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Group Selection and the Evolution of Myxomatosis

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ABSTRACT: Before it is possible to assess the importance of "group selection" in nature, it is necessary to rigorously define this term. A definition of group selection is derived from a critical analysis of conceptions common in the biological literature. This definition is then used to clarify the debate over the mechanism responsible for the evolution of myxomatosis in Australia.

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I. Introduction

Despite the tremendous success of Darwin's theory of natural selection in explaining biological phenomena, there is still considerable controversy with respect to the basic objects, processes, and patterns of evolution (Brandon and Burian 1984; Kincaid 1986). Many outstanding questions require additional empirical data for their resolution, but other questions concern the best way to *conceptualize* evolutionary processes. This paper addresses one issue with respect to which questions concerning the conceptual articulation of evolutionary theory come to a focus. The issue has a long history and remains at the forefront of evolutionary controversies today. This is the question of the meaning and proper referent of the term *group selection*.

Empirical and conceptual concerns are not, of course, unrelated. The assessment of claims that a given biological phenomenon is a product of "group selection" requires clarification of the precise meaning of this term. As Ernst Mayr has rightly said, "It is simply impossible to evaluate group selection properly until the term is rigorously defined" (Mayr 1988, p. 116). The central aim of this paper is to provide a rigorous definition of 'group selection'. In Section II various definitions of group selection abstracted from the biological and philosophical literature are critically examined. A more satisfactory definition is then proposed and explicated. Section III is devoted to an analysis of a purported case of group selection -- the evolution of myxomatosis in Australia. Using the proposed definition as a guide, I conclude that this should be attributed (at least in part) to group selection, provided that current information about this case is correct.

II. Defining Group Selection: Alternative Models

In order to make clear the characteristics of an adequate definition of group selection, I will introduce a series of definitions (or models) which gradually approximate a satisfactory formulation.[1] This approach is designed to show

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[1] The term "model" is being used here in the sense of: "A tentative ideational structure used as a testing device" (*American Heritage Dictionary*). I realize that some of these models (or definitions) may look like "straw men," erected simply to be demolished. They are not, especially if by the term "straw men" is meant "extreme or simplistic positions which no one holds anyway." The conceptions I discuss abstract the important features from formulations which one (still) constantly encounters in the literature on group selection. References after each definition direct the reader to biologists or philosophers who actually embrace a definition similar to each abstract definition given here.

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precisely where each conception succeeds and fails. This strategy will (hopefully) provide a clear rationale for each of the features of the final definition I will propose.

Consider first the following definition:

Def'n #1: Group selection occurs within a set of groups if and only if there is differential group success among the groups.[2]

Obviously this is too vague. What does "differential group success" mean? There has been an unfortunate tendency in some of the literature on group selection to assume that one group is more successful than another if it <u>grows</u> more rapidly than another.[3] But there are empirical as well as conceptual objections to such a view. First, this conception rests on the twin empirical assumptions that (i) the greater the current population <u>size</u>, the greater is the probability of the population's persistence over time, and (ii) an <u>increase</u> in size represents an accurate indicator of the population's fate in the near future. Both assumptions are questionable. A large and dense population may be subject to greater density-dependent mortality due to increased predation pressure or disease, or any of a number of other forces which can reduce the population's ability to persist. Likewise, a population that is rapidly expanding may be heading for population crash due to over exploitation of its resources. Clearly, increasing size is no <u>guarantee</u> of group success, and may well signify just the opposite.

Second, there is a conceptual problem with this notion of group success. Def'n #1 would license us to say that there is group selection if the number of organisms in group <u>A</u> increases relative to that of group <u>B</u>. But we must always keep in mind when considering group selection that we understand the concept of natural selection (of which group selection is a narrower instance) primarily as it applies to <u>organisms</u>.[4] We then apply this concept to entities on other biological levels.

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[2] This conception is implicit in the view of G.G. Simpson, one of the primary architects of the Modern Synthesis: "If one group is more successful than another under given (the same or similar) conditions of life, it is fair to conclude that it is better adapted. The surest criterion of such success is increase in relative abundance of the better adapted group. Such increase in relative abundance is evidence of selection...." (Simpson 1953, p. 161). This view is followed by Stern (1970) with regard to the concept of population adaptations: "Accepting these views, we may now define the level of adaptation of a population as a relative term comparing two or more populations such that those with the higher rates of increase are better adapted to their environments" (Stern 1970, p. 55). Again, "[W]e ... define an adaptation of a population as any characteristic of that population that causes, on average, a higher rate of increase in size than would occur in its absence" (Stern 1970, p. 57).

