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Behavioural Ecology of Insect Parasitoids (BEPAR)

from theoretical approaches to field applications

An ESF Standing Committee for Life, Earth and Environmental Sciences (LESC) Programme

The aim of the BEPAR programme is to foster research on the behavioural ecology of insect parasitoids in Europe and to promote the use of a behavioural-ecological approach in biological control of insect pests in agriculture. Theoretical and experimental results obtained will be used to optimise the employment of insect parasitoids in field applications. This will lead to improvements in the impact of biological control technologies in agriculture.

Behavioural ecology studies the fitness consequences of behaviour. Using different animals (e.g. mammals, birds, fishes and insects), this approach has been developed since the mid 60's. Parasitoids have played an important role in the development and tests of theory on foraging behaviour, clutch size and sex allocation, but not in other areas of behavioural ecology, e.g. sexual selection.
Parasitoids are fascinating organisms. Adult females lay their eggs in or on other insects, and larvae subsequently develop by feeding on host bodies resulting in their death. Natural selection acts strongly on parasitoids, because they cannot reproduce without attacking hosts. They have evolved a large variety of host search and attack strategies, based on elaborate behavioural mechanisms. This makes them an ideal model for testing evolutionary hypotheses, usually through predictions derived from mathematical models and the experimental testing of such predictions.
Since parasitoid reproduction results in killing hosts, they can be used on a large scale to control insect pests attacking a wide variety of crops. This crop protection technique is called "biological control" and can significantly reduce of the use of toxic pesticides.

Cover:
A *Venturia canescens* female attacking a larvae of its host *Ephestia kuehniella*.
Photo: Albin Hunia, Germany.

A *Telenomus busseolae* female attacking eggs of one of its host *Sesamia nonagrioides*.

Introduction

Crop losses due to arthropods, diseases and weeds across the world have increased from about 34.9% in 1965 to about 42.1% in the late 1990s. There is thus a need to find efficient and sustainable pest control strategies. Many tools for controlling insect pests are available. However, among them, biological control by means of importation and release of insect parasitoids has recently gained renewed interest because of environmental concerns and problems encountered with the use of pesticides. Biological control has a long history of use in pest management and has been outstandingly successful in many instances. It has permanently resolved a number of economically important pest problems in a highly cost-efficient manner. However, such successes remain limited in number and are largely restricted to the control of pests accidentally introduced in perennial ecosystems. There is thus a need to find means to improve the success of pest control strategies using insect parasitoids, especially in annual cropping systems.

Behavioural Ecology aims at understanding which behaviours animal should adopt in order to maximize their reproductive success. In the case of insect parasitoids, the production of progeny is directly linked to the reduction of the host population. Therefore, studying how parasitoids should optimize their reproductive output should directly provide means to improve pest control efficacy in biological control programmes.

Until the 1990s, behavioural ecologists largely focussed on developing and testing theoretical predictions for the fitness consequences of behaviour but devoted less effort to studying the behavioural rules (so-called proximate mechanisms) employed by the animals. In the last decade, behavioural ecologists have been trying to integrate the study of behavioural mechanisms with the functional approach of studying the fitness consequences of behaviour. A wealth of knowledge is available on the behavioural mechanisms employed by parasitoids to find hosts and allocate offspring to them, but how these mechanisms contribute to fitness or act as constraints on the optimization of reproductive behaviour of parasitoids is often poorly known. One main aim of the programme is thus to foster the development of theory in behavioural ecology that incorporates knowledge of the underlying mechanisms of parasitoid behaviour in models that predict maximal fitness. The results obtained that way can be used to define more efficient biological control technologies of insect pests in agriculture.

Framework of the scientific programme

The basic, unifying, principle of behavioural ecology is that behaviour, like any other characteristic of organisms, has been shaped, to a large extent, by natural selection. This assumption leads to hypotheses (frequently expressed in mathematical terms) that can be tested in the laboratory and under natural conditions. Thus, one aim of the BEPAR programme is to understand which rules real animals use to govern their behaviour. This can be achieved thanks to the heuristic power of evolutionary approaches. In many cases, animal behaviour does converge with theoretical predictions. In many other occasions, the most illuminating part of the exercise is to reflect on the differences between the experimental results and optimal (theoretical) behaviour. This process can reveal the weaknesses in our understanding and lead to further refinement of the hypotheses and experimental tests. Both ultimate and proximate explanations are addressed in the programme. Combining this approach with others – like behavioural and population genetics – will allow an improved understanding of how natural selection has shaped behaviour.

