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A TEST OF THE ROLE OF HAPLODIPLOIDY IN THE EVOLUTION OF HYMENOPTERAN EUSOCIALITY

RAGHAVENDRA GADAGKAR
Centre for Ecological Sciences and Centre for Theoretical Studies. Indian Institute of Science, Bangalore-560 012, INDIA.

The haplodiploid genetic system found in all Hymenoptera creates an asymmetry in genetic relatedness so that full-sisters are more closely related to each other (coefficient of genetic relatedness, $r = 0.75$) than a female would be to her daughters ($r = 0.5$). The multiple origins of eusociality in the Hymenoptera have therefore been ascribed to haplodiploidy (1). But a Hymenopteran female is related to her brothers by 0.25. A worker who rears equal numbers of brothers and sisters therefore has no advantage over a solitary nest foundress because her average relatedness to brood will be reduced to 0.5. But workers can potentially gain more inclusive fitness than solitary foundresses if they invest more in their sisters than in their brothers (2). When queens mate multiply and simultaneously use sperm from different males, they produce different patrilines of daughters who would only be related to each other by 0.25. This again reduces the inclusive fitness that workers can potentially gain. Whether or not the genetic asymmetry created by haplodiploidy can by itself be 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. To test the haplodiploidy hypothesis I assume that workers are capable of investing in their brothers and sisters in the ratio that is optimal for them and compute the threshold relatedness to sisters required for them to obtain a weighted mean relatedness to siblings of 0.5 and thus break even with solitary foundresses.

In an outbred Hymenopteran population where workers rear mixtures of sisters and brothers, the optimum number of females that a worker should rear relative to every brother reared is given by $r_f/0.25$ where r_f is her mean relatedness to sisters and 0.25 is that to her brothers. When workers successfully skew investment between sisters and brothers in the ratio $r_f/0.25 : 1$, their weighted mean genetic relatedness to siblings $\bar{r}$ is given by:

$$\bar{r} = [(r_f^2/0.25) + 0.25] \ / \ [(r_f/0.25) + 1] \qquad ......(1)$$

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

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

Equation (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, inspite of skewing investment between sisters and brothers in the ratio that is optimal for them. I will call this number namely 0.604 the *haplodiploidy threshold.*

Most published estimates of genetic relatedness are accompanied by standard errors and I therefore ask if these estimates are significantly greater than the haplodiploidy threshold. Of 141 such estimates (spread over 35 species) of relatedness between sisters only 16 estimates are significantly higher than the haplodiploidy threshold ($p < 0.05$). Of these, 5 pertain to ants, 4 to primitively eusocial bees and 7 to primitively eusocial wasps. Of 17 species of ants, only three have atleast one estimate which is significantly higher than haplodiploidy threshold. These are *Solenopsis geminata* for which 3 out of 5 estimates are higher, *S.invicta* for which only 1 out of 4 estimates is higher and *S.richteri* for which the only available estimate is higher. *Apis mellifera*, the honey bee does not have relatedness significantly higher than the haplodiploidy threshold. The two species of vespine wasps studied also do not have significantly higer values and of three species of swarm-founding wasps, none have even one estimate that is significantly higher than the threshold. Thus out of 20 species of highly eusocial Hymenopterans studied only three have atleast one estimate significantly higher than the haplodiploidy threshold. I conclude from this that the genetic asymmetry created by haplodiploidy is by itself insufficient to maintain the highly eusocial state.

Of 2 species of primitively eusocial bees only one, namely *Lasioglossum zephyrum* has values significantly higher than the haplodiploidy threshold but even here only 4 out of 14 estimates are significantly higher. Of the 8 estimates for the other primitively eusocial bee namely *Exoneura bicolor*, none are significantly higher. Of 17 species of primitively eusocial wasps, only 2 have estimates significantly higher than the haplodiploidy thrshold. One such species is *Microstigmus comes* in which only 6 out of 18 estimates are higher. The other is *Mischocyttarus immarginatus* in which the only estimate available is significantly higher. Thus of 15 species of primitively eusocial Hymenopterans studied only 3 have at least one estimate significantly higher than the haplodiploidy threshold. I conclude from this that the genetic asymmetry created by haplodiploidy is by itself insufficient to promote the origin of eusociality.

In computing the haplodiploidy threshold I have assumed outbreeding. This appears to be reasonable for most species used in this analysis. I have also assumed that workers are capable of skewing investment 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 is better to falsify a hypothesis inspite of giving it an unfair advantage.

1. Hamilton, W.D. 1964. J.theor.Biol., 7:1-52.
2. Trivers, R.L. and H. Hare. 1976. Science, 191:249-263.