Original Article

Recent Work on the Levels of Selection Problem

By

Samir Okasha

1. Introduction

The complex of problems falling under the 'levels of selection' rubric includes an intriguing mix of empirical, conceptual and philosophical issues. Roughly speaking, the key question concerns the *level of the biological hierarchy* at which natural selection occurs. Does selection act on organisms, genes, groups, colonies, demes, species, or some combination of these? Evolutionary biologists and philosophers of biology have devoted considerable attention to this question over the last forty years, so much so that in some quarters the debate is now regarded as stale. Despite this perception, recent years have in fact seen interesting and important new work on the levels of selection, some of which has significantly re-defined the terms of the traditional debate. This paper aims to introduce the reader to these new developments.

2. Multi-Level Selection and the Major Transitions in Evolution

The body of ideas known loosely as 'multi-level selection theory' takes as its starting point the notion the natural selection can operate *simultaneously* at different levels of the biological hierarchy. So the evolution of a given trait can be affected by selection at more than one level. This means that it is a mistake to ask what *the* level of selection is in a given scenario, or in general – there need be no single answer. Hence to oppose 'genic selection' to 'individual selection' or to 'group selection', as authors such as Dawkins (1976) and Williams (1966) did, is to commit a conceptual mistake: selection can operate at all of these levels, and others. Another central theme of multi-level selection theory is the idea that the *direction* of selection may be different at different hierarchical levels; for example, a trait may be selectively disadvantageous at the individual level, but selectively advantageous at the group level. According to its proponents, a properly inclusive evolutionary theory, which seeks to understand all the forces affecting biotic evolution, must recognise the possibility of selection at multiple levels.

Though the label is new, the basic ideas behind multi-level selection theory have actually been with us for some time. Darwin's famous discussion of the evolution of self-sacrificial behaviour among early humans in *The Descent of Man* (1871) makes the point that a trait or behaviour may be favoured by group selection

but disfavoured by individual selection; and as Gould (2002) has recently documented, August Weismann formulated very clearly the idea that selection can operate at multiple hierarchical levels, above and below that of the organism. Weismann (1903) wrote: "this extension of the principle of natural selection to all grades of vital units is the characteristic feature of my theories…this idea will endure even if everything else in the book should prove transient" (quoted in Gould (2002) p.223).

Despite this impressive pedigree, it is only relatively recently that biologists have come to see multi-level selection as a potent explanatory principle. A number of prominent evolutionary theorists, including Williams (1992), Maynard Smith and Szathmary (1995), Michod (1999), Frank (1999), Sober and Wilson (1998), and Gould (2002) – some of who were staunch *opponents* of higher-level selection in previous years – have recently endorsed versions of multi-level or 'hierarchical' selection theory, though each in slightly different ways and for different explanatory ends.

This growth of interest in multi-level selection is in some ways surprising, given that active discussion of the levels of selection has been going on since the early 1960s. What explains it? Part of the answer, I believe, stems from an increasing realisation that the traditional way of setting up the levels of selection question takes too much for granted. Traditionally, the question has been set up roughly as follows: "the biological world is hierarchically organised – genes are found on chromosomes, chromosomes in cells, cells in tissues, tissues in organs, organs in organisms, organisms in groups, groups in species etc. Moreover, the principle of natural selection can be formulated wholly abstractly – as Lewontin (1970) famously argued, selection will operate on any entities that exhibit 'heritable variation in fitness'. Entities at many hierarchical levels satisfy these three conditions, hence there is the potential for selection to operate at different levels."

The problem with this formulation is that it takes the existence of the biological hierarchy for granted, as if hierarchical organisation is simply an exogenously given fact about the organic world (Griesemer 1999). But of course, the biological hierarchy is *itself* the product of evolution – entities further up the hierarchy, such as multi-cellular organisms, have obviously not been there since the beginning of life on earth. The same is true of cells and chromosomes. So ideally, we would like an evolutionary theory which explains how lower-level entities became aggregated into higher-level entities, e.g. how independent genes joined up to form chromosomes, how organelles came to be incorporated in to prokaryotic cells to form eukaryotic cells, how single-celled organisms gave rise to multi-cellular ones, how solitary insects came to form integrated colonies, and so-on. (These are examples of what Maynard Smith and Szathmary (1995) call the 'major transitions' in evolution.) In short, we want to know how the biological hierarchy got there in the first place, rather than just treating it as a given.

