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Beyond eusocial insects: Studying the *other* social insects to better understand social evolution.

Joël Meunier[1], Sandra Steiger[2]

[1] Institut de Recherche sur la Biologie de l'Insecte (IRBI), UMR 7261, CNRS / University of Tours, 37250 Tours, France

[2] Institute of Insect Biotechnology, University of Gießen, 35392 Gießen, Germany

Fascinating social insects

When one thinks about social insects, the first reaction is generally to acknowledge the fascinating eusocial organization present in bees, ants, termites and wasps. This fascination generally comes from their complex societies in which up to several thousands of workers cooperate to build sophisticated nest architecture, to find large and distant food sources, as well as to defend each other against predators and pathogens [1]. Moreover, these societies often rely on a unique system of division of labor, in which very few individuals have access to reproduction (queens and kings), whereas the vast majority of colony members is specialized in non-reproductive tasks such as nursing, nest defense and foraging [1]. These fascinating social properties have driven the interests of biologists for centuries and generated results of fundamental importance in different fields of biology. For instance, they shed light on the genetic and epigenetic parameters shaping extreme forms of altruism, on the resolution of social conflicts that are inherent to group living, on the evolution of sophisticated communication systems and on the emergence of collective defenses against parasites and pathogens.

However, eusociality is but one form of social life in insects (it is present in only 2% of insect species [2]). For instance, caterpillars of many Lepidoptera species exhibit a social life, in which dozens of individuals gather and use sophisticated communication systems to express collective foraging activities and defenses against predators [3]. Similarly, temporary family life is another, non-eusocial form of social life [4] in which parents and juveniles exhibit frequent and tight social interactions reflecting forms of cooperation (e.g. parental care), as well as competition and conflict (e.g. sibling rivalry and sexual conflicts). This family life occurs, for instance, in earwigs and burying beetles [3]. Even in bees and wasps, eusociality is but one type of social

system. The vast majority of bee and wasp species are indeed solitary, whereas the rest exhibit social systems ranging from communal to semisocial [5,6]. Somewhat surprisingly, other findings also question the omnipresence of eusociality in ants. In colonies of the clonal raider ant *Cerapachys biroi*, for instance, there is no reproductive caste and all "workers" reproduce simultaneously and show communal breeding [7]. This lack of a reproductive division of labor does not fit with the definition(s) of eusociality [8] and underlines that unexpected fundamental variation in social systems can occur even within well-known biological social models such as ants.

The historical neglect of the *other* social insects

While insects encompass one of the greatest diversities of social systems across animal taxa [3], the term "social insects" has long been used – and is still used - as a synonymous for "eusocial insects" in the literature. This misleading and erroneous synonymy is a major issue, because it suggests that the 'other', non-eusocial insect societies are not social and are thus not pertinent to improve our general understanding of social evolution. However, only focusing on eusocial species to study social evolution also comes with major limitations. Eusocial species indeed exhibit highly derived and peculiar social traits (e.g. colony members have lost their capability to live alone and have evolved secondary traits to cope with their obligatory and permanent social life), which could make them of limited relevance to address fundamental questions such as why and how social life i) has originally emerged from a solitary state, ii) is maintained in a primitive form and/or evolve into different social systems, as well as why and how social life iii) can be lost and/or exhibit variable levels of complexity between sister species.

In 2006, a book written by James Costa and entitled “The other insect societies” [3] provided a first remarkable overview of the *other* social insects. Based on a comprehensive survey of the literature, this seminal book shed light on the broad diversity of forms of group living and social organization present across insects, as well as compiled the - sometimes very limited, sometimes relatively abundant - works conducted in these species. The main conclusion of this book was that the *other* social insects open scope for novel and promising research in social evolution (and in many aspects of social life), which thus call for more studies on these species. Twelve years later, did we follow the recommendation of this book? Are the *other* social insects still neglected compared to eusocial species? Did studies on the *other* social insects provide novel and important insights into our general understanding of social life and its evolution?

