Book Reviews

Evolution through group selection. V. C. Wynne-Edwards. Blackwell Scientific Publications, Oxford. 1986. Pp. x + 386. Price £29.50 HB, £14.95 PB.

A quarter of a century ago, Professor Wynne-Edwards initiated one of the most lively debates in evolutionary biology, with the publication of his *Animal dispersion in relation to social behaviour*. The argument of this book is well-known: much social behaviour serves an “epideictic” function, informing individuals of population density so that they can adjust their reproductive effort to a level that will not overtax their resources. This explicit avowal of group selection focussed attention on what had been until then a pervasive but ill-defined tendency to be satisfied with explanations involving an advantage to the population or the species. In doing so, it also focussed opposition, led by G. C. Williams in his essay on *Adaptation and natural selection*. The opposition has had the best of the argument so far, and I would guess that the majority of the current generation of evolutionary biologists have been brought up to regard group selection much as a Baptist regards incense. In the past few years, however, there have been signs of turbulence, with R. Dawkins insisting that even the individual represents too high a level of organisation to constitute a unit of selection, while D. S. Wilson claims to have developed a rigorous and precise mathematical theory of group selection with abundant and precise empirical support. It is at this interesting juncture that Wynne-Edwards has weighed in with a second damned thick, square book, whose title—*Evolution through group selection*—sufficiently explains its scope and intent. What has changed since 1962 to justify writing (and reading) another 400 pages on the same topic?

One thing that has not changed is Wynne-Edwards' views on the nature of social behaviour and the scope of group selection. If anything, they have hardened:

“Aphids normally limit the damage they inflict to levels their food plants can sustain” (p. 33).

“If the success rate of the larval stages [of trematodes] is sufficiently high, it appears likely that a signal does get through to the adult population ... its message may be that egg production should be reduced or stopped altogether in order to ease up on the hard-pressed hosts” (p. 44).

“[Animals which] live and feed gregariously ... avoid encroaching on each other's feeding space, to the mutual benefit of all” (p. 139).

This is, then, no half-hearted half-withdrawal of the author's previous views, but a full-blooded defence and extension of them. Its justification is that he has now discovered the “very simple” basic mechanism underly-

ing the effective group selection of self-regulated populations. This mechanism is outlined on p. 10:

“... individuals in species that regulate their food consumption do not make any personal sacrifices at all. On the contrary they find themselves born into a world of plenty. The fitnesses they enjoy are far higher than those attainable by a population of independent non-cooperators, exploiting similar habitats for personal gain without regard to the consequences. These self-seekers would live in a ravaged world by comparison; whereas social programs are good for all qualified individuals, since the group benefits they bring stem largely from the increased fitness of the members.”

This paragraph invites close scrutiny, since it is explicitly presented as the rationale for the book, and the basis of Wynne-Edwards' defence of group selection. I think that many people will find it less than convincing. There is little doubt that, if self-regulating populations were to evolve, their “qualified” members would have a greater absolute fitness than the members of a comparable selfish population living at the limits of subsistence. In the same way, as Wynne-Edwards points out, fishermen in a regulated fishery will secure a greater harvest than would be obtained in a free-for-all. But this scarcely seems to answer the basic objection to group selection: what if an individual were to ignore the social conventions in order to realise the greatest possible personal gain? Since its *relative* fitness would exceed that of individuals who limited their reproduction for the common good, the genes responsible for selfish behaviour will spread through the population. That their descendants would live in a ravaged world is no doubt the unacceptable face of Darwinism, but it is not clear how, in the natural economy, it can be avoided.

This does not, of course, exhaust what Wynne-Edwards has to say. In a long and closely-written book an abundance of material is advanced as support for his point of view. Some of this (such as the results of the grouse work, or the discussion of regulation in different trophic “industries”) is obviously original and interesting stuff which everyone will read with enjoyment, though opinion will continue to be divided about some of the interpretations. I was particularly struck by the paragraph on pp. 140–141, which until its final two sentences reads like a particularly clear introduction to a game-theoretic account of ritualised combat, only then to veer off in completely the opposite direction, towards an interpretation in terms of the good of the species. Indeed, one of the major weaknesses of the book is its consistent failure to compare its controversial interpretations of social behaviour with those given by the individualist, or genic, theories proposed by Williams,

Hamilton, Maynard Smith and others. In other places, these interpretations are pushed to an extreme which might cause many biologists to reject the rest of the book unread. In particular, I would prefer that the Gaia hypothesis be restricted to its natural habitat of station bookstalls, rather than polluting works of serious scholarship.

For readers of *Heredity*, the most interesting parts of the book will be those which refer to the two most notable recent sources of support for group selection: D. S. Wilson's theoretical work, and the experiments of M. J. Wade.

