Editorial overview: Behavioural ecology — molecular and neural mechanisms underpinning adaptive behaviour in insects

Lars Chittka

Lars Chittka

Department of Psychology, School of Biological and Chemical Sciences, Queen Mary University of London, Mile End Road, London E1 4NS, UK
e-mail: l.chittka@qmul.ac.uk

Sections Editors

Lars Chittka

Lars Chittka is distinguished for his work on the evolutionary ecology of sensory systems and cognition, using insect–flower interactions as a model. He developed perceptual models of bee colour vision, allowing the derivation of optimal receiver systems as well as a quantification of the evolutionary pressures shaping flower signals. Chittka also made fundamental contributions to the understanding of animal cognition and its fitness benefits in the economy of nature. He explored phenomena such as numerosity, speed-accuracy tradeoffs, false memories and social learning in bees. His discoveries have made a substantial impact on the understanding of animal intelligence and its neural-computational underpinnings.

Around the turn of the century, there was a perception in some circles that behavioural ecology was dead [1]. However, the fashions in behavioural ecology that were then seen in decline were in fact dead before they were born (as indeed any science that thrives on fashion rather than discovery). Fields such as 'fluctuating asymmetry' and 'UV vision' have sunk into oblivion for all the right reasons: they harboured a good number of workers who would never let a rigorous experiment get in the way of a cute story. It is also good to see that most entomologists never fell for these fads — UV sensitivity, for example, had been discovered in the Hymenoptera a good century before it became a fashion in behavioural ecology [2], and by the time it did, its systematic distribution and its behavioural and evolutionary significance had already been thoroughly explored in insects [3], without any hyperbole at any stage. One reason why insect scientists are so successful in the analysis of behavioural adaptation is that they never fully disentangled the analysis of mechanisms from ethology. Why would such disentanglement be a problem, given that some textbooks still inform us that we can neatly segregate proximate from ultimate perspectives on animal behaviour?

It is certainly possible to study *animal behaviour* without concern for the molecular and neurobiological mechanisms underpinning behaviour. However, *behavioural ecology* is the study of how an animal's behaviour is adapted to its environment [4] — which, most readers will agree, involves an evolutionary angle. It is not possible to study an evolutionary process — *any* evolutionary process — without knowing the traits that evolved. Many behavioural ecologists and some cognitive ecologists are under the impression that words (i.e. behavioural characteristics that fall under a certain operational definition) are traits. They are not. For example, in studies on 'animal personality', *boldness* is sometimes measured as time spent in open space [5]. But an animal's behaviour in such a situation could be controlled by sheer indifference to a threat, levels of phototaxis, deficits in various sensory modalities, overall locomotor activity, hunger levels, or indeed the fact that, depending on the animal's biology, open space can actually contain less predation threat than, for example, an area in vegetation which might harbour concealed predators. Animals scoring similarly on a 'boldness' scale might do so for entirely different reasons. You cannot begin to compare a trait between species or individuals, or explore a trait's plasticity, or its evolutionary history, if you do not have an idea what controls the trait, or indeed what the trait is [6]. This is why the present special volume contains a collection of papers that would perhaps not regularly be classified as behavioural ecology — the reviews focus on molecular and neurobiological

DM Gordon

Deborah M Gordon is a professor in the Department of Biology at Stanford University. Her lab studies how ant colonies work without central control using networks of simple interactions, how these networks evolve in relation to changing environments, and analogies with collective behaviour in other systems (http://www.stanford.edu/~dmgordon/).

underpinnings of behaviour, insofar is the editors think they may be useful for understanding behaviour adaptation.

The exploration of within-species differences in insects is as old as the study of animal behaviour. The founding father of the experimental and observational exploration of behaviour, Jean-Henri Fabre (1823–1915), observed between-population differences in how well a digger wasp dealt with an experimental disruption of an innate behavioural routine, and concluded that '…Intelligence is heritable… — there are clever and less clever kinds' [7]. To social insect scientists, the study of individual variation in colony organization is of course second nature. In this volume, Jandt and Gordon provide an overview of recent breakthroughs in between-colony and between-individual differences, and their molecular, physiological and neurobiological foundations. Notice how they manage to do so without once mentioning the buzzword 'personality'!

Buhl and Rogers explore the mechanisms underpinning collective movements in insect groups, drawing from locusts as a key model in this topic field. Work over the last decade has identified an array of elegantly simple mechanisms by which seemingly complex collective phenomena can be achieved. Buhl and Rogers also have an important message for the modellers in behavioural ecology: a match between a model and an observed behaviour does not mean that we have identified the mechanisms or strategies by which the animals behave — there might be a large number of models all predicting the behaviour equally well, especially in models that are deliberately adjusted to replicate a certain behaviour.

