

of dispersing daughters than do groups founded, by chance, by a lower proportion of hamiltonian females. Even though each hamiltonian female loses out locally to each fisherian female within every mixed group, the differences among groups in the production of dispersers favour the hamiltonian trait. The among-group advantage of female-biased progenies exceeds the disadvantage of this trait to individuals within groups, and the trait increases in frequency in the global population¹. The optimal female bias is more extreme when groups are smaller not because LMC is stronger (though it is), nor because inbreeding is greater (though it is) in smaller groups, but because smaller groups vary more in initial composition, and thus in the number of dispersers they export^{1,3,5}.

In the conditions of the models, it is impossible for female bias to evolve without the differential productivity of groups. This fact can be demonstrated by eliminating differential productivity, either by imposing a within-group carrying capacity⁵ or by suppressing variation in group composition, as argued above. By any reasonable definition, differential productivity of groups is the driving force of group selection—it is to groups what classical fitness is to individuals. I agree with Charlesworth and Toro that the critical role of group selection in the evolution of female-biased sex ratios is more apparent when groups are isolated from one another for more than a single generation of within-group mating. (In fact, D. S. Wilson and I⁵ produced such a model before I developed the one-generation model that is the focus of the present controversy¹, and Bulmer and Taylor⁶ independently derived a related multigeneration model.) But the selective forces acting in every generation of local mating—including the first—are identical, so there is no logical justification for drawing the line between one and two generations. Charlesworth and Toro also point out (apparently as a criticism) that the same evolutionary process¹ would operate when 'groups' have poorly defined boundaries. No doubt it does. The discrete 'group' of group selection is a conceptual

and mathematical convenience that should disturb no one used to dealing with theories of 'demes', 'populations', or 'communities'. I am persuaded that group selection should be defined not by the characteristics of groups, but by the characteristics of the process^{5,7-9}.

Borgia's belief (following Maynard Smith⁴) that inbreeding (sib mating) itself selects for female-biased sex ratios is mistaken, in the conditions of all published models¹⁻⁷. The argument is the same as for LMC: hamiltonian females indeed reduce the probability of redundant sib matings among their progeny, but nonetheless lose out to fisherian females in every mixed group. Inbreeding is greater in a group-structured deme than in a panmictic deme, but this is only an incidental fact, as far as sex ratios are concerned. I made no claim that "group selection is the only mechanism" for the evolution of female-biased sex ratios (Borgia), only that group selection is required in the conditions of existing models. For obligate sib mating ($n = 1$), or for some of the mechanisms discussed by Wildish, group selection is clearly not required. Borgia complains that I have neglected cases in which the size of 'spatial groups' is greater than the size of 'reproductive groups'. If sib mating is not obligate, but is commoner than expected for random mating, given n , then the effective group size n' satisfies $1 < n' < n$, and the evolutionarily stable proportion males is correspondingly lower. (Variable mating success among males has the same effect⁵.) There is no published model for the case, suggested by Borgia, of partially obligate sib mating, although I have derived one (unpublished). In it there are three selective forces at work: individual selection favouring female bias, based on forced sib mating (selection against LMC); individual selection against female bias among random-mating progeny (Fisher's principle); and selection between groups for productivity, favouring female bias. The magnitude of each force and the resultant balance depend on the biology of the organism. Only the group selection term, however, depends on group size (n). Therefore any data showing a positive correlation between number of founders and proportion males⁵ are evidence for group selection, whatever the proportion of obligate sib matings (assuming differential mortality is uncorrelated with group size).

Wildish adds interesting detail to the complex biology of female-biased populations, but I disagree with some of his interpretations. For the purpose of generality, the model I presented¹ relied on no particular mode of inheritance: it was explicitly based on the fitness of phenotypes, not genes or genotypes. The mode of transmission of the sex-ratio trait is unspecified because it is essentially irrelevant to the phenomenon the model demonstrates, contrary to Wildish's inter-

pretation. I would also dispute the notion that any gene affecting progeny sex ratio (more generally, investment ratio) could possibly be "selectively neutral" (Wildish), except in a very large, panmictic population with a stable, unbiased sex ratio¹⁰. For example, in the case of a panmictic population with a sex ratio biased by linkage of a 'sex-ratio' gene with a 'survival' gene, a mutant that retains the latter while producing an unbiased (fisherian) sex ratio among its progeny will have a great selective advantage.

ROBERT K. COLWELL

Department of Zoology,
University of California,
Berkeley, California 94720, USA

1. Colwell, R. K. *Nature* **290**, 401-404 (1981).
2. Hamilton, W. D. *Science* **156**, 477-488 (1967).
3. Hamilton, W. D. in *Sexual Selection and Reproductive Competition in Insects* (eds Blum, M. S. & Blum, N. A.) 167-221 (Academic, New York, 1979).
4. Maynard Smith, J. *The Evolution of Sex* (Cambridge University Press, 1978).
5. Wilson, D. S. & Colwell, R. K. *Evolution* **35**, 882-897 (1981).
6. Bulmer, M. G. & Taylor, P. D. *J. theor. Biol.* **86**, 83-89 (1980).
7. Charnov, E. L. *The Theory of Sex Allocation* (Princeton University Press, in the press).
8. Price, G. A. *Ann. hum. Genet.* **35**, 485-490 (1972).
9. Wade, M. J. *Science* **210**, 665-667 (1980).
10. Shaw, R. F. & Mohler, J. D. *Am. Nat.* **87**, 337-342 (1953).

Errata

In the letter 'Male and Female DNAs can be discriminated using retroviral probes' by S. J. Phillips *et al.*, *Nature* **297**, 241-243 (1982), the name of the fourth author is incorrectly spelt and should read 'Eva M. Eicher'. On page 242 the ninth line of text should read 'The number of virus-related sequences in male DNA'.

In *Nature* of 10-16 June 1982, credit should have been given to Mr Gene Moore who took the photograph used on the cover. The cover is also used on the reprints of the review article 'Radar research on thunderstorms and lightning' by W. D. Rust & R. J. Doviak, *Nature* **297**, 461-468 (1982).

Corrigendum

In the letter 'Electrophysiology of mammalian thalamic neurones *in vitro*' by R. Llinas & H. Jahnsen, *Nature* **297**, 406-408 (1982), line 4 in the right-hand column on page 407 should read 'suggesting the presence of early K conductance⁷', not Na conductance.

Matters Arising

Matters Arising is meant as a vehicle for comment and discussion about papers that appear in *Nature*. The originator of a Matters Arising contribution should initially send his manuscript to the author of the original paper and both parties should, wherever possible, agree on what is to be submitted. Neither contribution nor reply (if one is necessary) should be longer than 500 words and the briefest of replies, to the effect that a point is taken, should be considered.