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Editorial overview: Social insects: Integrative approaches to understanding insect sociality: why physiology is still highly relevant

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The study of physiology allows biologists to understand how organisms maintain homeostasis by dissecting the inner workings of cells, tissues, and organs. Therefore, by definition, physiology occurs at the interface of the organism and its ever-changing environment. However, the field of physiology has been viewed by some to be fading into the past, as the molecular revolution has progressed into the genomic era [1]. As a case in point, the heyday of insect physiology can be said to have occurred during the early and mid-20th centuries, during which time this field provided unprecedented insights into insect biology, pest control, and evolution [2,3]. Application of insect physiology to the study of social insects was equally fruitful, leading to impressive progress in our understanding of basic physiological processes underlying caste differences, division of labor, chemical communication, energetics, and providing insights into the mechanisms behind social evolution [4].

For example, studies on juvenile hormone provided key insights into queen-worker caste determination in bees and ants, worker behavioral division of labor in honey bees, and soldier differentiation in termites [5]. Studies on electrophysiology elucidated the complex sensory systems of social insects and their chemical world [6]. Studies on metabolics and energetics of flight provided important insights into how social insects forage, allocate energy, and maximize colony efficiency [7]. Thus, physiological studies truly led the way and revolutionized our 20th century understanding of how social insects function and the mechanistic underpinnings of the evolution of sociality. At the same time, research on ecological factors influencing the formation, stability, and organization of insect colonies has progressed steadily, leading to an increasing appreciation of the importance of ecological interactions in the maintenance and evolution of insect colonies [8,9].

Now, with the rise of molecular genetics in the latter part of the 20th century, and the strong emphasis on genomics in the 21st century, physiological studies have increasingly taken a ‘back seat’ to new technologies. Although some physiological studies continued throughout this period, the proportion of studies using physiological approaches declined, while those using emerging techniques in genomics and molecular biology increased. Without a doubt, these modern molecular approaches led to many new insights into social insect biology, including a better understanding of the molecular mechanisms of numerous social traits, including foraging and caste differentiation [10,12]. Genomics also contributed to important insights into molecular mechanisms of social evolution, such as novel genes, gene co-option, and shared genetic toolkits for sociality [9]. However, many of these studies focus only on the subcellular level, without a strong integration of organismal level information or perspectives. In addition, because no social insects have had the depth of genetic study as more developed model organisms, like *Drosophila*, gene function is usually unknown or inferred based on homology with other species. Therefore, the vast majority of molecular genetic and/or genomic studies provide little functional information about the actual roles of genes in the organism being studied. Although in practice many researchers have used molecular genetic and genomic data to 'replace' physiological level studies, in reality, these studies are rarely able to generate the functional explanations garnered from physiological studies. Therefore, the deepest insights into the mechanisms regulating social insect phenotypes can only be provided with a pairing of genetic/genomic and physiological-level studies. Further, by incorporating physiological experiments into genomic studies, researchers are better able to link modern datasets with the wealth of physiological data generated during the heyday of insect physiology.

With these thoughts in mind, the goal of this issue is to highlight a growing number of studies, especially in recent years, which have very intentionally integrated physiological information in an attempt to gain multi-level insights into social insect biology. In this issue of *Current Opinion in Insect Science*, we feature a diverse variety of interdisciplinary research approaches and ideas, all of which integrate different aspects of social insect physiology, including energetics, immunity, stress responses, neuroanatomy, and endocrine and exocrine systems. These studies showcase that physiological information continues to be just as relevant, if not more so, to understanding social insect biology. We suggest these studies represent the seeds of a re-invigoration of research in social insect physiology that is resulting from the integration of physiology with many other perspectives, including microbiological, genomic, neurobiological, chemical, and evolutionary.

In this issue, Korb and Belles use a comparative perspective that integrates physiology, molecular biology, and evolutionary biology to synthesize long-known information about the role of juvenile hormone in cockroach development, proposing a new way forward for understanding caste evolution in termites. In articles by both Woodard and Baudier and O'Donnell, the authors use physiological information about nutrition and temperature tolerance to provide new outlooks on social insect conservation, population declines, and responses to global change. At the interface of ecology and microbiology are studies of how microbes shape insect social interactions, their evolution (Biedermann and Rohlfs), and immune system function (Anderson and Ricigliano). In another fruitful intersection, neuroanatomy meets ecology to improve the understanding of factors that constrain and drive social wasp brain evolution and behavior (O'Donnell and Bulova). Smith and Liebig present a new synthesis on the evolution of fertility signaling, a key component of the chemical ecology of social insects. Finally, Kapheim uses a highly integrative approach, tying together ecological, genomic, and physiological studies to provide new insights and hypotheses for understanding insect social evolution.

Moving forward, we hope that this issue can help re-ignite interest in generating new physiological data while, at the same time, encouraging social insect researchers to consider 'old' (premolecular) literature on mechanisms of insect behavior. Ignoring physiology, particularly with an overly reductionist molecular approach, can miss out on important organismal insights. On the flip side, ignoring physiology while conducting more top-down ecological studies can miss opportunities to understand underlying mechanisms and physiological factors that constrain organismal responses to the environment. We posit that the ultimate goal of a deeper understanding of social insect biology is best achieved by integrating multiple levels of analysis, including molecular and ecological, with physiology [1]; In summary, the reintegration of physiology into multilevel studies of social insect biology continues to be an important component of a systems understanding of social insect colony organization and evolution.

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