Very probably, multi-level selection will have a role to play in explaining the transitions to new levels of hierarchical organisation. As Buss (1987), Michod (1999) and Maynard Smith and Szathmary (1995) have all stressed, we need to know why lower-level selection did not disrupt the formation of the higher-level entities, e.g. why intra-organismic selection at the cellular level did not disrupt the integrity of multi-cellular organisms. Clearly, selection on the higher-level entities themselves is one possible answer. If so, then we have a classic multi-level scenario: selection operates on lower-level entities, favouring those that survive best/replicate fastest without regard for the effect on the higher-level entity; selection *also* operates on the higher-level entities, ultimately leading to a high degree of functional integration and suppression of competition among the lower-level entities. So the levels of selection problem becomes, not just the problem of dis-

covering at which hierarchical level or levels selection *now* acts, but the problem of figuring out how the various levels in the hierarchy evolved initially.

This new 'diachronic' perspective gives the levels of selection question a renewed sense of urgency. Some biologists were inclined to dismiss the traditional levels of selection debate as a storm in a tea-cup – arguing that in practice, selection on individual organisms is the only important selective force in evolution, whatever about other theoretical possibilities. But as Michod (1999) stresses, multi-cellular organisms did not come from nowhere, and a complete evolutionary theory must surely try to explain how they evolved, rather than just taking their existence for granted. So levels of selection apart from that of the individual organism must have existed in the past, whether or not they still operate today. From this expanded point of view, the argument that individual selection is 'all that matters in practice' is clearly unsustainable. Michod's own models of the evolution of multi-cellularity involve two levels of selection – the organismic and the cellular – in a scenario interestingly reminiscent of the classical group selection model for the evolution of altruism. 'Selfish' cells, which abandon somatic duties in favour of increased replication are selected for at the cellular level; but at the level of the whole organism, there is selection against such cells, for they disrupt organismic function (Michod 1999). This particular model has been criticised, but the general principle of interacting levels of selection leading to the evolution of new hierarchical levels is widely accepted.

The contrast I have drawn between the modern 'diachronic' view of the levels of selection and the traditional 'synchronic' view should not be overdone. Even in the earlier discussions, there was always an awareness that entities at different levels of hierarchical organization form a temporal sequence, i.e. lower-level entities generally evolved before higher-level ones. But the importance of explaining the major transitions, and the need to invoke multi-level

selection theory to do so, was not widely appreciated until Buss's seminal *The Evolution of Individuality* (1987). Consider for example Richard Dawkins' (1982) brief discussion of how independent replicating units may originally have come together to form chromosomes. Dawkins says that it is "easily understood" why independent genes might have gained an advantage by "ganging up together" into cells, because their biochemical effects might have complemented each other (p.252). What Dawkins fails to realise is that his argument in effect invokes group selection! From the selective point of view, genes sacrificing their independence by combining to form higher-level functional units, e.g. chromosomes or cells, is strictly analogous to individuals combining themselves into higher-level functional units, e.g. groups. But Dawkins is an implacable *opponent* of group selection, insisting on the impotence of selection for group advantage as an evolutionary mechanism, compared with ordinary individual selection! Clearly, Dawkins has failed to realise that trying to explain the major transitions involves us in levels of selection issues closely analogous to those on which debate traditionally focused.

The surge of interest in multi-level selection among biologists has prompted many philosophers of biology to take another look at the levels of selection question, prompting a considerable body of new work. To some extent, this new philosophical work is continuous with work done in the 1980s by Sober, Brandon, Lloyd, Wimsatt, Sterelny, Kitcher and others; to some extent it reflects the new scientific developments. A brief summary of some of the main philosophical contributions is offered below.