This approach has already proven to be a most powerful means of studying parasitoid behaviour. Two illustrative examples are the study of superparasitism and patch-leaving decisions. Concerning superparasitism, the main question was why a female would sometimes attack a host that already contains a parasitoid offspring when usually only a single parasitoid will emerge from a host independently of the number of parasitoid eggs the host has received. The latter is the consequence of parasitoid larvae suppressing each other inside the host. For a long time, attacking an already parasitized host was considered a waste of resources and a consequence of poor discrimination capacity. However, evolutionary approaches have revealed that under some circumstances attacking an already parasitized host is a more appropriate strategy than avoiding it. This is so because there is often some probability to have offspring even from a parasitized host and this probability might lead to higher (fitness) gains than if the parasitoid would never find the opportunity to lay this egg in her life time. Comparing theoretical models with experimental results has revealed how exquisitely tuned the egg laying behaviour of many parasitoids is.

Another example is that of time-allocation. Parasitoids must find their hosts in a heterogeneous environment, and must decide how to allocate their time to different parts of the environment. A classical theory called “the Marginal Value Theorem” predicts that, when the number of hosts strongly varies among patches, each patch of hosts should be depleted to the average gain rate achievable in the habitat. This results in longer residence times in patches containing more hosts, in longer residence times with increasing average distance between patches, and in patches being further depleted in poorer habitats. Tests of these predictions with several parasitoid species have shown that they can behave according to the predictions of this model. Moreover, the behavioural mechanisms that parasitoids use to decide how long to stay in a patch have been identified and mechanistic models can predict similar patterns of patch time allocation. Finally, it has been shown that when hosts have a more regular distribution over patches, other leaving rules are adaptive, and that parasitoids belonging to species that live in such environments use a mechanism of patch time allocation obeying these rules.

The need for theoretical approaches

One of the tools that has most contributed to the success of behavioural ecology has been the building of models to study the behavioural strategy that animals adopt to maximise their fitness. Developing these models is a complex exercise because it depends on a wide range of assumptions: (1) Which alternatives are potentially open to an animal? (2) What should be optimised? (3) What are the constraints?
Of course, many relatively arbitrary decisions are taken in the course of model development. A good convergence between the behaviour of the animal and the results of the model is taken as an indication that the biological process has been well understood. Similarly, there is a wealth of information available on when a failing model should be discarded and when it should be amended.

Especially for insect parasitoids, different mathematical techniques are used depending on the characteristics of the behaviour under study. The simplest situation is that of behaviour whose outcome is assumed to be independent of the age and physiological state of the animal and of the behaviour of conspecifics. These models are termed “static optimality” models and are most often based on analytical

Trichogramma females attacking eggs of *Pieris brassicae*.

mathematical techniques. A more complex situation arises when the outcome of the behaviour of an individual depends on the behaviour of conspecifics. A classical example is a group of parasitoids exploiting a number of host patches together. As the departure of an individual from a patch would increase host availability to remaining animals, the foraging success of each animal would depend on the patch residence time adopted by others. In this case, the question asked is not whether a given behaviour is "optimal" but whether it is "evolutionarily stable" (i.e behaviour that, when adopted by the whole population, cannot be replaced by any mutant). Game theory, a mathematical technique used mainly in economics, has been adopted to solve this kind of problem with extraordinary success.

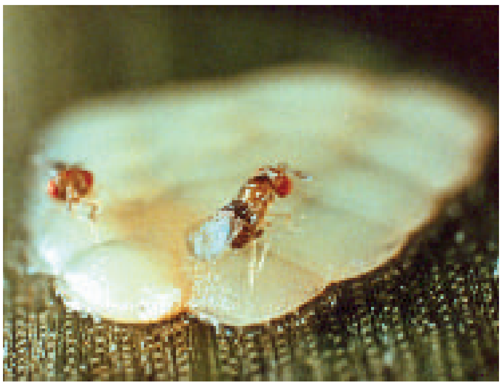
Which behaviour an animal should adopt depends in many cases on its age and physiological state. A typical example is whether to lay an egg in a parasitized host. The probability of dying with eggs that have not been laid would depend on the age and metabolic resources of the parasitoid. A young animal might have plenty of opportunities to search for more profitable hosts, opportunities that an ageing or starving animal might not have. Stochastic dynamic modelling is a powerful and simple technique that is used to solve this sort of problem.

Many behavioural decisions of parasitoids may be state-dependent as well as dependent on the behaviour of conspecifics. Only recently, dynamic game theory in the form of genetic algorithms or iterated stochastic dynamic modelling has been used to elucidate optimal behavioural solutions of parasitoids under such relatively complex ecological scenarios.

From behavioural ecology to evolutionary ecology

Behavioural ecology concentrates on behavioural traits and chiefly takes an experimental-manipulative approach to explore the fitness consequences of alternative actions. It is supported by models that seldomly incorporate explicit genetics and are often called phenotypic. Evolutionary ecology encompasses a broader range of problems and approaches. It often uses genetic techniques explicitly, and frequently emphasises the comparative approach based on phylogenetic methods.

