

Hawk is the better strategy when the opponent is Bully and Bully is better when the opponent is Hawk. Thus we have a system of frequency-dependent selection, leading to a stable mixture of Hawk and Bully. At this equilibrium, Hawk and Bully will have equal fitness on average and will therefore have frequencies: Hawk 0.575652; Bully 0.424348. In nearly all conflicts, the opponent will be Hawk or Bully, with frequencies just given, so that average pay-offs will be: Mouse 19.5000; Hawk 20.4311; Bully 20.4311; Retaliator 11.3932; Prober-Retaliator 13.6357.

Therefore, types other than Hawk and Bully are at a disadvantage and will not spread. These results will not be affected by the presence of a few individuals adopting strategy Mouse for non-genetic reasons, since Hawk and Bully are the best (equally good) strategies when the opponent is Mouse.

If, for simplicity, we regard the five strategies as reproducing asexually with fitnesses given by average weighted pay-offs, we find that the Hawk-Bully equilibrium is attained from some starting points, for example, with strategies given in the order above, (0.33, 0.33, 0.33, 0.005, 0.005) or (0.9, 0.025, 0.025, 0.025, 0.025). On the other hand, starting with all strategies of equal frequency, the ultimate population consist entirely of Retaliator. These results suggest strongly that some modification of the original model is required to explain the general occurrence of conventional strategies.

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¹ Maynard-Smith, J., and Price, G. R., *Nature*, 246, 15 (1973).

PROFESSOR MAYNARD-SMITH REPLIES—I am afraid that Gale and Eaves are quite right. They have found an alternative evolutionary stable strategy to the conflict which the late Dr Price and I investigated.

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Anti-Darwinism among the molecular biologists

OHATA¹ asserted that evolutionary change at the macromolecular level was caused primarily by "mutation pressure" rather than Darwinian selection. This view, upheld by an influential school of biochemists and molecular biologists (most of them named in Ohta's bibliography), strikes some of us as regressive and potentially dangerous to our science.

One major danger is that it will dissuade biochemists from looking for functional significances in sequence differences (for example those of cytochrome *c* from different species). There is also a more general danger, that of encouraging ahistorical, statistical and mathematical thinking at the expense of the search for causal and historical explanations of the particularities of organisms.

It was a Scottish philosopher of science who wrote that "Only in the last resource, when the heavenly powers fail us, should resort be had to the demons of the underworld, chance and probability"². In the case of macromolecular evolution, it does not seem to me that Ohta and those who think like him in any way have demonstrated the failure of the "heavenly powers" of Darwinian selection. Earlier, Kimura and Ohta³ had coined the phrase "naive pan-selectionism" for the ideas of those who disagreed with them, and this phrase was taken up by Wills⁴ in a paper, not cited in Ohta's bibliography, which criticised in some detail the arguments of Kimura and Ohta, and showed that the evidence was quite consistent with a selective origin for most, if not quite all, the protein differences met with in nature.

The major argument cited by the followers of Ohta and Kimura in favour of their attitude has been the alleged time-proportionality in the numbers of residues differing between species, for cytochrome *c* and other proteins. Reasons have been put forward, such as the "Red Queen hypothesis" of van Valen¹³, why a loose proportionality of this sort might be expected on the basis of ordinary selectionist theory. Ohta, however, treats it as an established fact that there exists a "proportionality far too accurate to be explained in this way. It needs to be pointed out that, in the graphs published to illustrate this proportionality, by Dickerson⁵ for cytochrome *c*, for example, and by Wilson *et al.*⁶ for haemoglobins, the apparent linearity of the relationships depends on the assignment of some very questionable ancestral ages for the taxa concerned. Thus Dickerson gives a mid-Cretaceous age (around 100 Myr) for the ancestries of the main orders of placental mammals, whereas fossil evidence⁷ would place this in the very late Cretaceous or early Palaeocene, perhaps 75 Myr ago. For a common ancestry of mammals and reptiles, that is an ancestral amniote, Dickerson cites a Lower Carboniferous (around 320 Myr) age, whereas fossil evidence⁷ would suggest an early Permian age of perhaps 270 Myr. For a common ancestor of Amphibia and Amniota, Dickerson's graph assigns a late Devonian age of some 350 Myr, whereas fossil evidence⁷ would rather suggest the mid-Carboniferous, some 300 Myr ago. Finally, the age given by Dickerson for a common ancestor of insects and vertebrates is late Pre-

Cambrian, perhaps 600 Myr old. This would be about the age of the celebrated Ediacara fauna of Australia, described by Glaessner⁸ in which quite advanced annelid and possible primitive types of arthropods are represented; undoubtedly, any common ancestry of the deuterostomian line (including Vertebrata) and the molluscan-annelid one from which the insects sprang must have been very considerably older, perhaps more than 700 Myr old.

The similar graph for the haemoglobins given by Wilson *et al.*⁶ assigns some even more questionable ancestral dates—for example, original separation of the cyclostome (lamprey) line from that of Gnathostomata, is placed in the Proterozoic, some 800 Myr ago, probably nearly as old as the entire metazoan line!

A further assumption of Ohta is that protein polymorphism in natural populations is non-adaptive and a result of mutation pressure. Where such polymorphism has been studied in detail for particular proteins, as pointed out by Johnson¹², the phenomena have been found to parallel closely those of polymorphism in ordinary phenotypic characters, selective control of which has been demonstrated, as pointed out by Ford¹¹ in another important and relevant work not mentioned in Ohta's bibliography. Selander and Kaufman⁹, also not cited, draw attention to a book by Levins¹⁰ in which the theory is developed of the long term adaptive advantages of maintaining certain critical degrees (varying with the characters and the circumstances) of heterozygosity of natural populations.

Ohta's evident pride in the mathematical sophistication of his methods of analysis prompts a scriptural gloss on his phrase "naive pan-selectionism": namely, that by adopting what he would consider as the naivety of "little children", the molecular biologists might improve their chances of entering into that "kingdom of heaven" in which the historic truths of evolution are revealed.

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¹ Ohta, T., *Nature*, 252, 351-354 (1974).

² Ritchie, A. D., *Studies in the History and Methods of Science* (Edinburgh University Press, 1958).

³ Kimura, M., and Ohta, T., *Nature*, 229, 467-469 (1971).

⁴ Wills, C., *Am. Nat.*, 107, 23-34 (1973).

⁵ Dickerson, R. E., *Scient. Am.*, 226, 58-75 (1972).

⁶ Wilson, E. O., and Eisner, T., *Life on Earth* (Sinclair Associates Inc., Stamford, 1973).

⁷ Harland, W. B., *et al.*, *The Fossil Record*. Geological Society, London, 1967.

⁸ Glaessner, M. F., *Rec. S. Aust. Mus.*, 13, 369-401 (1959).

⁹ Selander, R. K., and Kaufman, D. W., *Proc. natn. Acad. Sci. U.S.A.*, 70, 1875-77 (1973).

¹⁰ Levins, R., *Evolution in Changing Environments* (Princeton University Press, New Jersey, 1968).

¹¹ Ford, E. B., *Ecological Genetics*, third ed. (Chapman and Hall, London, 1971).

¹² Johnson, G. B., *Nature*, 242, 193 (1973).

¹³ van Valen, L., *J. molec. Evol.*, 3, 89-101 (1973).