

Where is behavioural ecology going?

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Since the 1990s, behavioural ecologists have largely abandoned some traditional areas of interest, such as optimal foraging, but many long-standing challenges remain. Moreover, the core strengths of behavioural ecology, including the use of simple adaptive models to investigate complex biological phenomena, have now been applied to new puzzles outside behaviour. But this strategy comes at a cost. Replication across studies is rare and there have been few tests of the underlying genetic assumptions of adaptive models. Here, I attempt to identify the key outstanding questions in behavioural ecology and suggest that researchers must make greater use of model organisms and evolutionary genetics in order to make substantial progress on these topics.

‘Behavioural ecology is a beguilingly simple subject’

J.R. Krebs and N.B Davies [1]

The romantic era of behavioural ecology

The core ideas that underlie modern behavioural ecology can be traced to a period during the 1960s and 1970s when a remarkable series of papers demonstrated that simple adaptive models, such as the marginal value theorem, could be used to tackle diverse puzzles that had remained largely untouched during the Modern Synthesis of evolutionary biology [2–14]. Building on the foundations laid by Fisher [15] and Haldane [16], these authors targeted topics as diverse as foraging, fighting, sex and cooperation. The models typically ignored detailed genetic mechanisms and instead predicted that even the most puzzling aspects of behaviour must have evolved because, on average, they increase the fitness of the individual. Such models were not designed to show that animal behaviour is perfectly optimal, but to identify and understand the kinds of payoffs and constraints that are important in behavioural evolution.

With the benefit of hindsight, there were several early works that pioneered the adaptationist approach to empirical studies of behaviour and ecology [17–23] and the fledgling field received popular syntheses in Wilson’s *Sociobiology* [24] and Dawkins’ *The Selfish Gene* [25]. But the conceptual unification of the field and, importantly, its focus on behaviour *per se*, did not occur until 1978, when Krebs and Davies published the first edition of their edited volume, *Behavioural Ecology: An Evolutionary Approach* [26]. In the opening sections of that book and in their subsequent introductory textbook [27], Krebs and Davies

wove together the theories developed over the preceding decade and championed a new empirical approach to investigating behaviour. The key element of this approach was the use of adaptation as the central conceptual framework, which gave behavioural ecologists a precise *a priori* expectation: behaviours should evolve to maximise the fitness of the individuals showing those behaviours.

Krebs and Davies also stressed the importance of two other principles [27]. The first was the need to quantify variation in behaviour accurately. Drawing attention to the new quantitative work that was being performed in some areas of ethology [28,29], they showed how this approach could be applied to a variety of behaviours. The second principle was to use subtle variation among individuals to test adaptive hypotheses. With the notable exception of some primatological studies [30], previous ethological studies had tended to regard all individuals of a species as behaving in the same way. By contrast, behavioural ecologists tested the consequences of individual variation in behaviour on subsequent reproduction and survival.

This combination of a testable adaptive framework and a quantitative empirical approach led to huge growth in behavioural ecological research during the late 1970s and 1980s. Foraging strategies and sex ratios emerged as key battle grounds regarding the effectiveness of optimality models [31,32]. By the beginning of the 1990s, the consensus within the field was that simple optimality models were often remarkably accurate, suggesting that such models captured the essential payoffs, tradeoffs and constraints that determine behavioural evolution [33,34]. Here I ask, what has happened in behavioural ecology since then? Have behavioural ecologists simply continued to study finer and finer details of foraging behaviour and sex ratios, or have they moved on to tackle new questions of broad conceptual importance?

The evolution of behavioural ecology

Behavioural ecology has changed in terms of both the broad topics and the specific questions that it addresses. Several of the original foci of behavioural ecology, such as optimal foraging, have become relatively less fashionable (Figure 1a). Other topics have already gone through boom-and-bust cycles, even within the short history of the field, with fluctuating asymmetry being a striking example (Figure 1a). However, these declining areas of activity have quickly been replaced by interest in other topics, some of which lie outside traditional definitions of behaviour, such as host–parasite interactions (Figure 1b). Also, a few of the original puzzles have