Though the BEPAR programme is primarily orientated within the behavioural ecology paradigm, a major goal is to make links between behavioural ecology and other aspects of evolutionary ecology. This is being done in several ways in the BEPAR programme. In studying the co-evolution of host resistance and parasitoid virulence, actual genes involved in these traits should soon be identified, and their dynamics in the field will be studied. This will enable us to test some old but little explored theories about host-parasite co-evolution. Recent studies have quantified genetic variation in a number of traits involved in foraging and sex ratio, allowing phenotypic behavioural ecology models to be compared with those from a quantitative genetic background. Finally, parasitoids were the subjects in some of the first comparative studies in behavioural ecology using different related species. More comparative work will be developed within the BEPAR programme, thanks to newly available improved (molecular) phylogenies.



Trichogramma brassicae females attacking eggs of *Ostrinia nubilalis*.

From behavioural ecology to population dynamics

One of the basic endeavours of biological science is to explain complex systems from the behaviour and interaction of their individual components. Studying how behaviour of individuals affects the dynamics of populations has become a major challenge to population ecology, especially in the case of insect parasitoids. Two facts make this approach particularly promising: (1) population ecology lacks a central, biological theory that guides research. Most of its concepts are drawn from other disciplines. Conversely, behavioural ecology has such a theory: the theory of evolution by natural selection, which is the major source of hypotheses and explanations. Linking population dynamics to behavioural ecology should expand the explanatory and predictive capacity of population ecology and give to it a more solid biological framework; (2) good knowledge of population dynamics can only be obtained through long and costly surveys of natural populations. Refining hypotheses on the basis of well understood biological processes would make the questions more precise and should result in a more economic use of human and financial resources.

Models of host-parasitoid interactions incorporating sketchy descriptions of animal behaviour have suggested that behaviour can indeed have a major influence on population dynamics. However, this work has often lead to contradictory predictions. As a consequence, many authors have called for the inclusion of more realistic descriptions of animal behaviour in these models. Optimality models allow a compact description of animal behaviour without the loss of realism. These descriptions can be easily incorporated to models of interacting populations (such as host-parasitoid systems). Both the consequences of convergence to the optimal behaviour and the deviation from these predictions can be analysed using powerful analytical tools and computer simulations.

The outcome of biological control depends to a large extent, and both directly and indirectly (i.e. through population processes), on parasitoid behaviour. An interesting example is the process by which parasitoids interfere with each other while exploiting a host patch. From the most practical point of view, interference can play an important role in determining the success of biological control, simply through the behaviour of the parasitoids at the moment of release. This is one of the reasons why so much care is put on the packaging and the process of releasing biological control agents. Also in a direct way, interference can decrease the efficiency of parasitoids through fighting or by forcing the animals to leave host patches too early. Conversely, through population processes, interference can lead to a more persistent parasitoid population and to a longer lasting protection of the crop. Behavioural ecological approaches might answer questions such as: (1) In which conditions should parasitoids share a patch without interference between them? (2) When should parasitoids try to gain exclusive possession of a patch? (3) Which distributions of parasitoids and of parasitoid attacks should result from interference of different intensities? (4) What would be the population consequences of different strategies of parasitoids towards conspecifics sharing the same patch?

Added European value of the programme

Co-operative work between European teams in this sort of scientific research appears to be particularly sound because some teams have already demonstrated their ability to develop the theory, while others are efficient in defining and conducting experimental work, and still others have a sound understanding of the statistical treatment of the data. Finally, Europeans have already demonstrated their efficacy in the development of field tests of the theoretical predictions available. However the work has highlighted the need for several different scientific disciplines to be combined in order to achieve high quality outputs. One important aim of the BEPAR programme is to achieve this by combining the expertise of research groups across European countries to work in partnership on a range of clearly defined research objectives. The multidisciplinary approach is thus forming the basis of work developed within the programme. Scientists working in the different European teams involved are developing scientific co-operations, sharing their expertise in diversified research areas (e.g. ecology, entomology, mathematics, statistics, chemistry, etc.). Such a pan-European multidisciplinary co-operative research programme appears to offer the most productive means of developing and executing research for producing sound theoretical predictions supported by experimental data generated by both field and laboratory work.

The programme concept

The concept of the scientific programme proposed is based on:

- The development of different complementary scientific activities at the European level. These include the development of theoretical approaches and their experimental examination in both laboratory and field tests, alongside the organisation of international workshops and conferences, and short-term fellowship grants for senior scientists to carry out collaborative work in a European country, other than their country of origin.

- Educational goals towards graduate students, PhD and post-doctoral students, including co-supervised PhD theses, summer schools, and European travel grants for PhD students and PostDocs.

- Distribution of information to the scientific community through a web site (http://bepar.antibes.inra.fr/), books and original publications in international scientific journals, etc.

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