[3] For example, one of the most prominent recent defenders of group selection writes that, "In all group-selection models, the term individual selection refers to allele frequency change within single groups, whereas group selection indicates the differential [genetic] contribution of groups to the global population" (Wilson 1983, p. 171). Alternatively, he identifies "the differential productivity of groups" with group selection (Wilson 1983, p. 169). The best way for groups to be more "productive" (of their containing genes) is, of course, to grow in size (numbers). Some biologists have actually used population size, or the instantaneous variation of this size, as a measure of group success. For example, according to Jacquard (1977): "The selection value of a population, during a given period of time, is proportional to the rate of variation of its size during that period" (Jacquard 1977, p. 105; quoted in Wallace 1984, p. 42). Sober's (1984) definition of group selection also allows differential group growth to count as group selection. (See note 14 below.)

[4] There has been a move recently in the philosophy of biology literature to treat as an <u>individual</u> any spatiotemporally distinguishable entity, whether this entity be an organism, a group (as traditionally understood), or a species (Ghiselin 1974;

We would not ordinarily consider it to be a case of organism selection when one organism *grows* in size relative to another.[5] But if differential organismic growth is not sufficient for organism selection, why should differential group growth be sufficient for group selection? Why should there be radically different criteria for what we *mean* by "selection" on different biological levels? No compelling reason has yet been proposed. An adequate definition of group selection must take seriously the fact that our conception of natural selection is most developed at the level of organisms, and seek to apply the insights gained about selection at this level to selection operating on the level of groups, while simultaneously taking into account the important *differences* between entities at the two levels.

A second definition attempts to do just this:

Def'n #2: Group selection occurs within a set of groups if and only if there is differential group persistence and/or multiplication among the groups.[6]

This formulation could be defended as follows: *Organism* selection can occur by at least two different routes. Differential survival/death is one way (mortality selection). Differential reproduction is another (fecundity selection).[7] If group

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Hull 1980; Eldredge 1985). In this paper I will use the term 'individual' interchangeably with the term 'organism', and contrast this with the term 'group'. This should not be taken to imply that 'groups' (in the traditional sense in which this term has been used) cannot be "individuals" in the technical philosophical sense. Indeed, a presupposition of all of the definitions discussed in this paper is that the groups in question are individuals (sensu Hull *et al*).

[5] As Brandon (1986) puts it, the slogan is "survival of the fittest," not "survival of the fattest." If I take up the habit of hanging out in bars and drinking beer, and as a consequence develop a beer gut, we would not say that I am on this account being selected over my more restrained companions, unless such behavior was *also* shown to be effective in prolonging life, securing mates and producing offspring. To the best of my knowledge, such a correlation has never been established ... or even investigated. [Although, for ideas about how such a process *might* come about, see Low *et al*. (1987) and Anderson (1988).] In this regard Wright's account of group selection is preferable: "Selection, with the deme as its unit, takes the form of more rapid growth of population of the better adapted ones and their more extensive dispersion into the territories of the less adapted with consequent grading up, or even replacement of the latter" (Wright 1956, p. 16). Here Wright links population growth with differential *colonization*, a point that will be emphasized shortly. It is still not clear in Wright's formulation, however, whether this is a process distinct from that of individual selection. See Provine (1986) for discussion.

[6] A definition like this one seems to be endorsed by a large number of biologists. For example, Grant (1985) in his recent overview of evolutionary theory writes, "Interdeme selection (also often referred to as group selection) is differential reproduction of different local populations" (p. 141). According to Wade (1977), "Group selection is defined as that process of genetic change brought about or maintained by the differential extinction and/or proliferation of populations" (p. 135). Uyenoyama and Feldman (1980) state that group selection is "the process by which certain demes make a greater genetic contribution to the next generation relative to other demes" (p. 393). Michod (1982) defines group selection as "the changes in gene frequency resulting from the differential extinction or productivity of groups" (p. 45). Beatty (1984, p. 191) lists many other examples. "The danger of this approach," as Nunney (1985, p. 219). points out, "is that if the between-group component of gene-frequency change is used as the criterion for defining group selection, then the division of almost any evolving population into groups will create an illusion of group selection." I agree with Nunney who concludes that, "Any definition of group selection based simply on the differential proliferation of groups [e.g., Wade 1976, 1978; Wilson 1979, 1980] falls into this logical quagmire."

selection is a process analogous to organism selection, then there should be analogues of organism survival and reproduction at the level of groups.[8] This would be differential group persistence and/or multiplication. Differential group persistence can be understood as some groups persisting in existence from time t to time t' while others go extinct in this interval. Differential group multiplication can be understood as the differential founding of entirely new groups, either through colonization, fissioning, or some other means.

