Exoskeletons out of the Closet

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In a landmark paper published 20 years ago in *Science*, Trivers and Hare (*1*) showed that a fundamental conflict of interest is expected between queens and workers within colonies of many species of ants, bees, and wasps (order Hymenoptera). Because they are unusually closely related to their sisters, workers (unlike queens) are predicted to strongly bias the allocation of resources toward the colony's female reproductive offspring. Ratios of males to females and other kinds of data imply that workers usually prevail in this worker-queen conflict (*1*, *2*), but we still know little about the mechanisms involved. Do workers induce the queen to lay eggs with a primary sex ratio contrary to her interests? Do they detect the sexes of larvae and cull them, or feed their sisters more than their brothers? In this issue of *Science*, Sundström *et al.* (*3*) show that workers in colonies of the ant *Formica exsecta* apparently kill queen-laid male larvae under circumstances where biasing their colony's investment toward female reproductives increases their inclusive fitness.

Impure altruism? Workers and two queens (marked by yellow and green paint) of the ant *Myrmica tahoensis* tend male and female larvae and pupae. In this species and others (including *F. exsecta*, see p. 993) worker-imposed male mortality may cause sex-ratio variation among colonies. [Photo by Jay Evans]

Male ants, bees, and wasps develop from unfertilized haploid eggs, but females are diploid. A female hymenopteran is therefore related to her brothers by only one-quarter, but to her full sisters by three-quarters (*4*). In many species where the female workers control the colony's allocation of resources to reproductive offspring, the population-wide ratio of allocation should equilibrate at 3:1 (female:male). At this ratio a worker is "indifferent" to her colony's allocation because her genes will be transmitted with equal efficiency through sisters and brothers (*5*). Queens, being equally related to their sons and daughters, are indifferent at a 1:1 ratio. This difference gives rise to a conflict because there is no population-wide ratio at which both queens and workers can be indifferent (*1*).

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Workers are probably unable to control the queen's egg production (and hence the primary sex ratio), but since they do all the work they should have many opportunities to affect the allocation of net investment, which is the quantity that matters (*1*, *5*). For example, they could feed female larvae more than males; they could turn larvae otherwise destined to be workers into sexual females; or they could eat males, partially recycling them from the male to the female side of the ledger (*2*). Each of these ploys has a price, however, in wasted time and resources. Losses will be reduced if workers can determine the sex of a larva before they put much work into it. Queens should be able to counter with ploys of their own, including all-male broods and stealthy male larvae that masquerade as females through several instars (*6*).

In species where some queens mate once but others mate twice (producing daughters with a mixture of full- and half-sib relationships), workers in both kinds of colonies would increase their inclusive fitness if those in the high-relatedness colonies specialized in female production while those in the low-relatedness colonies specialized in males (*7*). To effect this conditional sex-ratio strategy, workers would first need to assess the average relatedness within their colony and then bias allocation in the appropriate direction. "Split sex ratios" are also expected in species where the asymmetry of worker relatedness to males and females varies because colonies vary in queen number. Evans (*8*) recently used multilocus microsatellite genotyping and larval transfers between unrelated colonies, in the field, to show that workers in one such species apparently assess the genetic diversity within their colonies and adjust the sex ratios of larvae at advanced stages of development.

Formica exsecta is one of several single-queen ant species in which colony sex ratios are known to vary with the queen's mate number. Sundström *et al.* (*5*) surveyed the sexes of "eggs" (prehatching embryos) by cytological examination of chromosomes (*9*) and then compared their sex ratios to those of reproductive pupae. Primary sex ratios did not differ between high- and low-relatedness colonies, so the large difference in adult sex ratios must have been caused by events subsequent to egg laying. The average proportion of females increased from egg to pupal stages in high-relatedness colonies, implying disproportionate mortality of males—presumably as victims of their sisters. This finding will greatly sharpen interest in the twin problems of assessing average relatedness, on the one hand, and the sexes of individual larvae, on the other. When, where, and how do workers perform these feats? And do countermeasures ever evolve? Apparently, in *F. exsecta*, males are not very good at disguising themselves. But they might sometimes succeed, temporarily, in some species, until workers evolved the ability to discriminate new cues to larval gender.

References

1. R. L. Trivers and H. Hare, *Science* **191**, 249 (1976).
2. B. Holldobler and E. O. Wilson, *The Ants* (Harvard University Press, Cambridge, MA, 1990); L. Keller, Ed., *Queen Number and Sociality in Insects* (Oxford University Press, Oxford, 1993); A. F. G. Bourke and N. R. Franks, *Social Evolution in Ants* (Princeton University Press, Princeton, NJ, 1995); R. H. Crozier and P. Pamilo, *Evolution of Social Insect Colonies* (Oxford University Press, Oxford, 1996); S. Turillazzi and M. J. West-Eberhard, Eds., *Natural History and Evolution of Paper-Wasps* (Oxford University Press, Oxford, 1996).
3. L. Sundström, M. Chapuisat, L. Keller, *Science* **274**, 993 (1996).
4. W. D. Hamilton, *J. Theor. Biol.* **7**, 1 (1964); *Annu. Rev. Ecol. Syst.* **3**, 193 (1972).
5. R. A. Fisher, *The Genetical Theory of Natural Selection* (Clarendon Press, Oxford, 1930).
6. P. Nonacs and N. F. Carlin, *Proc. Natl. Acad. Sci. U.S.A.* **87**, 9670 (1990); P. Nonacs, in *Evolution and Diversity of Sex Ratio in Insects and Mites*, D. L. Wrensch and M. A. Ebbert, Eds. (Chapman & Hall, New York, 1993), pp. 384–401.
7. J. J. Boomsma and A. Grafen, *Evolution* **44**, 1026 (1990); *J. Evol. Biol.* **3**, 383 (1991).
8. J. D. Evans, *Proc. Natl. Acad. Soc. U.S.A.* **92**, 6514 (1995).
9. S. Aron, L. Passera, L. Keller, *J. Evol. Biol.* **7**, 403 (1994); S. Aron, E. L. Vargo, L. Passera, *Anim. Behav.* **49**, 749 (1995).