/2$ such matings and each produces $Y/2$ aa, $Y/2$ a.

Among the colonies, each worker produces Y offspring, r proportion of the offspring being female. *The colonies are of two types* ($aa \times A$, $Aa \times a$). Ignoring the output of aa or a, we have from these colonies:

(1) $Aa \times a$—there are $\varepsilon_2 X/4$ workers, thus the number of reproductives they raise are:

$$\frac{\varepsilon_2 XYr}{8}\,Aa;\ \frac{\varepsilon_2 XY(1-r)}{8}\,A.$$

(2) $aa \times A$—there are $\varepsilon_1 X/2$ workers, and the number of reproductives they raise are:

$$\frac{\varepsilon_1 XYr}{2}\,Aa.$$

Adding up all the offspring raised by workers or produced via the second mating, the results are:

$$\# A \simeq \frac{\varepsilon_2 XY(1-r)}{8}$$

$$\# a \simeq XY/4$$

$$\# Aa \simeq \frac{X\varepsilon_2 Y}{8} + \frac{\varepsilon_2 XYr}{8} + \frac{\varepsilon_1 XYr}{2}$$

$$\# aa \simeq XY/4.$$

The new genotype frequencies (in the fall, $T+1$) are ε_1' and ε_2' (and are given by):

$$\varepsilon_1' \simeq \# A/\# a \simeq \frac{(1-r)\varepsilon_2}{2}$$

$$\varepsilon_1' \simeq \# Aa/\# aa \simeq 2r\varepsilon_1 + \frac{(1+r)\varepsilon_2}{2}. \tag{A1}$$

Writing (A1) as matrix multiplication, we have

$$\begin{pmatrix} 0 & \dfrac{1-r}{2} \\ 2r & \dfrac{1+r}{2} \end{pmatrix} \cdot \begin{pmatrix} \varepsilon_1 \\ \varepsilon_2 \end{pmatrix} = \begin{pmatrix} \varepsilon_1' \\ \varepsilon_2' \end{pmatrix} \tag{A2}$$

The A gene is being selected for only if the dominant eigenvalue (λ) of (A2) is greater than 1. The characteristic equation is a simple quadratic given as follows

$$\lambda^2 - \frac{(1+r)\lambda}{2} - r(1-r) = 0. \tag{A3}$$

A plot of λ vs. r is provided in Fig. 1. Notice that λ increases with r, reaching a maximum of $\sim 1{\cdot}05$ when $r = \frac{3}{4}$. It is above one for all r above a half. This figure corresponds to the argument first put forward by Hamilton (1964). As clearly stated by Trivers & Hare (1976), selection favors eusocial behavior (*its origin*) under haplodiploidy when the workers rear sibs as reproductives provided the workers are able to bias the investment (here, the sex ratio) towards sisters ($r > \frac{1}{2}$). If this bias does not take place, $r = \frac{1}{2}$ (under Fisher's sex ratio theory) and the eusocial gene is of no selective advantage.

If we repeat the above argument, allowing the workers to produce some

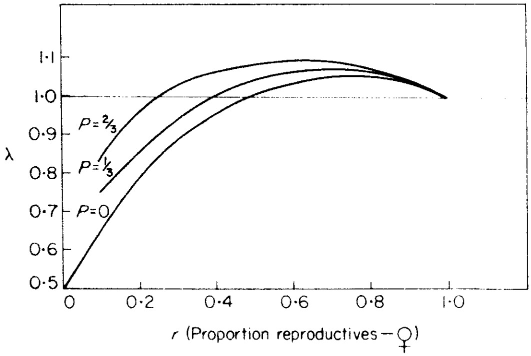

FIG. 1. Natural selection for a eusocial gene. λ gives the strength of selection for ($\lambda > 1$) or against ($\lambda < 1$) a gene for eusocial behavior, as a function of the worker's ability to invest resources into sisters (r). P is the fraction of male reproductives contributed by workers.

sons (P = proportion of males which are from worker-laid eggs), the characteristic equation becomes:

$$\lambda^2 - \lambda\left[\frac{+1+2\cdot(1-r)p}{2}\right] + \frac{p\cdot(1-r)(r+1)}{2} - r(1-r) = 0. \tag{A4}$$

Figure 1 shows λ vs. r for various P.