The crux of Wade's experiments is that selection between subgroups set up randomly from an initially heterogeneous stock can result in the evolution of a lower rate of increase. Wynne-Edwards argues that these experiments demonstrate group selection, and therefore support his interpretation of social behaviour. But these are really two separate claims, and while I agree with the first I can still deny the second. Wade's experiments are correctly designed and analysed, and in this sense they supply a *vera causa* for group selection comparable to that which Darwin argued was provided by artificial selection between individuals for his theory of natural selection. But (unlike Darwin's case) their relevance to evolution in natural populations seems highly questionable. Suppose that we begin by crossing a number of inbred lines to create a base population in which there is substantial genetic variance for the rate of increase. We can then proceed to lower the rate of increase of groups by applying downward group selection. But equally, we can reduce the mean rate of increase of individuals by applying downward individual selection. After all, there is no difficulty in selecting for characters whose effect in natural populations would be to reduce fitness. The result is called agriculture. But this will not persuade most people that natural selection often acts so as to reduce rates of increase. What Wade's experiments show is that artificial group selection can be made stronger than countervailing individual selection; it is an ingenious demonstration, but it is also not a proposition that anyone would vehemently deny. What they do not show is that group selection favouring lower rates of increase will ever be stronger than the opposing individual selection pressure under natural conditions.

The other recent development that might cause some to reconsider their opposition to group selection is the simple and elegant "trait group" model of D. S. Wilson, and, just as important, the demonstration by R. K. Colwell that the model correctly predicts the sex-ratio of populations with a trait-group structure as the outcome of a tension between individual and group selection. Since the same predictions were originally made by W. D. Hamilton on the basis of what seemed to be an impeccably individualist argument, Colwell's results have created some controversy. Since Wilson and Colwell's models represent the main theoretical novelty in any reconsideration of Wynne-Edwards' position, they are worth looking at closely.

The basic argument derives the fitness of a rare variant producing a fraction a of sons in a mating group

of N other individuals who each produce a fraction $\bar{a}$ of sons as:

$$w = (1 - a) + a \left[\frac{(1 - a) + N(1 - \bar{a})}{a + N\bar{a}} \right].$$

The Evolutionarily Stable State is usually obtained by maximising w to yield $a^* = \frac{1}{2} [N/(N+1)]$, the Hamiltonian allocation to sons, as the optimal strategy. But we may object that what should be maximized is not absolute but relative fitness. Since the mean fitness in the group is,

$$\bar{w} = \frac{2N(1 - \bar{a}) + 2(1 - a)}{(N+1)}$$

we obtain $a^* = \frac{1}{2}$ by maximizing $w/\bar{w}$. This Fisherian allocation of $\frac{1}{2}$ can be shown to be stable in groups of any size, however small. What Wilson and Colwell claim is that the Hamiltonian allocation arises from the conflict between individual reproductive success within groups, favouring a sex-ratio of $\frac{1}{2}$, and group selection based on the differential productivity of groups, favouring a sex-ratio of zero (or, more realistically, the smallest fraction of males which ensures that all females are fertilised). If there are M groups, and a fraction g of zygotes remains within the natal group, the remainder $1 - g$ dispersing at random, then the ESS is

$$a^* = \frac{1}{2} [1/(1 + X)],$$

$$\text{where } X = (1/N)[(1 - g)M/(1 + gM)(M + 1)].$$

If $g = 1$ then group selection is precluded and selection is Fisherian, with $a^* = \frac{1}{2}$. On the other hand, if $g = 0$ then group selection is given its widest scope and $a^* = \frac{1}{2} [N/(N + y)]$ where $y = M/(M + 1)$ is of order unity, and for large M the outcome of selection is nearly Hamiltonian. The role of group selection in this process is quite clear: the optimal sex-ratio becomes steadily more female-biased as differential group productivity becomes more important, with increase in M and decrease in g . It is easy to show that precisely analogous results hold for a continuously-distributed population in which individuals mate only with neighbours, forming a completely overlapping series of "trait-groups". But this does not in the least contradict Wynne-Edwards' views of social behaviour, in which grouse, for instance, form just such a continuously overlapping population. Since, then, we have a theory which is mathematically and genetically sound, and which correctly predicts observed patterns of sex allocation, are we not compelled to admit the force of Wynne-Edwards' argument?

I remain unconvinced, for two reasons. The first is that the process of group selection in Wilson's models rests exclusively on the greater success of groups which produce more progeny. This scarcely seems to support the crucial Wynne-Edwardsian contention of greater success for groups which produce fewer progeny. The second is that Wynne-Edwards is quite explicit in stating that his mechanism of group selection will work only if groups occupy the same site for long periods of time.

