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What if Workers in Social Hymenoptera *Were* Males?

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In social wasps, bees and ants, the worker caste is always female. Utilizing the approach of Trivers & Hare (1976), the sex-ratio of investment in reproductives which is preferred by different types of colony members is calculated, under the imaginary circumstance that female and male workers are equally possible. The preferred ratio of a male worker is identical to that of his mother. A queen or female worker who can lay male-worker eggs therefore gains allies in her struggle to bias the investment ratio in her favor. This can have various social consequences, depending on whether the queen or female workers lays the male eggs, and on whether female workers are the queen's daughters or sisters. The principal prediction of this imaginary situation is that if males can be just as good workers as females, the queen should prefer that all workers be male. Yet this never happens, even when the queen controls the sex of all colony offspring. This supports the view that it is an inability to be good workers which excludes hymenopteran males from the worker caste.

Introduction

It has been known for centuries that the worker caste in social wasps, social bees and ants, unlike in termites, is made up entirely of females. Workerlike acts are occasionally noted in hymenopteran males (Starr, 1985*a*,*b*), but in no known species do they contribute significantly to the functioning of the colony. And it is quite certain that in no species is the worker caste male.

Two quite different types of ultimate causes have been adduced for male non-workerness. West-Eberhard (1975), Charlesworth (1978) and Starr (1985*a*), as well as some earlier authors, emphasize a number of physical and behavioral traits which render males unfit to undertake key social roles. Hamilton (1964, 1972) noted that males, unlike females, have no extraordinary relatedness to their sisters; he concluded that it is this which initially determines that if some offspring are to altrustically assist their mothers they will be females. As pointed out by Trivers & Hare (1976), such a bias requires that females distinguish sister from brother larvae and be able to preferentially invest in sisters. Otherwise, the average relatedness of females

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to siblings is the same as that of males (if the mother is singly mated) or less (if she is multiply mated).

It is often an illuminating approach in biology, when trying to account for a given trend, to allow the opposite situation and then to follow it through to its consequences. What I will do here is to introduce this sort of *reductio ad absurdum* into Trivers & Hare's (1976) analysis, by assuming that males *can* be workers. My goal is to contribute to answering the question of why they never are.

The Interests of Male Workers

For simplicity, let male workers have the same productive value per investment as female workers. Further, let the castes in each sex be distinct, so that workers never mate, though female workers may lay unfertilized, male-producing eggs. From this, we may analyze the preferred ratio of investment of different classes of colony members in female and male reproductives, following the logic of Trivers & Hare (1976, summarized by Starr, 1984). I introduce no additional assumptions to those of Trivers & Hare, and remove the assumption of single mating. The changes modeled here are all within the colony cycle, i.e. we are not concerned with any changes in gene frequency.

Two starting situations are considered here: (1) a single queen with offspring workers, and (2) a single queen with sibling workers. The first occurs, for example, when a new honey bee colony is founded by a swarm containing the mother queen; the second occurs when the swarm contains a new queen. I will show below that a consideration of these two situations suffices also for others, and thereby accounts for nearly all of those found in social hymenoptera.

(1) Figure 1 shows the preferred ratio of investment, x, in male/female reproductives of the queen, a laying worker, and non-laying workers, for all values of p, the fraction of male eggs laid by the queen. For simplicity, and in order to draw the greatest distinction between the interests of a worker which lays eggs and one which doesn't, all eggs not laid by the queen come from a single worker. The figure illustrates the extremes in relatedness between sister workers. In Fig. 1(a) the queen has mated with just one male (effective promiscuity, $P_e = 1$), so that all female workers are full-sisters. In Fig. 1(b), effective promiscuity is infinite, so that all female workers are half-sisters. The main effect of increased promiscuity is to separate the interests of laying and non-laying workers, while drawing those of the queen and non-laying workers closer together. I have suggested

