



NEW BIOLOGICAL BOOKS

The aim of this section is to give brief indications of the character, content, and cost of new books in the various fields of biology. More books are received by *The Quarterly* than can be reviewed critically. All submitted books, however, are carefully considered for originality, timeliness, and reader interest, and we make every effort to find a competent and conscientious reviewer for each book selected for review.

Of those books that are selected for consideration, some are merely listed, others are given brief notice, most receive critical reviews, and a few are featured in lead reviews. Listings, without comments, are mainly to inform the reader that the books have appeared; examples are books whose titles are self-explanatory, such as dictionaries and taxonomic revisions, or that are reprints of earlier publications, or are new editions of well-established works. Unsigned brief notices, written by one of the editors, may be given to such works as anthologies or symposium volumes that are organized in a fashion that makes it possible to comment meaningfully on them. Regular reviews are more extensive evaluations and are signed by the reviewers. The longer lead reviews consider books of special significance. Each volume reviewed becomes the property of the reviewer. Most books not reviewed are donated to libraries at Stony Brook University or other appropriate recipients.

The price in each case represents the publisher's suggested list price at the time the book is received for review, and is for purchase directly from the publisher.

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SOCIAL EVOLUTION: DOES COLLAPSING TAXONOMIC BOUNDARIES PRODUCE A SYNTHETIC THEORY?

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A review of
COMPARATIVE SOCIAL EVOLUTION.

*Edited by Dustin R. Rubenstein and Patrick Abbot.
Cambridge and New York: Cambridge University Press.
\$115.00 (hardcover); \$64.99 (paper). xii + 465 p.;
ill.; index. ISBN: 978-1-107-04339-8 (hc); 978-1-
107-64792-3 (pb). 2017.*

This publication is an epic effort by 28 authors led, inspired, directed, and perhaps policed by two editors. It attempts to bring together into a single volume essentially everything that we know about social evolution in diverse taxa, invertebrate and vertebrate. Even more importantly, it aims to produce a synthesis of the essential features, trajectory, and logic of social evolution, a synthesis that hopes to dissolve all taxo-

mic boundaries and produce a single, unified narrative meaningful throughout the animal kingdom. Sociality is encountered in about 2% of insects, 5% of mammals, 9% of birds, and more rarely in other groups of animals. The book succeeds admirably in the first task of bringing everything together. There are individual chapters on sociality in ants, bees, wasps, termites, aphids and thrips, spiders, shrimps, primates, nonprimate mammals, birds, fishes, and even lizards. Reading the volume is like climbing the peak of a very high mountain on a clear day and surveying the vast landscape in all directions. Read from cover to cover, the book gives readers a truly breathtaking experience of the mind-boggling diversity of animal social life. Individual

chapters allow you to dig as deeply as possible with the current knowledge into the intricacies and variations in social life in different groups of animals that show at least some form of social behavior. Never before has something like this been attempted and executed so successfully, at least not since Wilson's *Sociobiology* 43 years ago (Wilson 1975). But there is a crucial difference between Wilson's tome and this one. Wilson's was a top-down approach and this one aims to be a bottom-up approach, but more on that later because this difference concerns the second aim of the book, namely synthesis.

Comparative Social Evolution is poised to be a one-stop destination for almost anything you want to know about animal social evolution. If it does not explicitly tell you what you want to know, it will almost certainly tell you where to go and find that information, or it will tell you that no one knows. It is hard to overemphasize the importance of bringing all of the references cited in the various chapters into a single volume. For this reason, I am a bit surprised and disappointed that all of the references were not pulled together at the end of the book into one collection rather than be distributed (and often repeated) at the end of individual chapters. Be that as it may, *Comparative Social Evolution* can indeed serve as an encyclopedia with a large number of entries that you can look up and read individually and independently. This has been made possible because of the very concerted and disciplined effort of the editors in planning the volume. I have had a little ringside view of the missionary zeal of the editors in this regard, as I was part of an early planning meeting, although I had to withdraw from being a coauthor of the chapter on wasps, due to other commitments. The authors of individual chapters were indeed given a template that they had to fill up diligently, even if a particular heading did not apply to their group. The authors of the chapter on ants, for example, complain that "[a]dapt[ing] our chapter to the structure of this book provided some difficulties because no solitary ants exist and many aspects of their life histories fit into several sections" (p. 21). The editors probably said *put that down in writing and we will print that also*. The template contained the various headings to be used, primary, secondary, and even tertiary headings that are uniform for all of the groups. This gives the book its encyclopedic nature. The headings provided to the various authors are very instructive indeed.

