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BOOK REVIEW

Evolution Through Group Selection

By V C WYNNE-EDWARDS. Blackwell Scientific Publications, London, 1986; pp. xi + 386

This book is not what its title and length might suggest – a comprehensive up-to-date evaluation of group-selection theory in relation to alternative hypotheses. Rather, it is a reassertion of the idea (Wynne-Edwards 1962) that widespread patterns of social, sexual, and dispersal behavior are products of selection at the group level for self-regulation of population size. Most readers of *Journal of Genetics* interested in ecology and social behavior are probably aware that it was Wynne-Edwards' 1962 book, *Animal Dispersion in Relation to Social Behaviour*, that sparked a heated controversy over levels of selection. That controversy led to a revolution in thinking, showing how genic and individual selection can account for the evolution of apparently individually costly traits, such as helping behavior or limited brood size – traits attributed by Wynne–Edwards and many previous authors to selection for the good of the group. It also led to a large literature, partially reviewed in this new book, specifying the circumstances in which group selection might operate; and to the eventual realization on the part of most researchers that selection can occur on many different levels, including the genic, individual, social-group, population, and species levels. However, for many compelling reasons (summarized by Williams 1966, Lewontin 1970, E O Wilson 1975, Trivers 1985, and Wittenberger 1982) selection acting on phenotypes expressed at the individual level is now thought to be the primary (although not exclusive) means for the evolutionary establishment of characters – even those beneficial at a group level. As a result Wynne-Edwards' 1962 book fell into disrepute, and the synthesis it represented is no longer widely appreciated.

This fate was not entirely deserved. Albeit (in retrospect) for the wrong reason, Wynne-Edwards was the first to perceive several widespread patterns of social behavior, all of them associated with limited resources, strong intraspecific competition, and reduced survival or reproduction by some individuals. He was the first to broadly relate intraspecific competition with alternative patterns of behavior and morphology (or "alternative strategies"), and hence social structure. And he saw many common elements in social and sexual competition, including the crucial role of ritualized display in structuring groups by diverting differently endowed individuals into different social and reproductive roles. Furthermore, he achieved an apparent reconciliation of what had seemed a contradiction between the facts of competitive behavior and the long-term persistence of populations. If Wynne-Edwards' 1962 book had been written with individual or genic selection (rather than group selection) as its underlying theme – and this would have been perfectly

compatible with all of the broad patterns he surveyed – it would be viewed to this day as a brilliant achievement, an unprecedented synthesis of the facts of social behavior and population ecology with the theory of natural selection, approaching in scope the works of Darwin himself. It is no wonder that, until its group-selection basis was widely discredited, Wynne-Edwards' book inspired many young biologists with an interest in the general implications of sociality. Robert Trivers (1985, p. 84), describes his generation as retaining a "soft spot in our hearts" for Wynne-Edwards; and Stephen Jay Gould (1982, p. xv) describes him as a victim of "ignorant ridicule," berating evolutionary biologists for "the hooting dismissal of Wynne-Edwards and group selection in any form during the late 1960s and most of the 1970s".

This new (1986) book comes into a changed world. Now, rather than assuming that observed behaviors benefit either individuals or species, biologists have learned to think in terms of the spread of genetic alleles, whose effects act either directly on phenotypes affecting individual survival and reproduction, or, indirectly on the reproduction of individuals (especially relatives) bearing identical alleles. Most, if not all, of the phenomena discussed by Wynne-Edwards (1962) have been reinterpreted in these terms (for examples see Hamilton 1964, Williams 1966, and Wittenberger 1982). In a detailed and careful argument, Williams (1966) concluded that when both a genic- or individual-level interpretation and a group-level one can be applied, the lower (genic or individual) level explanation is preferable. In addition, there is a large volume of literature specifying the conditions in which group selection can conceivably occur and even override individual selection (reviewed in Wade 1978, E O Wilson 1975, and D S Wilson 1980). Does the new book confront this altered world and guide us to a better understanding of evolution by group selection, building on the past twenty years of efforts to understand how the different levels of selection may interact during evolution? No, it does not. It is difficult to praise (or take very seriously) such an extensive reassertion of the 1962 theory which fails to even cite its most important critique, Williams' 1966 book *Adaptation and Natural Selection*! Does the new book cogently discuss the idea of kin selection, now widely used to explain many of the phenomena it treats? No, it does not. In fact, it commits (p. 172) a formerly common and now usually avoided error, defining inclusive fitness to include all of the reproduction of nearby relatives, devalued by their relatedness to the individual concerned (rather than, properly, only the individual's effects on the reproduction of relatives). Numerous field tests of the predictions of kin selection theory applied to "group" adaptations connected with sociality in insects, birds, primates, and other mammals are not mentioned.

