

Social Revolution
Review essay on Andrew F. G. Bourke: Principles of Social Evolution, Oxford
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Abstract

Andrew Bourke's *Principles of Social Evolution* identifies three stages that characterize an evolutionary transition in individuality and deploys inclusive fitness theory to explain each stage. The third stage, social group transformation, has hitherto received relatively little attention from inclusive fitness theorists. In this review, I first discuss Bourke's "virtual dominance" hypothesis for the evolution of the germ line. I then contrast Bourke's inclusive fitness approach to the major transitions with the multi-level approach developed by Richard Michod, Samir Okasha and others. I suggest that, rather than choosing between these approaches, we should exploit the strengths of both. Finally, I stress the need for a firmer conceptual grasp of the nature of social group transformation.

Like all the best books in evolutionary biology, Andrew Bourke's *Principles of Social Evolution* (2011) is one long argument. Here's the conclusion:

Hamilton's inclusive fitness theory (kin selection theory) provides a general theory of social evolution powerful and versatile enough to serve as the conceptual foundation for understanding the major transitions in evolution. (p. 27)

In synthesizing a vast array of theoretical and empirical work within a unifying Hamiltonian framework, Bourke makes a powerful case. Even those left unmoved by the book's core argument, however, will still find countless invaluable insights along the way. Indeed, when a book is so rich in fascinating examples, so deft in its handling of subtle conceptual and theoretical issues, and yet so accessible to non-specialists, it seems a shame to give away too many spoilers. In this review, I focus selectively on the most novel aspects of Bourke's framework and on the philosophical issues to which they give rise.

In the next section, "Social group transformation", I highlight the bold ambitions of Bourke's project. In "Virtual dominance", I examine Bourke's "virtual dominance" hypothesis for the evolution of the germ line. In "Kin selection and its rivals", I contrast Bourke's inclusive fitness approach to the major transitions with the multi-level approach developed by Richard Michod, Samir Okasha and others. I suggest that, rather than choosing between these approaches, we should exploit the strengths of both. In "The elusive individual", I stress the need for a firmer conceptual grasp of what the process of social group transformation consists in. In "In praise of big pictures", I consider the distinctive value of the broad-brush theorizing exemplified by *Principles of Social Evolution* in a field in which formal modelling increasingly predominates.

Social group transformation

There is no denying the audacity of Bourke's project. The book is a manifesto for an "expanded view of social evolution" that brings within the scope of sociobiology phenomena well outside its traditional heartland:

Social evolution has grown outwards from the study of the beehive and the baboon troop to embrace the entire sweep of biological organization. It claims as its subject matter not just the evolution of social systems narrowly defined, but the evolution of all forms of stable biological grouping, from genomes and eukaryotic unicells to multicellular organisms, animal societies, and interspecific mutualisms. (p. 7)

Bourke's goal, in short, is to elucidate principles that apply whenever new levels of biological organization come into being. To this end, he identifies three stages through which any such process must pass: (i) social group formation, (ii) social group maintenance, and (iii) social group transformation. These three explananda form the backbone of the book.

As Bourke is keen to emphasize, most work in sociobiology is directed at one of the first two stages. Yet the major transitions are about more than the evolution of stable social groups: they also involve the transformation of those social groups into unified, higher-level individuals. Bourke suggests that his focus on the problems of social group transformation is the central novelty of his approach (see pp. 21–22). Accordingly, it will be central topic of this review.

One might imagine that an expanded view of the explananda of sociobiology would call for novel explanatory resources—new mechanisms, new concepts, new theories. But the second audacious feature of Bourke’s project is its theoretical conservatism: in Bourke’s eyes, the resources we already have—specifically, W. D. Hamilton’s (1964) inclusive fitness theory—are adequate to the task. This claim sounds mild enough in the context of Bourke’s second stage, social group maintenance: inclusive fitness theory was, after all, designed to explain how altruistic (and spiteful) behaviour can be evolutionarily stable. It sounds bolder, however, in the context of Bourke’s first stage, where the aim is to explain not the stability of cooperation given certain kinds of group structure, but the origin of group structure itself (see Calcott 2008 for more on this distinction). And it sounds boldest of all in the context of Bourke’s third stage, where the aim is to explain the dizzying functional complexity that characterizes an integrated, higher-level individual. If inclusive fitness theory can explain all this, it will have explained far more than it was originally intended to explain.