Although Def'n #2 captures the crucial idea of differential group persistence and/or multiplication, it is still inadequate. To see clearly the crucial defect in this definition, we need to fix our ideas with regard to organism selection again. Although organism selection involves differential organism survival and/or reproduction, neither of these is sufficient to constitute organism selection. A by-now-famous example, suitably refined, makes this point clearly (Scriven 1959). Suppose that a pair of phenotypically and genetically identical twins are strolling along an unprotected ridge when suddenly a thunderstorm appears. One of the twins is struck dead by a bolt of lightning, while the other escapes with mildly singed hair. Here we have differential organism survival, but it was not due to natural selection. Presumably it was just a chance event that the one twin was struck by lightning but the other was not. It was not an instance of natural selection because the differential survival of the individuals was not due to any fitness differences between them. They were, as stipulated, phenotypically and genetically identical and occupied the same environment.[9] The survival of the one twin, we can suppose, was not due to any special features which he possessed but his less fortunate brother lacked. So differential organismic survival alone is not sufficient to guarantee that natural selection has occurred. Some reference must be made to fitness differences between the individuals.

Likewise in the case of groups. That one group persists while another goes extinct could be due to any number of factors other than natural selection. If a freak accident can terminate the existence of one organism and spare another, then the same could happen to entire groups. The forest fire that sweeps through a valley is not necessarily an agent of natural selection with respect to the flora and fauna in its path. All the organisms and groups may get destroyed, regardless of any differences between them. For natural selection to be the operative factor in the differential survival and/or reproduction of biological entities, differential success must be attributable to fitness differences among the entities.[10]

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[7] For explication of these terms, see Endler (1986). Natural selection should be understood as encompassing both differential survival and reproduction, because these two processes affect the two main phenomena evolutionary biology is concerned with understanding: the present representation of phenotypes in the world (e.g., their diversity, distribution, ecological interactions, etc.) and the changes in the representation of phenotypes in the world over time (e.g., their origin, evolution, adaptation, etc.). Brandon's (1982, 1985, 1988) explication of group selection ignores differential group persistence as a possible mode of group selection, and focuses exclusively on differential group multiplication. It could, however, be easily amended to include differential group persistence.

[8] Here I follow Stanley (1977), Gould and Eldredge (1977), Damuth (1985) and others who have emphasized the need to conceptualize higher-level selection processes in terms analogous to those used to describe selection at the level of organisms.

[9] This assumption is more controversial than it looks. Some of the difficulties are explored in Beatty (1984), and in Shanahan (1989). For a careful analysis of the concept of 'environment', see Brandon (1990).

[10] One might argue (as an anonymous referee did) as follows: "If there are only two populations, and one increases or survives or proliferates colonies more than the other, we have no grounds for saying there is selection; replication of each of two types (randomized over environment) is needed." A distinction needs to be made

Given the necessity of there being fitness differences among groups involved in group selection, the following definition suggests itself:

Def'n #3: Group selection occurs within a set of groups if and only if there is differential group persistence and/or multiplication due to fitness differences among the groups.

This definition seems to remedy the flaws we noted in the previous definitions.[11] Here differential group persistence and/or multiplication depends on there being fitness differences between groups. But despite its improvement over previous definitions, this definition still contains a crucial defect. We can imagine a case in which differential group persistence and/or multiplication is indeed due to fitness differences between groups, yet in which it would be misleading to say that group selection was occurring. The following example represents such as case.[12]

Suppose that we have an ensemble of six groups of organisms. Each group is internally homogenous for height. The first group contains all one foot tall individuals, the second group all two feet tall individuals, and so on up to six feet. Thus all the variation in height is *between* groups. There is no *within*-group variation in height at all. Upon reaching maturity offspring of individuals in each group disperse to form new groups of individuals with the same heights as the parents (i.e., height is heritable). Suppose further that greater height contributes to organismic survival and reproduction, so that because of their

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here between the empirical identification of selection events and the conceptual definition of a unit of selection. For the former empirical issue, we do indeed need replication of the two types randomized over environments (the more the better). But for the conceptual issue we do not, for here we are concerned with the task of clarifying the essential conditions for a selection event of a certain sort to obtain. The main reason for the difference is that for the empirical question the more data we have the better shall be able to identify the properties actually responsible for differential survival and/or reproduction in a particular case. Hence replication of such events is necessary. My view is simply that some of these events are themselves selection events. The reason that we do not need replication of these events for the conceptual issue is that we can construct a *Gedankenexperiment* in which we define certain conditions into the situation. The core of the conceptual issue is not "Is this a case of selection?", but rather "What do we *mean* by [group] selection?" Once this latter question is settled (or a proposal is made), we can compare actual events in nature to the model to see how well the latter illuminates the former. This distinction between conceptual and empirical issues is discussed at greater length in Lloyd (1988, 1989). Thought experiments have much in common with laboratory selection experiments in that they both have access to certain kinds of crucial information, thus bringing the phenomena of interest into the sharpest focus. On this point see Griesemer and Wade (1988). Once the distinction between empirical and conceptual questions is recognized, claims like that made by the anonymous referee can be seen to be important to the implementation, but not to the evaluation, of a definition of group selection.

