2 Haplodiploidy and the evolution of eusociality: worker revolution.

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Recommendations:

Very Good **03 Sep 2014**

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Explaining the occurrence of altruism has perplexed biologists ever since Darwin first advanced his theory of evolution by means of natural selection {1}. After all, if natural selection favors those individuals that produce the most surviving young, how can a behavior evolve that entails helping others to survive and reproduce, especially if it reduces the helper's own survival and reproduction? Nowhere is this problem more apparent than in species that have evolved eusociality, in which non-reproductive castes exist to care for the reproductive members of the society {2,3}.

Eusociality is especially common among ants, bees, and wasps, i.e. members of the insect order Hymenoptera {4}. Moreover, unlike most species, the Hymenoptera have an unusual system of sex determination, known as 'haplodiploidy'. With haplodiploidy, unfertilized (haploid) eggs become males, whereas fertilized (diploid) eggs become females {4}. Interestingly, in the Hymenoptera, all non-reproductive (worker) individuals are females {4}.

These facts led the evolutionary biologist W. D. Hamilton to propose a hypothesis for the evolution of eusociality. Hamilton's hypothesis was an extension of his better-known kin selection or inclusive fitness theory for the evolution of altruism (the latter theory holds that a gene can spread in a population if it increases the reproduction of relatives, even if it reduces its bearer's personal fitness {5,6}). According to Hamilton's 'haplodiploidy hypothesis' {5-7}, Hymenoptera were predisposed to evolve eusociality because a worker would be more closely related to her full sisters (coefficient of relatedness [R]=3/4) than to her own daughters (R=1/2). In other words, all else being equal, natural selection should favor workers that help their mother (the queen) rear additional sisters, even at the expense of producing their own daughters.

Although this theory was immediately attractive because it explained a long-standing problem in biology (the evolution of eusociality in the Hymenoptera), it quickly became apparent that all else was generally not equal. For example, haplodiploidy also makes a worker less related to her brothers (R=1/4) than to her sons (R=1/2). Additionally, a female-biased sex ratio would tend to increase the mating success of the (rarer) males produced by the colony, which would tend to devalue the females that the workers helped to produce.

In a highly influential paper, Trivers and Hare {8} suggested how Hamilton's haplodiploidy hypothesis could overcome the above problems. For instance, they proposed that workers might preferentially replace the queen's sons with their own sons (workers are often capable of producing unfertilized eggs, which develop into males {9}). They further suggested that workers might bias the sex ratio of the queen's brood toward females. In other words, there should be a 'worker revolution'.

In the present paper, Joao Alpedrinha, together with two leading theorists in the realm of social evolution, Andy Gardner and Stuart West, re-evaluate the Trivers and Hare version of the haplodiploidy hypothesis in light of new information on the life histories of the Hymenoptera. Although their re-appraisal is theoretical in nature, their theory is nicely informed by the natural history and biology of the Hymenoptera.

The salient conclusions to emerge from Alpedrinha, Gardner, and West's analysis are (1) worker reproduction will tend to inhibit, rather than promote, the evolution of helping behavior and (2) worker control of sex allocation might facilitate helping, but it tends to have a relatively weak and short-lived effect. Overall, these results suggest that the presence of haplodiploidy has a negligible effect on fostering the evolution of eusociality.

This paper is important because it represents a re-appraisal of a cherished idea in the field of social evolution {8}. Furthermore, the authors suggest that rather than haplodiploidy being important in the evolution of eusociality, other factors, such as inclusive fitness considerations, were likely critical in explaining the evolution of helping 'behavior' (broadly defined) throughout the tree of life {2,3}.

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Disclosures
None declared

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Abstract:

ABSTRACT

Abstract Hamilton suggested that inflated relatedness between sisters promotes the evolution of eusociality in haplodiploid populations. Trivers and Hare observed that for this to occur, workers have to direct helping preferentially toward the production of sisters. Building on this, they proposed two biological scenarios whereby haplodiploidy could act to promote the evolution of eusociality: (a) workers biasing the sex allocation of the queen's brood toward females and (b) workers replacing the queen's sons with their own sons. This "worker... more »
revolution," whereby the worker class seizes control of sex allocation and reproduction, is expected to lead to helping being promoted in worker-controlled colonies. Here, we use a kin-selection approach to model the two scenarios suggested by Trivers and Hare. We show that (1) worker control of sex allocation may promote helping, but this effect is likely to be weak and short lived; and (2) worker reproduction tends to inhibit rather than promote helping. Furthermore, the promotion of helping is reduced by a number of biologically likely factors, including the presence of workers increasing colony productivity, workers being unmated, and worker control of sex allocation being underpinned by many loci each having a small effect. Overall, our results suggest that haplodiploidy has had a negligible influence on the evolution of eusociality.

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