In the most original and compelling part of the book (Ch. 6), Bourke argues that an inclusive fitness perspective does indeed yield insights into the origins of complexity. Expanding on an earlier paper (Bourke 1999), he argues that inclusive fitness considerations predict the existence of a positive feedback loop between group size and social complexity. The proposal, in a nutshell, is that an increase in group size affects the inclusive fitness interests of the group members in ways that promote greater complexity, while an increase in complexity enables the evolution of ever larger social groups. Bourke’s in-depth defence of this “size-complexity hypothesis” makes for a fascinating foray into largely uncharted territory. I now want to consider in greater detail one aspect of this argument.

Virtual dominance

In a particularly striking section, Bourke applies the apparatus of reproductive skew theory to the problem of the origin of the germ line (see pp. 179–183, 186). Reproductive skew theory comprises a cluster of modelling strategies deployed to explain reproductive inequality in social groups (see Johnstone 2000). So-called “transactional” models (see, e.g., Johnstone and Cant 1999; Reeve 2000) consider two individuals, a dominant and a subordinate, and aim to predict how much output the dominant will concede to the subordinate to discourage it from leaving. Inclusive fitness considerations are central to such models: unsurprisingly, they tend to predict that a subordinate will require less of a personal fitness incentive to cooperate when it is closely related to the dominant.

What do transactional models predict when we allow for more than two interacting individuals, and when control of the reproductive skew is distributed evenly throughout a

social group rather than concentrated in the hands of a single dominant? A model due to Reeve and Jeanne (2003) suggests that, even when control is evenly distributed throughout a multi-member group, reproductive capacity will still end up concentrated in the hands of a single “virtual dominant”—namely, the individual (or class of individuals, in the event of a tie) to which the rest of the group has the greatest mean relatedness.

As Reeve and Jeanne note, the virtual dominant in an insect colony will tend to be the queen. Somewhat less intuitively, the virtual dominants in a group of cells produced by clonal cell division from a unicellular ancestor will be members of the cell line which accumulates the fewest mutations over time. Since mutations occur during cell division, this will tend to be the slowest dividing cell line. If the “virtual dominance” hypothesis is correct, therefore, it suggests a novel explanation for the origins of the germ line: the germ line originated as the slowest dividing cell line in a multicellular group, and it holds exclusive rights to reproduction by virtue of being the line to which the other cell lines have the greatest mean relatedness.

Though Reeve and Jeanne were the first to articulate this hypothesis, Bourke is the first to apply it in detail in the context of the major transitions, and the first to bring it to the attention of an audience beyond theoretical biology. He should be applauded on both counts—it is an intriguing proposal, and its application to the evolution of multicellularity is particularly innovative. There is no doubt, however, that the hypothesis is still extremely tentative.

Here is one reason for caution: Reeve and Jeanne’s model assumes that individuals will relentlessly attempt to alter the reproductive skew in favour of their closest relatives, with a degree of intensity proportional to the relatedness between actor and recipient minus the mean relatedness between the actor and the other individuals in the group (Reeve and Jeanne 2003, p. 1043). From this assumption it follows that, at any given moment, there is always a net transfer of reproductive resources in favour of the individual to which the other group members have the greatest mean relatedness (Reeve and Jeanne 2003, p. 1043). This transfer of resources continues until it hits an exogenous constraint—when, for example, one dominant individual holds all the reproductive power, or when the average fitness of the group falls below some critical threshold for group stability. In short, the virtual dominance outcome stems directly from a non-trivial assumption of the model, viz., that the intensity with which an actor will attempt to alter the skew in favour of some individual scales linearly with its differential relatedness to that individual.

There are reasons to doubt whether this assumption will hold in general. For instance, the intensity of an individual’s skew-altering behaviour might depend on the frequency of other individuals disposed to alter the skew in the same direction: if no one shares your interests, attempting to alter the skew alone may well be futile; but if too many of your group mates share your interests, there may well be an incentive to free-ride on their efforts. A more detailed model would endogenize the trade-off a group member makes between its interest in shifting the reproductive skew and its other fitness interests, and it remains to be seen

whether the equilibria of such a model would still indicate the presence of a virtual dominant.¹

This is a serious caveat, but it should not blind us to the potential value of the virtual dominance hypothesis. It may yet represent a major breakthrough, for it provides a putative account of how germ-soma separation arises purely through the social interactions of lower-level entities. More generally, the application of reproductive skew theory to the major transitions represents a promising avenue for future research.

