Transitions and Social Evolution

A Review of *Principles of Social Evolution*,

by Andrew F.G. Bourke, Oxford University Press, 2011

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The concept of the major evolutionary transitions has excited a large number of highly qualified researchers in the last fifteen years; Bourke's book is a very useful contribution to this expanding field. David Queller has distinguished egalitarian and fraternal transitions, which correspond to cases where the emerging higher-level units arise from unlike and like lower-level units, respectively. Bourke focuses mainly on fraternal transitions, analyzing the evolution of multicellular organisms and animal societies in the framework of Hamilton's kin selection (inclusive fitness) theory. The supporting evidence is substantive and very up-to-date, and the book offers a remarkable collection of relevant facts. However, the picture of egalitarian transitions is painted somewhat crudely, and thus some of the most exciting theoretical questions are not asked. Nevertheless, the book is an excellent stimulant for further thinking.

KEYWORDS

Egalitarian transitions • Fraternal transitions • Group selection •
Kin selection • Major transitions • Social evolution

This is a lovely and very useful book. It deals with the emergence of higher and higher level units of evolution, especially regarding what Queller (1997) called "fraternal major transitions." These are evolutionary transitions where the lower-level units that gang up are genetically alike and, therefore, the initial advantage is likely to come from the economy of scale rather than the complementation of function, as in the case of "egalitarian transitions." Simple division of labor may arise from simple conditions (such as some cells being inside, others outside, so that even with the same physiological reactivity the responses of the two cell types may differ), but the spectacular forms arise from evolved epigenetic mechanisms (Jablonka and Lamb 2005).

Professor Bourke deals, in separate chapters, with the formation (coming together), maintenance (controlling the reproduction of units that have come together) and transformation (evolutionary increase in complexity) of social groups. The real merit of the book is the compilation of as much evidence as possible in favor of the postulated hypotheses. A good example is Table 4.3—"Ecological factors promoting social groups in the origin of multicellularity and eusociality (including cooperative breeding)"—running for five pages, citing all of the relevant papers. This achievement is admirable. Undoubtedly, many (including the present reviewer) are going to use this book to teach a modern view of the major evolutionary transitions.

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Received 22 January 2012; Accepted 14 February 2012

The reader will be fascinated to learn about the controversies, such as those concerning the possible reasons for the existence of a segregated germ line in many multicellular organisms. Bourke lists four alternative hypotheses for the evolution of soma and germ, but firmly states that none of them can account for the variation within and across animal phyla in the timing of the divergence of germ cells from others. Although he favors the “size-complexity hypothesis for social group transformation” in general, Bourke tends to be rather critical even of his own pet theories. For example, he sums up the topic of germ divergence in a qualified manner: “several models exist that propose cogent reasons for why larger multicellular organisms might evolve a segregated, early-diverging germ line. But the association of size with early divergence of the germ line is tentative and alternative hypotheses for the segregation of the germ line exist” (p. 183).

Beyond the general appeal of this authoritative treatise, everyone is likely to find especially intriguing parts. I found three items very interesting: the discussion of the role of dispersal in the maintenance of social groups, the explanation and application of the idea of the “virtual dominant,” and the role of maintained variation in further evolution toward increased complexity. On the latter Bourke observes that, “some evidence suggests that, for long-term stability, complex social groups require features that maintain within-group genetic variation” (pp. 195-196), which is not immediately obvious from the point of view of kin selection theory. The elegant concept of the virtual dominant (Reeve and Jeanne 2003) deserves more attention in the future. Imagine a social group in which no group member is physically superior to others. Even in such a group one may find a member to whose offspring the other group members are, on average, most related. Take again the example of germ line segregation. Germ line cells undergo fewer cell divisions than somatic cells (the reasons for this are discussed in reference to some of the hypotheses mentioned before), and hence accumulate fewer somatic mutations. Therefore, somatic cells will be more related to germ line cells than to each other, so the latter will socially dominate the former, which means that selection, on average, will favor the interests of the germ cells. This is a nice example of successful reasoning based on inclusive fitness and relatedness.

The theoretical basis of the whole book is rooted in the idea of kin selection/inclusive fitness. Bourke explains these theoretical foundations in a very accessible way, yet I think that some essential components are being overlooked. These are the limitations of kin selection and the applicability of multilevel selection theory to the major transitions, especially the egalitarian ones. As Bourke acknowledges, the units coming together in egalitarian transitions are not related, hence a simple kin selection approach does not work. The initial advantage must be some complementation of function between the unrelated units. Because they are unrelated, no reproductive division can emerge either: mitochondria cannot delegate their reproduction to plastids, and *vice versa*. Apparently, the whole topic of egalitarian transitions is somewhat distant from Bourke’s focus—this is perfectly acceptable since nobody can do research on everything—but this distance leaves us with a fuzzy image of the egalitarian transitions. In the caption to Table 3.1 (“Major transitions classified by whether they occur between- or within-species and between relatives and non-relatives”) he writes, “the transition from separate replicators (genes) to a cell enclosing a genome is omitted because it almost certainly involved both egalitarian and fraternal elements” (p. 78), by which he means that several copies of the same gene, as well as copies of unrelated genes, are likely to have joined. This is true, as indeed it was assumed in a model of this process (Szathmáry and Demeter 1987), which happened to be one of the dominant co-stimulants of the whole major transitions project. The snag is that the same mixed status is likely to apply to all of the so-called egalitarian transitions (presumably, a population of proto-mitochondria and not just one such prokaryote was engulfed but not eaten by the ancestor of the nucleo-cytoplasm, and so on). But this leaves untouched the observation that the important aspect here is the cooperation between non-kin.