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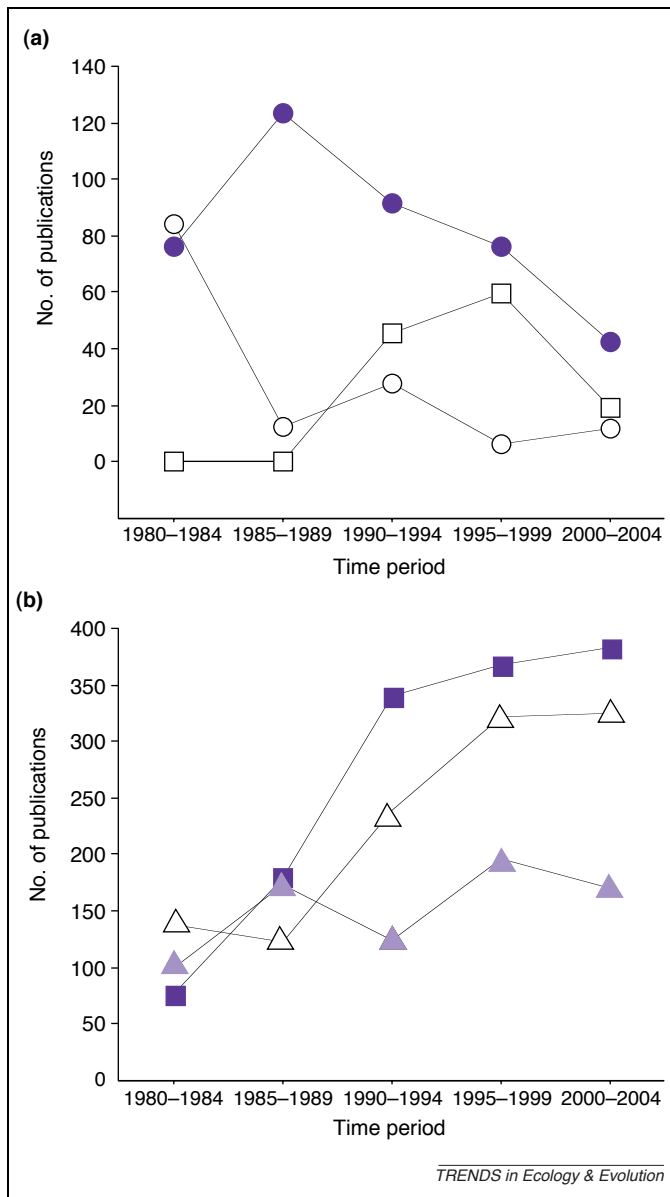


Figure 1. Differences in the pattern of publication among behavioural ecological topics over the past 25 years. **(a)** Topics declining in relative frequency over time (open circles, optimal foraging; closed circles, mating systems; open squares, fluctuating asymmetry). **(b)** Topics increasing over the same period (closed squares, sexual selection; open triangles, host–parasite interactions; closed triangles, animal signals). The number of publications is the number of papers on a topic per 10 000 papers published in the field during the period in *Behavioural Ecology*, *Animal Behaviour* and *Behavioural Ecology and Sociobiology*. Data are based on searches of titles only from the ISI Web of Knowledge™ (<http://wok.mimas.ac.uk>). Searches were performed in November 2005 using the following terms: optimal foraging, optimal forag*; Mating systems, mating system* or polyg* or polya*; Fluctuating asymmetry, fluctuating asymmetry; Sexual selection, sexual selection or mate choice or mating success; Host–parasite, parasit* or immuno*; Animal signals, signal*.

retained their interest. Sexual selection in birds, for instance, remains a major area of activity. But behavioural ecology is not just the study of sexual selection in birds: as a field, behavioural ecology tackles a range of behaviours, and makes use of a variety of organisms (Figure 2a).

There has also been a shift in the type of questions being posed. Some of these shifts in emphasis are idiosyncratic to particular topics, but my view is that there are also some general trends. I detect a growing appreciation of studies that attempt to estimate the

relative importance of competing proximate mechanisms, that use long-term databases to understand the demographic consequences of behavioural variation, or that explain the ecological basis of differences in behaviour among species (Table 1). This is true even for topics of long-standing interest, such as sexual selection, where the goal posts have now moved on from simply demonstrating that sexual ornaments are used as cues in mate choice, to estimating the relative importance of indirect (genetic) and direct (nongenetic) benefits to mate choice [35], or the role of sexual selection in speciation (Table 1). Similarly, whereas previous studies of cooperation have revealed that apparent cases of phenotypic altruism within species are in fact genetically selfish, a new challenge is to discover whether the mechanisms responsible for cooperation are common across different taxonomic groups, or across different levels of organisation (Table 1).