Kin selection and its rivals

For Bourke, all three stages of a transition in individuality are characterized in terms of groups and the changes they undergo: groups are formed, they are stabilized, and they are transformed. Given this, it is perhaps a little surprising that Bourke so assiduously avoids any appeal to group-level properties or processes in explaining these phenomena. In Bourke's framework, the formation, maintenance and transformation of a social group is to be explained wholly in terms of the inclusive fitness of the lower-level entities: concepts such as group selection, group adaptation, group fitness and group heritability have no part in the story. This disappearance of the group seems all the more curious given that a highly influential approach to social group transformation—that of Richard E. Michod and colleagues—conceives of the process explicitly in terms of fitness trade-offs at the group level (see, e.g., Michod 1999, 2005, 2006; Michod and Nedelcu 2003; Okasha 2006, 2009).

Though Bourke comments favourably on Michod's work (see pp. 179–80), the two theorists plainly conceive of social group transformation in very different terms. For Michod, the evolution of individuality essentially involves the “fitness decoupling” of a group from its members, and the consequent “export” of fitness from the parts to the whole. He argues that these processes culminate in the lower-level entities ceasing altogether to be bearers of Darwinian fitness (see Michod 1999, 2005). By contrast, Bourke eschews any ascription of fitness to groups. Even in the final stages of a transition, Bourke sees the fundamental bearers of fitness as the lower-level group members, which evolve ever more sophisticated forms of cooperation in order to maximize their own inclusive fitness.

While it seems clear that Bourke's inclusive fitness perspective leads to many valuable insights, one wonders if we can really afford to jettison the concepts and methods of the multi-level framework Michod and colleagues have developed. This leads naturally to a deeper worry that cuts to the heart of Bourke's project: is the theoretical unity for which he strives necessary—or even desirable—in the context of explaining the major transitions? Can we not, in David Queller's (1997) words, “have it both ways”?

It is no secret that inclusive fitness theorists and multi-level selection theorists rarely see eye to eye, let alone pause to consider the possibilities for fruitful interaction (see Okasha 2006, 2010; Borrello 2010). Yet given the formal similarities between the two approaches, the animosity between their respective proponents is hard to justify. Both approaches typically begin with an a priori partition of the Price equation. In the kin selection partition, we split

the change attributable to selection into components separately attributable to the average direct and average indirect fitness effects of the social behaviour under consideration (see, e.g., Queller 1992a; Gardner et al. 2011). In the multi-level partition, we split the change into components separately attributable to selection within groups and selection between groups (see, e.g., Price 1972; Wade 1985; Okasha 2006).² In each case, the relevant parameters may be estimated in order to predict the response to selection. From the kin selection partition, we derive Hamilton's famous rule that a social behaviour will be favoured by selection if and only if the relatedness between actor and recipient exceeds the cost-benefit ratio (Hamilton 1964). From the multi-level partition, we may derive an analogous rule: an altruistic behaviour will be favoured if and only if selection for the trait between groups is stronger than selection against the trait within groups. The approaches are predictively equivalent in the following sense: if the relevant parameters are measured accurately, the two approaches will always make the same prediction regarding the direction of the response to selection (see Marshall 2011).

Though long recognized in some quarters (see, e.g., Hamilton 1975; Grafen 1984; Queller 1992b), the point appears to be lost on a surprising number of kin selection's recent critics, who persist in constructing ever more ingenious models in which multi-level selection theory is alleged to deliver a prediction that cannot be derived within a kin selection framework (see, e.g., Wilson and Hölldobler 2005; Traulsen and Nowak 2006; Traulsen 2010). In all such cases, Hamilton's defenders have shown that the supposed predictive failures of kin selection theory arise from a misinterpretation of the relevant parameters, not a genuine non-equivalence between the theories (see, e.g., Foster et al. 2006; Lehmann et al. 2007; Gardner et al. 2011). The debate has an odd and often frustrating feel, since, on the standard formalizations of the two theories, one can prove that they are predictively equivalent.

Kin selection does not deserve the pummelling it so often receives, and Bourke's robust advocacy of the theory in the face of recent critiques (see especially Chapter 2, pp. 57–71) is very welcome. Yet I worry that Bourke, like many of his Hamiltonian allies, has been pushed by the protracted and somewhat bitter nature of the debate towards a monist standpoint on which a multi-level framework is acknowledged as a mathematically equivalent alternative only so that it can be ignored for serious explanatory purposes. When Bourke, having shown the widely acknowledged equivalence between the two frameworks, adds that “[t]he present book uses the methodology and language of inclusive fitness theory because they have proved useful for the issues it addresses” (p. 65), it is hard not to see this as a subtle gibe at the multi-level alternative—and indeed multi-level selection receives no further mention in the book.³