There has been a lot of heated discussion about the merits and potential deficiencies of kin selection theory. I think it remains very useful in many ways. The fact, emphasized by Bourke, that all known forms of eusociality evolved under conditions of high relatedness is perhaps more convincing than endless calculations. But this is not the whole story. Bourke’s Box 2.3—“In defence of inclusive fitness theory”—reflects on several objections to kin selection theory, but the clearest and potentially most challenging analysis by Van Veelen (2009) is missing. There are a few serious blows. First, it is not true, as held by many, that kin selection and group selection approaches can always be applied and are equivalent (Van Veelen et al. in press), and that one should prefer the former because of its “methodological unity” and “standardized

nature.” There are frameworks in which a group selection rendering is always possible, whereas the kin selection formalism is not. (This by itself does not mean that the former would always be superior to the latter.) Second, for public goods games with non-linear payoffs, kin selection is not the approach offering insight. Third (as an illustration of the second), cooperation can be dynamically stable locally in the absence of positive assortment in the teamwork dilemma with sigmoid benefit functions (cf. Szathmáry 2011). A further interesting case is generalized reciprocity (helping if you got helped last time by anyone), which can evolve in large groups without positive assortment (Barta et al. 2011).

The observation that the problem of egalitarian transitions can be put in the category of cooperation “in the narrow sense” of Hamilton’s inclusive fitness theory (positive gains for both partners in terms of the expected numbers of offspring) is valid, but does not explain much. As Queller (1997) put it, the greatest hurdle is the control of conflicts. If there are mutual gains, where then is the conflict? It is precisely with respect to this question that I think Bourke’s view is fuzzy on the egalitarian transitions. As Eigen and Schuster (1979) analyzed for the case of cooperation among naked genes, “cooperation in the narrow sense” does not solve the problem of cooperation, since the two partners are likely to have different growth rates (typically, with nonlinear interactions), and this creates the conflict! Eigen thought the conflict could be resolved with the concept of the hypercycle, a kind of n-species mutualism, where replicators help each other, superimposed on the individual replication cycles. But, as Maynard Smith (1979) emphasized, the hypercycle is evolutionarily unstable because it is vulnerable to cheaters. Cooperation can be guaranteed for a limited number of genes provided they “sit in the same boat,” i.e., in a reproducing compartment (protocell: Szathmáry and Demeter 1987), without hypercyclic coupling. This picture readily lends itself to a group selection approach, but how kin selection theory would help is far from obvious. To say that sitting in the same boat “aligns the inclusive fitness of both partners” is true insofar as inclusive fitness is a good guide in the given situation. Cooperation of genes before and in protocells is typically a case of non-linear interactions; hence the standard theory of inclusive fitness is inapplicable. In lectures I used to offer a bottle of excellent champagne to someone able to build a detailed and convincing kin selection version of the stochastic corrector model (Szathmáry and Demeter 1987)—there cannot be one.

I am forced, therefore, to conclude that Bourke has not provided us with a unified theoretical framework of the major transitions. Where he comes close is the case of fraternal transitions, which were earlier analyzed from the perspective of kin selection/inclusive fitness anyway (Maynard Smith and Szathmáry 1995). Whether a true unification of group and kin selection approaches is meaningfully (productively) possible is an open question. The fact that quantum field theory and general relativity in physics have resisted attempts at their unification could be taken to suggest that we also may have to wait a long time in evolutionary biology. Rules derived from kin selection theory are not as robust as they are often portrayed (cf. Van Veelen 2011); some of its developments have the odor of Ptolemaic epicycles. Meticulous, impartial analyses pay off in the end.

Literature cited

- Barta, Z., McNamara, J.M., Huszár, D., and M. Taborsky. 2011. Cooperation among non-relatives evolves by state-dependent generalized reciprocity. *Proceedings of the Royal Society B: Biological Sciences* 278: 843-848.
- Eigen, M. and P. Schuster. 1979. *The Hypercycle: A Principle of Natural Self-Organization*. Berlin: Springer-Verlag.
- Jablonka, E., and M. Lamb. 2005. *Evolution in Four Dimensions: Genetic, Epigenetic, Behavioral and Symbolic Variation in the History of Life*. Cambridge, MA: MIT Press.
- Maynard Smith, J. 1979. Hypercycles and the origin of life. *Nature* 280: 445-446.
- Maynard Smith, J., and E. Szathmáry. 1995. *The Major Transitions in Evolution*. Oxford: Oxford University Press.
- Queller, D. 1997. Cooperators since life began. *Quarterly Review of Biology* 72: 184-188.

- Reeve, H.K., and R.L. Jeanne. 2003. From individual control to majority rule: extending transactional models of reproductive skew in animal societies. *Proceedings of the Royal Society B: Biological Sciences* 270: 1041-1045.
- Szathmáry, E. 2011. Evolution. To group or not to group. *Science* 334: 1648-1649.
- Szathmáry, E., and L. Demeter. 1987. Group selection of early replicators and the origin of life. *Journal of Theoretical Biology* 128: 463-486.
- Van Veelen, M. 2009. Group selection, kin selection, altruism and cooperation: when inclusive fitness is right and when it can be wrong. *Journal of Theoretical Biology* 259: 589-600.
- Van Veelen, M. 2011. A rule is not a rule if it changes from case to case (a reply to Marshall's comment). *Journal of Theoretical Biology* 270: 189-195.
- Van Veelen, M., Garcia, J., Sabelis, M.W. and M. Egas. in press. Group selection and inclusive fitness are *not* equivalent; the Price equation vs. models and statistics. *Journal of Theoretical Biology*.

ACKNOWLEDGMENTS

I thank M. van Veelen and M. Taborsky for useful correspondence.

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ISSN 1949-0739