3. Philosophical Issues in Multi-Level Selection Theory

One recurring themes in philosophical discussions of multi-level selection is the issue of realism versus 'pluralism' or 'conventionalism' about the levels of selection. Roughly speaking, realists maintain that there is always a 'fact of

the matter' about the level or levels of selection operating in a given scenario. Pluralists hold that in at least some cases there is no such fact. So for example, a given selection process could equally well be viewed as group selection or as individual selection – we are faced with a choice of perspective, not fact, according to pluralists. Pluralism first raised its head in debates over 'genic selection' in the 1980s, where the main issue was whether the 'gene's eye' view of evolution, championed by Dawkins and G.C. Williams and others, was ultimately equivalent to the orthodox organismic viewpoint or not (cf Sterelny and Kitcher 1988, Waters 1994). On balance, most participants in this debate came down on the 'pluralist' side. Aided by Hull's replicator/interactor distinction, it was argued that to oppose genic selection to individual selection was to commit a category mistake, for genes are replicators while individual organisms are interactors, and entities of *both* sorts are involved in any selection process. This sort of pluralism simply stems from our freedom to focus on replicators or interactors, when describing natural selection.

In the 1990s, however, a somewhat different realist/pluralist dispute arose, that could not be resolved simply by distinguishing replicators from interactors, for the issue at stake was individuals versus *group*s – both of which are interactors, not replicators. The dispute hinged around a particular class of evolutionary models, often called 'trait-group' models after D.S. Wilson (1975, 1980), or 'intra-demic' selection models. In these models the evolution of a trait, typically a social behaviour, is affected by population structure – individual organisms engage in fitness-affecting interactions with certain other members of the population (which form the individual's 'trait-group'), generating evolutionary outcomes that would not occur in a freely-mixing, unstructured population. The key question is: do such models involve a component of group selection or not? Some authors, including Sober and Wilson (1998), have insisted that the answer is 'yes' – since the trait-

groups that make up the population typically exhibit differential productivity, there is selection between groups as well as selection between organisms within groups. Sober and Wilson thus favour a resolutely realistic line – it is a matter of fact, not convention, whether or not group selection is occurring in a trait-group scenario. However others theorists, including Dugatkin and Reeve (1994) and Sterelny (1996) have defended a pluralistic line. They argue that trait-group models *can* be construed as multilevel selection as per Sober and Wilson, but can equally be regarded as pure individual selection, simply by treating the organisms in a particular individual's trait-group as part of that individual's selective environment. There is no fact of the matter as to which is right, on this view.

One notable recent contribution to this debate comes from Kerr and Godfrey-Smith (2002a, b); see also the replies by Maynard Smith (2002), Sober and Wilson (2002), and Dugatkin (2002). Kerr and Godfrey-Smith offer a highly sophisticated defence of pluralism. They construct a simple evolutionary model of selection in a structured environment, and show that the model's dynamics can be fully described by two sets of parameter values, one of which ascribes fitness values only to individuals, the other of which ascribes fitnesses to groups *and* individuals. The former is called a 'contextual' parameterization, for the fitness of an individual depends on its group context, while the latter is called a 'multi-level' parameterization, for both individuals and groups are ascribed fitnesses. Kerr and Godfrey-Smith demonstrate that the two parameterizations are mathematically equivalent – each set of parameter values can be derived from the other. This does not *prove* that pluralism rather than realism is the correct position to take on trait-group selection – for it might be argued that that only one of the parameterizations correctly captures the causal facts, even though the two are mathematically interchangeable, hence computationally equivalent. But Kerr and God-

frey-Smith's work certainly makes a strong case for pluralism, as well as bringing a new degree of rigour to this ongoing debate.

One persistent source of philosophical concern in the levels of selection debate concerns the concept of causality. Virtually everybody agrees that the theory of natural selection is a causal theory – it aims to provide a causal-historical explanation for changes in gene/trait frequency over time (though see Walsh, Ariew and Matthen (2002) for a dissenting view). Therefore, where multiple levels of selection are in play, it follows that causes must be operating at more than one hierarchical level. Sober's seminal (1984) book contained a detailed attempt to use philosophical ideas about causality to help understand multi-level selection. Recent work by Okasha (2003a, b) also addresses the issue of causality, though from a somewhat different angle. Most conceptual/philosophical work on the levels of selection has addressed a purely *qualitative* question, namely, what are the level(s) of selection in a given situation? Okasha argues that this traditional focus fails to address an important *quantitative* question, namely, given the levels of selection that are in play, what fraction of the total evolutionary change can be attributed to each? For example, suppose we agree that individual and group-level selection are both operating in a given situation. How do we tell how *much* of the resulting evolutionary change is due to selection at each level? Okasha explores two different statistical techniques designed to address this question, and finds that they yield incompatible results – each technique decomposes the total change into different components, allegedly corresponding to distinct levels of selection. This raises an interesting, and as yet unresolved, philosophical issue: how do we choose between the two techniques? Or is there perhaps 'no fact of the matter' about which is correct? Focusing on the quantitative rather than just the qualitative question takes the realist/pluralist dispute into new and uncharted territory.