[11] Cf. Alexander and Borgia (1978): "To the extent that group selection means simply the occurrence of differential extinction (or reproduction) of groups of individuals, no biologist is likely to deny its existence. As Williams [1966, 1975] notes, however, *differential extinction of groups can account for the direction of evolutionary change in a trait only when groups differ in the trait and when this difference accounts for the difference in extinction rate*. We regard this as the criterion of group selection" (p. 450). The point to notice in the present context is that Alexander and Borgia define group selection as the differential extinction of groups due to a trait with respect to which groups differ. This formulation suffers from the same defects as Def'n #4.

[12] This example and the one following are borrowed with only slight modification from Sober (1984).

height advantage the six-footers survive longer and reproduce at a greater rate than individuals of lesser stature. The six-footers thereby produce more offspring at a greater rate, and hence found new colonies more rapidly, than do shorter individuals, some of whom, perhaps the one-footers, do not survive to reproduce at all. This is the scenario we are considering.

In the case just sketched there are fitness differences among groups, and in virtue of such fitness differences there is differential group persistence and multiplication among the groups. This process would, according to Def'n #3, represent an instance of group selection. But there is something highly peculiar about this conclusion, because selection for the _organismic_ property of _being tall_ seems to be the only evolutionary force at work. The differential persistence and multiplication of groups is entirely an _effect_ of selection operating on the properties of organisms. The fact that organisms are found in groups of phenotypically similar individuals is irrelevant to the selection process at work. The mere fact that differential group persistence and/or multiplication is due to fitness differences entirely between groups is insufficient to define group selection as an evolutionary process distinct from that of organism selection.

In defining group selection what we want is to describe a process which acts on groups as such. This suggests that we need to specify some _group property_ in virtue of which some groups do better than others. Suppose that we again assume the initial conditions as in the foregoing example: groups internally homogenous for height, but heterogenous between groups. This time, however, suppose that the _reason_ that the tall groups outmultiply the short groups is _not_ because tall organisms outreproduce short organisms, but rather because organisms in a group with the large _average_ height enjoy survival and reproductive advantages over organisms in a group with a small _average_ height. In other words, organisms enjoy survival and reproductive advantages or suffer survival and reproductive disadvantages because of the properties of the _groups_ to which they belong (in this case, the properties of having a _large average height_ or a _small average height_).[13]

This idea is embodied in the following definition:

Def'n #4: Group selection occurs within a set of groups if and only if there is differential group persistence and/or multiplication due to some group property affecting group fitnesses.[14]

In order for there to be group selection on this definition, there must be differential group persistence and/or multiplication because of the presence of a group-level property among the groups. In the foregoing example this group-level

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[13] "Average height" is used in the examples for ease of exposition. A biologically more realistic group property would be "frequency of altruists in a group." It is on the basis of such a group property that D.S. Wilson (e.g., 1977) argues on behalf of a process he terms "intrademic group selection." If the considerations raised here are cogent, then the process Wilson describes may represent organism, but not group, selection.

[14] This definition captures the essence, if not the particularity, of Sober's (1984) definition. According to Sober, "there is group selection for groups that have some property _P_ if (and only if)

1. Groups vary with respect to whether they have _P_, and
2. There is some common causal influence on those groups that makes it the case that
3. Being in a group that has _P_ is a positive causal factor in the survival and reproduction of "organisms" (Sober 1984, p. 280).

Note that on this definition a group property contributes to the survival and reproduction of _organisms_. I do _not_ want to deny that such processes are important, but I do want to deny that such processes should be called "group selection". I would claim that Sober's model, as well as the "Type I" model of Mayo and Gilinsky (1987) and the "Multilevel [1]" model of Damuth and Heisler (1988) represent at best a process of "group-mediated organism selection."

property was the average height of organisms in a group. It was this property which accounted for the differential survival and reproduction of organisms, and consequently for the differential group multiplication. The greater the value of this group property (within limits set by the environment), the greater the group fitness and hence multiplication.

The role of the group property "average height" in the foregoing example needs to be analyzed more carefully. In what sense is it responsible for differential group multiplication? And if it is responsible, does this entail that group selection is operative? I take it that "average height" is a genuine group property. An individual organism has a height, and perhaps has an average height over the course of its individual lifetime, but it does not have an average height at an instant in time. Groups, however, do. The critical issue here is not whether "average height (or some suitable substitute) is or is not a group property. The critical issue is how (i.e., in what capacity) this property functions in the selection process described, and whether this function represents a process of group selection.

If we reconsider the last example, we see that the group-level property of "average height" functions in the selection process as part of the environment of individual organisms. Organisms which find themselves in groups with a greater average height enjoy greater fitness benefits than those organisms which find themselves in groups with a lesser average height.[15] The fact that a part of their environment is itself capable of multiplying is an interesting but strictly irrelevant observation. As our earlier discussions show, the question of group selection concerns the cause(s) of differential group persistence and/or multiplication, not merely an effect of a certain sort. For selection to operate at the level of groups, groups need to be considered in relation to their selective environments. Requiring group properties is not sufficient.

