Maynard Smith on the levels of selection question

SAMIR OKASHA

Department of Philosophy, University of Bristol, 9 Woodland Road, Bristol BS8 2HH, UK (e-mail: Samir.Okasha@bris.ac.uk)

Abstract. The levels of selection problem was central to Maynard Smith's work throughout his career. This paper traces Maynard Smith's views on the levels of selection, from his objections to group selection in the 1960s to his concern with the major evolutionary transitions in the 1990s. The relations between Maynard Smith's position and those of Hamilton and G.C. Williams are explored, as is Maynard Smith's dislike of the Price equation approach to multi-level selection. Maynard Smith's account of the 'core Darwinian principles' is discussed, as is his debate with Sober and Wilson (1998) over the status of trait-group models, and his attitude to the currently fashionable concept of pluralism about the levels of selection.

Introduction

The levels of selection question – which asks whether natural selection operates on genes, individuals, groups, species, or some other units – occupied John Maynard Smith throughout his career. In part, this is because Maynard Smith held a fascination for biological phenomena that appear anomalous from the Darwinian standpoint, as Szathmáry and Hammerstein (2004) note, and such phenomena invariably force us to think carefully about the unit of adaptive advantage, hence of selection. Thus consider for example the evolution of sex, one of Maynard Smith's life-long concerns (cf. Maynard Smith 1978). Females that reproduce sexually are at a fitness disadvantage vis-à-vis those that reproduce parthenogenetically, as the latter do not incur the cost of producing males. So why is sexual reproduction so common? Is it perhaps advantageous at the level of the species, rather than the individual? Or consider ritualised fights between animals of the same species, which rarely lead to escalation. Why is it advantageous to an animal to engage in such rituals, rather than fighting properly? Or does the advantage perhaps accrue to the group, rather than the individual animal? It was through consideration of this latter question that Maynard Smith was led to the concept of an evolutionary stable strategy (ESS), arguably his greatest contribution to biology (cf. Maynard Smith and Price 1973). Other topics on which Maynard Smith wrote that raise levels of selection issues include the evolution of recombination, altruism, symbiosis, the origins of life and the 'major transitions' in evolution (cf Maynard Smith 1979, 1983, 1988a, b, 1991; Maynard Smith and Szathmáry 1995).

This paper traces the development of Maynard Smith's views on the levels of selection from the 1960s to the time of his death. Section 1 examines his legendary opposition to group selectionist thinking, particularly of the 'unconscious' variety, and explores its sources. Section 2 contrasts Maynard Smith's position with those of two other prominent neo-Darwinists – G.C. Williams and W.D. Hamilton – with whom he shared many of the same concerns. I argue that all three started with similar positions on the levels question, but Williams' and Hamilton's underwent significant transformation over the years while Maynard Smith's did not. The underlying reasons for this difference are considered. Section 3 focuses on conceptual and philosophical issues. Maynard Smith's abstract formulation of the 'core Darwinian principles' is considered, along with his distinction between 'units of selection' and 'units of evolution' (cf. Maynard Smith 1987). His attitude towards the philosophical thesis known as 'pluralism', which says that there is sometimes no 'fact of the matter' about the true level of selection, and the related idea that a single selection process can often be modelled in multiple ways, is discussed. Section 4 looks at the major evolutionary transitions, a topic which became increasingly important for Maynard Smith from the late 1980s onwards, and which is intimately bound up with the levels of selection question. I argue that in studying the major transitions, it is necessary to construe the levels question in 'diachronic' rather than 'synchronic' terms. The implications of this change in perspective are briefly explored.

Maynard Smith and the question of group selection

Textbooks on the evolution of social behaviour often give a potted history of the subject's development along the following lines. In the early half of the 20th century, biologists routinely interpreted animal behaviours as adaptations designed to promote the welfare of the whole group (or species), often without realising that ordinary individual-level selection does not necessarily lead to group-beneficial outcomes. Matters changed suddenly in the 1960s, thanks to the work of G.C. Williams, W.D. Hamilton and John Maynard Smith. These authors showed the inherent fragility of group selection as an evolutionary mechanism, and proposed alternative explanations for how pro-social or altruistic behaviour could evolve, such as kin selection, reciprocal altruism, and evolutionary game theory. As a result of their work, the hypothesis of group selection fell out of favour in evolutionary biology, where it remains today.

Potted histories of this sort, though inevitably oversimplified, are basically accurate. (More detailed, nuanced histories of the group selection debate can be found in Sober and Wilson (1998) and Segersträle (2000)). Certainly, Maynard Smith himself regarded the rejection of the 'good of the group' tradition as a turning point in twentieth century evolutionary biology, that was fundamentally necessary for the subsequent development of the subject. Unlike certain modern evolutionists, who regard the wholesale rejection of group

selection in the 1960s and 70s as an overreaction, Maynard Smith remained adamant that it was not an overreaction but a crucial conceptual advance. In one of his last papers on the subject, he recalls reading Konrad Lorenz's description of ritual fighting behaviour while a zoology undergraduate in the 1940s: "I remember that the behaviour was explained by Julian Huxley by saying that ritual evolved because escalated fighting would 'militate against the survival of the species'. Even as a student I knew that had to be wrong" (2002 p. 524). Interestingly, G.C. Williams recounts a similar experience on first encountering the "superorganism" concept of Allee and Emerson.[1] Williams' experience led him to write *Adaptation and Natural Selection*; Maynard Smith's led him to devise ESS theory, to repeatedly warn against invoking selection for group advantage unless necessary, and to develop a life-long interest in evolutionary scenarios that involve conflict between levels of selection.

In 'The Logic of Animal Conflict', co-authored with George Price, Maynard Smith returned to the issue of ritualised fighting that he had read about as an undergraduate some thirty years previously. The purpose of the paper was to suggest an explanation for the puzzling phenomenon of ritualised fights *without* appealing to selection at the group or species level. The paper made the key point, now taken for granted in evolutionary studies of animal behaviour, that the optimal strategy for an individual may depend on what other individuals in the population are doing. An immediate corollary is the need to use game-theoretical methods, rather than traditional optimisation theory, to understand behavioural evolution. Maynard Smith and Price used a simple game-theoretic model of an animal contest to show that conflict limitation, rather than all-out war, *can* boost individual fitness (essentially, by increasing the probability that the individual will survive and mate in the future). Thus the anomaly of ritualised fighting becomes explicable, by selection acting only at the individual level, once explicit account is taken of the fact that the fitness of any strategy depends on what other strategies are present in the population. Huxley's appeal to the 'survival of the species' is unnecessary.

The strategic or game-theoretic mode of analysis introduced by Maynard Smith and Price hinged around the concept of an evolutionary stable strategy (ESS) – a concept which was "fundamental to their argument" (1973, p. 15). An ESS is a strategy such that if all members of the population are using it, no rival strategy will be fitter; it thus defines an equilibrium state from which the population will not deviate under the pressure of selection. Though precursors of the ESS concept can be found in both Fisher and Hamilton, it was Maynard Smith who articulated the concept precisely, recognised its full biological significance, and built an impressive body of theory around it (cf. Maynard Smith 1982). For the levels of selection question, the main significance of ESS theory is that it provided a paradigm for how to explain co-operative and altruistic behaviours *without* invoking higher-level selection. Moreover, unlike the forms

---

[1] This incident is described in Sober and Wilson (1998) p. 36.

of co-operation and altruism explicable by kin selection, ESS theory can explain co-operative interactions between members of different species, and thus symbiotic alliances.