Why might a kin selection approach be more useful in general than a multi-level approach? One reason often cited is that relatedness is easier to measure than the parameters of a multi-level model, since it may be determined using molecular markers (see Queller and Goodnight 1989). This is true of Bourke's favourite example—the eusocial Hymenoptera—and many social vertebrates. Yet Bourke's “expanded view of social evolution” requires us to look for social phenomena beyond these traditional and much-studied cases; and, while this broad

conception of the field provides new and exciting work for kin selection theory, it is also a source of novel complications. Two examples spring to mind. One is social evolution in microbial populations, where, owing to horizontal gene transfer, a high rate of genetic mutation, and the difficulty of determining who is interacting with whom, the measurement of relatedness can be problematic (see West et al. 2007). Though a multi-level approach to microbial evolution may well encounter serious difficulties of its own, its ability to avoid this particular methodological hurdle suggests that it may be an option worth pursuing (see Velicer and Vos 2009 for some initial steps). The other is social evolution in human populations, where recent work has placed considerable emphasis on models of “cultural group selection” (see, e.g., Heinrich and Boyd 2001; Heinrich 2004; Boyd and Richerson 2010). While the equivalence of kin and group selection suggests that any such model could be reformulated as a model of “cultural kin selection”, the relevant relatedness coefficient would concern cultural rather than genetic correlation between group members, and it is not clear how this “cultural relatedness” ought to be measured. These cases suggest that, at least in principle, a multi-level perspective may earn its keep in contexts where the relevant relatedness coefficient is not straightforwardly measurable.

Bourke formulates his core thesis (see p. 27, and the opening paragraph of this review) in a way that makes it seem in tension with the thought that a multi-level perspective may be preferable for some explanatory purposes in major transition theory. Yet even if one maintains that there are, at present, no clear-cut examples in which a multi-level approach unambiguously helps, it would surely be rather premature to assume that this will always be the case. Bourke might do better to avoid any such bet. All the evidence on which he draws in *Principles of Social Evolution* is equally compatible with a pluralist position on which kin selection theory, remarkably versatile though it may be, is not the only route to an understanding of the major transitions.

The elusive individual

Social group transformation culminates in the evolution of new, higher-level individuals. But what is an “individual”? In the opening chapter, Bourke suggests the following definition:

By “individual” in this book I mean some stable, physically discrete entity that is composed of interdependent parts acting in a coordinated manner to achieve common goals and is typified by the very property of lacking a high degree of within-individual conflict (p. 8).

In emphasizing stability, interdependence, coordination in pursuit of common goals, and the absence of conflict, Bourke’s definition of the individual has affinities with a number of recent attempts to characterize the organism (see, e.g., Queller and Strassmann 2009; West and Kiers 2009; Okasha 2011). The consensus on these matters is far from complete, however, and one need not look hard to see bones of contention.

For instance: in what sense do the parts of an organism “pursue common goals”? If the thought is that individuality (or organismality) requires genuine teleology, Bourke’s

definition seems to carry radical metaphysical commitments.⁴ But if Bourke is referring merely to apparent teleology, one might fear that the extension of “individual” will turn out to depend too much on contingent features of human psychology—on our subjective propensity to read purpose and design into some living systems rather than others. If we want “individual” to denote a real biological kind, such anthropocentricity seems problematic.

Bourke is not the only recent author to characterize the biological individual in explicitly teleological terms, and is not the only author to equivocate between ascriptions of real and merely apparent purpose.⁵ Clarifying the link between purpose and individuality remains a deep and urgent task for the philosophy of biology. It is, alas, far too big a task to undertake here.

A different worry concerns the extent to which Bourke’s characterization can accommodate the diversity of biological individuals. Like many definitions before it, Bourke’s could reasonably be charged with over-emphasizing the properties of animals to the neglect of other kingdoms. For instance, plants are often able to survive the loss of major parts (see Sterelny and Griffiths 1999), and can tolerate surprisingly high levels of within-group conflict (see Clarke 2011). The story here is a familiar one: for every general definition of the organism ever offered, serious counterexamples have invariably followed. Intuitions vary widely regarding problematic cases, and disagreement about which properties matter to individuality is compounded by meta-disagreement regarding how, if at all, we can ever settle the question in a manner which goes beyond table-thumping and appeals to intuition.