Another author might have used kin selection to effect a reconciliation between group selection (*sensu* Wynne-Edwards 1962) and later developments in evolutionary theory. However, this book adopts a different approach. The author begins (preface, p. x) with the confession that in the first book he was "unable to suggest" a process of selection "that would allow the welfare of the group to take precedence over the self-interest of the individual". "Now", he continues, "I have what seems to be a reasonable suggestion to make. The way I have approached it may appear at first sight unnecessarily devious. The reason is that the reality has been difficult to grasp, and I believe one needs to be led along a particular path of experience in order to appreciate it". That "path of experience" was twenty years of research on

the red grouse, and an interesting and useful review of it takes up a large portion of the book. It also included the discovery of D S Wilson's (1975) theoretical work on group selection, which Wynne-Edwards (p. 316) says "was enough to get me started on this book". The crucial new insight is first revealed on page 13, where Wynne-Edwards briefly summarizes the point of this new book: "As originally presented, the (group selection) hypothesis rightly insisted that adaptations for the common good could not evolve through individual selection, pure and simple, but only through selection acting between groups. I was, however, unable to suggest how social cooperators would be able to equal, much less exceed, the fitness of freeloaders. Consequently most evolutionists rejected it, notwithstanding the weight of circumstantial evidence in its favour. The present work sets out to rectify this defect, and establish the explanation . . . that *cooperators, bequeathing productive resources as well as genes to posterity*, have developed an unsurpassed strategy for survival" (italics mine). He then shows how marginally reproductive or non-reproductive members of groups (e.g., the subordinate "outcasts" among the red grouse) give in and die rather than continuing to consume resources, in effect passing the intact resources via successful territorial individuals to a posterity that is composed of the group's own descendents (or a descendent group of relatives). For, red grouse, like many other social animals, are philopatric – they tend to reproduce near where they were born. Put in what are now familiar terms to most biologists in this field (after Hamilton 1964): group-living animals often exhibit population "viscosity" which leads to the formation of groups containing relatives. In such groups, individually costly cooperation can be explained via benefits to the offspring of genetic relatives (kin selection). So, if we take the statements of the preface (cited above) at face value, we are led to the remarkable conclusion that during the same twenty years in which many field biologists were learning to apply and test the ideas of Hamilton, Wynne-Edwards was independently deriving them via studies of red grouse! Almost, but not quite, for incredible as it may seem, this book never mentions the obvious similarity between its own conclusions and those of Hamilton. Instead, it persists in regarding phenomena explainable in terms of individual and kin selection as evidence for group selection, and devotes extensive discussion to models of group selection (e.g. Wade 1980, D S Wilson 1980) whose conditions seem to show a weaker correspondence to the observations of red grouse than does a straightforward kin selection model. The final conclusion regarding kin selection is (p. 332) that it "offers no advantage over individual selection as an explanation for the evolution of the group adaptation connected with sociality", and (p. 335) that its predictions are met "only under group selection conditions" – a conclusion that could as well be reversed to read – "group selection predictions are met only under conditions favorable to kin selection."

There is a semantic issue at stake here which, like most such issues, is not "merely" semantic. The Wade model applied to a family (or extended family) group is a kind of kin-selection model, and the similarities of trait – group selection (D S Wilson 1975a) and kin selection have been discussed by Maynard-Smith (1976). Wade (1980) is among those who have pointed out that kin selection can be considered group selection, if seen as depending on the differential success of different sets (groups, families) of interacting relatives (some authors even refer to "kin-group" selection). This view of kin selection is not wrong, but it does not acknowledge the degree to which kin selection, seen (alternatively) as an indirect

effect of individual phenotypes acting through relatives, may be fine-tuned during evolution: insects and other animals are known to be able to distinguish different degrees of relatedness that can occur *within* family groups (reviewed by Gadagkar 1985) and they may evolve so as to adjust the amount and direction of their cooperative behavior accordingly. In any case, careful discussions by Wade (1980) and others (e.g., Maynard-Smith 1976) regarding the distinctions and similarities between kin selection and group selection are barely alluded to in this book, which as a result may confuse or mislead some readers.

What the new book does, in sum, is to reiterate the old argument regarding group selection, adding recent theoretical and experimental evidence that tends to support it. It does not answer critics or adequately discuss data suggesting that all of the phenomena discussed can be explained by individual and/or kin selection. One obvious reconciliation of the two sets of evidence is to admit that both kinds of selection can occur, and that when a trait is favored at both levels it is likely to be established especially rapidly (e.g., see Wade 1980), or persist especially effectively through time (West-Eberhard 1979). The question is no longer whether one or the other type of selection can occur, but when and to what extent each is important in a given case in nature: "The argument is quantitative, not qualitative" (Maynard-Smith 1976). Research beginning at that point is not advanced by this book, since it never comes to grips with the fact that both individual (or kin) selection and group selection could be operating, simultaneously or sequentially, to produce (and allow the persistence of) observed patterns of social behavior. (For example, a territorial system like that of the red grouse, with environmental feedback regulating territory size so as to promote individual defensive and trophic efficiency, could become established by purely individual selection, then, secondarily, function to protect its population from extinction. This sequence seems reasonable given Wynne-Edwards' data, and Williams' 1966 arguments for the primacy of lower levels of selection.) Wynne-Edwards continues to insist that the group function is not just primary but is the *only* explanation possible. As a result, he fails to seek the reconciliation of group and individual selection which most readers would now require, and misses the chance to salvage the many valuable insights of his 1962 book (see West-Eberhard 1979).

On this and related issues Wynne-Edwards persistently neglects an extensive literature that is unfavorable to his theory. For example, one section (p. 321 ff) that describes interspecific mutualisms and symbioses as "impossible to account for wholly in terms of individual selection" is credible only because it fails to cite widely known attempts to do so (e.g., Williams 1966, Trivers 1971, Axelrod 1984). I resist critically discussing any further such points, when they should have been treated properly in the book itself. As a review of twenty years of research on the social behavior and ecology of red grouse this book can be recommended; as a review of twenty years of thought on levels of selection it is most disappointing. It will not satisfy readers who believe that a scientific argument is acceptable only if it deals

perceptively and thoroughly with previous and contradictory alternative hypotheses.

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