Though Maynard Smith was sceptical about group selection, he did not dismiss it altogether. In his 1964 paper 'Group Selection and Kin Selection', which was a critical discussion of Wynne-Edwards' views, he constructed a simple model to explore the evolution of altruism by group selection. The model described a hypothetical mouse species which lives in haystacks, where each haystack is colonised by a single fertilised female. The resulting population structure makes for two levels of selection – between individuals within haystacks, and between the haystacks (groups) themselves. In theory, a behaviour which is individually disadvantageous but group-beneficial can evolve, so long as the balance between the selective forces is right. Though Maynard Smith's own aim was to show the unlikelihood of such an outcome, the haystack model has been resurrected by later theorists interested in selection for group advantage (cf. Wilson 1987, Kerr et. al. forthcoming). And the general point made by the haystack model, that population structure permits evolutionary outcomes not possible in an unstructured population, plays an important role in the discussion of pre-biotic evolution in *The Major Transitions in Evolution* (Maynard Smith and Szathmáry 1995).

Furthermore, Maynard Smith often endorsed the suggestion that selection at the species level might have played in role in the maintenance of sexual reproduction (cf. Maynard Smith 1978, 1984, 1988c, 2002). The taxonomic distribution of parthenogens strongly suggests that purely asexual taxa are destined to rapid extinction, perhaps because of the accumulation of deleterious mutations via Müller's ratchet, or perhaps because of their inability to evolve fast enough in response to environmental stress. This has led a number of theorists to speculate that sexual reproduction may be an adaptation of species – i.e. that selection for sexuality at the species level has offset the short-term advantage of parthenogenesis. Though sympathetic to this idea, Maynard Smith emphasised that at most it could explain the *maintenance* of sexual reproduction, not its original evolution, so could not be the whole story. And while he accepted the logical cogency of the concept of species selection, he never accepted the prominence accorded to it by macroevolutionary theorists such as Stanley, Gould and Eldredge. For these theorists, species selection was part of a broader attempt to 'decouple' macro and microevolution, i.e. to show that macroevolution is not just microevolution writ large, but is governed by autonomous dynamics of its own. This idea held little attraction for an arch neo-Darwinist such as Maynard Smith; species selection for him was a minor addendum, not a rival, to conventional microevolutionary forces (cf Maynard Smith 1988c).

The group selection debate has been characterised by perennial disagreements over concepts and terminology, as well as empirical fact. For example, there are disagreements over whether group selection and kin selection are substantially different evolutionary mechanisms; over whether groups must be

reproductively isolated to be selected as units; over whether frequency-dependence automatically generates a higher level of selection; and more. Maynard Smith regarded these as important conceptual questions, not trivial semantic ones, and discussed them often (cf. Maynard Smith 1976, 1987, 1998, 2002). Many of his most fruitful exchanges with philosophers of science resulted from discussions over how best to conceptualise selection at the group level.

Maynard Smith's starting point was that for groups to be units of selection, they must exhibit "variation, multiplication, and heredity", where heredity means "like begetting like"; this followed straight from the logic of the Darwinian process (Maynard Smith 1987). Thus in a 1976 review of the subject, he argued that group selection "requires that groups be able to "reproduce", by splitting or by sending out propagules, and that groups should go extinct" (1976, p. 282). The process envisaged by Wynne-Edwards, in which reproductively isolated demes give rise to other such demes, satisfies these conditions, Maynard Smith argued, as does the process of species selection as described by Gould and Eldredge, in which speciation plays the role of demic reproduction. However, Maynard Smith insisted that orthodox kin selection does *not* count as group selection, for it does not require the existence of discrete groups at all, less still a well-defined process of group reproduction; it requires only that relatives interact with each other. (The alternative view that kin selection is a type of group selection is defended by Nunney (1985), Queller (1992), Hamilton (1975a, b), Uyenoyama and Feldman (1980), Sober and Wilson (1998) and others.) Similarly, Maynard Smith was always reluctant to consider D.S. Wilson's 'trait group' model as *bona fide* group selection, on the grounds that the periodic 'blending' of groups into the mating pool prevents the groups themselves from exhibiting the requisite heredity (cf. Wilson 1975, 1980, Maynard Smith 1976, 1987). While Wilson stressed the continuity of the trait-group model with traditional Wynne-Edwards style group selection, Maynard Smith stressed the differences, preferring to regard the trait-group model as individual selection with fitness-affecting interactions between neighbours, much like kin selection.

To some extent, Maynard Smith's disagreement with Wilson stems from competing definitions of what a 'group' is, though this is not the whole story (cf. Okasha 2001, 2006a, b). For Wilson, groups come into existence wherever there are fitness-affecting interactions between individuals, however fleeting (cf Sober and Wilson 1998); while for Maynard Smith, groups need to be spatially discrete, at least partially isolated from other groups, and preferably functionally organised. Interestingly, the idea that 'genuine' groups are distinct from mere collections of interacting individuals, which Maynard Smith originally advanced in a sociobiological context, re-appears in his later work in a very different context. In their treatment of pre-biotic evolution in *The Major Transitions*, Maynard Smith and Szathmáry (1995) consider Manfred Eigen's theory of hypercycles, which are co-operative networks of RNA molecules (cf. Eigen and Schuster 1979). Eigen's basic idea was that such networks could

have evolved if different RNAs catalysed the replication of each other. For example, RNA type 1 might catalyse the replication of type 2, type 2 that of type 3, and type 3 that of type 1, leading to a co-operative three-member hypercycle in which each member does better than it would do alone (see Figure 1).

It may seem tempting to regard a hypercycle as a new evolutionary unit, and thus to envisage a process of selection at the level of hypercycles. But Maynard Smith and Szathmáry caution against this: "note that the hypercycle is not an individual in the sense that a bacterium is. It is, rather, a population of molecules interacting ecologically. Lacking individuality, it cannot be a unit of evolution" (1995, p. 53). So in the initial evolution of hypercycles, selection takes place at the level of the *individual RNA molecule*, they argue. However, they then go on to consider a modification of Eigen's model which involves compartmentalising the hypercycles by enclosing them within a membrane, permitting stronger selection for cooperation (cf. Eigen et al. 1981). With compartmentalisation, we *do* have a new evolutionary individual which can function as a unit of evolution, Maynard Smith and Szathmáry argue – for when compartments divide, there is "vertical transmission of genetic information, from parent to offspring" (1995, p. 53). The difference between the hypercycle model with and without compartmentalisation is closely analogous to the difference between processes such as kin, trait-group and frequency-dependent selection on the one hand, and "genuine" group selection on the other. In both cases, Maynard Smith's position was clear: selection on interacting individuals is logically distinct from selection on groups.
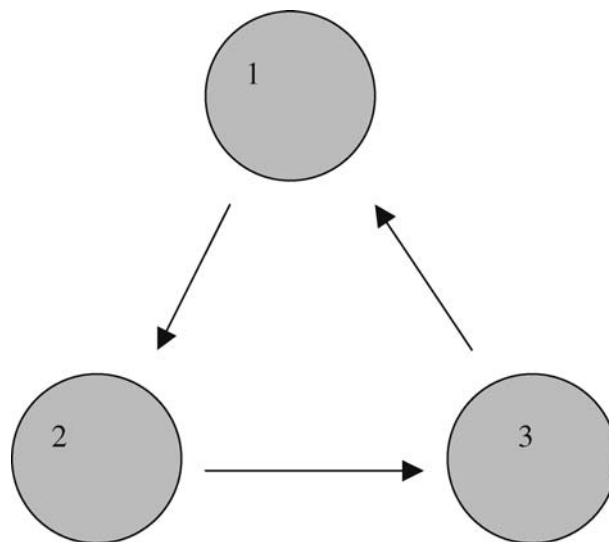

Figure 1. A three-membered hypercycle.