Molecular tools

Behavioural ecology has also changed in terms of the types of tools used to investigate animal behaviour. One obvious one is the application of molecular markers to behavioural questions [36,37] (Figure 2b). When Krebs and Davies wrote the first editions of their textbooks, metaphorical selfish genes were about as close as they got to molecular biology [26,27]. By the time of the third edition of *Behavioural Ecology: An Evolutionary Approach* in 1991, there was a DNA fingerprint on the front cover [38]. Given the fondness of behavioural ecologists for birds and sexual selection, it is not surprising that the molecular revolution in behavioural ecology was first felt in the study of mating systems in birds, where the widespread application of methods for assigning genetic paternity has overturned the dogma that birds are largely monogamous [39].

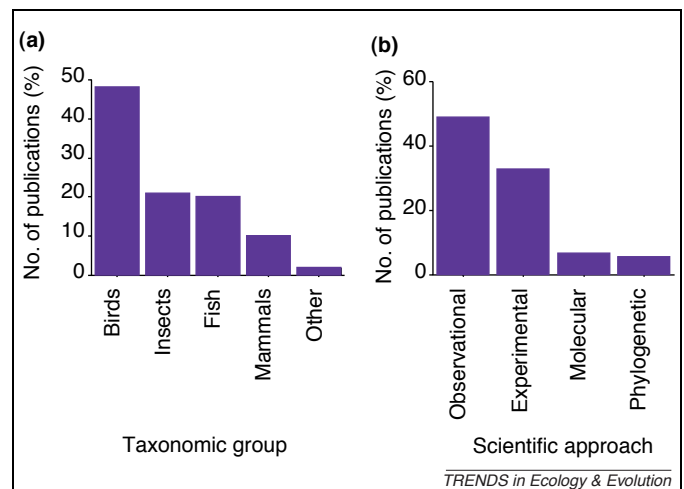


Figure 2. Approaches used in modern behavioural ecology. **(a)** Taxonomic affinity of study organisms. **(b)** Scientific method used. The number of publications is measured as a percentage of the total papers published between 2001 and 2005 in *Behavioural Ecology*, *Animal Behaviour* and *Behavioural Ecology and Sociobiology*. Data are based on searches on both the titles and abstracts from the ISI Web of Knowledge™ (<http://wok.mimas.ac.uk>). Searches were performed in November 2005 using the following terms: Birds, bird* or avian; Mammals, mammal*; Fishes, fish* or pisces; Reptiles, reptil* or lizard* or snake*; Insects, insect* or butterfly* or moth* or grasshopper* or cricket* or fly or flies; Observational studies, observation* or correlation*; Experimental studies, experiment* or manipul*; Molecular studies, molecular or fingerprint* or DNA or nucle* or satellite*; Comparative studies, comparative or phylog*.

Table 1. A personal list of questions in behavioural ecology

Topic	Questions answered satisfactorily	Questions remaining
Adaptation and optimality	Can simple adaptive models help explain complex behaviours?	Yes
	Are there constraints to behavioural adaptation?	Yes
	Is gene-level selection typically more useful in explaining behaviour than group-level selection?	Yes
Sexual selection and signals	Are the runaway process and the handicap principle plausible?	Yes
	Do females commonly show active mate choice?	Yes
	Are some traits consistently favoured through mate choice?	Yes
	Can there be genetic benefits to female choice?	Yes
	Can there be nongenetic benefits of female choice?	Yes
Life histories	Are there life-history tradeoffs?	Yes
	Are phenotypic observations sufficient to show these?	No
	Do life-history tradeoffs vary across species?	Yes
	Is variation among individuals in life history often adaptive?	Yes
Cooperation and altruism	Is cooperation typically directed towards genetic kin?	Yes
	Are there examples of non-kin benefits to cooperation?	Yes
	Does kin conflict also occur in social groups?	Yes
	Is cooperation nonrandom with respect to phylogeny?	Yes
Host-parasite interactions	Are there tradeoffs between immunity and life history?	Yes
	Is there genetic variance in parasite resistance?	Yes
	Do hosts and parasites coevolve?	Yes

Molecular techniques are now routine in the investigation of behaviour, as illustrated by the recent findings of cryptic differences between populations in large-scale patterns of migration behaviour [40].

Proximate mechanisms

Behavioural ecologists are also making increasing use of techniques from other areas of cellular and molecular biology. In large part, this is a result of an increasing interest in the proximate mechanisms that determine behaviour [41]. One area receiving particular attention is that of ecological immunology [42,43], where techniques from medicine have now been used to test theories linking immunocompetence with sexual ornamentation [44], colouration [45] and life histories [46]. The rush into a new area is not without its problems and several authors have cautioned about an over-reliance on a limited number of rather crude techniques that assay only one particular aspect of immunity [47,48]. It is worrying, for instance, that we still know so little about what these simple immune assays tell us about resistance to real parasites in wild populations, how different aspects of immunity interact, or the genetic basis of links between immune responses and traits such as body condition and sexual ornamentation.