But this is precisely the situation in the sex-ratio model—with g approaching unity—which is associated with the greatest scope for individual selection, and the evolution of a Fisherian sex ratio. Wilson and Colwell's claim to have demonstrated a form of group selection seems perfectly reasonable, but it is very different from the form of group selection advocated by Wynne-Edwards.

I doubt that anyone could defend the Panglossian hypothesis of adaptive density-regulation with more erudition or skill than Professor Wynne-Edwards, and I am sure that his book will be widely read and enjoyed for its many merits. Nevertheless, I finished it with a sense of disappointment that the new mechanism of group selection on which his thesis centres seems as vulnerable as ever to the standard criticisms, while the new developments that he describes do not, it seems to me, rescue his theory. Whether it will reopen the great group selection controversy remains to be seen; but I suspect that it will mark the end of an old controversy rather than the start of a new one.

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Molecular evolutionary genetics. Ross J. MacIntyre (ed). Plenum Press, New York. 1985. Pp. xxi + 610. Price \$79.50 US.

At last the book we've (all?) been waiting for. The first comprehensive account of the data and implications of the new molecular evolutionary genetics. There have been several attempts to bring molecular biologists and population geneticists within the covers of a single book but they generally reveal a lack of patience by the latter to come to grips with the bewildering complexity of the data of the former, before prematurely crunching some morsels of them through the great theory machine in the sky. Selfishly accumulating DNA and mobile elements (although a genomic rarity) seem to be the few events that have stirred our generals' equilibria. The editor Ross MacIntyre has kept the mathematicians out of it and commissioned some of the leading front-line troopers to review the scene in all its glory. They have done this magnificently. These are some of the best constructed, and thought-provoking reviews I have read, and are destined to have long shelf-life even in this rapidly advancing field.

Evolution by means of natural selection has always been an easy process to understand. Even Richard Dawkins gets the order of events right by the time of his third book. There is random mutation, meiosis and sex. Together they ensure, barring accidents, that there is no long-term change in the genetic composition of a population. Wheel on selection (the constant need to survive in a hostile world) and there we have it. Plug in the numbers and behold the organisms in all their harmonious beauty flickering on the computer screens of our armchair selection fundamentalists—in MacIntyre's

words, "an unpleasantly austere neo-Darwinian view of evolution". The new molecular genetics has made children of us all again "in an enchanted forest, wandering aimlessly from discovery to discovery. For the moment let us be thankful that the pleasures of the forest are so numerous and diverse".

Wen-Hsiung Li and colleagues kick off with 84 pages (almost a monograph in itself) on the evolution of DNA sequences: a compilation of information, thoroughly analysed by their own new and realistic methods, to provide the database on which all discussion of rates, clocks, codon usage, pseudogenes, duplications can be based. In this chapter we begin to see the hard neutralist and selectionist lines breaking down: a job completed by George Miklos, Carl Schmidt and James Shen, Raoul Benveniste and Susan Gerbi in later sections. There are no cosmic DNA clocks ticking at a universal rate; not unless we grossly distort the known times of separation between many species. Li and friends show this conclusively. Hominoids are slowing down and rodents are speeding up for reasons nobody is sure about. It might be due to differences in numbers of germ-line mitoses, DNA repair rates, or the rates and biases of a variety of DNA turnover mechanisms which seriously confine the idea that DNA is passively picking up mutations and drifting through time to a premolecular age.

This latter point is supported by Li, Luo and Wu's account of concerted evolution and the variety of internal mechanisms responsible for it. Miklos and Gerbi do a better job of describing and dissecting this widespread phenomenon but the first chapter points us in the right direction. I have the feeling that at the time of writing the authors had not completely absorbed the data and potential significance of this phenomenon. There's no need, for example, to set up some gladiatorial contest between gene conversion and unequal crossing over as responsible for the homogeneity patterns, given that we know that both processes (in addition to transposition and slippage) often operate simultaneously within a given family. This is a fact of genomic life which makes it highly unlikely that I personally can be described as having said that conversion is more important than unequal crossing over. More serious problems arise with the authors' proposition that large differences in the degree of family homogeneity, for example between rDNA and the immunoglobulin gene family, is linked to their functional requirements. This idea was originally proposed by Gojobori and Nei who miscalculated the supposedly slow rates of gene conversion in the latter family on the false assumption that the unit under comparison is the unit of conversion. As with globins, chorions, MHC and other multigene families, conversion units are often tiny compared to the length of the gene, leading to highly variable mosaic genes. Rates of turnover by gene conversion cannot be calculated from observed levels of variability between arbitrary chosen units of comparison, no matter how logical they might be from a functional point of view. (I've been waiting to say that for a long time.)

The issue of function of the more obvious highly abundant tandem or dispersed families of non-genomic