Perspective

Relatedness, Sex Ratios, and Controls

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FIFTEEN YEARS AGO TRIVERS AND HARE (*1*) SHOWED THAT Fisher's sex-ratio theory (*2*) and Hamilton's inclusive-fitness theory (*3*) together imply that conflict over the sex ratio should be nearly universal in colonies of social Hymenoptera (ants, bees, wasps). The exact form of the conflict is expected to depend on various details of colony and population structure, but in many cases workers are predicted to evolve behaviors that tend to increase the proportion of females among their colony's reproductive offspring, while principal reproductives ("queens") are predicted to evolve behaviors that tend to increase the proportion of males. Trivers and Hare compiled sex-ratio data for many species of social insects, and found that strongly female-biased ratios of investment did indeed occur, especially among those species of ants in which there is typically just one queen per colony. These are the kinds of species in which we should expect to find the most strongly female-biased sex ratios, if workers have the upper hand. This result was (and still is) widely viewed as a stunning confirmation of Fisher's and Hamilton's theoretical insights, and as a demonstration that offspring can evolve behaviors that advance their own (here, vicarious) reproductive interests at the expense of their parents'.

The Trivers and Hare paper appeared in 1976, when the study of insect sociality was already beginning to expand rapidly. It laid out a rich, quantitative framework within which both the origin of sociality and the strategic behavior of individuals could be studied, thereby giving shape to a research program that has produced hundreds of empirical and theoretical studies that test, refine, and extend the original model and analysis of data. The extensions are so many and varied that the model has grown into a paradigm; it now motivates and organizes a wide range of issues and findings in social insect behavior and evolution (*4, 5*).

On page 442, Mueller (*6*) describes an experiment designed to test the idea that within a population, colonies with different patterns of relatedness should produce different sex ratios. One version of this idea goes back to Trivers and Hare, and it has recently been generalized by Grafen (7) and Boomsma (*4*). The central claim of the Trivers and Hare model is that under certain circumstances the relatedness asymmetries caused by haplodiploidy give rise to sex-ratio biases. The overwhelming majority of attempts to test this hypothesis (and others derived from the basic model) have employed the method of interspecific comparisons, which exploits evolution as a "natural experiment." This has been the favored method because it can be used to address predictions in a relatively direct way, and with a large enough number of independent contrasts it can be powerful. For example, one of the more compelling contrasts presented by Trivers and Hare is that between monogynous (single-queened) and polygynous (multiple-queened) species of ants in the genus *Myrmica*. As predicted, the investment ratios of the monogynous species are more female-biased than those of the polygynous species. A weakness of the comparative method, however, is its assumption that "all else" is effectively equal, at least on average, between two groups of species or other taxa that differ with respect to the variable of interest. We can try to find situations where this assumption is relatively likely to be true, but in any given instance there is no guarantee. Who knows what else may differ among, for example, the monogynous and polygynous *Myrmica*, or in what ways (other than those entailed by the theory) monogyny and polygyny may incline them to have different investment ratios?

A completely different approach is to design tests involving just a single species, so as to eliminate the uncontrolled variation associated with the evolutionary histories of different species. Here the aim must be to find and exploit some form of intraspecific variation than can be taken to reflect the variables of interest. One such test, related in focus to Mueller's experiment, was discovered by Ward (*8*), who found that monogynous colonies of *Rhytidoponera* increase their relative female investment when their local population contains a high proportion of queenless (male-producing) colonies. This supports the hypothesis that workers are in control, because the estimated investment ratios are very close to the theoretical predictions. But qualitatively, any controlling agent should adjust in this way. And the comparisons are among geographically separated populations that could differ, like species, in unknown ways.

Yanega (*9*) recently showed that the original foundress disappears from a substantial proportion of nests in a sweat bee, *Halictus rubicundus*, and is replaced by one of her daughters. Because the relatedness asymmetry is absent in such nests, workers (now sisters of the principal reproductive) should prefer male over female offspring. As predicted, such nests produce a more male-biased sex ratio than do neighboring nests where the mother survives. All else may seem to be truly equal here, but in fact more has changed than relatedness: females of different generations differ in size; workers are absolutely less related to the brood in nests lacking foundresses; the population of such a nest is reduced by one individual (possibly significant, because colonies of this species are very small); and we do not know why the foundress disappeared.

In Mueller's experiment on a related species, *Augochlorella striata*, foundresses are removed experimentally, so the cause is known. As in *H. rubicundus*, such disappearances happen frequently in nature; thus the response (again, a relative male bias) is likely to be biologically meaningful. Indeed, a few control nests that naturally lost their foundresses also produced relatively male-biased sex ratios. This result supports both the basic theory and an interesting extension, and it illuminates the biology of an important group of primitively social bees. But it also shows that even a carefully conceived manipulative experiment may be less than perfectly controlled. Here, as in Yanega's study, more things change than just relatedness when the foundress disappears. It is fortunate that theoretical, comparative, and experimental studies have different strengths and weaknesses, and it seems likely that Mueller's paper will stimulate attempts to design similar experimental approaches to a range of issues in the behavior and evolution of social insects. Such approaches should gain support and inspiration from the broad interest now developing in the general problem of condition-dependent behavioral plasticity.

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