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Editorial overview: Behavioural ecology: Behavioural ecology of insects: current research and potential applications

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Eric Wajnberg is a population biologist, specialized in population genetics, behavioural ecology, statistical modelling and biological control. For over thirty years, he developed several scientific programmes leading to better understand what are the most important behavioural traits involved in the efficacy of insect parasitoids to control crop pests in biological control programmes. Theoretical approaches are developed — mainly using Monte Carlo simulations and Genetic Algorithms — and experiments are conducted in order to verify the predictions obtained. The main traits studied are (1) those involved in progeny and sex allocation (sex ratio), (2) locomotory mechanisms involved in discovering hosts (video tracking), (3) patch exploitation strategies, etc. He is the editor-in-chief of the international journal BioControl and has published more than 10 books on insect ecology and biological control.

Why has the use of insects as biological models in behavioural ecology been so successful? The first reason is, without question, their diversity. Class Insecta contains the largest number of species in Animalia [1]. They have colonized all terrestrial ecosystems and present a huge diversity of life history traits and behaviours that makes them fascinating organisms to answer the key historical question in behavioural ecology, that is, what is the adaptive value of observed behaviours in different environments? The second reason is their size. Thanks to their small size, and thus to our ability to rear them easily in many cases, insects always were — and still are — wonderful biological models for running laboratory experiments. Over the years, this has enabled us to address important questions related to animal behavioural ecology, leading us both to verify experimentally existing model predictions and to foster further theoretical developments. Such a strong dialogue between theoretical and experimental work on insects has greatly contributed to the development of our current knowledge of behavioural ecology in general.

Since the 70s, studies on the behavioural ecology of insects have tried to understand the adaptive value of decision-making processes adopted by individuals in different environmental contexts. One striking example concerns the optimal decisions adopted by reproductive animals. This is the case, for example, for the optimal clutch size and the optimal sex ratio females should lay, or the optimal time foraging animals should remain on patches of resources. In this respect, insect parasitoids are one the most studied guilds of insects, leading to a large number of important findings (see e.g. [2–4]).

This classical approach is always fruitful, and determining the adaptive value of behaviour is always at the core of this scientific field [5]. In the Special Issue, three papers illustrate such a classical approach, and develop new ideas and concepts on nutritional ecology, mate choice and polyembryony. Raubenheimer and Simpson present an integrative approach — nutritional geometry — that brings together two historical disciplines: foraging and feeding. Nutritional geometry allows us to model graphically and elegantly the interactions between different diet components and their effects across several levels, including physiology and ecology, on individual behaviour and reproductive success. Such a promising approach, which has yet to be used in the field in insects, should allow us to integrate all facets of nutritional activity in animals. Another classical question in behavioural ecology is sexual selection and particularly mate choice. Kelly presents recent research on the identification of factors — both intrinsic and extrinsic — of the females explaining variation in their mate preference for sexually selected traits in males. The author focuses on the

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Emmanuel Desouhant is professor at the University of Lyon, France. He is a specialist of evolutionary and behavioural ecology in insects. His work focuses on the use of information and decision-making processes in the context of foraging and sexual selection to address, for example, questions on mate choice and kin recognition. He combines experiments in the laboratory and in the field to decipher the mechanisms (physiological and molecular) that underline the behavioural responses in animals, and to estimate the adaptive value of behaviours. His research focuses mainly on phytophagous and parasitoid insects.

impact of the social environment of females (constituting both con-specifics and hetero-specifics) on their mate choice. Such a new paradigm of mate choice will lead to numerous future experimental tests in insects to quantify the role of variation in sexually selected traits among males relative to that of variation in female mating preferences for those male traits. Finally, the classical approach in behavioural ecology of insects enables us to investigate fascinating reproductive strategies that are barely observed in other animals. This is the case, for example, for polyembryony in insect parasitoids, a reproduction system in which several embryos (sometimes over thousands) can develop from a single egg. Ode *et al.* nicely summarize, for example, recent development in the understanding of why such an efficient progeny-production strategy has actually not invaded all parasitic wasp families. They identify the evolutionary constraints involved in this particular, atypical mode of reproduction.

As stated above, the small size of insects can sometimes be a convenient feature since it makes laboratory rearing and accurate laboratory experiments rather easy. However, it has in many cases curbed our ability to study carefully several of their behaviours, especially in real natural settings. Building relevant *in natura* experimental designs still remains a challenging task for the scientific community. Two papers in the Special Issue propose solutions to this challenge, that is, for learning and dispersal. Nieberding *et al.* review our knowledge concerning the adaptive value of learning in non-social insects. While learning abilities are widespread in insects, the fitness consequences are poorly described. The authors identify several issues. The main one is that learning is generally studied under laboratory conditions with individuals generally showing low genetic variation and that are reared for several generations under highly standardized conditions. They propose guidelines to circumvent these issues and to study in the field fitness-learning relationships in an eco-evolutionary framework. Similarly, dispersal in the environment is another barely studied behaviour in insects, as it is very difficult to implement relevant and accurate mark-recapture experimental designs. In this respect, Asplen provides an overview of recent conceptual and technological advances on this topic that should see a boom in the coming years, with potential interesting applications in terms of biological control, or disease vector control.