Phylogenetic approach

An analytical tool that has a rich history in behavioural ecology but that is now being applied with increasing sophistication is that of phylogenetic comparative techniques (Figure 2b). Recent advances are based on the development of methods designed to test for links between traits that vary in a complex manner among closely related species, of which behavioural traits are a prime example [49,50]. Together with new molecular phylogenies, large-scale behavioural databases and fast computers, these new comparative techniques have generated renewed interest in the comparative approach. In addition to increasingly sophisticated analyses of well established questions regarding social organisation and life histories

[51], there is an exciting thrust towards the testing of the role of behaviour in determining large-scale patterns of speciation and extinction [52,53]. Recent comparative studies of cichlid fish, for instance, have demonstrated the potential role of male mating behaviour in the famous radiations of the East African lakes [54].

Future challenges

‘Behavioural ecology is the soft underbelly of evolutionary biology’

David Reznick

For a field so heavily influenced by evolutionary thinking, behavioural ecology shows a surprising ignorance of quantitative genetics. With a few notable exceptions [55], it is still relatively rare to read a paper in a behavioural ecological journal, or hear a talk at a behavioural ecological conference, that contains information about the genetic relationships among traits. Instead, behavioural ecologists typically assume, first, that the observed phenotypic patterns of behaviour accurately reflect the underlying genetic patterns and, second, that the details of genetic architecture will not seriously influence the evolution of those behaviours. Krebs and Davies characterised this attitude as ‘think of the strategies and let the genes look after themselves’ [27], whereas Grafen formalised it as the ‘phenotypic gambit’ [56].

The phenotypic gambit should be safe under some circumstances, such as when studying a behaviour that is at a long-term evolutionary equilibrium. This is because, given enough time, evolution should lead to behavioural adaptation irrespective of the underlying genetic architecture [34]. In other circumstances, however, the difference between phenotypic and genetic patterns can be crucial. In the study of sexual selection, for instance, it matters a great deal whether a link between the showy ornamentation of the father and the longevity of his son is due to the good genes of the father or to his attentive parental care [35,57]. More generally, it might be

dangerous to assume that all the behaviours that we observe are at evolutionary equilibria; once we become interested in the evolutionary dynamics of behaviour then genetics again become potentially important. This is because selection theory predicts that genetic correlations among traits are likely to be common and that these correlations can affect the evolution of individual traits [58,59]. Indeed, a recent reassessment of the influence of genetic limits on evolutionary change advocates that a multivariate approach is vital to understanding the evolution of complex traits, and suggests that the potential for evolutionary change is often limited by a lack of genetic variation in the multidimensional direction favoured by selection [60].

Genetic basis of behaviour

How can behavioural ecology respond to the increasing need for quantitative genetic information? The challenge is not trivial because the types of traits that are of interest to behavioural ecologists are likely to have low genetic heritability and/or complex genetic correlations with other traits. Also, whereas traditional quantitative genetic studies can use experimental breeding designs to tease apart genetic and environmental effects, such experiments are usually prohibitively demanding in wild populations. It is particularly exciting, therefore, to see the development of new techniques for obtaining quantitative genetic information about complex traits in wild populations.

One such technique is the incorporation of pedigree information into statistical models to estimate quantitative genetic parameters [61]. This 'animal model' approach has already been used to great effect in a some well studied populations, estimating the heritability of fitness in the red deer *Cervus elaphus* of Rum [62] and the genetic correlation between life-history parameters in the Gotland collared flycatchers *Ficedula hypoleuca* [63]. The fact that the technique has so far been limited to populations that have been the subject of long-term studies is no coincidence because they typically require a multigenerational pedigree. Even the requirement for a pedigree can be dropped, however, under another new approach that proposes the use of molecular markers to reconstruct genetic relationships among individuals and then use statistical models to extract information about quantitative genetic parameters [64]. The potential promise of this 'marker-based' approach to behavioural ecology is substantial, but it remains far from clear whether it can deliver robust parameter estimates from wild populations of mobile animals. Although there have been few empirical tests to date, the available evidence suggests the animal model approach will have the larger impact on behavioural ecological research [65].

