

## The haplodiploidy threshold and social evolution

Raghavendra Gadagkar

Centre for Ecological Sciences and Centre for Theoretical Studies,  
Indian Institute of Science, Bangalore 560 012, India

Workers in eusocial insect species help in rearing their siblings and other genetic relatives instead of producing their own offspring. The multiple origins of such eusociality in the Hymenoptera have been ascribed to haplodiploidy because this genetic system makes a female more closely related to her full sisters than she would be to her offspring. To test this so called haplodiploidy hypothesis, I first assume that workers are capable of investing in their sisters and brothers in the ratio that is optimal for them. I then define a *haplodiploidy threshold* as that value of genetic relatedness between workers and their sisters such that they have a weighted average relatedness to the brood they rear of 0.5 and thus have the same fitness as solitary nesting females. Using 177 published estimates of relatedness between sisters in social hymenopteran colonies, I show that in 29 out of 35 species studied, there is not even one estimate of relatedness that is significantly higher than the haplodiploidy threshold. I conclude therefore that the multiple origins of eusociality in the Hymenoptera cannot be ascribed solely to the genetic asymmetry created by haplodiploidy.

EUSOCIAL insects such as termites, ants and many species of bees and wasps exhibit three characteristic features namely, overlap of generations, co-operative brood care and caste differentiation into fertile reproductive castes and sterile worker castes<sup>1,2</sup>. These sterile worker castes present an obvious challenge to Darwin's theory of natural selection<sup>3</sup>. The seminal work of Hamilton<sup>4,5</sup> was the first serious attempt to meet this challenge. Hamilton developed the concept of inclusive fitness and showed that fitness can also be gained by helping genetic relatives in addition to or, indeed, instead of producing offspring.

One reason for the instant appeal of Hamilton's ideas was that the haplodiploid genetic system found in the insect order Hymenoptera creates an asymmetry in genetic relatedness such that full sisters are more closely related to each other (coefficient of genetic relatedness,  $r=0.75$ ) than a female would be to her offspring, ( $r=0.5$ ). In the light of this, it is striking that eusociality is known to have arisen at least eleven times independently in the Hymenoptera compared to only twice (once in the termites and once in the naked mole rat) outside that insect order<sup>2,6</sup>. This idea that the genetic asymmetry created by haplodiploidy can promote the evolution of eusociality in the Hymenoptera may be termed the haplodiploidy hypothesis.

There are however at least two hurdles that have to

be overcome before the haplodiploidy hypothesis becomes plausible. The first is that although hymenopteran females are related to their full sisters by 0.75, they are related to their brothers merely by 0.25. A hymenopteran worker who rears equal numbers of sisters and brothers has therefore no advantage over a solitary nest foundress because her average relatedness to the brood she rears is equal to 0.5. Trivers and Hare<sup>7</sup> suggested that this hurdle can be overcome if workers discriminate between their sisters and brothers and bias their investment in favour of sisters. A combination of Fisher's sex ratio theory<sup>8,9</sup> and Hamilton's kin selection theory<sup>3,4</sup> predicts that a ratio of investment between female and male broods which is equal to the ratio of relatedness to the two classes of brood is evolutionarily stable from the worker's point of view<sup>10-15</sup>. There is however considerable controversy about whether investment is under the control of workers and whether workers in fact achieve the ratio of investment that is optimal for them<sup>16-18</sup>.

The second hurdle is that many hymenopteran females mate with more than one male, store sperm in their spermathecae and produce different patrilineages of daughters who are related to each other by 0.25 (ref. 19-22). This again reduces the inclusive fitness that workers can potentially gain. Whether the genetic asymmetry created by haplodiploidy is by itself sufficient to allow workers to have more inclusive fitness than solitary foundresses thus depends on their relatedness to their sisters and on their ability to skew investment in favour of sisters. A number of estimates of genetic relatedness between sisters in hymenopteran colonies have now been published. However an objective test of whether the genetic asymmetry created by haplodiploidy by itself can select for worker behaviour has not been performed. To test the *haplodiploidy hypothesis* I first assume that workers are capable of investing in their brothers and sisters in the ratio that is optimal for them, namely, in the ratio of their genetic relatedness to their sisters and brothers. I then compute the threshold relatedness to sisters required for workers to obtain a weighted mean relatedness to siblings of 0.5 and thus break even with solitary foundresses.

The optimum number of females that a worker should rear relative to every male reared is given by  $r_f/r_m$  where  $r_f$  is her mean relatedness to female brood and  $r_m$  is the relatedness to male brood. When workers successfully skew investment between females and males in the ratio  $r_f/r_m:1$ , their weighted mean genetic relatedness to the brood they rear is given by

$$\bar{r} = [(r_f^2/r_m) + r_m] / [(r_f/r_m) + 1]. \quad (1)$$

In an outbred hymenopteran population where workers rear mixtures of sisters and brothers,  $r_m$  is expected to be 0.25 and the relatedness between a

solitary nesting female and her offspring is expected to be 0.5.

To thus solve eq. (1) for  $\bar{r}=0.5$ , I rewrite it as

$$16r_f^2 - 8r_f - 1 = 0. \quad (2)$$

Eq. (2) yields a value of 0.604 for  $r_f$ . This means that a genetic relatedness between workers and their sisters of 0.604 is required if workers are to gain as much fitness as solitary individuals *in spite of skewing investment between sisters and brothers* in the ratio that is optimal for them. I will call 0.604 the *haplodiploidy threshold*.

Most published estimates of genetic relatedness are accompanied by standard errors and it is therefore possible to ask if these estimates are significantly greater than the haplodiploidy threshold. Of 177 such estimates (spread over 35 species) of relatedness between sisters, only 22 estimates are significantly higher than the haplodiploidy threshold ( $P < 0.05$ ). Of these, 5 pertain to ants, 4 to primitively eusocial bees and 13 to primitively eusocial wasps. Of 20 species of highly eusocial hymenopterans studied only three have at least one estimate significantly higher than the haplodiploidy threshold (Table 1). I conclude from this that the *genetic asymmetry created by haplodiploidy is by itself insufficient to maintain the highly eusocial state*. Of 15 species of primitively eusocial hymenopterans studied only 3 have at least one estimate significantly higher than the haplodiploidy threshold (Table 1). I conclude from this that the *genetic asymmetry created by haplodiploidy is by itself insufficient to promote the origin of eusociality*.

Thus only 6 out of the 35 species of social hymenopterans studied have at least one estimate of genetic relatedness between sisters that is high enough for haplodiploidy by itself to select for worker behaviour. It is therefore quite unreasonable to ascribe the multiple origins of eusociality in the Hymenoptera solely to the genetic asymmetry created by haplodiploidy. In computing the haplodiploidy threshold I have assumed outbreeding. This appears to be reasonable for most species used in the analysis. I have also assumed that

Table 1. A test of the haplodiploidy hypothesis.

Group	No. of species for which estimates of genetic relatedness between sisters, with standard errors, are available	No. of species for which at least one estimate is significantly greater than the haplodiploidy threshold
Ants	15	3
Vespine wasps	2	0
Swarm-founding wasps	3	0
Primitively eusocial bees	2	1
Primitively eusocial wasps	13	2
Total	35	6

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workers are capable of skewing investment between female and male brood in the ratio that is optimal for them. This may or may not hold. If it does not, then I am giving an unfair advantage to the haplodiploidy hypothesis. But that is just as well because it makes my falsification of the haplodiploidy hypothesis more robust.

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