Part I is about social diversity, including how common sociality is in the group being considered, what are the forms of sociality in the group, and why do the members of this taxon form social groups in the first place? Is it because of ease of resource acquisition, predator avoidance, homeostasis, securing mates,

or for providing offspring care? What is the role of ecology in shaping sociality in the group, including the role of habitat and environment, biogeography, and ecological niches occupied? What is the role of the evolutionary history in shaping sociality in the group? Part II concerns social traits and is organized into two sections—traits of social species and traits of social groups. In the traits of social species, what is the role of cognition and communication? What is the longevity and life span of members of the group or of the groups themselves? What is the fecundity of the members of the group, the age at first reproduction? What is the dispersal mechanism? Traits of social groups include genetic structure of groups, breeding structure, and sex ratio. Finally, each chapter is expected to provide its own social synthesis, including a summary of sociality in that group and what comparative perspectives are possible by studying that group. Now imagine what would happen if each of these subheadings is populated with a considerable amount of text, data, and a large number of references by all authors covering all animal groups with any level of sociality. It will turn into an encyclopedia and, in this case, lead to this unique volume, *Comparative Social Evolution*.

The inclusion of "less than" eusocial species, especially communal taxa, has added to the diversity and complexity of the patterns of social evolution being considered here. Indeed, the editors "wherever possible . . . asked the authors to frame the life histories of social species in the context of closely related non-social species" (p. 11). Such inclusivity, which is more conducive to the study of social evolution (Gadagkar 1994), also shows how rare sociality is in the animal kingdom and how rare eusociality is among social animals. To entice you to read this book, I will provide a few brief quotes from different chapters that leapt out at me from the page. Ants: "It is futile to try condensing all that is worth knowing about the fascinating world of ants into a single chapter" (p. 21); bees: "bees are essentially vegetarian digger wasps most of which are solitary ground-nesters with some species showing tolerance for social interactions and nest cohabitation" (pp. 50–51); wasps: "Order Hymenoptera has about 115,000 described species out of an estimated one million" (p. 84); termites: "Compelling insights have been advanced regarding the selective landscape favoring termite eusocial evolution compared with factors influencing eusocial origins and elaborations in other animals" (p. 144); thrips and aphids: "thrips and aphids are two of the 'most studied of the understudied' social insect groups" (p. 155); spiders: "the architecture of the webs built is a key determinant of the social system that develops" (p. 188); shrimps: "eusocial crustaceans, if they were to be discovered,

would have a suite of traits predisposing them to living in family groups—including some form of parental care and non-dispersing juveniles—and that they would use a long-lived, predator-free domicile” (p. 231); primates: “researchers have amassed a large body of information about the social behavior and ecology of many of the more than 400 primate species” (p. 253); nonprimate mammals: “Social structure has been characterized for roughly 2,500 (46 percent) of the approximately 5,400 species . . . [t]he majority (approximately 70 percent) . . . are solitary . . . [t]he remaining approximately 30 percent . . . are social” (p. 285); birds: “has all of our effort delivered the promised rewards? ‘Yes’ in the sense that many authors have identified factors promoting the transition to cooperation within their species, but an emphatic ‘no’ when it comes to the question of why some avian lineages exhibit sociality and cooperative breeding while others do not” (p. 341); fishes: “A particular feature of fish . . . is the fact that the vast majority of fishes does not stop growing after reaching maturity . . . groups usually consist of both small and large members which strongly affects behavior and social structure” (p. 367); and lizards: “social behavior is relatively simple and easily quantifiable” (p. 391).

But is the whole greater than the sum of its parts? Is the volume greater than the sum of its chapters? This is a legitimate question that any reader might ask, given the title of the book—*Comparative Social Evolution*. The question is even more important for the authors and especially for the editors. It is fair to say that making the whole greater than the sum of its parts was the *raison d'être* of the volume in the first place. *Comparative Social Evolution* begins with an interesting foreword by Bernard Crespi who, along with Jae Choe, had undertaken a rather similar exercise 20 years ago, by editing a pair of volumes entitled *The Evolution of Social Behavior in Insects and Arachnids* and *The Evolution of Mating Systems in Insects and Arachnids* (Choe and Crespi 1997a,b). In reviewing these books at the time, I had observed that “[a]lthough both [books] have introductory and concluding chapters purporting to unify conceptually the myriad threads of data from diverse taxonomic groups, the varied and even discordant facts that emerge from reading the individual chapters are more striking and more impressive than the heroic . . . attempts at generalization encountered in the opening and concluding chapters. This is indeed no fault of the editors or authors writing these chapters. It’s just a bit too early and so reminiscent of Steven Weinberg’s predicament” (Gadagkar 1998:123). Weinberg said, “The final theory may be centuries away and may turn out to be totally different from anything we can imagine” (Weinberg 1993:211) and Richard Feyn-

man’s solution was that “I’m just looking to find out more about the world and if it turns out that there is a simple ultimate law which explains everything, so be it. . . . If it turns out it’s like an onion with millions of layers . . . that’s the way it is” (Feynman 1999:23).

