# Book review
# BOURKE, A.F.G. 2011: Principles of social evolution

Oxford University Press, Oxford, 288 pp; Paperback, ISBN13: 9780199231164, Price: £ 29.95

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Myrmecol. News 16: 24 (online 7 June 2011)
ISSN 1994-4136 (print), ISSN 1997-3500 (online)
Received 18 April 2011; accepted 19 April 2011

Charles Darwin's theory of evolution through natural selection is often popularized in metaphors such as "struggle for life", which emphasize the importance of individual selfishness and conflict in evolution. This rather unbalanced interpretation of how evolution works is in part attributable to Thomas Henry Huxley, "Darwin's bulldog," who portrayed the animal world as being "on about the same level as the gladiator's show." For Darwin himself, however, evolution had facets beyond conflict, and cooperation is a particularly important one. John MAYNARD SMITH & Eörs SZATHMÁRY (1995) showed that cooperation abounds in evolution and underlies the "major transitions" from simple to complex biological entities. Andrew BOURKE's new book accentuates this view of cooperative life and shows how the very same principles of social evolution are useful to explain a wide range of apparently different phenomena, such as the evolution of genomes, eukaryotic cells, multicellular organisms, and animal societies.

Following David QUELLER (2000) and others he distinguishes between "fraternal" major transitions, in which genetically related entities cooperate (e.g., cells in multicellular organisms or individuals in eusocial insect societies), and "egalitarian" ones, in which unrelated entities cooperate (e.g., organelles in a eukaryotic cell or algae and fungi in lichens). Firmly founded on Hamilton's inclusive fitness theory, BOURKE highlights similarities and differences among fraternal and egalitarian cooperation. In particular the ecological and genetic foundations of cooperation among cells in multicellular organisms show striking parallels to those that underlie the evolution of eusociality. Analogies between multicellular organisms and insect societies abound not only concerning division of labor but also the internal and external threats such more complex entities have to cope with. All systems that are characterized by mutual help and altruism are sensitive to parasites and freeloaders, be it egoistic endosymbionts and organelles in eukaryotic cells, tumor cell lineages in metazoans, or selfish egg-laying workers in insect societies. The group can persist as an "individual" only through powerful control mechanisms that suppress conflict among its units, including self-inhibition, but also coercion and policing – the dark side of the (super)organism.

Elaborating his model from 1999, BOURKE proposes that an increased number of constituents lead to increased complexity with more pronounced reproductive and non-reproductive division of labor among individual units. This size-complexity hypothesis appears to apply as well to multicellular organisms, where, e.g., vertebrates with trillions of cells have more different types of somatic cells than freshwater polyps or *Trichoplax*, as to insect societies, where leafcutter ants show a more marked caste diphenism and division of labor than, say, paper wasps. BOURKE contrasts systems with high and low complexity, both obviously the endpoints of a continuous range of different levels of complexity.

The book will be highly attractive to all those who are interested in the evolution of sociality, whether in insects or among individual cells. Its well-understandable account of inclusive fitness theory comes at a perfect time. It will rescue those who are confused by the current resurgence of models claiming that altruism, such as shown by the sterile somatic cells in our bodies or the workers in the societies of ants or termites, can evolve without relatedness. BOURKE clearly sets this right: Altruism in its strict sense is best explained in terms of Hamilton's rule and requires an above-zero relatedness: Altruism runs in families. Traditional misconceptions about inclusive fitness theory that have been unearthed again during the past few years are duly corrected and the reader is given clear guidance about what Hamilton's rule means and when it does not apply. Renewed criticism about the assumed genetic limitations and stringent requirements of inclusive fitness theory, such as its applicability under strong selection and non-additivity, are not covered, but such more mathematical details will not be missed by a broad readership and have been dealt with professionally in recent papers such as that by GARDNER & al. (2011). Even though ant enthusiasts might feel more at home with BOURKE & FRANKS' (1995) book on *Social evolution in ants*, the much broadened, theoretical approach of this new book makes it an excellent complement to more descriptive treatises of conflict and cooperation.

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