4. Further and Related Issues

The biological and philosophical work summarised in the previous two sections deals with what might be called the levels of selection question *sensu strictu*. However, there is a set of related issues sometimes included under the 'levels of selection' or 'units of selection' rubric, though they really concern the units of *inheritance* rather than selection, that have been the focus of considerable recent discussion. A very brief summary of some of this work is offered below.

The distinction between selection and inheritance is conceptually straightforward, or at least should be (though see Michod (1999) who argues for their inseparability). Selection concerns which variants survive best/reproduce the most, while inheritance concerns the transmission of genotypic and phenotypic characters across generations. Thus quantitative geneticists typically distinguish between selection itself and the evolutionary response to selection – where the latter depends on the heritability of the trait selected for. Nonetheless, issues about selection and inheritance were often run together in the traditional levels of selection debate, particularly by advocates of genic selection. Thus Dawkins, for example, used facts about *inheritance*, e.g. that genes are faithfully replicated across generations while whole genotypes and organismic characters are not, to privilege the gene as the unit of *selection*. In retrospect it is clear that arguments of this type wrongly conflating two distinct issues, and equivocate on the expression 'unit of selection'. One of the merits of Hull's replicator/interactor distinction was to make this equivocation clear. (It is partly for this reason that I used the expression 'level of selection' rather than 'unit of selection' in the previous section; in Hull's terminology, the issues of the previous section concern the level of interaction, not replication.) Nonetheless, questions about the units of inheritance/replication, and the primacy or otherwise of genes in the evolutionary process, are interesting and important in their own right,

even if they are orthogonal to questions about selection itself.

Advocates of the 'gene's eye' or 'replicator first' view of evolution, and many others, have tended to regard genes as somehow more important than the other causal determinants of biological form (such as the environment), at least from an evolutionary point of view. While no biologist would officially deny the importance of environmental factors in development, nor the importance of cytoplasmic as well as nuclear inheritance, genes are nonetheless often invested with a special significance. Dawkins emphasised the fidelity of DNA replication as a reason for thinking of genes as the 'ultimate beneficiaries' of evolution, for whom all adaptations are 'for the good of'. The use of informational vocabulary to characterise genes, enshrined in the (metaphorical) notion that genes constitute 'blueprints' for building organisms, is closely bound up with this privileged status accorded to genes. G.C. Williams (1966) emphasised the necessity of thinking of a gene as a store of information, rather than a physical DNA molecule, in order to fully appreciate the significance of the 'gene's eye view' of evolution. Whether or not the notion of genetic information is an essential aspect of the 'gene's eye' viewpoint, it is undoubtedly the case that many genic selectionists have emphasized that notion.

In recent years a number of theorists - biologists, philosophers and others - have subjected the hegemony of the gene, and the concept of genetic information, to intense critical scrutiny. In particular, advocates of 'developmental systems theory' (DST) such as Paul Griffiths, Russell Gray and Susan Oyama, have argued that genes are just one among many causal factors involved in development, and not uniquely responsible for the reliable transmission of biological form across generations (Griffiths, Gray and Oyama (2001)). Supporters of DST argue that in treating DNA as the master-molecule containing the 'information needed to build an organism', biologists have lost sight of the ob-vious fact that parents transmit far more to their offspring than nuclear DNA, and that many causal factors apart from genes are essential for normal development. There is no particular reason to single out genes as the prime determinants of organismic form, these theorists argue; from the logical point of view, all causal factors responsible for producing the normal adult phenotype are on a par. Population geneticists generally define evolution as 'change in gene frequency over time', a definition which has considerably influenced genic selectionists such as Dawkins, but from the DST viewpoint this is a seriously distorted conception.