Twenty years on, and with so much progress, are we in a significantly better position today? Crespi himself appears to be rather pessimistic, claiming in his foreword that “[t]he behavioral ecological paradigm, at least back then, was the prediction of behavioral from ecological variation” and concluding that “[m]ore than three decades later, we still cannot truly predict social systems from ecology, can we, with any substantial degree of confidence?” (p. xi). He concedes that this book “brings convergences, divergences, and social diversity to the fore, and will certainly serve as a leaping-off point . . . I am hoping to [have] a more predictive social behavioral ecology” (p. xi). I largely agree with Crespi’s assessment but would argue that considerable progress has been made. To be fair, the editors of this volume were not so ambitious as to explicitly attempt to predict the social from the ecological, but merely took the “admittedly optimistic view of animal sociality, arguing that there are convergent and common themes that span vertebrate and invertebrate societies” (p. 1) and aimed “to comparatively survey the diversity of vertebrate and invertebrate societies, and lay the groundwork for a new generation of theoretical, empirical, and competitive studies of animal social evolution” (p. 8) and asked if we can “ultimately achieve the social synthesis that kin selection and reproductive skew theory promised decades ago?” (p. 13).

I believe that they have achieved some success in their stated goal but only because of the explicit steps and precautions they took before undertaking this ambitious task. First they argued that “it takes a ‘bottom-up’ rather than ‘top-down’ approach to explore social evolution” (p. 8). This is a radical departure from the dominant paradigm in the field—it has almost always been the case by potential synthesizers that they produce an overarching theory or framework and attempt to explain observed facts about different species and explain away those that do not fit, in a top-down manner. On the other hand, Rubenstein and Abbot have preferred to examine and systematically organize knowledge of the natural history, biology, and life-history characteristics of different groups and attempted to extract from such systematization, broad patterns in social evolution—the hope is that general rules and patterns of social evolution will inevitably emerge from such an exercise. After characterizing various traits of the social groups themselves, and also of the social species,

they decided to use the traits of social groups to describe social organization and the traits of social species to describe social syndromes. As a result of this exercise, they consider four key social traits of groups, namely group structure, reproductive structure, alloparental care, and genetic structure. And they infer two social syndromes, namely central place foraging and fortress defense. These syndromes were of course known but they reaffirm their faith in this classification based on all of the old and new information contained in the various chapters. Finally, they identify three traits, namely longevity, fecundity, and developmental mode as the most promising traits for future investigation, especially in a comparative mode across different invertebrate and vertebrate societies. As they note, these traits are clearly important and reasonably well studied, but their role in organizing societies and promoting social evolution remains entirely unclear. They propose communal breeding as an area deserving a major new focus. This makes sense because it is probably the surest way of bringing social invertebrate and vertebrate societies under a common investigation paradigm.

In order to achieve even such limited synthesis, the editors worked hard first in attempting to define sociality in as universally a way as possible and to collapse the different terminologies used by researchers studying diverse social species into a common, consistent lexicon. Their compromise definition of sociality is simply "cooperative group living" (p. i). This is what allows them to gather under one roof a very diverse potpourri of species with varying degrees of commitment to social life. They make the reasonable argument that diversity in terminology has hindered previous attempts at synthesis. Their strict and uniform structure of each chapter goes a long way in facilitating the use of common terminology for different groups.

I found two claims they repeatedly make to be rather weak. The first is the claim that they use Hamilton's rule to guide their synthesis, but I do not see any evidence of this other than an implicit assumption of kin selection being at the heart of social evolution. I am surprised that the recent criticisms

of kin selection and Hamilton's rule, apart from one dismissal in the chapter on ants and one tangential reference in the chapter on wasps, is not approached head-on. There is also repeated reference to the "genomic era" and the "age of genomics," but again there is nothing explicit—it is not clear how we should do things differently in the genomics era or how genomics can transform our understanding of social evolution. Crespi (in the foreword) is also cautious: "I fear, and reason, that for some decades genomes will remain far too complex and too far from social systems for any tight connections to be drawn" (p. xii). I am even more skeptical because I think that the new genomics-related technology will spawn more raw data collection and feed people's desire to reanalyze everything once again at the molecular level, pushing back the possibility of synthesis even further. In any case we must ask why the editors and authors of this book did not achieve more, in terms of a synthetic narrative and predictive theory, in spite of trying very hard indeed. One possibility is that not much more is feasible and that "[t]he laws of biology are written in the language of diversity" (Wilson 1989:243). Personally I would prefer to keep that as a last resort and intensify efforts at developing a synthetic and predictive theory. So what more needs to be done? Perhaps the problem with past efforts was the reliance on a pure top-down approach and the problem with the present approach is the reliance on a pure bottom-up approach. Can we then combine the two? Perhaps, but that will mean that we must revisit evolutionary theories of individual, kin, and group selection and embrace multilevel selection more sincerely. Above all, we must face the present standoff with respect to kin selection (Gadagkar 2010) and either find a common meeting ground or settle the issue once and for all. Both sides cannot continue to pretend that they have vanquished the enemy and won the war. We should not underestimate the negative fallout of the present impasse on outsiders who watch our field and on students who wish to consider entering it. *Comparative Social Evolution* is probably as good a springboard as we can have to launch a new search for the Holy Grail.

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