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Editorial overview: The integrative study of animal behavior

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For more than a century, the systematic study of animal behavior has been a diverse and dynamic discipline. Historically, the study of animal behavior has often been limited to relatively simple processes and questions, which often failed to holistically explain the complexity of animal behavior in nature. For example, studying complex behavior in the field (e.g., mating behavior or group living) often fails to reveal its physiological underpinnings and developmental origins, whereas mechanistic studies of simplified behavioral contexts in the laboratory (e.g., resident-intruder paradigm or affiliation) often do not consider the functional consequences or evolutionary history of a given behavior. Expanding on the insights of earlier scholars, Nikolaas Tinbergen [1] recognized over 50 years ago that a richer grasp of animal behavior required an understanding of both the proximate and ultimate and mechanisms. These 'levels of analysis' are best viewed as complementary to each other, rather than as alternatives to be pursued in isolation [2]. Yet, for many decades, studies of the proximate and ultimate explanations of animal behavior typically proceeded independently. With the advent of new and powerful resources and tools in genomics, genome editing, physiology, neuroscience, movement tracking, etc., it is now possible to not only integrate across levels of analysis in the same studies, but also study increasingly more complex behaviors in more detail and in increasingly naturalistic contexts than ever before [3–5].

As important as Tinbergen's 'levels of analysis' have been in guiding the animal behavior research agenda for the last half century, the integrative study of animal behavior is more than just combining studies of proximate and ultimate explanations. True integration in animal behavior studies requires that researchers ask questions at multiple levels of biological organization, in a diversity of taxonomic groups, and across a range of spatial and temporal scales, and then answer those questions using a variety of tools and techniques [6]. Behavior is a phenotype that lends itself to this type of integrative biological study because it is the quintessential complex trait, shaped not only by the interactions of genes and their products as well as neural and endocrine processes, but also by interactions among individuals (of the same or different species) and with the broader environment. Of course, the study of animal behavior has, to some degree, always been integrative as even in the early days of the discipline ethologists carried out empirical research in a wide variety of species in field settings while comparative psychologists studied model species such as rats and pigeons in the lab. Moreover, the study of animal behavior has always been intimately linked with mathematical and statistical modeling approaches, and remains to this day steeped in evolutionary theory. Yet, in recent years

Seewiesen, he conducted postdoctoral research at Stanford University. As a Bauer Genome Fellow at Harvard University he pioneered behavioral and neurogenomics to analyze and understand the molecular and neural basis of social behavior and its evolution. Hofmann co-led the cichlid genome consortium, which successfully completed the sequencing of five cichlid genomes. He received the prestigious *Alfred P. Sloan Foundation Fellowship (in Neuroscience)* and was awarded the *Frank A. Beach Early Career Award* from the Society for Behavioral Neuroendocrinology.

the study of animal behavior is becoming more integrative than ever before, largely because modern tools and techniques can increasingly be applied in non-traditional model systems [3–5] and often even in naturalistic field settings [7]. This integrative approach to the study of animal behavior that spans levels of analysis or scales of biological organization is enabling critical tests of long-standing theory, while also generating novel insights and opening up new areas of inquiry. Ultimately, integrative research can both generate novel hypotheses or reject or support long-standing ones, often in ways that traditional approaches cannot do [6,8].

The idea for a special issue on the *Integrative Study of Animal Behavior* originated at a workshop on this topic that was organized by us in August 2014, with support from the US National Science Foundation [6]. The workshop brought together mostly junior and mid-career scientists, who had distinguished themselves through innovative and integrative behavioral research. While some would call themselves ecologists or conservation biologists, others would say they are evolutionary biologists or geneticists; and still others would refer to themselves as neuroscientists, neuroendocrinologists, or engineers. Yet, they all study the behavior of animals in more than one way and from multiple angles. Many of the workshop participants, along with several other authors, agreed to contribute short review papers for this issue that reflect the breadth of concepts and the multitude of approaches animal behaviorists use in their research. Our goal was to show that no matter what the primary research focus, taking an integrative approach to animal behavior can enrich its study.

Social behavior is a primary focus of many of the papers in this issue. To begin, Rubenstein and Hofmann develop a framework for exploring a series of mechanistic candidate pathways through which the social and ecological environments might influence the social phenotypes of individuals. They highlight a series of non-mutually exclusive candidate pathways that could potentially unlock the 'black box' that underlies the evolution of vertebrate sociality. Similarly, Taborsky and Taborsky also develop a model to link the genetic and physiological mechanisms underlying social behavior. Next, Akçay *et al.* argue that to take full advantage of the transformative potential of many new empirical approaches for studying social behavior, new types of theory are needed. They emphasize gene regulatory networks and try to link them with social theory. Approaching the subject from a completely different angle, Bongard then discusses how robots can be evolved *in silico* to understand the evolution of adaptive behavior and to generate novel hypotheses about why and how specific social traits have evolved in nature.

There are several neuroendocrine pathways underlying social behavior that have received particular attention in the literature: those relying on steroid hormones and nonapeptides as signaling molecules. It thus comes as no surprise that several papers in this issue review and critically assess recent progress in these areas. First, Kelly and Ophir remind us that the reliance on standard model systems in biomedical research has led to a lack of generalizability of experimental results. Using nonapeptide systems as an example, these authors then proceed to demonstrate how comparative approaches can reveal unifying principles underlying social behavior. Similarly, Kingsbury draws upon elegant recent work in estrildid finches to highlight the diverse functions of vasoactive intestinal polypeptide (VIP) in affiliation, gregariousness, pair bonding, nesting, and aggression, as well as biological rhythms, in addition to its well-known role in vertebrate parental behavior via the regulation of prolactin secretion. While both of these papers explore the pro-social effects of nonapeptides on social behavior, Beery discusses the less studied antisocial effects of oxytocin and proposes that both oxytocin and social behavior must be considered in more nuanced ways as some antisocial behaviors can be part of prosocial processes. Next, Vahaba and Remage-Healey review our current understanding of the role of rapid estrogen synthesis in the brain and how this affects cognitive processes, especially as they relate to the encoding of recent experience. Finally, Calisi and MacManes explore how new techniques can be used to expand the scope of these more focused studies. They describe how studying gene expression using RNAseq can help us understand complex behavioral systems and emphasize how techniques like these are well-suited for the study of non-model organisms.