Given the importance he attached to this distinction, it is no surprise that Maynard Smith reacted strongly to Sober and Wilson's (1998) claim that 2-person evolutionary game theory is simply a limiting case of group selection, in which the 'groups' are pairs of interacting individuals. Sober and Wilson's reasoning can be illustrated with reference to a standard Prisoner's Dilemma game with two strategies, co-operate (C) and defect (D), with a payoff matrix as shown below (Figure 2). This game would normally be described as a type of individual selection, in which an individual's fitness depends not only on its own strategy but also on its opponent's. However, Sober and Wilson prefer a 'multi-level' description; selection operates on individuals within pairs (favouring D over C) and on the pairs themselves (favouring (C, C) over the other pairs.) The overall evolutionary dynamics thus depends on the balance between the two levels of selection, just as in Maynard Smith's 'haystack' model described above. Co-operation can only spread if the advantage enjoyed by defectors in mixed groups (i.e. (C, D) pairs) is offset by the superior fitness of (C, C) pairs. Therefore, evolutionary game theory involves a component of group selection after all!

In response to this argument, Maynard Smith (1998) accuses Sober and Wilson of using the expression "group" far too liberally, and thus having changed the meaning of "group selection". This may seem fair. But it would be wrong to imply, as Maynard Smith does, that Sober and Wilson's assimilation of evolutionary game theory to traditional group selection stems *solely* from a semantic decision about what to call a group. Rather, their point is that there is a fundamental commonality in the underlying evolutionary mechanisms in both cases, that the multi-level description helps brings out (cf. Okasha 2006a). Nonetheless, there is something undeniably paradoxical about Sober and Wilson's position. For as we have seen, Maynard Smith originally devised evolutionary game theory to help explain the evolution of social behaviours *without* invoking group selection. So to argue that game-theoretic and ESS models are actually *versions* of group selection is more than a bit odd. The logic behind Sober and Wilson's argument is clear, but it leads to strange places.

	Player 2	
	Co-operate	Defect
Player 1		
Co-operate	11, 11	0, 20
Defect	20,0	5,5

Payoffs for (Player1, Player 2) in units of fitness

Figure 2. The prisoner's dilemma game.

I think Maynard Smith's disagreement with Sober and Wilson partly reflects his general reductionist philosophy of science, and his related preference for some modeling strategies over others – such as his dislike of Price's equation as a tool for modeling selection in hierarchical systems, discussed below. It also partly reflects his view that groups must exhibit a high degree of internal cohesion before they qualify as genuine evolutionary individuals. But at root, it was his conviction that unconscious 'good of the group' thinking had done so much harm in the past that led Maynard Smith to be wary of any attempt to revive group selectionist ideas, even in the trimmed down version promoted by Sober and Wilson, and thus to resist the idea that kin selection and ESS theory are usefully conceptualised in multi-level terms.

Maynard Smith, Hamilton, and Williams: a longitudinal comparison

The evolutionary ideas of Maynard Smith, Hamilton and Williams have a lot in common. All three were committed neo-Darwinists, and they shared many of the same concerns, e.g. the evolution of social behaviour, sex, and intra-genomic conflict. All three championed the gene's eye view of evolution and stressed the dangers of unconscious group selectionist thinking. Despite these points of commonality, however, their views on the levels of selection question diverged somewhat over the years. In particular, Maynard Smith remained firmly wedded to the gene's eye approach, while both Williams and Hamilton expressed sympathy for 'hierarchical' approaches to evolution, though for quite different reasons. The roots of this divergence are worthy of exploration.

The essence of the gene's eye approach was captured in Hamilton's remark: "despite the principle of the 'survival of the fittest', the ultimate criterion which determines whether a gene G will spread is not whether the behaviour [for which it codes] is to the benefit of the behaver, but whether it is to the benefit of the gene G" (1963, p. 7) Hamilton argued that pro-social or altruistic behaviours, which seem anomalous from the traditional organismic viewpoint, are easily understood from the gene's viewpoint, so long as they are preferentially directed towards kin. The logic of this argument was extended further by Williams (1966) and Dawkins (1976), who argued that *all* organismic adaptations, not just pro-social behaviours, can be thought of as strategies devised by genes to increase their future representation in the gene-pool. Thus Dawkins argued that the only "true" unit of selection is the individual gene, organisms being mere "vehicles", while Williams wrote that "only genic selection ... need be recognised as the creative force in evolution" (1966, p. 124).

Maynard Smith was deeply sympathetic to gene's eye thinking, which he thought helped illuminate disparate evolutionary phenomena. Indeed, his understanding of the gene's eye view was in one respect superior to that of Williams and Dawkins. For in their early writings, both of the latter erroneously contrasted 'genic selection' with 'group selection', implying that these are

alternative explanations for how a trait might evolve. Thus for example, Dawkins (1976) rejects Wynne-Edwards' theory that reproductive restraint in bird species evolved by group selection, arguing that a "selfish gene theory" can explain the pertinent data much better. The implication is that if Wynne-Edwards' theory were right, the selfish gene explanation would be wrong and vice-versa. Similarly, Williams (1966) argues that the absence of group-level adaptations in nature is evidence for the pervasiveness of genic selection. But this is a mistake: group selection is a *means* by which a gene might increase in frequency over its alleles, so is perfectly compatible with the gene's eye view (cf. Buss 1987, Sober and Wilson 1998).[2] Maynard Smith never fell prey to this confusion, realising from the outset that the gene's eye view was a heuristic perspective, not an empirical hypothesis about the course of evolution.

The gene's eye view has of course been criticised, in both the biological and philosophical literatures. Some have argued that it merely records the outcome of evolution while saying nothing about underlying causes (cf. Sober and Wilson (1998), Gould (2002)); others argue that phenomena such as epistatis, heterosis, and epigenetic inheritance cannot easily be accommodated by the genic view (cf. Wright (1980), Sober and Lewontin (1982), Avital and Jablonka (2000)). Maynard Smith was aware of these various criticisms, but basically unmoved by them (cf. Maynard Smith 1987). He was likewise unmoved by Leo Buss' claim in *The Evolution of Individuality* that a "hierarchical" approach is superior to a "genic" approach for understanding evolutionary transitions between units of selection. (Buss wrote: "to adopt a gene selection perspective is not wrong. It simply does not help unravel the central dilemma of our science" (1987, p. 55)). Though Maynard Smith's own work on the major transitions was deeply influenced by Buss, as he acknowledged, he did not accept Buss' argument for the superiority of the "hierarchical" approach; indeed, he argued that Buss' failure to adopt the gene's eye view had led him to some questionable conclusions (Maynard Smith and Szathmáry 1995, pp. 244–245).