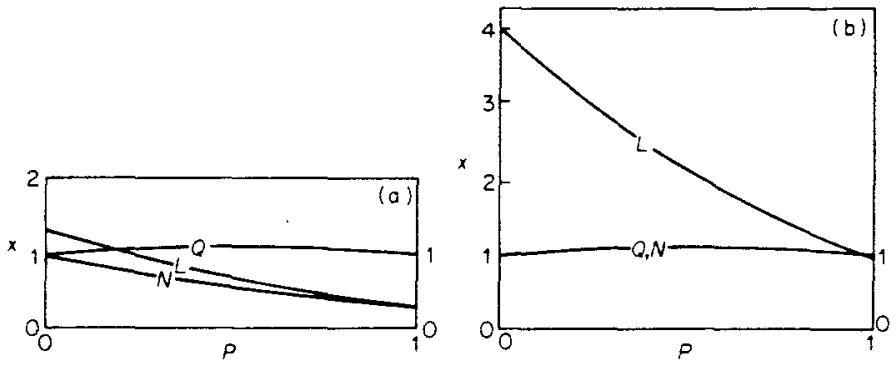

FIG. 1. Preferred ratio of investment x of queen (Q), laying daughter worker (L), and non-laying daughter workers (N), under varying fraction, p, of male eggs laid by the queen. (a) The queen mates just once ($P_e = 1$). (b) The Queen has very many mates ($P_e = \infty$).

elsewhere (Starr, 1984) that this is in fact the function of multiple mating, a tactic of the queen in her struggle to maximize her own fitness†.

(2) Figure 2 is the counterpart situation where female workers are the queen's sisters, rather than daughters. Here, the effect of increased promiscuity is quite different. It broadens differences of interest between

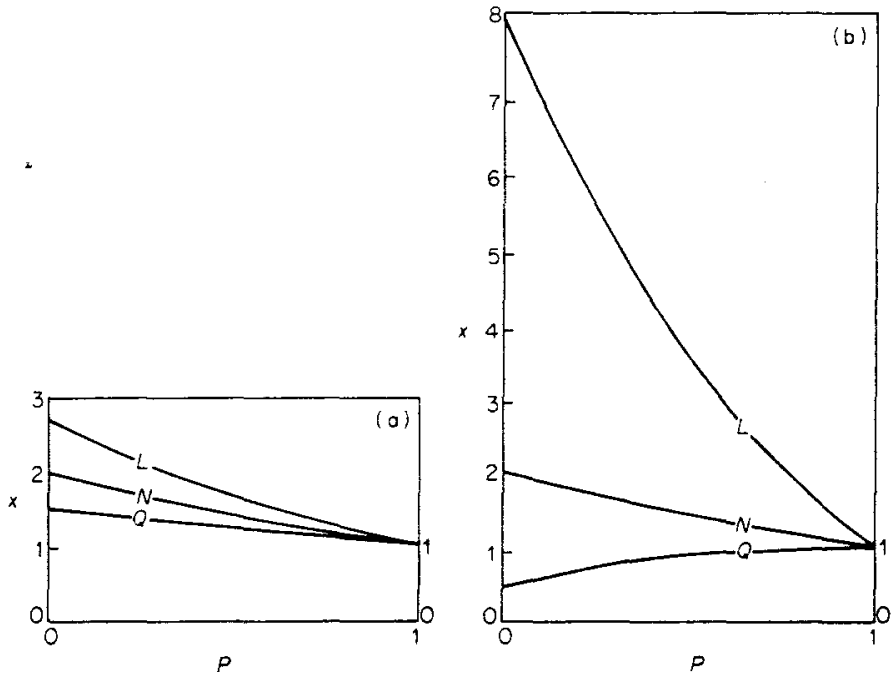

FIG. 2. Preferred ratio of investment, x, of queen (Q), laying sister worker (L), and non-laying sister workers (N), under varying fraction, p, of male eggs laid by the queen. (a) The queen mates just once ($P_e = 1$). (b) The queen has very many mates ($P_e = \infty$).