Behavioral interactions occur not only within species, but among species as well. Archie and Tung argue that interactions between animals and their microbiome can influence fitness and behavior in a reciprocal relationship. They suggest that animal social interactions can affect microbiome composition, but that microbiomes can also drive host social behavior through the production of chemical signals and the manipulation of a host's nervous system.

Sexual selection and mate choice is one of the best-studied topics in animal behavior. Hutton *et al.* argue that the framework for studying signaling is often over-simplified. Through the topic of animal coloration, they explore the dynamic nature of signal production and highlight the sensory processes that animal use to decode complex signals and make mating decisions. Next, Escobar-Camacho and Carleton discuss the diverse sensory capabilities of cichlid fishes, which provide one of the most powerful model systems for integrative studies of evolution, behavior, diversity, and speciation. Importantly, Cummings and Ramsey argue that studies of female choice should also consider cognitive processes in addition to the traditional view of signaling as a sensory process. In systems with alternative male reproductive tactics where females have to choose among very different types of males, they suggest that cognition may be critical to mate choice. Fuxjager and Schlinger then focus not on female mate choice, but on male signaling to attract mates. Summarizing his work on the elaborate courtship displays of the male golden-collared manakin, he discusses how androgen-sensitivity has evolved not only in the brain and the spinal cord, but also in the skeletal musculature, which is related to the physical and metabolically expensive nature of the displays. Rittschof *et al.* show that energy metabolism is not just important for mating behavior, but also for aggression. Using honey bees as a model system, they explore the relationship between energy metabolism and aggressive behavior in the brain.

A variety of papers explore parental care, including both how it evolves and how it influences offspring development. Roland and O'Connell suggest that the neurobiology of parental care is poorly studied in many organisms. Using Tinbergen's levels of analysis as a guide, they argue that poison frogs offer a potential model system to study the evolution of parental care in vertebrates. O'Rourke and Renn explore the fundamental life history trade-off between current and future reproduction with a focus on the neuromolecular basis of parental care and feeding behavior. Next, Guillette and Healy argue that nest building provides a useful model system for investigating cognition and its neural basis, as this behavior requires experience-dependent changes in dexterity and flexible decision making. MacDougall-Shackleton emphasizes the challenges associated with developing ecologically valid and experimentally controlled stressors in behavioral research, and then critically examines the evidence for the notion that developmental stress impairs performance of adult behaviors, using birdsong as an example. Related to the processing of stressful events, Greggor *et al.* examine the disparate and often conflicting studies on neophobia (i.e., the avoidance of novel stimuli). They argue that understanding the causes and functions of neophobia requires both cognitive and ecological approaches.

Over the past few years, there has been a renewed focus on the importance of considering individual differences in animal behaviors. Alonzo discusses how phenotypic variation within a population may represent the adaptive plasticity that allows organisms to respond to environmental change, or the heritable variation that underlies evolutionary change. She develops a mechanistic framework that integrates genes and hormones into studies of behavioral variation. Next, Bell and Dochtermann discuss the importance of quantitative genetics for understanding individual variation and plasticity of animal behavior, and underscore the challenges we face as we begin to integrate molecular mechanisms into quantitative genetic theory. Finally, Barron *et al.* suggest that these individual differences can influence the transmission of parasite infections. They argue that integrating individual behavioral variation into studies of disease ecology may allow ecologists to better characterize an individual's role in a host-parasite system.

Integration is not only working down from the organism to the level of the gene or molecule — from function to mechanism — but also up to the level of the population. By describing the neurobiological and neuroendocrine mechanisms underlying avian migration, Ketterson *et al.* discuss how integration can be used to study how populations adapt to changing environments. The integrative study of animal behavior can also be relevant to conservation biology. Blumstein and Berger-Tal argue that understanding how animals perceive the world and process information can be useful for preserving species. In a world where humans have modified landscapes everywhere, thinking about how animals perceive light pollution or anthropogenic noise might mitigate the effects of these human-induced rapid environmental changes. Finally, Roth and Krochmal argue that the field of conservation itself has a lot teach the field of animal behavior. For example, studying invasive species from a conservation perspective may be informative for understanding how animals respond to novel stimuli.

More than half a century after Tinbergen's seminal essay on the levels of analysis in studies of animal behavior, the need for an integrative understanding of behavior has become pressing. If we are to provide deeper insights into what drives behavior and how it works; if we are to apply the study of behavior in new biomedical and neurobiological discoveries; and if we are to conserve biodiversity through knowledge of how animals adapt to global change and other anthropogenic stressors, an integrative understanding of animal behavior — and organismal biology more generally — will be essential [9]. Such an approach requires comprehensive analyses at a variety of levels of analysis, across levels of biological organization, in a diversity of taxonomic groups, and at a range of spatial and temporal scales [6]. The papers in this issue illustrate but a few examples of this integrative approach to studying animal behavior.

Conflict of interest statement

Nothing declared.

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