Interestingly, both Williams and Hamilton *did* come to accept elements of a "hierarchical" approach, though without rescinding their commitment to gene's eye thinking. Williams became convinced that the genic neo-Darwinism of his earlier years, while essentially correct as a theory of microevolutionary change, could not account for evolutionary phenomena over longer time scales, and was thus an "utterly inadequate account of the evolution of the Earth's biota" (1992, p. 31). In particular, he became a staunch advocate of *clade selection* – a generalisation of species selection to monophyletic clades of any rank – which could potentially explain phenomena such as adaptive radiations, long-term phylogenetic trends, and biases in rates of speciation/extinction. In *Natural Selection* (1992), Williams argued that these phenomena cannot be explained by selectively-driven allele substitutions within populations, the

---

[2] Though Dawkins later acknowledged that opposing group to genic selection was a mistake, for genes are 'replicators' while groups are (potential) 'vehicles'; see Dawkins (1982).

evolutionary mechanism he had originally championed over all others. This book thus represents a substantial departure from the position of *Adaptation and Natural Selection*. Maynard Smith did not follow suit. He was unconvinced that there existed a broad class of evolutionary phenomena which genic neo-Darwinism could not explain, so could not see the need for the hierarchically expanded evolutionary theory that Williams advocated. Maynard Smith remained wedded to a thoroughgoing explanatory reductionism, closer to Williams' earlier than his later position.

Hamilton's views on the levels of selection also changed over time, primarily as a result of his interaction with George Price – with whom Maynard Smith co-authored his famous paper on animal conflicts, discussed above (cf. Hamilton 1996, Sober and Wilson 1998). Price's major contribution to evolutionary theory was to devise a novel formalism for describing a population's evolution over time, and to derive a simple equation describing the change in average phenotype from one generation to another – which has became known as "Price's equation" (Price 1972, 1995). The basic idea behind Price's equation is extremely simple. Imagine a population of organisms undergoing directional selection for a given character (e.g. height); we therefore expect the average population character (e.g. average height) to change over time. Price showed that the cross-generational change in average character can be written as the sum of two terms, one of which captures the effect of natural selection on the character, the other the fidelity with which the character is transmitted from parent to offspring (see Frank 1995, 1998, Grafen 1985, Michod 1999 or Okasha 2004 for details).[3] Though Price's equation is really no more than a mathematical tautology, applicable to any evolving system, it has proved valuable for thinking about many evolutionary problems, particularly where multiple levels of selection are involved.

Hamilton (1996) reports that his own attitude towards group selection changed when he discovered Price's work. Initially he had shared Williams' and Maynard Smith's scepticism, but Price convinced him that group selection, and multi-level selection more generally, deserved reconsideration (cf Sober and Wilson 1998, Okasha 2006a). In some ways this is odd, for Price's equation is simply a useful way of describing evolution, so implies nothing about the causal forces actually at work in nature. Price (1972) did briefly apply his formalism to selection in a group-structured population, but more by way of illustrating its flexibility that as an endorsement of group-level selection. Why then did Hamilton change his attitude towards group selection on discovering Price? The answer, I think, is that Price's formalism helps us understand what it *means* for selection to act simultaneously at multiple levels, and to appreciate the likely evolutionary consequences; it thus brings conceptual clarity to the levels of selection problem. Additionally, in the light of

---

[3] The first term is the covariance between character value and relative fitness, the second is the fitness-weighted average of the deviations in character value between parent and offspring.

Price, the range of evolutionary scenarios meriting the label 'group selection' seems larger than before; or so Hamilton thought.

From the brief description given above, it may be unclear *how* Price's equation achieves any of these things. Without going into the technical details (for which see Frank (1995), Hamilton (1975a) or Okasha (2006a)), the key point can be explained as follows. In a 'multi-level' evolutionary scenario, where smaller replicating units are nested within larger ones, Price's equation permits us to describe the *combined* effects of two (or more) levels of selection on the overall evolutionary change. This is because *natural selection at one level affects the transmission fidelity at the next level up*, thus leading to recursions between levels. So for example, suppose the two levels are individuals and groups. By applying the basic Price equation to the groups, as described above, we can write the overall evolutionary change as the sum of two terms, one reflecting selection on the groups, the other the fidelity with which groups transmit their 'character' to the next generation. But the latter depends, in part, on selection at the individual (within-group) level. If there is lots of within-group selection, then a group composed, for example, of individuals of two types A and B in equal proportion, may produce offspring predominantly of type A; the group will thus have a low transmission fidelity. So transmission bias at the group level corresponds to selection at the individual level. Thanks to this principle, Price's technique allows us to write the combined effects of individual and group selection in a single equation.

In a famous paper, Hamilton (1975a) showed how Price's equation can be generalised to an indefinite number of hierarchical levels, thus achieving, as he put it "a formal separation of the levels of selection" (p. 333). This in turn allows a number of key conceptual points to come across. Firstly, it shows that the balance between levels of selection depends on how much variance in fitness there is at each level. Thus in a two-level scenario, if most of the fitness variance is between groups then group selection will be strong; but if the variance is mainly within groups, individual selection will predominate. Secondly, it shows that selection at lower levels will tend to reduce the heritability at higher levels, thus weakening the response to selection at those levels. Thirdly, it suggests that for higher-level selection to win out, conflict-reducing mechanisms may be necessary, to reduce the fitness variance, hence opportunity for selection, among the lower-level units. (This principle plays a key role in Michod's work on evolutionary transitions in individuality – see Michod 1999). Finally, Price's equation permits an extremely simple derivation of Hamilton's famous rule – $r > c/b$ – for the spread of altruistic adaptations, as Hamilton himself showed (cf. Hamilton 1970; Grafen 1985; Frank 1998).

It bears re-emphasis that Price's equation itself does nothing to resolve empirical issues about the levels of selection in nature. However, the equation does suggest a criterion for how to identify the level(s) of selection in any given case – namely, there is a component of selection at any hierarchical level at which there is character-fitness covariance (cf. Okasha 2006a). This in turn suggests that Maynard Smith's requirements for group selection are excessively

strong. Recall that for Maynard Smith, group selection requires the existence of cohesive, spatially discrete groups, that "reproduce" by sending out propagules, and that go extinct. However as Hamilton noted, from a Price equation perspective this seems unnecessary; *any* population with discernible group structure, and where the groups differ in productivity, can legitimately be described as undergoing group selection. Indeed Hamilton wrote: "it may be best, using something like the Price formulation of selection, to think of *most* selection processes as having components at group, individual and haploid levels and to talk about the relative magnitudes of these components, rather than try to force all effects to submit to any one term" (1975b, p. 365, my emphasis). So for example, the idea that evolutionary game theory involves two levels of selection, which as we have seen Maynard Smith rejected, makes good sense from a Pricean perspective.

Maynard Smith was never a fan of Price's equation, despite having collaborated with Price, and did not employ it in his own work. The hierarchical picture of natural selection suggested by Price's equation did not appeal to him; he preferred to track evolutionary change directly, by adopting the gene's eye view. Interestingly, he explained this in terms of an abstract preference for reductionist methods in science: "I find the gene-centred approach both mathematically simpler and causally more appropriate, but this may merely reflect the fact that I prefer microscopic to holistic models: Maxwell–Boltzmann to classical thermodynamics, and Dawkins to Price's equation" (2002, p. 523). To understand this remark, it is crucial to note that the gene-centred and hierarchical or multi-level approaches are not in conflict; they are alternative ways of describing evolution, not alternative empirical hypotheses. This is a generalisation of the point stressed above, that group selection is perfectly compatible with the gene's eye view.