As these considerations suggest, the main problem is that of defining group selection as a distinct causal process operating at the level of groups per se. Consequently, the central thesis in the definition I want to defend is that selection operates on the level of groups only if groups differentially interact with some part of their environments in virtue of some group-level property with respect to which the groups differ. This suggests a necessary (but not sufficient) condition for selection to operate at the group level. When combined with the considerations raised in criticism of earlier definitions, it provides the basis for the following definition which is intended to capture necessary and sufficient conditions for group selection to occur.

(GS): Group selection occurs if and only if:
(1) a group, G, possesses some group-level property, P (where P determines some component of G's fitness);
(2) G differs from at least one other G-level entity with respect to P in a shared selective environment, E;
(3) G interacts with E in virtue of (or "through") P in such a way that P causally contributes to the differential persistence and/or multiplication of G relative to these other G-level entities.[16]

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[15] The same kind of point can be and has been made with regard to Dawkins' genic selectionism. In a sense I am doing exactly what Dawkins (1976, 1982) is accused of doing, i.e., treating various x-level (here gene-level) entities as part of the environment of a given focal x-level entity. This kind of approach has been criticized by Sober and Lewontin (1982) and by Sober (1987). However, I agree with Maynard Smith (1987) and Sterelny and Kitcher (1988) that there is nothing unjustified in this procedure. In fact it is required in a consistent application of Dawkins' viewpoint.

[16] Norman Gilinsky has remarked on the similarities between my model and the "Type II" model put forth in Mayo and Gilinsky (1987). While the agreements between us are substantial, there are some important differences as well. Two such

The first clause embodies the idea that there are distinctive group-level properties, some of which causally determine the group's chances of persisting and/or multiplying. Some examples of group-level properties might be average generational time, population size, area of territory occupied, division of labor among members, having a smooth or convoluted periphery, and so on.[17] What is important is that the property in question be one which attaches to the group itself, and that the property determine a component of the group's fitness.

The second clause expresses two important requirements. First, there must be differences among groups with respect to the property in question in order for there to be selection at that level. Second, the groups which are said to be participating in a given selection process must share a common selective environment. (On the concept of a selective environment, see Brandon 1990). Note that this clause does *not* require that such entities be members of a monophyletic group. If evolutionary theory (viewed from the most abstract level) concerns explaining the distribution and changes in biological properties in the biosphere, there is no reason why taxonomically diverse biological entities could not participate in the same selection process. It might be *unlikely* that they would participate in the same selection process, because it would be unlikely that they would be subject to the same selection pressures. But this is strictly an empirical, not conceptual, issue. The important point in this context is that the groups being considered have their fitnesses determined in part by common environmental or "critical factors" (Darden and Cain, 1989).

The third clause introduces the requirement that interaction occur between the group(s) in question and their common selective environment in virtue of some group-level property. This requirement has recently been emphasized by several authors (Brandon 1988; Hull 1988; Vrba 1984). The notion of fitness differences introduced in the first clause is here deployed so as to exclude differential group persistence and/or multiplication due to chance.[18] Group function in group

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differences will be noted here. Their definition of [Type II] group selection requires that group properties be "irreducible," whereas mine is (purposely) silent on this issue. (John Damuth has convinced me that this concept introduces needless difficulties.) In addition, there is no requirement in their model that differences in some group property or process *do* result in differential group multiplication (or persistence), but only that such differences result in fitness differences among the groups. One interesting (and to me disturbing) consequence of this view is that group selection can (on their model) occur in cases in which *no differential group multiplication or persistence obtains*! So, if as a result of some group property one group has its fitness augmented relative to some other group, then this is, on their model, a case of group selection. This is so even if all of the groups are destroyed by a natural disaster before any of them can multiply! Instead of defining group selection in terms of resultant fitness differences among groups, my analysis requires that for group selection to obtain, there must be an actual *change in group representation* within some more encompassing ensemble of groups. Merely the *likelihood* (which is what talking of resulting fitness differences amounts to) for such results to obtain is insufficient.

[17] Unlike Vrba's definition (Vrba 1984, Vrba and Eldredge 1984, and Vrba and Gould 1986) my definition does *not* require that the group-level property be an "emergent" one. It might just as well be an "aggregate" property, so long as it is in virtue of *this* property that the group interacts with its environment, resulting in differential group persistence and/or multiplication. (See Lloyd 1988; Damuth and Hiesler 1988). In addition, my model does not require that variation be heritable for selection to operate on it. I have defended this claim in detail elsewhere (Shanahan 1990). Heritability is necessary, however, for evolution by natural selection.

selection processes as "interactors" (Hull 1980). This clause does not require that P be the only causally relevant factor in the differential group persistence and/or multiplication, nor that it be the most important factor, or even that the differential group persistence and/or multiplication would not have come about except through P. This leaves open the possibility that selection may be operating on several different levels at once, each selection process making some contribution to the differential group persistence and/or multiplication.