Recent advances in our understanding of social insects

The main goal of this issue of *Current Opinion in Insect Science* is to provide an up-to-date appraisal of the recent research conducted across all social insects and stress how recent studies in the *other* social insects have provided key information for our general understanding of social life and its evolution. The reviews presented here survey recent advances in the study of insect social life in terms of genomics, behaviors and physiology.

The genomic aspects of social life are discussed in two reviews. The first one by Kronauer and Libbrecht, discusses how the genomic data currently available supports (or not) alternative trajectories in eusocial evolution and explains how studies investigating the molecular bases of brood care and nest defense in the *other* social insects would provide novel and unique opportunities of functional analyses. The

second review by Taylor et al makes the case that the broad diversity of social systems present in Vespid wasps provides a unique opportunity for testing hypotheses about the molecular mechanisms underlying the different evolutionary transitions from solitary to eusocial life.

The behavioral (in its broad sense) aspects of social life are discussed in four reviews. The first review by Smiseth and Royle presents how recent works in the *other* social insects changed our current view on the nature and outcomes of social interactions between family members and call for a major shift from the traditional emphasis on conflict to a greater emphasis on the balance between conflict and cooperation. The second review by Van Meyel *et al* emphasizes how and why social defenses against pathogen infections can and/or have emerged in almost all forms of social life in insects and argue that these defenses could have played a central role in the early evolutionary transition from solitary to group living. In the third review by Onchuru *et al*, the authors survey the different mechanisms of transmission of symbiotic microbes (gut microbiota) across all social insects and emphasize that social transmissions could be of key importance to promote the evolution of social behaviors and insect eusociality. Finally, the fourth review by Nehring and Steiger explores the link between social and communication system complexities and argue that further studies on the communication system of the *other* social insects are required to fill some of our current gaps in the conceptual and empirical understanding of this link.

The physiological aspects of social life are discussed in two reviews. The first review by Trumbo investigates whether the link between juvenile hormones and parental care reported in subsocial insects could provide major insights into a key assumption of social evolution, which is that the mechanisms regulating reproductive versus non-reproductive phases of the life cycle of solitary ancestors are

key drivers of reproductive division of labor in eusocial species. The second review by Lihoreau *et al* focuses on insect nutrition and argues that conceptual advances used to study nutrition in solitary and gregarious insects provide a robust framework to explore the role of food constraints in the evolution of insect social life.

Finally, the review by James Costa takes a broader perspective on the *other* social insects. In this review, the author discusses ongoing issues with the terminologies of social life, provides a brief and up-to-date overview of the main traits of interest in the *other* social insects and finally presents emerging fields of inquiry that derived from recent studies in these species.

Future directions

Even if the number of studies on the *other* social insects has increased over the last decade, this number is still low. Yet, the reviews presented here emphasize that these few studies provided major improvements in multiple fields of social evolution including behavioral ecology, physiology, genomics and chemical ecology. So how can we further promote the study of these *other* social insects in a near future? One simple option would be to abandon the synonymy between “social” and “eusocial” insects both in the literature and in the mind of social insect researchers and instead, to consider as “social insect” every insect species exhibiting a form of social life. Disrupting the dichotomy between eusocial and the *other* social insects would enforce researchers interested in different forms of social life to unify their frameworks (e.g. in terms of terminologies, theory and model assumptions) and ultimately promote the development of novel, comprehensive and robust paradigms in social evolution. Such a unification will be difficult, as terminologies can be dramatically different even within eusocial species [9]. But it has already started – notably with the book “Comparative

social evolution" which proposed a unified approach to compare eusocial vertebrates and invertebrates [2], and thus needs to be continued and strengthened further. Moreover, considering social insects in their broad diversity would allow us to put aside the question of their social classification when not essential (such as: is this species gregarious, subsocial, semi-social, quasi-social, primitive eusocial or true eusocial?), and instead allow focusing on the knowledge a work can provide to our general understanding of social life. Hence, this simple change in social terminology – which has been already called for at different degrees [10–12] - should profoundly strengthen our current understanding of social evolution, as well as provide novel and unexpected avenues for its further development. It is thus time for such a change.

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