APPENDIX B

Worker Investment in Sons

Consider a eusocial species (with discrete generations) homozygous at a locus of interest (♀*aa*, ♂*a*). Introduce into this population a dominant mutant (A) where its bearers produce sons, rather than sisters and brothers. Let the queen mate n times, and let the sperm from different fathers be used at random (thus $n = 1$ is equivalent to multiple inseminations with clumped sperm—Charnov, 1978). Let the frequency of A among the males be ε_1; Aa among the females ε_2. There are three colony types which occur with frequency $> \varepsilon^2$.

(i) $Aa \times \{a\}_n$ where $\{a\}_n$ refers to her mates (n of which were a).

(ii) $Aa \times \{a\}_n$

(iii) $aa \times A \times \{a\}_{n-1}$.

Ignoring second order terms, the frequencies of these types are 1, ε_2, $n\varepsilon_1$ respectively. The output in terms of reproductives, assuming that Aa (mutant workers) rear αY sons, compared to Y reproductives per aa worker, is as follows. Let the population primary sex ratio be r proportion females.

(1) $aa \times \{a\}_n$: This colony type contributes $Yr - aa$ and $Y(1-r) - a$.

(2) $Aa \times \{a\}_n$: Half of the workers are Aa and they rear only their own sons

$$\frac{\varepsilon_2 \alpha Y}{4} - A.$$

The other workers are aa, and rear sisters and brothers. They contribute:

$$\varepsilon_2 Yr/4 - Aa \text{ and } \varepsilon_2 Y(1-r)/4\ A.$$

(3) $aa \times A \times \{a\}_{n-1}$: $1/n$ proportion of the workers are Aa; these contribute $\varepsilon_1 \alpha Y/2 - A$. $(n-1)/n$ proportion of the workers are aa; they raise r proportion sisters ($1/n$ of these are Aa). Thus these workers contribute

$$\frac{\varepsilon_1(n-1)Yr}{n}\ Aa.$$

The genotype frequencies in one generation (ε_1', ε_2') are approximately

$$\varepsilon_1' \sim \frac{\text{number of } A \text{ produced}}{\text{number of } a \text{ produced}};\ \varepsilon_2' = \frac{\text{number of } Aa \text{ produced}}{\text{number of } aa \text{ produced}}.$$

In terms of the output of the three colony types, we have (written as a matrix product)

$$\begin{pmatrix} \dfrac{\alpha}{2(1-r)} & \dfrac{\alpha+(1-r)}{4(1-r)} \\ \dfrac{n-1}{n} & \frac{1}{4} \end{pmatrix} \cdot \begin{pmatrix} \varepsilon_1 \\ \varepsilon_2 \end{pmatrix} = \begin{pmatrix} \varepsilon_1' \\ \varepsilon_2' \end{pmatrix}. \tag{1}$$

The characteristic equation of (1) is

$$\lambda^2 - \lambda\left(\frac{\alpha}{2(1-r)} + \frac{1}{4}\right) + \frac{\alpha}{8(1-r)} - \left(\frac{n-1}{n}\right)\left(\frac{\alpha+1-r}{4(1-r)}\right) = 0. \tag{2}$$

The mutant is selected for if $\lambda > 1$. Since λ increases with increasing α, it is useful to ask for α = [function of n when $\lambda = 1$]. Consider two cases. *Case* 1: Worker control of r: From Charnov (1978);

$$1 - r = \frac{n}{2n+2}.$$

Putting this in equation (2) and setting $\lambda = 1$ provides

$$\alpha = \frac{n(2n+1)}{(n+1)(5n-2)}. \tag{3}$$

Case 2. Queen control of r: Here $r = \frac{1}{2}$, which provides (for $\lambda = 1$)

$$\alpha = \frac{2n+1}{5n-2}. \tag{4}$$