Insects, especially the social ones with their unique division of labour, offer unique insights into the mechanisms by which the same genome can be expressed differently to produce entirely different behavioural phenotypes depending on environmental need. Maleszka's paper explains the epigenetic processes involved in such plasticity, and also considers the role of epigenetics in learning and memory, and the possibility of transgenerational epigenetic inheritance.

The social brain hypothesis, positing that the cognitive demands linked to sociality profoundly influenced brain evolution, was, in an early version, first presented for insects by Felix Dujardin in 1850 [8], well over a century before it was explored for primates [9]. Farris rigorously tests this hypothesis by comparing the brains, and specifically the mushroom bodies (sites of multisensory integration and learning) of a large number of insect species, with a focus on the solitary and social Hymenoptera. While there are clear between-species differences in brain organization and neuropil sizes, these are not correlated with group size or indeed sociality, but instead with feeding ecology, illustrating that transitions from a solitary to social lifestyle (and from small to large groups) can be generated by relatively minor tweaks of neural circuitry, rather than changes in gross neuroanatomy.

One conclusion from Farris' chapter is that the need for spatial memory in central place foragers might be more important in driving brain evolution than sociality. Indeed, as Webb and Wystrach point out in their chapter, multiple brain areas are involved in innate orientation mechanisms as well as learning landmarks and routes. The authors guide us through recent developments in neuroethology and neural network modelling that have led to fundamentally new insights of how insects' complex orientation is tailored to environmental need.

Since the 1970s, plant–insect interactions have been a model system for understanding signal-receiver coevolution, and foraging as a model for the adaptiveness of behaviour. Recent breakthroughs in neural recording methods now facilitate the understanding of signal processing and memory storage at an unprecedented level in insect pollinators. Rusch et al. focus on insect pollinators' olfactory system to show how the study of neural mechanisms can have direct implications for floral signal evolution. The olfactory system is of course as important in mate recognition as it is in foraging, and Namiki and Kanzani use the silk moth as a model for pinpointing the brain areas and neural circuits that guide orientation and movement patterns for target search in the olfactory domain.

There is a traditional view that insects are simple reflex machines, responding to sensory input in deterministic and predictable manners. In recent years, through both electrophysiological work and psychophysics, it has become clear that insects use attentional mechanisms for filtering incoming information to make sense of their environment. De Bivort and Swinderen explain how the molecular-genetic and neuroscientific toolkit available in Drosophila can be used to understand the relevance of attentional processes that animals use to focus on what's important in their environment.

Several insect model systems have been at the forefront in understanding how memory dynamics and memory capacity are tailored to the economy of nature. The paper of Smid and Vet evaluates a variety of insect species to investigate how memory dynamics can evolve, as well as quantification of fitness costs and benefits of various cognitive capacities (and their neural-molecular underpinnings).

The editors are aware that some behavioural ecologists may not immediately see the relevance of such mechanistic, and often high-tech laboratory work under relatively artificial conditions, for what such scientists may feel can be achieved by field observations combined with optimality modelling. However, we are not simply waving the 'interdisciplinarity flag' because it's politically correct to do so. We feel that the idiosyncratic collection of articles we have selected represents some of the finest approaches of how behavioural ecology can be informed directly by work on molecular and neurobiological underpinnings of behaviour. Integrating such work with more field-based, classical approaches to ethology will hopefully provide some rewarding future avenues of research.

References

1. Dugatkin LA: **Closing thoughts**. In *Model Systems in Behavioral Ecology: Integrating Conceptual, Theoretical, and Empirical Approaches.* Edited by Dugatkin LA. Princeton University Press; 2001:533-534.

2. Lubbock J: *Ants, Bees and Wasps: A Record of Observations on the Habits of Social Hymenoptera edn (New edition, based on the 17th, 1929)..* Kegan Paul, Trench, Trubner, and Co.; 1882.

3. Chittka L, Menzel R: **The evolutionary adaptation of flower colors and the insect pollinators' color vision systems**. *J Comp Physiol A* 1992, **171**:171-181.

4. Gordon DM: **The fusion of behavioral ecology and ecology**. *Behav Ecol* 2011, **22**:225-230.

5. Mamuneas D, Spence AJ, Manica A, King AJ: **Bolder stickleback fish make faster decisions, but they are not less accurate**. *Behav Ecol* 2015, **26**:91-96.

6. Chittka L, Rossiter SJ, Skorupski P, Fernando C: **What is comparable in comparative cognition?** *Philos Trans R Soc B-Biol Sci* 2012, **367**:2677-2685.

7. Fabre J-H: *Souvenirs Entomologiques*. Librairie Ch Delagrave; 1879.

8. Dujardin: **Mémoire sur le systeme nerveux des insectes**. *Ann Sci Nat Zool* 1850, **14**:195-206.

9. Dunbar RIM, Shultz S: **Evolution in the social brain**. *Science* 2007, **317**:1344-1347.