† As usual in modern times, by "fitness" is meant inclusive fitness.

the three types of females, while maintaining their relative positions. The queen, then, cannot ally her own interests with either of the other types through her control over their relatedness to each other, and the interests of non-laying workers to retain a compromise position between the other two. Note also for all levels of promiscuity the three types have identical interest—a balanced investment ratio—when the queen lays all the male eggs.

Where do the interests of male workers fit in? The answer is extremely simple. The preferred investment ratio of any unmated male, for all values of p and P_e in both situations considered above and all others I have analyzed, is identical with his mother's.

The Impact of Male Workers

The introduction of a large fraction of male workers, then, represents an important advantage for the female who controls the provenance of male eggs. In struggling to maximize their own fitness, male workers will ally themselves entirely with her. In view of this, let us see (a) what the consequences are when $p = 1$, and (b) what they are when $p = 0$, for the two situations.

(a) In situation (1) with P_e very large (Fig. 1(b)), and in situation (2) for all values of P_e (Fig. 2), this takes on an odd aspect if the queen lays all male eggs, as all types of females then have identical preferred investment ratio. The oddness of this result is that it can be seen either as trivial or very significant. On the one hand, what is a victory if it occurs under circumstances in which there is no dispute? On the other hand, what more decisive victory can be imagined than one resulting from bringing the adversaries' interests in line with one's own?

In situation (1) with single mating (Fig. 1(a)), a queen's monopoly on male eggs has the opposite effect. It unites all female workers (trivially, since there are no layng workers) in a preferred investment ratio far removed from the queen's. This is the situation principally considered by Trivers & Hare (1976). Here, the queen may maximize her fitness not through manipulating a reconciliation, but by more conventional approaches to defeating her adversaries.

(b) In situation (1), when a single worker lays all male eggs she separates her interests from the now united interests of the queen and non-laying workers. This increases with increasing promiscuity, so that when P_e is infinitely large (Fig. 1(b)) the difference is about the same as that between queen and workers when P_e and p are each equal to 1 (Fig. 1(a)), a factor of 4 as compared to one of 3.

As mentioned above, in this particular situation, if workers can only be female, it seems clearly advantageous to the queen to multiply mate, as she then allies the non-laying workers with herself. If workers can be male, the queen's options are not so clear and may even be strongly contradictory. She may still ally herself with non-laying workers through promiscuity, but the presence of male workers devalues this alliance. The laying worker is automatically allied with male workers, and if these form a substantial fraction of the workforce, they can be a significant adversary. In that case an egg-laying race is expected, with an outcome reaching beyond the immediate simple score of female vs male eggs laid. Such a race is expected wherever there is a conflict of interest, but high promiscuity raises the stakes. Inasmuch as the queen still controls her own mating, and she cannot decisively win the egg-laying race, it may be to her advantage to keep the stakes low through low P_e.

Situation (2) presents a similar sharpening of conflict with increasing P_e at low p, but nothing more complex. Changing P_e cannot promote any alliance, as the relative positions of the three preferred investment ratios are constant. What is more, if we regard conflicts of interest geometrically, non-laying workers (which include male workers in this case) have no reason to favor either the queen or the laying sister worker over the mother. Their interests are a compromise between those of the other two; the ratio $x_L : x_N$ is never very different from $x_N : x_Q$, where x_L, x_N and x_Q are the preferred investment ratios of laying workers, non-laying workers and the queen, respectively. Under these circumstances, what should the adversaries do? The laying worker should pursue her sole option, to lay male eggs. The queen should do two things: (i) lay as many female eggs as she can, to dampen the effects of the new male workers, and (ii) mate only once, to lower the stakes in a conflict which is going badly for her. It is also to her advantage if she can in fact lay some male eggs; this will both take some fitness away from the laying worker and decrease the conflict between them.