A definition of group selection must be evaluated using two different kinds of considerations. Conceptual considerations concern the degree to which the definition aids in the clarification of actual biological phenomena falling within its scope. The bulk of this paper so far has been concerned with conceptual considerations. We turn next to an empirical application of the proposed definition.

III. The Evolution of Myxomatosis: An Analysis

Parasitologists have noted for a long time that parasites typically have less harmful effects on their hosts if the association is old than if it is recent (Ewald 1983; Holmes 1982; May and Anderson 1983). An example that is often cited as an illustration of this fact concerns the parasite-host relationship between the myxoma virus and the European rabbit *Oryctolagus cuniculus*. This rabbit was originally introduced into Australia by European settlers around 1859. The rabbits multiplied rapidly and spread throughout a large region. In order to control the burgeoning rabbit population that was reaching pest proportions and effectively defoliating much of the continent, the myxoma virus, whose normal host was the South American tropical forest rabbit *Sylvilagus brasiliensis*, was introduced in Australia in 1950 (Ratcliffe et al. 1952; Fenner and Marshall 1957). At first the virus operated as intended, causing immense mortality, killing 99.8% of the rabbits that were infected within 9-13 days after infection (Fenner and Myers 1978). But over the course of the next decade mortality rates fell drastically, so that by 1964 the virus killed only 8.3% of infected rabbits (Fenner 1965). How is this to be explained?

One explanation that appeals to ordinary mechanisms of organism selection is that the rabbits evolved greater resistance to the virus. Rabbits which, for whatever genetic and physiological reasons, enjoyed any degree of resistance to the virus, fared better than those with less (or no) resistance. Consequently, rabbit genotypes conferring resistance spread rapidly in the rabbit population. This hypothesis was confirmed when wild rabbits and laboratory-maintained rabbits were inoculated with a pure (laboratory-maintained) strain of the virus. Just as would be expected on the hypothesis, it was found that the wild rabbits exhibited greater resistance to the virus than the laboratory rabbits. So the population of wild rabbits, with the myxoma virus as its selective agent, had evolved greater resistance to the virus.

Further tests, however, suggested that this was not the complete explanation for the lower rates of mortality among wild rabbits. When wild and laboratory rabbits were inoculated with a wild strain of the virus, it was found that both kinds of rabbits showed fewer effects than when they were both inoculated with the pure strain of the virus. This suggests that while the rabbits were evolving greater resistance to the virus, the virus was evolving lower virulence with

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[18] For the purposes of explicating the concept of group selection within the context of evolutionary theory, it is necessary to discriminate between differential persistence and/or multiplication due to selection and that due to chance. This is because our current theories treat these as two different (albeit interacting) evolutionary processes. When we consider the process of evolution per se, however, it becomes much less clear that this distinction cuts nature at her joints. See Rosenberg (1988) for an illuminating discussion.

respect to the rabbits. But whereas the evolution of resistance on the part of the rabbits is easily explained on the hypothesis of organism selection, the trend toward avirulence in the viruses is not. To understand why it is not, one must understand the relationship between level of virulence and viral reproductive rates. The extent to which the myxoma virus weakens or kills rabbits is (at least in part) a function of the number of viruses within any given rabbit. Viral strains with a higher reproductive rate attain a greater level of virulence in a rabbit than those with a lower reproductive rate. But organism selection cannot account for lower rates of reproduction.[19] On the contrary, organism selection can be expected to maximize the rate of individual organismic reproduction and, as a consequence, the frequency of virulent genotypes among the viruses should increase. How then is the trend toward avirulence to be explained? Lewontin (1970) proposed the following answer.

> The key is that the myxoma virus is spread by mosquitoes, which mechanically transfer a few virus particles to the rabbits they bite.... Each rabbit is a deme from the point of view of the virus. When a rabbit dies, the deme becomes extinct since the virus cannot survive in a dead rabbit. Moreover, the virus cannot spread from that deme because mosquitoes do not bite dead rabbits. Thus there is a tremendously high rate of deme extinction, with the result that those demes are left extant that are least virulent. This causes a general trend toward avirulence of the pathogen despite the complete lack of selective advantage of avirulence within demes (Lewontin 1970, p. 15).

The mechanism Lewontin proposes can be explained by comparing it to the process described as "group selection" by Wynne-Edwards (1962, 1963). Each rabbit is a pool of resources from which a population of viruses draws its sustenance. If a viral group overexploits its resources, it kills its host and, in the process, causes its own extinction. Viral groups with lower viral reproductive rates have a lower ecological impact on their resources than those with higher rates, and are thus in a better position to survive and spread (or be spread) to other rabbits by mosquitoes which only bite living rabbits (Myers et al 1954; Day 1955). Although a maximum rate of individual reproduction is favored by organism selection, lower reproductive rates are favored by group selection operating via differential group extinction. An individually disadvantageous characteristic (lower reproductive rate) is thereby explained in terms of selection operating at the level of groups.[20]

* * *

[19] It is true that producing less offspring per breeding season than is physiologically possible may be in the reproductive interests of some organisms, especially if this increases the likelihood of survival of those offspring which are produced. Clutch size in birds, for example, can be expected to vary closely around a figure well below the potential number of offspring that could (physiologically) be produced (Lack 1954). But individual selection predicts that organisms will attempt to maximize their lifelong genetic contribution to the next generation. In organisms that do not have the option of allocating their reproductive efforts over a number of breeding seasons (e.g., like viruses), higher immediate reproductive rates will be favored by individual selection.