In an interview given shortly before his death, Maynard Smith went further, claiming that he "could not understand" Price's equation.[4] Obviously he did not mean this literally – the equation uses only the elementary statistical concepts of covariance and expectation, which Maynard Smith understood as well as anyone. What he meant, I think, is that he found Price's way of describing evolutionary dynamics non-perspicuous, i.e. he found it hard to attach biological significance to the components of Price's equation. By contrast, many other biologists, including ones whose evolutionary interests overlap with Maynard Smith's, have followed Hamilton in extolling the virtues of Price's equation, both as a modelling tool and as a source of conceptual insights (cf. Frank (1998), Michod (1999), Wade (1985), Sober and Wilson (1998)). This difference of opinion between Maynard Smith and Hamilton over Price's equation has left an important intellectual legacy; for it is reflected in the divergent approaches to studying the major evolutionary transitions, discussed below.

---

[4] The interview is available at http://www.peoplesarchive.com/browse/movies/3701

As has often been noted, the levels of selection question stems ultimately from the *abstract* nature of the principle of natural selection. Darwin argued that if a population of organisms vary in some respect, and if some variants leave more offspring than others, and if parents tend to resemble their offspring, then the composition of the population will change over time. But it is easy to see that Darwin's reasoning applies not just to individual organisms. *Any* entities which vary, reproduce differentially as a result, and beget offspring that are similar to them, could in principle be subject to Darwinian evolution. The basic logic of natural selection is the same whatever the "entities" in question are.

This fundamental point has been captured in different ways by different authors. Thus for example, Lewontin (1970) argued that natural selection can operate on any entities that exhibit "heritable variation in fitness"; such entities he called "units of selection" (p. 1). Thought Lewontin's analysis seems to capture the abstract Darwinian logic neatly, Hull (1981) and Dawkins (1982) offered a more elaborate ontology, arguing that *two* sorts of entity are involved in the Darwinian process, not one. "Replicators" are entities that bequeath structural copies of themselves to future generations, while "interactors" or "vehicles" are entities in which replicators are housed, and that interact with the environment in a way that leads to differential proliferation of variant replicators.

Though Maynard Smith was sympathetic to the Dawkins/Hull approach, and accepted the utility of the replicator/vehicle distinction, his preferred formulation of the "basic Darwinian principles" was actually closer to Lewontin's. Thus in a 1988 paper he wrote: "any population of entities with the properties of multiplication (one entity can give rise to many), variation (entities are not all alike, and some kinds are more likely to survive and multiply than others), and heredity (like begets like) will evolve. A major problem for current evolutionary theory is to identify the relevant entities" (1988a, p. 222). Interestingly, whereas Lewontin had used the label "units of selection" for entities satisfying these three conditions, Maynard Smith preferred the label "units of evolution". This is because he held that natural selection often operates on entities that satisfy the first two conditions, but lack heredity. Such entities can legitimately be called units of selection, Maynard Smith argued, but not units of evolution, since lacking heredity, they cannot be expected to evolve adaptations (1987, 1988a).

The distinction between units of selection and units of evolution does not feature in Maynard Smith's early work; he appears to have first formulated it in the mid-1980s. One use Maynard Smith made of the distinction was to suggest a novel way of conceptualising the trait-group models of D.S. Wilson. In his earlier writings, Maynard Smith was reluctant to regard the trait-group model as a genuine type of group selection at all, preferring to think of it as individual selection in a structured population with frequency-dependent fitness (cf. Maynard Smith 1976 and Section 3 above.) But in later papers,

Maynard Smith offered a different analysis, arguing that trait-group models *do* involve selection at the group level, but that the groups are not units of *evolution* (Maynard Smith 1987). This is because trait-groups do not satisfy the requirement of heredity – they do not give rise to daughter trait-groups with similar composition (unlike in the type of group selection envisaged by Wynne-Edwards). So although there can be selection between trait groups, with interesting evolutionary consequences, we would not expect trait groups themselves to evolve adaptations, according to Maynard Smith.

In *Unto Others*, Sober and Wilson (1998) contest this argument, in effect by questioning the distinction between units of selection and of evolution. They argue that a process of group-level selection is only evolutionarily interesting if the groups themselves exhibit heredity – on the grounds that a response to selection at any level requires the heritability of traits *at that level*. But trait-groups *do* exhibit heredity, they argue – despite periodically blending into the global mating pool. This periodic blending is simply the group-level analogue of sexual reproduction – it results in daughter trait-groups having multiple parents, rather than just one parent. But since sexual reproduction among individual organisms is compatible with organismic traits having positive heritability, the same must true at the trait-group level, Sober and Wilson reason. Thus trait-groups *can* evolve adaptations, and Maynard Smith's distinction between units of selection and of evolution is shown to be theoretically redundant.

How should this issue be resolved? In Okasha (2006a), I argue that Maynard Smith and Sober and Wilson are both partially correct. Maynard Smith is right that the role of the groups in trait-group models is disanalogous, in one crucial respect, to the role of groups in "traditional" discussions of group selection. However, Sober and Wilson are right that a certain *sort* of group heritability is still present in the trait-group model, and that it determines the response to group-level selection. The key to this reconciliation lies in an important distinction between two types of multi-level selection, emphasised by Damuth and Heisler (1988). (Precursors of the distinction can be found in Sober (1984) and Arnold and Fristrup (1982)). In multi-level selection 1 (MLS1), the individuals are the "focal" units, and the fitness of a group is defined as the average fitness of the individuals within it. MLS1 models thus deal with the evolution of an *individual* character in a group-structured population, as in Wilson's trait-group scenario. In multi-level selection 2 (MLS2), the groups themselves are the "focal" units, and group fitness is not defined as average individual fitness, but rather as expected number of offspring *groups*. MLS2 models thus deal with the evolution a *group* character, not an individual character. Damuth and Heisler (1988) show that a failure to distinguish between MLS1 and MLS2 has led to considerable confusion in the literature; see also Okasha (2001, 2006a).

The distinction between MLS1 and MLS2 helps resolve the tricky issue of the status of trait-group models. These models are of the MLS1 type – they are designed to explain the evolution of an individual character, often altruism, in a group-structured population, and thus define group fitness as average

individual fitness. By contrast, certain other treatments of group selection, e.g. that of Wynne-Edwards (1962), have described an MLS2 process, in which the groups themselves are the units whose demography we track. To that extent, Maynard Smith is right. However, Sober and Wilson are right that the concept of heredity can apply to trait-groups. If selection between trait-groups is to produce an evolutionary response, it is necessary that the set of individuals produced by a given trait-group be similar in composition to that trait-group itself, which constitutes group heritability of a sort. In Okasha (2006a), I use a formal description of the evolutionary dynamics to show that different notions of group heritability are relevant in MLS1 and MLS2.

Maynard Smith was never fully clear about the distinction between MLS1 and MLS2, though he was certainly aware of the logical differences between different models of higher-level selection. In part, this may have stemmed from his general dislike of multi-level approaches to evolution, discussed in Section 3 above. I suggest that had Maynard Smith appreciated the significance of the MLS1/MLS2 distinction, he would not have needed his distinction between units of selection and evolution, for to some extent the two distinctions are motivated by similar concerns. Furthermore, a number of the philosophical issues about the levels of selection, with which Maynard Smith grappled on many occasions, are considerably clarified by the MLS1/MLS2 distinction. One such issue is pluralism, which I discuss next.