Suppose we were to abandon all hope of there being any general, informative account of biological individuality. Would it matter? Does anything hang on whether the class of biological individuals exhibits any substantial unity (cf. Wilson 2000)? After all, an acknowledgement of nature’s inherent disunity can often serve as a pragmatic, pluralistic antidote to idle philosophical worrying (see, e.g., Dupré 1993). In the present context, however, the pluralist’s refrain rings somewhat hollow, because the worrying is not idle. In Bourke’s picture, the final stage in a major transition, social group transformation, is defined as a process by which groups become individuals. If there is nothing one can say in general about what individuality amounts to, there will be nothing one can say in general about social group transformation. Bourke’s definition is no free-spinning cog: it frames the explanandum for the book’s final third.

Bourke is not alone in staking a considerable amount on there being some cross-taxon, cross-level unity to individuality and the processes by which it evolves. If there were no such unity to be had, a great deal of theoretical and experimental work on the major transitions would have much less generality than is usually supposed.⁶ There would, for instance, be no strong reason to suppose that studies of the evolution of individuality in a single lineage could underwrite substantial projections regarding the evolution of individuality in general. Yet this form of projection from model taxa (in particular, the volvocine algae) lies at the heart of Michod and colleagues’ work on the transitions (see Michod 2006, 2007; Herron and Michod 2008). There is a pressing need in major transition theory for a firmer grasp of what, if

anything, biological individuals in different lineages and at different levels have in common. Consensus, however, remains elusive. Bourke closes *Principles of Social Evolution* with a list of “open questions in social evolution”. The question of how best to characterize the biological individual—and, by implication, the process of social group transformation—deserves a place on that list.⁷

In praise of big pictures

The study of social evolution predates its mathematical formalization: the problem of explaining how sociality evolves vexed Darwin long before Hamilton and Price (see Herbers 2009; Ratnieks et al. 2011). Yet fifteen decades on, social evolution theory seems increasingly synonymous with formal, game-theoretic modelling. Against this backdrop, perhaps the most pleasing aspect of *Principles of Social Evolution* is its continuity with that quintessentially Darwinian tradition of patient, verbal system-building. There are no detailed formal models in the book, and precious few equations. Bourke’s main concern is to piece together and unify the histories of real lineages in which individuality has evolved, and this is a task for which the “one long argument” approach seems particularly well suited.

Bourke’s methodology seems most fruitful of all in the case of social group transformation, where modelling work is thin on the ground—perhaps because the phenomenon has at times been overlooked, but mostly owing to the difficulties involved in making tractable models of the evolution of complexity. While Bourke’s argument in part comprises a discussion of models that support a link between size and complexity, it is to his credit that he avoids excessive reliance on any particular modelling assumptions, opting instead to synthesize a highly diverse range of theoretical and empirical data in support of a broad, qualitative hypothesis. The result is that the limitations of the models on which he draws do little to undermine the plausibility of the overarching hypothesis.

While this form of big-picture theorizing does not obviate the need for more formal representations of evolution, our understanding of the major transitions would be much the poorer without it. In its short history as a unified research programme, the study of the major transitions has often been propelled in promising new directions by works of qualitative, speculative synthesis.⁸ *Principles of Social Evolution* is another landmark contribution.

Notes

1. The particular limitations of Reeve and Jeanne’s model are indicative of broader problems for reproductive skew theory. Many models rely on questionable assumptions (see Kokko 2003) and have a chequered empirical track record (see Nonacs and Hager 2011). The extension of reproductive skew theory to groups of more than two individuals has proven especially problematic (see, e.g., Kokko et al. 1999; Johnstone et al. 1999).

2. Of course, we might want to incorporate more levels than this, and the recursive nature of the multi-level partition makes this possible. In most cases where the framework has been applied, however, only two levels are under consideration.

3. Many kin selection theorists are far less diplomatic than Bourke in their assessment of the utility of a multi-level approach (see, e.g., West et al. 2008).
4. Walsh (2009) argues that we should bite this bullet, but this remains an unorthodox view.
5. Compare, for example: “natural selection leads to organisms that appear designed for a single purpose, that purpose being maximization of their inclusive fitness ... it is exactly this shared purpose that defines an organism” (West and Kiers 2009, p. R1080); “the most salient feature of organisms is adaptation, the seeming goal-directedness that makes organisms different from merely physical entities... we suggest that the essence of organismality lies in this shared purpose” (Queller and Strassmann 2009, p. 3144).
6. McShea and Simpson (2011) argue that this is indeed the case.
7. See Clarke (2010) for further discussion of this issue.
8. See, e.g., Buss (1987), Bonner (1988), Maynard Smith and Szathmáry (1995).

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