Closely allied to this critique of the causal primacy of genes in development is a critique of the very notion of genetic information itself. (Moss (2002) offers a particularly sophisticated critique of both notions.) The historical significance of informational and 'coding' language for the genesis and development of molecular biology cannot be doubted, but many recent philosophers and biologists have wondered how seriously we should take the notion of genetic information. Is there any literal sense in which genes contain 'information' for building organisms, or even for producing proteins, in which *other* factors relevant to development, or to transcription/translation, do *not* contain information? Why do we speak about genetic information but not environmental information, for instance? Moss argues that there are in fact two quite different concepts of the gene in modern biology, and that the idea that genes contain the information needed to build an organism represents an illegitimate conflation of the two. An extended discussion of the notion of genetic information, and how if at all it should be understood, can be found in *Philosophy of Science* 2000, with contributions from Maynard Smith, Sarkar, Godfrey-Smith and Sterelny.

5. Conclusion

It may seem surprising that the levels of selection debate is still live today, given that it traces right back to Darwin. The reason lies partly in the difficulty of resolving the relevant

empirical issues, and partly in the fact that the levels of selection question, like so much in evolutionary biology, involves a mixture of empirical and conceptual issues (cf. Sterelny and Griffiths (1999)); and conceptual issues are generally much harder to resolve definitively than empirical issues, where they admit of definitive resolution at all. I hope that the foregoing survey, incomplete though it is, conveys some sense of the direction in which the debate is currently moving.

Samir Okasha, Lecturer in Philosophy, University of York, Heslington, York YO10 5DD, United Kingdom. Email: so5@york.ac.uk.

References

NB: This bibliography includes all works cited in the text, plus some other relevant recent work. It does not aim to be exhaustive.

Buss, L. (1987). *The Evolution of Individuality*. Princeton NJ: Princeton University Press.

Darwin, C. (1871). *The Descent of Man and Selection in Relation to Sex.* New York: Appleton.

Dawkins, R. (1976). *The Selfish Gene.* Oxford: Oxford University Press.

Dawkins, R. (1982). *The Extended Phenotype.* Oxford: Oxford University Press.

Dugatkin, L. A. (2002). 'Will Peace Follow?' *Biology and Philosophy,* 17, 4, 519-522.

Dugatkin, L. A. and Reeve, H. K. (1994). 'Behavioural Ecology and Levels of Selection: Dissolving the Group Selection Controversy', *Advances in the Study of Behaviour,* 23: 101-33.

Frank, S. (1999). *Foundations of Social Evolution.* Princeton NJ: Princeton University Press.

Godfrey-Smith, P. (2000). 'Information, Arbitrariness and Selection: Comments on Maynard Smith', *Philosophy of Science,* 67, 2, 202-207.

Godfrey-Smith, P. (2000) 'The Replicator in Retrospect', *Biology and Philosophy,* 15, 403 - 423.

Gould, S. J. (2002). *The Structure of Evolutionary Theory.* Cambridge MA: Harvard University Press.

Griesemer, J. (1999). 'Materials for the Study of Evolutionary Transitions'. *Biology and Philosophy,* 14, 127-142.

Griffiths, P., Gray, P. and Oyama, S. (2001). *Cycles of Contingency: Developmental Systems and Evolution.* Cambridge MA: MIT Press.

Jablonka, E. and Lamb, M. (1995). *Epigenetic Inheritance and Evolution: the Lamarckian Dimension.* Oxford: Oxford University Press.

Keller, L. (1999). (Ed.). *Levels of Selection in Evolution.* Princeton NJ: Princeton University Press.

Kerr, B. and Godfrey-Smith, P. (2002a). 'Individualist and Multi-level Perspectives on Selection in Structured Populations', *Biology and Philosophy,* 17, 4, 477-517.

Kerr, B. and Godfrey-Smith, P. (2002b). 'On Price's Equation and Average Fitness', *Biology and Philosophy,* 17, 4, 551-565

Leigh, E. (1995). 'The Major Transitions of Evolution', *Evolution,* 49, 1302-1306.

Lewontin, R. (1970). 'The Units of Selection', *Annual Review of Ecology and Systematics,* 1, 1-18.