Pluralism is the idea that the choice between certain theoretical alternatives is conventional, rather than factual – there is "no fact of the matter" about which alternative is correct. This idea has often surfaced in the levels of selection debate. Thus for example, Hamilton (1964) showed that the evolution of altruism can either be understood from an "inclusive fitness" or a "gene's eye" viewpoint – both are valid perspectives on the facts, rather than competing empirical hypotheses. Similarly, Dugatkin and Reeve (1994) argue that certain evolutionary phenomena can either be interpreted in terms of group or individual selection; there is objective answer about which is right. More recently, Kerr and Godfrey-Smith (2002) have developed a general argument for pluralism. They construct a simple evolutionary model of selection in a hierarchically structured population, and show that the model's dynamics can be fully described by two sets of parameter values. The first set ascribes fitness values only to the lower-level individuals; the second set ascribes fitness values to both individuals and groups.[5] Kerr and Godfrey-Smith demonstrate that the two parameterisations are mathematically equivalent – each set of parameter values can be derived from the other, so the overall evolutionary change can be expressed in terms of either.

Maynard Smith was sympathetic to pluralism, though had reservations. He agreed that a single evolutionary process could often be modelled, or mathematically described, in alternative ways, and that the choice between the

[5] 'Individual' and 'group' have purely abstract meanings here. For example, the individuals and groups could be cells and multi-celled organisms, or organisms and colonies.

alternatives was heuristic, not factual (cf. Maynard Smith 1987, 2002). However, unsurprisingly, he also admitted to a general bias in favour of lower-level descriptions where possible. Thus in the inclusive fitness versus gene's eye case, he argued that the gene's eye approach was "both mathematically simpler and causally more appropriate" (2002, p. 523). Similarly, he argued that a multilevel description of evolutionary game theory, in which the 'groups' are pairs of interacting individuals, of the sort championed by Sober and Wilson (1998), was "formally possible [but] causally inappropriate" (2002, p. 524). Far better to treat the individual as the unit of adaptive advantage, Maynard Smith thought, than the ephemeral pair. In particular, Maynard Smith stressed the oddity of regarding a pair of interacting individuals as an adaptive unit when the interaction is competitive, rather than cooperative.

I think Maynard Smith's ambivalence regarding pluralism had two sources. Firstly, he realised that a pluralistic, or conventionalist, resolution cannot apply to *all* levels of selection disputes – in some cases there *is* a fact of the matter. For example, when Wynne-Edwards (1962) and Lack (1966) disagreed over whether reproductive restraint in birds had evolved by group selection, their disagreement was a factual one about the course of evolutionary history; it would be absurd to suggest that there is no objective fact about who was right. Secondly, even in cases where alternative mathematical descriptions are possible, the intuition that one of the descriptions is more causally faithful than the other is often very strong. As the quoted remarks in the foregoing paragraph show, Maynard Smith himself had such intuitions, which he expressed in terms of "causal appropriateness". I think he realised that this notion of causal appropriateness would be difficult to spell out precisely, thus explaining his circumspection regarding the idea of pluralism.

In forthcoming work, I have tried to develop a systematic approach to these tricky issues (Okasha 2006a). The first problem is to determine which levels of selection disputes admit of a conventionalist resolution and which do not, i.e. which are like the Wynne-Edwards/Lack case and which are not? Here the distinction between MLS1 and MLS2 plays a crucial role. In an MLS1 scenario, i.e. where the lower-level individuals are the focal units, it will always be possible to describe the evolutionary dynamics in both single-level and multilevel terms, as the Kerr and Godfrey-Smith result shows. (The Price equation permits an even simpler proof of this result.) But in an MLS2 scenario, in which the higher-level groups are the focal units and possess autonomously-defined fitnesses, this is not so. Evolutionary change, in an MLS2 scenario, refers to change in the frequency of different types of *groups*, not individuals; it is thus impossible to capture the evolutionary dynamics in lower-level terms, without ascribing fitnesses to groups as units. Pluralism is therefore not an option; any description of the system's evolution that does not invoke group selection will simply be false.

The second problem is to unpack the idea that one of a pair of mathematically inter-changeable descriptions may be more "causally appropriate" than the other. A good way of addressing this problem, I argue, is to use Price's

covariance formulation of selection (Okasha 2006a). Price teaches us that natural selection requires character-fitness covariation; this is the essence of his equation. So in order to determine the potential level(s) of selection in any given case, the first task is to figure out the hierarchical level(s) at which character and fitness covary. But this does not resolve the causal question, for it is obvious that two variables may covary even if there is no direct causal link between them. Therefore, we need to determine which character-fitness covariances are due to a direct causal link between the variables in question, and which are not. In particular, we must consider the possibility that a character-fitness covariance at one hierarchical level may be a side-effect, or byproduct, of causal processes taking place at a *different* level. If we can make sense of this possibility, we can provide substance to the idea that one description may be more causally appropriate than another, despite their mathematical interchangeability. In Okasha (2006a), I show how causal graphs can be used to address this problem in precise terms.

I do not know whether Maynard Smith would have been happy with this way of fleshing out what it means for one mathematical description of an evolving system to be more causally appropriate than another. There is some reason to think he would not, given his reservations about the covariance formulation of selection. However, it is obvious that *something* must be said about how the notion of causal appropriateness should be understood, given the centrality that Maynard Smith accorded it in his discussions of pluralism. Construing the notion the way I suggest, i.e. taking causally appropriate descriptions to be ones in which all of the posited character-fitness covariances are the result of direct causal links between the variables in question, permits general philosophical lessons about causality to be brought to bear on the problem.

The major transitions in evolution and the re-formulation of the levels question

In their treatment of the 'major transitions in evolution', Maynard Smith and Szathmáry (1995) accord a pivotal role to the levels of selection issue. On their characterisation, a major transition occurs whenever there is a "change in the method of information transmission" between generations (p. 6). From this it does not *necessarily* follow that major transitions have anything to do with the evolution of new hierarchical levels, but many of them turn out to. For Maynard Smith and Szathmáry say: "one feature is common to many of the transitions: entities that were capable of independent replication before the transition can replicate only as part of a larger whole after it" (p. 6). Examples are the transition from prokaryotes to eukaryotes, from single-celled to multi-celled organisms and from solitary organisms to colonies. Such transitions immediately raise two questions. Why was it advantageous for the lower-level units to give up their free-living existence and coalesce into a larger unit? And why is the integrity of the larger unit not disrupted by selection among the lower-level units? This is of course a classical levels of selection problem – the

larger unit's integrity requires that higher-level selection win out over lower-level selection, e.g. by evolving mechanisms for conflict suppression.

In the work of Buss (1987) and Michod (1999), the centrality of the levels of selection issue to the problem of evolutionary transitions is even clearer. This is because unlike Maynard Smith and Szathmáry (1995), these authors do not characterise the transitions in terms of "information transmission", but rather directly in terms of the evolution of new levels of "individuality". So for Maynard Smith and Szathmáry, it is simply a contingent fact that many of the transitions involve smaller replicating units coalescing into larger ones, but for Buss and Michod this is a necessary fact – it is what they take an "evolutionary transition" to be. Despite this difference, the approach of all three authors is fairly similar; indeed, both Michod and Maynard Smith and Szathmáry note their indebtedness to Buss. However, whereas Buss and Michod favour adopt a "hierarchical" approach (and in Michod's case, makes extensive use of Price's equation), Maynard Smith and Szathmáry favour a genic approach. They write: "the transitions must be explained in terms of immediate selective advantage to individual replicators: we are committed to the gene-centred approach outlined by Williams (1966) and made still more explicit by Dawkins (1976)" (1995, p. 8).

