

NOTES AND COMMENTS

UNMATEDNESS AND THE EVOLUTION OF EUSOCIALITY

Eusociality has evolved between ten and twenty times and, with the two exceptions of termites and naked mole rats, always within the insect order Hymenoptera (Wilson 1971; Trivers 1985). Hamilton (1964) suggested that this predisposition toward eusociality resulted from the haplodiploid genetic system of the Hymenoptera, in which males develop from unfertilized eggs. The haploidy of males ensures that, when the mother mates only once, sisters receive all, and therefore share all, their paternal genes. This extra relatedness, in comparison with diploidy in which they share only half their paternal genes, makes sister-sister altruism (such as rearing sisters) more likely.

Hamilton (1964) and Trivers and Hare (1976) pointed out a hurdle to be overcome in the argument linking haplodiploidy with a predisposition to eusociality. Although a female may be selected to rear sisters, indiscriminate sib rearing, as would occur if the insect could not distinguish between brothers and sisters, is not likely to be favored. The link between eusociality and haplodiploidy therefore seems to depend on the arising of a mutant that causes both sib rearing and discrimination in favor of sisters. It is possible that simultaneous mutants are found in species in which the mother already discriminates between sons and daughters in her maternal care, but sidestepping this hurdle has been a major theme in the literature. The first attempts, by Hamilton (1964) and Trivers and Hare (1976), were to argue that a female-biased population sex ratio would favor sib rearing. Showing that this was not sufficient, Craig (1979) established the principle that, when the equilibrium sex ratio is equality, the sib rearers must produce a sex ratio that is biased relative to the population sex ratio. As males become more rare, they enjoy a proportional mating advantage that exactly counterbalances the benefits accruing to the sib rearers from producing extra females. The extra boost to eusociality thus depends on some way of ensuring that females rear more sisters and fewer brothers than the population average sex ratio (Craig 1979, 1980; Grafen 1986). Seger (1983) and Grafen (1986) have suggested mechanisms for securing this boost through sex-ratio distortions and overlapping generations. The purpose of this note is to describe a new mechanism that almost certainly operates in many haplodiploid species.

Our argument is based on a hypothetical comparison between two solitary species that are identical except that one is haplodiploid and the other diploid. We

are concerned only with the initial spread of the sib-rearing trait because we believe that, once the trait is common, further steps toward eusociality do not depend on the trait's becoming fixed, but on refinements that adapt morphology or behavior to the worker role. This approach differs from that of Craig (1980), who saw the likelihood of fixation of the trait as a measure of the importance of sex-ratio biases in the evolutionary origins of eusociality.

Males in haplodiploid species develop from unfertilized eggs; an unmated female (or a female unable to fertilize her eggs for other reasons) is thus able to produce viable male offspring. If the population is at sex-ratio equilibrium, such that the marginal male is of the same value to its mother as the marginal female, then the unmated mother in a panmictic population suffers no disadvantage in comparison with a mated female that produces sons and daughters. There is therefore no selective disadvantage from this source to oviposition before mating, or even to avoiding mating altogether. This is relevant because it suggests that unmatedness among mothers may become common. (Unmatedness cannot spread too far because, sooner or later—depending on whether mated females adjust their sex ratio in response to the level of unmatedness—producing males must become a disadvantage. Furthermore, selection pressures on males to find females and mate with them is strong.)

The above argument suggests that virgin oviposition may be common in nature. In the parasitic Hymenoptera, a group that has been particularly closely studied because of its economic importance, virgin oviposition in the laboratory is normal (Clausen 1940). There is some field evidence of virgin oviposition: gregarious hymenopteran broods are sometimes composed exclusively of males, indicating that the mother was unable to produce females (Godfray, MS), but further evidence, especially from aculeate Hymenoptera, is desirable. Virgin oviposition by unmated workers is common in the eusocial Hymenoptera (Wilson 1971).

The major consequence of unmatedness is that there are two classes of mothers: the unmated and the mated. A gene for sib rearing expressed in daughters only would therefore be expressed in the broods of mated females only. These broods are female-biased relative to the average in the population. This effect is present whether or not mated females compensate for the excess of males produced by unmated mothers by biasing their own offspring ratios toward females. (Supra-binomial variance in sex ratio from any cause would, of course, have a similar effect.) This overcomes Hamilton's and Trivers and Hare's hurdle and does not require sib sex discrimination.

One apparent corollary that turns out not to be true should be mentioned. The advantage to sib rearing arises automatically when some virgins lay all-male clutches, and it does not depend on a compensating female bias in the clutches of mated females. It is tempting to believe that such compensation would increase the advantage to sib rearing through the extra female bias in the clutches in which sib rearing first arises. In fact, the reverse is true, and such compensation decreases the advantage of sib rearing. The potential gain to a sib rearer through producing more sisters in its own clutch is exactly counteracted by the change in the population sex ratio that the population-wide compensation brings about. The net effect of compensation on a sib-rearer's reproductive success therefore de-

pend solely on the reduction in the number of males among its sibs. This must decrease the success of a sib rearer. The same argument applies whether compensation is achieved by altering the primary sex ratio of eggs laid or by altering the secondary sex ratio by preferentially rearing females.

It is now firmly established that haplodiploidy can have the kind of influence on eusociality first suggested by Hamilton. There are competing explanations, however, for the concentration of eusociality in the Hymenoptera (Charnov 1978). In this note, we have not tackled the historical problem of whether Hamilton's mechanism did in fact influence the evolution of eusociality, though in our view the argument presented here does make it likely that haplodiploidy had a positive effect.

ACKNOWLEDGMENTS

We thank P. Harvey and a reviewer for valuable comments and discussion.

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Submitted August 6, 1986; Revised February 12, 1987; Accepted May 28, 1987

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