

SUDDEN EUSOCIALITY IN THE HYMENOPTERA

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ABSTRACT: The Order Hymenoptera comprises the ants, bees, and wasps. This insect Order is haplodiploid. Females develop from diploid fertilized eggs and males develop from haploid unfertilized eggs. An implication of haplodiploidy is that sisters share 75% of their genes if their mother mates only once. These sisters share with their own offspring only 50% of their genes. So-called "eusociality" has arisen at least eleven times independently in this Order. An earlier explanation of this fact states that a female would rather raise sisters than her own offspring due to the genetic relatedness above. Here another explanation--the male haploidy explanation--is proposed to explain eusociality. A new sister-raising mutation passed to a male through its mother would be transmitted to all of its daughters (since all of its sperm are genetically identical), and if their mother had mated only once, the foundation of a eusocial colony would exist. All female offspring would have the mutation and so most would raise sisters. Assuming incomplete penetrance, a few daughters would mate and reproduce elsewhere. Selective advantages may explain spreading of the mutation and thus eusociality in populations.

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It has long been wondered why eusociality has evolved apparently independently at least eleven times in the haplodiploid Order Hymenoptera (ants, bees, and wasps). Interest has focussed on their genetic system (males develop from unfertilized eggs which are thus haploid and females develop from fertilized diploid eggs). The issue of eusociality in this Order has recently been discussed by Hölldobler and Wilson (1990) and by Seger (1991).

Hamilton (1964) proposed a widely accepted explanation of the origin of eusociality in these insects. If the mother queen mates only once before raising her young, her daughters will share with one another 75% of their genes, while sharing only 50% of their genes with their own offspring. (The "shared" genes must be "identical by descent".) Thus, wrote Hamilton, it was to the advantage of daughters to stay in the nest and help raise sisters rather than to reproduce themselves.

In the present paper, quite a different argument is proposed. It will be suggested that eusociality can initially arise in a few generations instead of evolving more gradually as generally supposed.

Before we get started, the reader may wish to note the recent "head start" model of Queller (1989). However, this model is not

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alternative to Hamilton but yet another example of an inclusive fitness approach.

I do not feel that my following new explanation of eusociality would replace Hamilton's. Rather, it might be useful in conjunction with Hamilton's. This new explanation may be termed the "male haploidy explanation".

Suppose a female were mutated in one of the cells in the precursor of her ovaries at a young age, as the result for example of background radiation. This mutation was transmitted to the genotype of one of her eggs. When she became adult and mated, that egg remained unfertilized and so became a haploid male. The mutation was such that the male was not led to raise siblings, but this male's daughters were so led. Perhaps the male did not express sibling-raising due to epistatic interactions in his genome. The mutation may have affected him negatively to some extent, but not enough to prevent later successful mating. It is assumed that every one of the male's gametes carried the mutation, which is why we stipulated that the original mutation occurred very early in the life of this male's mother. (A male's gametes are genetically identical because, since he is haploid there is thus no meiosis and no crossing-over during gamete formation.)

A female mated with this male and no others. (Note that single matings are an assumption in Hamilton's argument as well.) All of her female offspring inherited his complete haploid genotype. Because of the mutation, almost all of them raised young siblings instead of own offspring. That is, they were behaviourally sterile. (None of the original queen's sons inherited the eusocial gene, because they received only their mother's genes.) Penetrance of the mutant allele was incomplete, so that a small number of females (daughter queens) grew to reproduce instead of raising siblings. This state of affairs constituted almost instantaneous eusociality in this first colony in the population.

In the next generation, in the daughter queens' own colonies, only 1/2 of the daughter queens' female offspring possessed the mutation. The noneusocial 1/2 simply left the colony and reproduced elsewhere. Thus once again the daughter queens would have passed the eusocial gene to 1/2 of their sons and these sons would have produced wholly eusocial colonies (if females in the population mated only once.)

It is important to note that the situation described so far would not lead automatically to a spread of the mutation in the population, because the other alleles at the same locus as the mutation would be transmitted in exactly the same way by other nonmutant males. We must invoke selection.