In a previous paper, I have argued that the recent work on the evolutionary transitions has led the traditional levels of selection question to be subtly transformed (Okasha 2006b). Briefly put, the transformation is as follows. The traditional formulation of the levels question, exemplified by works such as Lewontin (1970), has a 'synchronic' orientation. The biological hierarchy with its various levels of nestedness is assumed to be already in place; the question is about the level(s) at which selection currently acts, or acted in the recent past. But as Griesemer (2000) insightfully notes, such formulations say nothing about how the biota came to be hierarchically organised in the first place; they simply take it as a given. By contrast, recent work on the major transitions construes the levels question in a 'diachronic' way – the aim is to understand how the various levels in the hierarchy came to exist. From the diachronic perspective, the levels of selection question is not simply about the evolution of adaptations at pre-existing hierarchical levels, but about the evolution of the biological hierarchy itself.

The shift from a synchronic to a diachronic perspective gives the levels of selection debate a new sense of urgency. Some biologists (though not Maynard Smith) were inclined to dismiss the traditional debate as a storm in a teacup, 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. The same is true of cells and chromosomes. 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.

Another respect in which the traditional discussions sit uneasily with the new diachronic perspective concerns the very *concepts* used to understand natural selection. Consider for example the Dawkins/Hull replicator/interactor conceptualisation, discussed above. Replicators are entities which "pass on their structure intact" and are characterised by their "longevity" and "copying fidelity"; interactors are entities which "interact as cohesive wholes with their environment". This account of evolution of natural selection proved valuable for certain purposes, but it is not well-suited to studying the major transitions, for a simple reason. The longevity and copying fidelity of replicators (such as genes) and the cohesiveness of interactors (such as organisms) are highly evolved properties, themselves the product of many rounds of cumulative selection (Griesemer 2000). The first replicators must have had extremely poor copying fidelity, and the earliest multi-cellular organisms must have been highly non-cohesive entities, owing to competition between their constituent cell-lineages (Buss 1987, Michod 1999). If we wish to understand how copying fidelity and cohesiveness evolved in the first place, we clearly cannot build them into the very concepts used to describe evolution by natural selection.

In light of this point, what becomes of Maynard Smith and Szathmary's insistence on a "replicator first" approach to studying the major transitions? If replicators were relatively late arrivals on the scene, how can they form the basis for a general theory of evolutionary transition? Part of the answer may be that Maynard Smith and Szathmáry are using "replicator" in a somewhat looser sense than Dawkins, without the requirement of high-fidelity copying. But this does not resolve the matter entirely. Griesemer (2000) makes the important point that in a major transition, it is not strictly the case that old replicators get packaged into new ones, as Maynard Smith and Szathmáry (1995) say. For the new entities that evolve during transitions, e.g. multi-celled organisms, insect colonies, human societies etc. clearly do not even approximate the definition of a replicator. Griesemer argues that these entities are *reproducers*. (This is not just a new word – he offers a sophisticated analysis of what a reproducer is.) Interestingly, in a paper written after their book, Szathmáry and Maynard Smith (1997) accept Griesemer's account of the ontology of the major transitions, agreeing that reproducers rather than replicators are the fundamental units. This in turn brings Szathmáry and Maynard Smith closer to the "hierarchical" approach of Michod and Buss, for in effect it constitutes a shift away from a strict genic methodology.

These reflections suggest that moving from a synchronic to a diachronic formulation of the levels question necessitates a certain amount of conceptual revision. The concepts needed to understand adaptation at pre-existing hierarchical levels differ somewhat from those needed to understand the evolution of the hierarchy itself. Furthermore, a number of topics discussed under the traditional levels of selection rubric look substantially different from a diachronic perspective. One such topic is group selection.

We saw above that in 1960s and 1970s, a consensus emerged that group selection was a relatively minor evolutionary force, thanks in part to Maynard Smith's contributions. The apparent paucity of co-operative groups in nature, by contrast with the all-pervasiveness of individual adaptation, lent support to this view. But in the light of the major transitions, this view needs re-consideration. For as Michod (1999) has emphasised, multi-celled organisms *are* groups of co-operating cells, and (eukaryotic) cells are groups containing nuclear chromosomes and organelles. Since cells and multi-celled creatures obviously have evolved, and function well as adaptive units, the efficacy of group selection cannot be denied. Just as the blanket assumption that the individual organism is the sole unit of selection is untenable from a diachronic perspective, so too is the assumption that group selection is a negligible force. For by 'frameshifting' our perspective downwards, it becomes apparent that individual organisms *are* co-operative groups, so are the *product* of group selection!

Does this imply that the rejection of group selection in the 1960s and 1970s was based on faulty arguments? I suspect that Maynard Smith would have answered "no", primarily because he insisted on a sharp distinction between group and kin selection, as we have seen, and argued that kin selection was what permitted multi-cellularity to evolve. The cells within a typical multi-celled organism are clonally derived from a single fertilised zygote, so are highly related to each other. The integrity of the organism is thus explained by classical kin selection. Of course, one *can* study the evolution of multi-cellularity using multi-level selection theory, as Michod (1999) does, and thus think in terms of selection within and between groups; but this does not alter the fact that kinship between cells is the key factor.[6] Kinship plays a critical role in many of the other evolutionary transitions too. Since Maynard Smith was adamant that kin and group selection were different evolutionary mechanisms, I doubt he would have accepted the argument that the major transitions show the power of group selection. The issue is not clear-cut, though, for in at least some of the transitions co-operative groups are formed by *unrelated* individuals, e.g. prokaryotes → eukaryotes, so kin selection cannot have been the driving factor.

To conclude, it is striking how the levels of selection issue, which began life as an important but local discussion within sociobiology, has ramified so broadly in recent years, as its relevance to the theory of evolutionary transitions has become clear. Given that Maynard Smith was an active participant in the original sociobiological discussions, and was later instrumental in bringing the topic of evolutionary transitions to centre-stage, it is unsurprising that the levels issue was so important to him. On this issue as on many others, his clarity of thought, analytical power, and intellectual honesty were unsurpassed, setting a benchmark for others to aspire to in their own work.

---

[6] In multi-level terms, the effect of kinship is to increase the between-group variance and decrease the within-group variance (where a 'group' is a group of cells, or proto-organism), thus increasing the relative power of group selection.

References

Arnold A.J. and Fristrup K. 1982. The theory of evolution by natural selection: a hierarchical expansion. Paleobiology 8: 113–129.

Avital E. and Jablonka E. 2000. Animal Traditions: Behavioural Inheritance in Evolution. Cambridge University Press, Cambridge.

Buss L. 1987. The Evolution of Individuality. Princeton University Press, Princeton.

Damuth J. and Heisler I.L. 1988. Alternative formulations of multi-level selection. Biol. Philos. 3: 407–430.

Dawkins R. 1976. The Selfish Gene. Oxford University Press, Oxford.

Dawkins R. 1982. The Extended Phenotype. Oxford University Press, Oxford.

Dugatkin L.A. and Reeve H.K. 1994. Behavioural ecology and levels of selection: dissolving the group selection controversy. Adv. Study Behav. 23: 101–133.