Inasmuch as only the queen is mated, could she assert her control by laying no female eggs, and, as the shorter-lived female workers die off, taking over the laying of male eggs? Conceivably she could, though only if she were sufficiently long-lived and almost certainly at tremendous cost. If the workers have immediate control of caste differentiation, as is usually supposed for all large colonies, they might well find it in their interests to raise all offspring as reproductives, thereby bringing that colony cycle to a close. In any event, such a bizarre strategy on the queen's part would call swarm founding into question.

One peculiarity of the queen's expected preference for single mating under situation (2) is that situation (2) will usually (including in honey

bees) give way to situation (1). And at least when workers are female, the queen in situation (1) has reason to prefer high promiscuity. This gives rise to the hypothesis that a honey bee queen mates with just one male at the beginning and flies out some weeks later for additional matings; this hypothesis is of course false. There has recently been some discussion, occasioned by contradictory results, of just how a queen treats the sperm from her different mates. Taber's (1955) purported finding of a strong separation of sperm packets in the spermatheca was until recently unchallenged and considered very significant. Martinho (1979) and Kerr, Martinho & Gonçalves (1980) reported that sperm packets are not only segregated but are rotated in their utilization, with a period approximately equal to the development time of a queen. Page (1980) found considerable mixing of the sperm, though, and questions Martinho's results and Kerr *et al.*'s interpretation on methodological grounds (R. E. Page, pers. comm.). Could it be that a queen begins with segregated sperm, mostly utilizing those from a single male, and later mixes them? This ornate hypothesis is neither falsified nor supported by what we now know.

In an illuminating treatment of colony-founding in social wasps, Jeanne (1980) showed that the basic patterns are based on two variables: founding may be by one queen (haplometrosis) or several (pleometrosis), and it may involve only the queen(s) (independent founding) or workers as well (swarm founding). There seems to be no reason why these terms will not serve as well to describe colony-founding in other social insects. The two situations treated above involve haplometrotic swarm-founding. For present purposes, the number of same-generation queens does not affect the results of the analysis, so that what has been said above, is equally applicable to pleometrotic swarm founding.

The apparent best option for an independent-founding queen is extremely simple. Given that male workers are just as productive as female workers, and that there is no conflict of interest between an unmated male and his mother, the queen can start with full control by producing only male workers. And at no later stage would she benefit by departing from this policy. Again, the same applies to independent-founding groups. Although the founding queens may be in sharp conflict, none of them gains an advantage from producing female rather than male workers.

Conclusion

The above discussion leaves aside some relevant situations (e.g. acceptance back into the colony of mated daughter queens in some ants), but covers most basic social patterns in hymenoptera.

The general conclusion to emerge is that male workers would have a very significant effect on conflicts within the colony and therefore on social organization. The identification of their interests with those of their mothers means that (1) queens should prefer that all workers be male, and (2) where this is not possible, there should be an intense struggle for control over laying male eggs. Inasmuch as each small advantage in this struggle can serve to produce increased control, a stable equilibrium between the extremes ($0 < p < 1$) may not be possible. This factor raises the stakes.

The first point is the more important, as all swarm founding appears to have evolved from independent founding (Jeanne, 1980).

The conclusion that male workers, if they existed, should figure prominently in hymenopteran societies supports the view that it is their unfitness as workers which makes all workers female (Starr, 1985*a* and *lit. cit.*)

An assumption not mentioned until now is that caste differentiation of brood is under the control of adults, or at least that the caste of colony offspring is under queen control. This is not essential to the argument, but if offspring can themselves choose their caste, then, largely consistent with Hamilton's (1964, 1972) argument, it is less in the interest of males than of females to become workers.

The line of reasoning used here is that of Trivers & Hare (1976). Although this has not in itself been subject to testing, it is a direct and intimate outgrowth of kin-selection theory, which in its 20 years of existence has been amply corroborated throughout its breadth. Any concusion from it is therefore consistent with present-day theory.

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