An alternative method for obtaining behavioural genetic information is the candidate gene approach, which is based on the finding that some complex behaviours are strongly influenced by a small number of genes of large effect [66]. Some of the best examples of this approach come from the study of social behaviour, where it has now been shown that behaviours as diverse as social hierarchies and mate recognition can be determined by

such genes [67]. In the fire ant *Solenopsis invicta*, for instance, a single genetic element is responsible for determining variation in an important aspect of colony-level social organization [68]. It now remains to be discovered how many other behaviours have a similarly simple genetic basis, and whether the candidate gene approach can be successfully extended to organisms where genetic resources are more limited.

Model organisms

Another potential solution to the need for genetic information would be for behavioural ecologists to join mainstream biology in the use of model organisms. Behavioural ecology has been informed by studies based on *Drosophila*, such as the recent demonstration of dynamic sexual conflict [69], but such examples remain relatively rare in behavioural ecological journals. Of more than 2500 articles published in the three leading behavioural ecological journals between 2001 and 2005, <2% made use of traditional model animals such as the nematode worm *Caenorhabditis elegans*; the fruit fly *Drosophila melanogaster*; the zebra fish *Danio rerio*; the chicken *Gallus domesticus* and the mouse *Mus musculus*. Why is this? In part it is probably a reflection of the fact that behavioural ecologists are genuinely more interested in the behaviour of wild organisms. Although traditional model species have many other useful attributes, their natural history in the wild is typically very poorly known. But that cannot be the whole story because behavioural ecology also makes extensive use of laboratory studies, particularly of invertebrates and fish (Figure 2a). My feeling is that behavioural ecologists have shunned model organisms simply because of cultural tradition.

Whatever the cause, the result has been that behavioural ecology has failed to make use of the wealth of genetic information accumulated in the biomedical literature, or exploit the genomic resources already available for commercially important model species. The use of model organisms remains a largely unexplored route in behavioural ecology, but surely one of great promise [35]. Indeed, even for those studies requiring wild populations, there is nothing to stop behavioural ecology developing its own model systems, based either on particularly widespread taxa or on close relatives of the traditional models.

Replication across studies

Increased use of model organisms in behavioural ecology would also help to deal with another important limitation of the field, which is the lack of precise replication across laboratories. This problem is certainly not unique to behavioural ecology *per se* but the use by researchers of an extraordinary diversity of study species makes it particularly difficult to replicate important findings. In other biological fields, the use of model organisms enables precise comparisons between studies and there is a culture for researchers to be wary of a potentially important discovery until it has been confirmed in other laboratories. By contrast, in behavioural ecology the lack of model systems means that even the classic studies are very rarely subject to robust scrutiny.

One potentially useful development in this area is the importing of meta-analyses from the medical and social sciences [70]. Meta-analyses are statistical procedures designed to test the generality of support for a particular hypothesis by comparing results across a large number of empirical studies while simultaneously controlling for variation in potentially confounding factors, such as sample size and experimental technique. So far, the application of meta-analyses to behavioural ecological questions has been relatively limited, but it has been used to good effect in areas including adaptive sex ratios and fluctuating asymmetry [71]. At its best, meta-analyses might enable behavioural ecologists to continue to study a wide variety of species while simultaneously performing tests of generality.

Conclusions

One of the most important developments regarding behavioural ecology is that the adaptationist approach has now been applied to many other fields and to topics as diverse as the organisation of genomic elements, immunological cascades and human demography. It would be too much to claim that behavioural ecologists are entirely responsible for this because the core principles of the modern adaptationist approach clearly go back at least as far as Fisher and Haldane, but I think behavioural ecology has had a role in making this approach accessible and popular.

Within the field of behavioural ecology itself, a new series of questions has emerged to replace those that have already been answered (Table 1). Many of these new questions are of a subtly different type and require a more detailed understanding of the genetic and physiological mechanisms that underlay behavioural traits. Here, I have argued that, to tackle these outstanding questions, behavioural ecologists would benefit greatly from embracing the opportunities offered by model organisms and evolutionary genetics.

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<http://www.vertpaleo.org>

17–19 November 2006

E-Bird International meeting. Coping with environmental change: integrating avian ecology and endocrinology. University of Glasgow UK
<http://e-bird.cefe.cnrs.fr/final-workshop.htm>

4–7 December 2006

5th International Conference on Ecological Informatics, Santa Barbara, CA, USA
<http://www.isei5-conference.elsevier.com>

2007

12–18 August 2007

30th Congress of the International Association of Theoretical and Applied Limnology, Montréal, Canada
<http://www.sil2007.org>

20–25 August 2007

11th Congress of The European Society for Evolutionary Biology, Uppsala, Sweden
<http://www.eseb.org/>