Maynard Smith, J. (2000). 'The Concept of Information in Biology', *Philosophy of Science*, 67, 2, 177-194.

Maynard Smith, J. (2000). 'Reply to Commentaries', *Philosophy of Science*, 67, 2, 214-218..Maynard Smith, J. (2002). 'Commentary on Kerr and Godfrey-Smith', *Biology and Philosophy,* 17, 4, 523-527.

Maynard Smith, J. and Szathmary, E. (1995). *The Major Transitions in Evolution.* New York: W.H. Freeman.

Michod, R. (1999). *Darwinian Dynamics.* Princeton NJ: Princeton University

Press.

Moss, L. (2003). *What Genes Can't Do*. Cambridge MA: MIT Press.

Okasha, S. (2001). 'Why Won't the Group Selection Controversy Go Away?'. *British Journal for the Philosophy of Science,* 51, 25-50.

Okasha, S. (2002). 'Genetic Relatedness and the Evolution of Altruism', *Philosophy of Science,* 69, 1, 138-149.

Okasha, S. (2003a). 'Multi-Level Selection, Covariance and Contextual Analysis', *British Journal for the Philosophy of Science,* (forthcoming).

Okasha, S. (2003b). 'Multi-level Selection and the Partitioning of Covariance: a Comparison of Three Approaches', *Evolution,* (forthcoming)

Okasha, S. (2004). 'The 'Averaging Fallacy' and the Levels of Selection', *Biology and Philosophy,* (forthcoming)

Sarkar, S. (2000). 'Information in Genetics and Developmental Biology: Comments on Maynard Smith', *Philosophy of Science,* 67, 2, 208-213.

Sober, E. (1984). *The Nature of Selection*. Chicago: Chicago University Press.

Sober, E. and Wilson, D. S. (1998). *Unto Others: The Evolution and Psychology of Unselfish Behaviour*. Cambridge MA: Harvard University Press.

Sober, E. and Wilson, D. S. (2002). 'Perspectives and Parameterizations: Commentary on Benjamin Kerr and Peter Godfrey-Smith's 'Individualist and Multi-Level Perspectives on Selection in Structured Populations'', *Biology and Philosophy,* 17, 4, 529-537.

Sterelny, K. (1996). 'Explanatory Pluralism in Evolutionary Biology', *Biology and Philosophy,* 11, 193 - 214.

Sterelny, K. (1996). 'The Return of the Group', *Philosophy of Science*, 63, 562-84.

Sterelny, K. (2000). 'The 'Genetic Program' Program: A Commentary on Maynard Smith on Information in Biology', *Philosophy of Science,* 67, 2, 195-201.

Sterelny, K. and Griffiths, P. E. (1999). *Sex and Death: An Introduction to the Philosophy of Biology*. Chicago: University of Chicago Press.

Sterelny, K. and Kitcher, P. (1988). 'The Return of the Gene', *Journal of Philosophy,* 85: 339-360.

Walsh, D., Ariew, A. and Matthen, M. (2002). 'Trials of Life: Natural Selection and Random Drift', *Philosophy of Science,* 69, 429-446.

Waters, C.K. (1994). 'Tempered Realism about the Forces of Selection', *Philosophy of Science,* 58, 553-573.

Weismann, A. (1903). *The Evolution Theory*. London: Edward Arnold.

Williams, G. C. (1966). *Adaptation and Natural Selection*. Princeton: Princeton University Press.

Williams, G. C. (1992). *Natural Selection: Domains, Levels, Challenges*. Oxford: Oxford University Press.

Wilson, D. S. (1975). 'A Theory of Group Selection', *Proceedings of the National Academy of Sciences USA,* 72, 143-146.

Wilson, D.S. (1980) *The Natural Selection of Populations and Communities*. Menlo Park CA, Benjamin Cummings.

Wilson, D. S. (1997). 'Altruism and Organism: Disentangling the Themes of Multi-level Selection Theory', *American Naturalist,* 150: S122-S134.

Wilson, R. (2003). 'Pluralism, Entwinement and the Levels of Selection', *Philosophy of Science*, (forthcoming).

Wynne-Edwards, V. C. (1993). 'A Rationale for Group Selection', *Journal of Theoretical Biology,* 162, 1-22.