[20] Like the mechanism proposed by Wynne-Edwards, the mechanism proposed by Lewontin operates on and between groups, involves differential group extinction and colonization, and serves to counteract an organismically advantageous but group disadvantageous trait -- maximum organismic reproduction. The major difference between the two mechanisms is that the evolution of avirulence in the myxoma virus does not, unlike Wynne-Edwards' process, involve social interactions between members of a randomly mating local population. Viruses are asexual, and thus do not form a deme in the strict sense. In addition, viruses in a rabbit form a "group" only because their fates are tied together in virtue of their common host. They do not (so far as we can tell) constitute a social unit. A further difference

Lewontin's account provides a plausible explanation of why avirulence might have evolved in the viral population. However, Futuyma (1979), starting from the same empirical data, proposed a very different interpretation of this case, one which relies solely on individual selection to explain the phenomenon.

> If the fitness of an individual parasite or its offspring is lowered by the death of its host, avirulence is advantageous.... because the virus is transmitted by mosquitoes that feed only on living rabbits, virulent virus genotypes are less likely to spread than benign genotypes. Avirulence evolves not to ensure a stable future supply of hosts, but to benefit individual parasites (Futuyma 1979, p. 455, emphasis added).[21]

Which of these interpretations is correct? Is the evolution of avirulence in the myxoma virus due to group selection, as Lewontin's discussion suggests, or is it due to ordinary organism selection, as Futuyma's remarks suggest? A perusal of the biological literature indicates that professional opinion about this case is divided. Like Lewontin, E.O. Wilson (1975) and Levin and Kilmer (1974) cite the myxoma case as a probable example of interdemic (group) selection. Like Futuyma (1979), Alexander and Borgia (1978) interpret this as a case of organism selection. The case thus provides a good opportunity to apply the model of group selection defended above (GS).

Consider this case in terms of each of the clauses which constitute (GS). The first clause requires that a group, G, possess some group-level property, P (where P determines some component of G's fitness). Let P be the level of virulence of a group (measured, perhaps, by the severity of symptoms of infected hosts). Note that this property is a by-product of the reproductive rates of individual viruses. Such rates are in turn the product of individual viral genotypes. However, the fact that P is decomposable or "reducible" to properties of individual organisms does not in the least disqualify this property from being a genuine group property. Having level of virulence "X" sufficient to cause "Y" degree of symptoms in a host is something a group can rightly be said to have or lack. Group properties may well be "summative" in nature. In the myxoma case, having the group property "X level of virulence" determines rather directly a component of the fitness of groups, namely, a group's ability to persist and/or multiply. So interpreted, the first clause of (GS) is satisfied.

The second clause requires that a group, G, differs from at least one other G-level entity with respect to P in a shared selective environment, E. In the myxoma case, groups differ with respect to their level of virulence. Note that it does not matter on this view why the groups differ. They might differ because groups are either (i) [relatively] homogenous or (ii) [relatively] heterogenous with respect to their containing viral genotypes. One group might have a given level of virulence because it contains a few viruses with high reproductive rates and many with low reproductive rates (a relatively heterogenous group). Another group might have the same level of virulence because it consists almost entirely of viruses with average reproductive rates (a relatively homogenous group). What matters here is not the reasons why groups differ in level of virulence, but simply that they do so differ.[22]

* * *

is that whereas Wynne-Edwards' groups can take over areas vacated by other groups that have gone extinct, the viruses in a rabbit cannot do so, because group extinction in the case of the viruses includes the death of the host and consequently renders that "habitat" unsuitable for other would-be colonizers.

[21] I introduce Futuyma's interpretation here only to provide contrast with that of Lewontin, to show how different interpretations of the same empirical data are possible. In the second edition of his Evolutionary Biology (1986), Futuyma omits the above interpretation and puts forward a group selection explanation of the phenomenon.