Gradualistic selection would have begun to operate once eusociality appeared. Eusocial colonies would have competed against noneusocial females and their offspring and with each other. Primitive eusociality might confer such advantages as anti-predator and anti-parasite superiority, improved brood care, and perhaps enhanced exploitation of patchy environments. Thus probably brood survival would have been increased and the mutation would have spread in the population.

Clearly the mutant allele is dominant if the argument is to work.

The author does not think that he is discussing some mysterious macromutation. The circuitry in the brains of insects must be tightly

packed and parsimoniously organized. A mutation might disrupt the development of a single neuronal circuit or pathway and thus make mating behavior impossible. The female insect so affected might retain parental motivation and so turn to sister-raising. This phenomenon would be an indirect influence of a gene on behavior.

That single genes may influence behavior strongly in insects has been documented by such writers as Rothenbuhler (1964) and de Belle, Hilliker and Sokolowski (1989). The developmental pathways which lead to such genetic influence are unknown.

A reviewer has objected that kin selection must operate in this scheme because of the .75 relatedness among females. The author cannot detect kin selection in the first three generations although it may operate later. Following is a detailed response to the kin selection objection.

The key process occurs when a male carrying the mutation passes it on to all of his daughters because he is haploid and thus produces genetically identical gametes. This step does not involve kin selection.

Secondly, the daughter queens transmit the mutation to 50% of their daughters and 50% of their sons not because of kin selection but because they share half of their genes with each offspring.

Hamilton's account implies that a female hymenopteran could effectively make a choice between producing its own young ($r=.5$) and raising sisters ($r=.75$). The capacity to make such a choice would have to involve at least one extra mutation. In my model, the "choice" is automatic due to the properties of my postulated mutation. Further, sterility in workers does not here evolve gradually as it must with kin selection but suddenly (in one generation) due to the postulated mutation.

When most daughters raise siblings this does not spread the mutation in the manner described by kin selection theory because both daughters and their female siblings are sterile from the beginning (as a result of the mutation). The few females who escape sterility because of incomplete penetrance of the mutation ("daughter queens") are not helped by workers in the standard kin selection way, because the probability that a daughter queen and a helping worker both share the mutation is not .75 (as according to the kin selection hypothesis) but 1.00 (as according to the male haploidy hypothesis).

It is true that Hamilton in the very beginning deduced that sisters are related to one another by 75% of their genes because of male haploidy. My argument is based upon the same fact certainly, but the emphasis is quite different. I emphasize the male haploidy itself, while Hamilton emphasizes the resultant relatedness between offspring sisters. I reason that male haploidy has properties which lead to a unique transmission of a mutation resulting in sudden primitive eusociality.

What I have written can neither include nor exclude kin selection. However, the latter does not operate at the origin at very least of eusociality, which makes my account differ from Hamilton's.

The recent discovery of eusociality in another haplodiploid insect Order (the Thysanoptera or thrips) strengthens the genetic approach to eusociality (see Crespi, 1992) to the extent that it provides further correlation between eusociality and haplodiploidy. Of course, some research is disconfirming. Queller, Strassman and Hughes (1988) found the juxtaposition of sister-raising and low relatedness in colonies of

neotropical swarm-founding wasps (with multiple queens). Both Hamilton's and our models are questioned by these findings unless special phenomena such as nepotism (preferentially raising only one's own full sisters) are demonstrated. However, the author still feels that single matings by single foundresses constitute a reasonable ancestral scenario.

A colleague has been working on a numerical model designed to describe the propagation of the altruistic sister-raising mutation proposed here. This model initially shows that the mutation would slowly spread in a population. However, it appears that a polymorphism rather than complete fixation would result, because crosses between selfish non-sister-raising recessive homozygotes would always generate some selfish individuals. Nevertheless, these selfish individuals would be in the end rare. This result could be assumption-sensitive.

This paper has put forth a new explanation of eusociality in the Hymenoptera, which is related to but distinct from Hamilton's (1964) kin selection hypothesis.

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