Thanks to several breakthroughs in both physiology (e.g. accurate hormone level quantification) and genetics (e.g. widely available molecular markers, and genomic, transcriptomic and epigenomic approaches, [6]), it is time to consolidate the proximate mechanisms and ultimate (phylogeny and adaptive value) approaches proposed by Tinbergen for behavioural studies [7]. For example, nowadays new molecular and statistical tools enable us to build sound phylogenies, leading us to use phylogenetic comparative techniques to check the evolutionary relevance of model predictions in behavioural ecology [8,9]. This is of utmost importance for a field so heavily influenced by evolutionary thinking and especially in insects that show immense biodiversity. In the Special Issue, Mayhew shows elegantly how comparative analyses, based on 'omics' approaches addressing phenotypic behavioural traits, allows us to decipher the evolutionary meaning of proximate and ultimate causes in animal behaviours. Among the proximate causes of behaviours, ontogeny (i.e. the study of different phases of development of an organism during its lifetime) was historically less studied. Some insect species (both holo-metabolous and hemi-metabolous) have a peculiar feature, that is, metamorphosis, that makes them relevant for studying the link between ontogeny during immature stages and adult behaviours. Metamorphosis has been recognized as a neglected opportunity to test ontogeny of personality in animals [10]. Amat *et al.* illustrate how ontogeny may influence individual trajectory and consistent inter-individual variability. They review recent studies in insects with metamorphosis and elaborate a verbal model to predict the changes we should observe in trait personality with incomplete or complete metamorphosis. This study illustrates the long-standing characteristic of behavioural ecology where predictions and experimental results fruitfully feed each other.

Of course, behavioural ecology, especially in insects, remains an up-to-date, active field of research anchored in societal questions. In the Special Issue, three papers deal with societal issues addressing global changes, invasion biology and biological control to reduce pesticide use. There are nowadays relevant models to study the impact of Human Induced Rapid Environmental Changes (HIREC). In this respect, Caro and Sherman [11] predicted that understanding the adaptive value of behaviours will be impeded by HIREC, because these behaviours become maladaptive under such anthropogenic conditions. van Baaren and Candolin illustrate this statement with insects, showing that movement, foraging, reproduction, habitat selection and social interactions may indeed be strongly affected by HIREC. However, they also suggest that such maladaptation opens interesting questions on the adaptive role of behavioural plasticity, its limits and costs. Biological invasion is tightly linked, among other behaviours, to the dispersal ability of insects. In this respect, releasing a biocontrol agent to control a targeted pest is actually nothing more than a planned invasion. Abram and Moffat propose in this Special Issue an analysis of biological control based on recent advances in invasion biology. This enables us to understand what life history and behavioural traits efficient biological control agents should have, what biotic and abiotic parameters are involved, and also what ecological and evolutionary constraints act on these agents once they are released into the field. This can provide key information to select the correct species and/or strain to be released in particular agro-ecological situations. Finally, Mills and Heimpel summarize the theoretical framework used to understand and to study the spatial dynamics of host-parasitoid interactions and thus the spatial dynamics of biological control. This appears to be needed to accurately quantify the foraging responses of successful biological control agents.

Conclusions

After several decades of both theoretical developments and experimental work, the behavioural ecology of insects remains a very active field of research. The scientific questions addressed are fundamentally grounded in strong interdisciplinary approaches tackling simultaneously both the ultimate and proximate causes of behaviours, nowadays supported by accurate molecular and phylogenetic data. The growing knowledge in this field is now able to provide relevant information for societal questions, as can be seen from several papers in the Special Issue, for example, on invasion biology and biological control. Other aspects like those dealing with conservation biology could also be studied and understood through a behavioural ecology point of view [12].

There still remain, however, challenges to be faced. For example, detailed and accurate analyses of insect behaviour in the field are always difficult. Advances in computer-assisted devices can now be of great help, eventually coupled with the use of molecular markers to follow each individual separately and/or their progeny. Another challenge is to aggregate the huge amount of information regarding life history and behavioural traits in insects available in the literature into shared and structured databases. This will enable us to explore, in an efficient way, for example, the effects of environmental conditions on the tremendous diversity of those traits in insects.

Finally, as far as behavioural ecology of insects is concerned, the Special Issue timely addresses several important and relevant questions, but we are aware that some are missing. This is the case, for example, for the analysis of the evolutionary meaning of the behavioural traits involved in sex ratio and sex allocation, the link between individual behaviour and community structure and function, and the associated implications in conservation biology, just to mention a few. We believe that the Special Issue will foster new research on the behavioural ecology of insects, leading to the production of exciting results with potential important applied outputs, for example, to improve the efficacy of biological control programmes.

Conflict of interest statement

Nothing declared.

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