The common selective environment for the viral groups consists of Oryctolagus cuniculus, mosquito vectors, and other relevant Australian environmental factors. The fact that different viral groups (by definition!) exist in different rabbits does not affect this claim. What determines selective environment on this view is not common location, but rather similar selective pressures. The selective pressures exerted on viral groups are those determined by the physiology of Oryctolagus cuniculus, the mechanics of viral transmission by mosquito vectors, and so on. If viral groups are parceled into discrete hosts which can move about and hence change their location in relation to each other, I can see no reason to deny that biological entities in general could be participating in a selection process even though the entities be separated by large spatial or temporal distances.[23]

Finally, the third clause of (GS) requires that a group, G, interact with the environment, E, in virtue of property P, in such a way that P causally contributes to the differential persistence and/or multiplication of G relative to these other G-level entities. In the myxoma case viruses interact with their rabbit hosts both individually and as groups. Individual interactions determine individual survival and/or reproduction.[24] But it is also the case that groups, in virtue of a group-level property they possess to greater or lesser extent, interact with their hosts, determine some condition of their hosts, and thereby affect group persistence and multiplication.[25]

This can be seen by considering the specific ways in which a group property (level of virulence) determines the fate of viral groups. The evidence suggests that mosquitoes preferentially bite rabbits with open sores which provide easy access to blood, the mosquitoes' food (May & Anderson 1983). These lesions or sores, in turn, are caused by the presence of the myxoma virus. If P (the level of virulence in a rabbit) has a relatively high value, the infected rabbit develops an abundance of open lesions which facilitate spread of the virus. However, in this case its lifespan is greatly diminished, thereby limiting the

* * *

[22] Lloyd (1988, 1989) emphasizes the importance of determining the genotypic constitution of the groups in the myxoma case. On my view this is indeed important information to have, but does not affect the determination of whether group selection is or is not operative.

[23] Sober (1984, p. 274, n. 40) argues that it would make no sense to view groups living on opposite sides of the universe as participating in the same selection process. He does not, however, specify how close the groups must be to participate in the same selection process. Damuth (1985) gives sound theoretical reasons why we might not (given the tools of current evolutionary theory) want to consider non-localized entities as participating in the same selection process.

[24] This is where the viral composition within rabbits becomes important. If the viruses within a rabbit are genotypically identical, then there can be little room for individual selection within rabbits. If the viruses within a rabbit are genotypically heterogenous, then conditions favor individual selection within rabbits. The tendency to suppose that group selection is operative only in the case of genotypically homogeneous viral groups comes from the mistaken (but still prevalent) assumption that group selection always acts contrary to individual selection. Note that this account would still allow a distinction between Sober's tall-short example and the myxoma case. In Sober's example, differential group multiplication was the effect of differential interaction between individuals and their environments. In the myxoma case, however, differential group multiplication is not merely a result of differential viral interaction with their environment. Rather, it is an effect of an interaction between a group property -- average level of virulence -- and the environment (the host).

[25] This is, incidentally, a beautiful example of how biological entities not only respond to selection pressures from the environment, but themselves help to shape this very environment through their behavior (Oldling-Smee 1988).

opportunity for it to be bitten by mosquitoes and to have its viral strain spread (Levin and Pimentel 1981; May & Anderson 1983). If *P* has a relatively low value, then the infected rabbit is less likely to develop sores, and to have its lifespan cut inordinately short, but is also less likely to be bitten by mosquitoes and to have its viral strain spread to other rabbits. Finally, if *P* has a value in the intermediate to high range, then the infected rabbit develops exposed lesions, providing mosquitoes with access to the rabbit's blood, while the intermediate level of virulence allows the rabbit to survive for a considerable length of time. Such a condition seems to be optimal for the spread of the virus, i.e., for the multiplication of viral groups. Note that on this account selection for a group property causes differential group persistence and multiplication, one of the *effects* of which is to increase the frequency of certain genotypes in the regional population. This is a good example of the distinction between "selection" as a *cause* of evolutionary change and "sorting" as an *effect* of selection at another level (Vrba and Gould 1986).

Conclusions

I conclude that the evolution of myxomatosis in Australia was due to group selection. In this account, selection at the level of groups determines sorting among entities at lower levels (viruses and viral genotypes), resulting in evolution -- of properties, such as avirulence, and of gene frequencies. This is the same conclusion as that reached by Lewontin, but notice that it was reached by a different path, one which analyzed the biological factors involved in terms of an independently developed definition of group selection. The value of this approach, I wish to suggest, is not only that it clarifies the conditions under which group selection can be said to be operative, but also that with slight modification it can be used to analyze selection at any level in the biological hierarchy. For instance, using this framework, a "unit of selection" could be defined as follows:

(*US*) *S* is a unit of selection if and only if:
(1) *S* possesses some *S*-level property, *P* (where *P* determines some component of *S*'s fitness);
(2) *S* differs from at least one other *S*-level entity with respect to *P* in a shared selective environment, *E*;
(3) *S* interacts with *E* in virtue of *P* in such a way that *P* causally contributes to the differential persistence and/or multiplication of *S* relative to these other *S*-level entities.

Substituting a specific "gene" or "species" for *S* produces defining conditions for genic and species selection. The approach defended in this paper, therefore, is congenial to the development of a hierarchical analysis of selection -- the need for which is becoming increasingly apparent (Vrba and Eldredge 1984).

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