Eigen M. and Schuster P. 1979. The Hypercycle, a Principle of Natural Self-Organization. Springer-Verlag, Berlin.

Eigen M., Schuster P., Gardiner W. and Winkler-Oswatitsch R. 1981. The origin of genetic information. Sci. Am. 244(4): 78–94.

Frank S.A. 1995. George Price's contribution to evolutionary genetics. J. Theor. Biol. 175: 373–388.

Frank S.A. 1998. Foundations of Social Evolution. Princeton University Press, Princeton.

Gould S.J. 2002. The Structure of Evolutionary Theory. Harvard University Press, Harvard.

Grafen A. 1985. A geometric view of relatedness. Oxf. Surv. Evol. Biol. 2: 28–89.

Griesemer J. 2000. The units of evolutionary transition. Selection 1: 67–80.

Hamilton W.D. 1963. The evolution of altruistic behaviour. Am. Nat. 97: 354–356, reprinted in Hamilton (1996), 6–8.

Hamilton W.D. 1964. The genetical evolution of social behaviour I. J. Theor. Biol. 7: 1–16, reprinted in Hamilton (1996), 31–46.

Hamilton W.D. 1970. Selfish and spiteful behaviour in an evolutionary model. Nature 228: 1218–1220, reprinted in Hamilton (1996), 177–182.

Hamilton W.D. 1975a. Innate social aptitudes in man: an approach from evolutionary genetics, reprinted in R. Fox (ed.) Biosocial Anthropology. Wiley, New York, pp. 133–155, reprinted in Hamilton (1996), 315–352.

Hamilton W.D. 1975b. Gamblers since life began: barnacles, aphids, elms. Q. Rev. Biol. 50: 175–180, reprinted in Hamilton (1996), 357–367.

Hamilton W.D. 1996. Narrow Roads of Gene Land Volume 1: Evolution of Social Behaviour. W.H. Freeman, New York.

Hull D. 1981. Units of evolution: a metaphysical essay. In: Jensen U.J. and Harré R. (eds), The Philosophy of Evolution, Harvester Press, Brighton, pp. 23–44.

Kerr B. and Godfrey-Smith P. 2002. Individualist and multi-level perspectives on selection in structured populations. Biol. Philos. 17: 477–517.

Kerr B., Neuhauser C., Bohannan B.J.M. and Dean A.M. (forthcoming). Local Migration Promotes Competitive Restraint in a Host-Pathogen 'Tragedy of the Commons'.

Lack D. 1966. Population Studies of Birds. Clarendon Press, Oxford.

Lewontin R.C. 1970. The units of selection. Annu. Rev. Ecol. Syst. 1: 1–18.

Maynard Smith J. 1964. Group selection and kin selection. Nature 201: 1145–1147.

Maynard Smith J. 1976. Group selection. Q. Rev. Biol. 61: 277–283.

Maynard Smith J. 1978. The Evolution of Sex. Cambridge University Press, Cambridge.

Maynard Smith J. 1979. Hypercycles and the origin of life. Nature 20: 445–446.

Maynard Smith J. 1982. Evolution and the Theory of Games. Cambridge University Press, Cambridge.

Maynard Smith J. 1983. Game theory and the evolution of cooperation. In: Bendall D.S. (ed.), Evolution from Molecules to Man, Cambridge University Press, Cambridge, pp. 445–456.

Maynard Smith J. 1984. Paleontology at the high table. Nature 309: 401–402.

Maynard Smith J. 1987. How to model evolution. In: Dupré J. (ed.), The Latest on the Best: Essays on Evolution and Optimality, MIT Press, Cambridge, MA, pp. 119–131.

Maynard Smith J. 1988a. Evolutionary progress and the levels of selection. In: Nitecki M.H. (ed.), Evolutionary Progress, University of Chicago Press, Chicago, pp. 219–230.

Maynard Smith J. 1988b. Selection for recombination in a polygenic model – the mechanism. Genet. Res. 51: 59–63.

Maynard Smith J. 1988c. 'Current Controversies in Evolutionary Biology', in Did Darwin Get it Right?. Chapman-Hall, New York.

Maynard Smith J. 1991. A Darwinian view of symbiosis. In: Margulis L. and Fester R. (eds), Symbiosis as a Source of Evolutionary Innovation, MIT Press, Cambridge, MA, pp. 26–39.

Maynard Smith J. 1998. The origin of altruism. Nature 393: 639–640.

Maynard Smith J. 2002. Commentary on Kerr and Godfrey-Smith. Biol. Philos. 17(4): 523–527.

Maynard Smith J. and Price G.R. 1973. The logic of animal conflict. Nature 246: 15–18.

Maynard Smith J. and Szathmáry E. 1995. The Major Transitions in Evolution. Oxford University Press, Oxford.

Michod R.E. 1999. Darwinian Dynamics: Evolutionary Transitions in Fitness and Individuality. Princeton University Press, Princeton.

Nunney L. 1985. Group selection, altruism, and structured-deme models. Am. Nat. 126: 212–230.

Okasha S. 2001. Why won't the group selection controversy go away?. Br. J. Philos. Sci. 52(1): 25–50.

Okasha S. 2004. Multi-level selection and the partitioning of covariance: a comparison of three approaches. Evolution 58(3): 486–494.

Okasha S. 2006a. Evolution and the Levels of Selection. Oxford University Press, Oxford, (in press).

Okasha S. 2006b. Multi-level Selection and the Major Transitions in Evolution, Philosophy of Science (Proceedings of the 2004 PSA) (in press).

Price G.R. 1972. Extension of covariance selection mathematics. Ann. Hum. Genet. 35: 485–490.

Price G.R. 1995. The nature of selection. J. Theor. Biol. 175: 389–396 (written circa 1971).

Queller D.C. 1992. Quantitative genetics, inclusive fitness, and group selection. Am. Nat. 139: 540–558.

Segerstråle U. 2000. Defenders of the Truth: The Battle for Science in the Sociobiology Debate and Beyond. Oxford University Press, Oxford.

Sober E. 1984. The Nature of Selection. Chicago University Press, Chicago.

Sober E. and Lewontin R. 1982. Artifact, cause and genic selection. Philos. Sci. 49: 157–180.

Sober E. and Wilson D.S. 1998. Unto Others: the Evolution and Psychology of Unselfish Behavior. Harvard University Press, Cambridge, MA.

Szathmáry E. and Hammerstein P. 2004. John Maynard Smith (1920–2004). Nature 429: 258–259.

Szathmáry E. and Maynard Smith J. 1997. From replicators to reproducers: the first major transitions leading to life. J. Theor. Biol. 187: 555–571.

Uyenoyama M. and Feldman M.W. 1980. Theories of Kin and group selection: a population genetics perspective. Theor. Popul. Biol. 17: 380–414.

Wade M. 1985. Soft selection, hard selection, kin selection, and group selection. Am. Nat. 125: 61–73.

Williams G.C. 1966. Adaptation and Natural Selection. Princeton University Press, Princeton.

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

Wilson D.S. 1975. A theory of group selection. Proc. Natl. Acad. Sci. USA 7(2): 143–146.

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

Wilson D.S. 1987. Altruism in Mendelian populations derived from sibling groups: the haystack model revisited. Evolution 41: 1059–1070.

Wright S. 1980. Genic and organismic selection. Evolution 34: 825–843.

Wynne-Edwards V.C. 1962. Animal Dispersion in Relation to Social Behaviour. Oliver and Boyd, Edinburgh.