

Evolutionary biology

Sex ratios in wasps and aphids

from Robert M. May and Jon Seger

DARWIN seems to have framed most of the major problems in evolutionary ecology, and to have showed, at least in outline, how they might be solved. But he failed to crack the problem of the sex ratio. "In no case . . . would an inherited tendency to produce the sexes in equal numbers or to produce one sex in excess, be a direct advantage or disadvantage to certain individuals more than to others; . . . I formerly thought that when a tendency to produce the two sexes in equal numbers was advantageous to the species, it would follow from natural selection, but I now see that the whole problem is so intricate that it is safer to leave its solution for the future." The future began in 1930 with R.A. Fisher; that it continues is shown by papers in *Science*² and this issue of *Nature*³.

Fisher pointed out that if we count grandchildren (rather than children), then it follows at once that there is an advan-

tage to producing the minority sex, whose members enjoy greater reproductive success, on average, than do members of the majority sex⁴. Thus males and females will be produced in equal numbers at the evolutionary equilibrium. If the cost of producing a male offspring differs from that of producing a female, then we need to state Fisher's result in its more general form, which says that at the equilibrium there is equal total investment in the two sexes. Darwin might easily have discovered this principle some 60 years before Fisher, had he thought to look ahead two generations instead of one when evaluating an individual's reproductive success.

Fisher's result assumes that there is population-wide competition for mates. In 1967, Hamilton⁵ showed that the ratio to investment may be dramatically female-biased under certain kinds of mating systems in which, owing to the physical

isolation of sibships, brothers compete to inseminate their sisters. Hamilton marshalled evidence demonstrating large female biases in a number of insects (mainly parasitoid wasps) that are likely to experience intense 'local mate competition' (LMC).

Hamilton's paper stimulated interest in many different kinds of problems concerning sex allocation. LMC itself has developed into a substantial industry, in part because its mathematics are seductively elegant, and in part because it explains patterns that do not have plausible alternative explanations based simply on the mechanics of sex determination. For example, it has often been claimed that the 1:1 sex ratios of mammals and birds are mere side-effects of the X-Y (or Z-W) chromosomal mechanism of sex determination. A recent book by Bull⁶ stands this reasoning on its head, by considering the evolution of a wide range of sex-determination mechanisms, taking into account their effects on the sex ratio.

Wasps have no sex chromosomes, being haplodiploid, so they can play

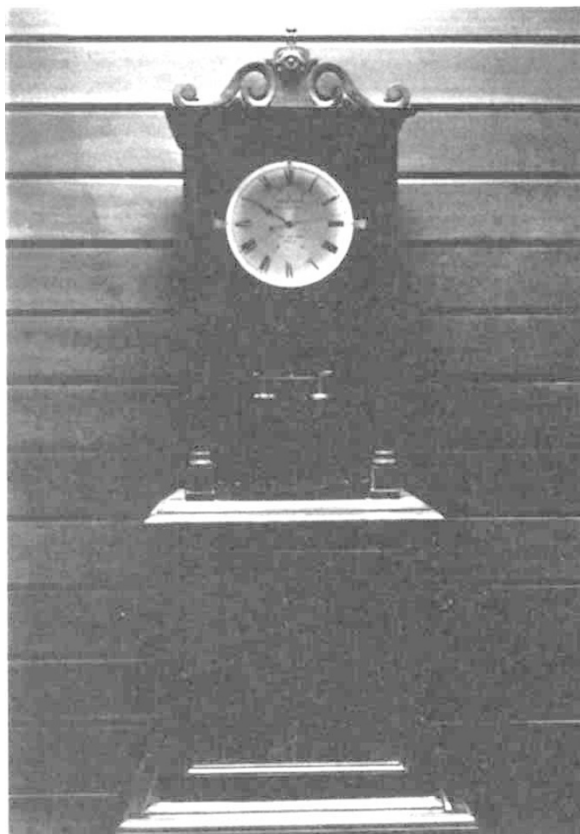
sophisticated sex-ratio games' involving extreme biases and, more interestingly, conditional responses to local variation in the environment or in the structure of the population. Theorists have explored the strategic possibilities at some length, and experimentalists have tested many of the resulting predictions using laboratory populations of the wasp *Nasonia vitripennis*, which has become the *Drosophila* of sex-ratio research. In no other field of evolutionary biology has it been possible to verify so many detailed quantitative predictions. Recent books by Charnov⁷ and by Trivers⁸ review the work on LMC and on many topics in the theory and practice of sex allocation.

Some of the most exciting recent advances have come not from the laboratory, but from the field. For several years there has been uncertainty as to whether the female-biased sex ratios seen under LMC are responses only to the competition for matings that occurs within groups of brothers, or whether they are also responses to the inbreeding with which such competition is almost always confounded. By comparing three species of fig wasps, Herre has recently shown that the biases reflect both the level of sib-competition and the average level of inbreeding⁹. Theoretical predictions, some derived for the first time by Herre, call for the more highly inbred species to show stronger female biases for any given number of foundresses in an individual fig (that is, for a given intensity of LMC). This is exactly what Herre sees in the three species. Not only are their sex ratios ranked in the expected order, but the actual data fall remarkably close to the theoretical curves relating sex ratio to foundress number. Herre's test of the subtle distinction between inbreeding and LMC was made possible by the existence both of variation within species in the number of foundresses per fig (supplying variation in LMC) and of variation between species in the average number of foundresses per fig (supplying variation in inbreeding levels).

A paper by Yamaguchi¹⁰ on page 460 of this issue also combines advanced theory and field data novel in at least two important respects. First, they add aphids to the list of major animal groups in which LMC appears to cause large sex-ratio biases. This is exciting news, in part because aphids have diploid genetics and chromosomal sex determination. How, then, do they control their sex ratios? The generation of aphids that infest plants throughout the summer are parthenogenic clones of XX females. But at the end of the summer, the last parthenogenic generation produces sexual females (who are XX) and males (who are XO). The male embryos are created by elimination of one X chromosome during a modified mitosis.

A second and strikingly novel pattern seen in Yamaguchi's data concerns sex-ratio differences among females who produce the sexual generation. These found-

Long-running experiments (II)



Although it has sometimes been stopped by mechanical failure, by the need for cleaning or when the ambient temperature has not fluctuated sufficiently, in principle this atmospheric clock has not needed winding since it was built in 1864. Now in the Physics Department of the University of Otago in Dunedin, New Zealand, its mechanism is driven by fluctuations in ambient temperature which expand and contract the air in an air-tight box. It is described in *European Journal of Physics* 5, 195-197; 1984, with a request for other examples of such experiments.