

Behavioural Ecology in the 21st Century

Stuart A. West¹, Sasha R.X. Dall², J. Paul Cunningham³, Suzanne H. Alonzo⁴ & Ashleigh S. Griffin¹

¹Department of Biology, University of Oxford, Oxford OX1 3RB, UK

²Centre for Ecology & Conservation, University of Exeter, Cornwall Campus, Penryn TR10 9FE, UK

³Agriculture Victoria Research, AgriBio Centre, 5 Ring Road, Bundoora, VIC 3083, Australia

⁴Department of Ecology and Evolutionary Biology, University of California Santa Cruz, Santa Cruz, California, USA 95060

stuart.west@biology.ox.ac.uk

Behavioural ecology research has explained traits from foraging and cooperation to mating strategies and sex allocation. However, the size and interdisciplinary nature of this research can obscure the broader contributions that behavioural ecology has made and the major tasks for the future. We first assess the contributions that behavioural ecology has made to fundamental science, for both understanding nature and the scientific method. Secondly, we explore the application of behavioural ecology research to global challenges, from pests and pathogens to conservation and mitigating human impact. In all cases, progress has relied on a hypothesis driven approach that combines mathematical modelling with empirical testing, and the strategic choice of simplifying assumptions.

Introduction

Behavioural ecology aims to understand how organisms are adapted to their environments¹. It focuses on evolutionary questions about *why* natural selection has favoured different traits (Box 1). The aim is to explain both the precise forms of traits in single species, and why traits vary across species. This behavioural ecology approach can be applied to any trait from simple behaviours to more complex life history strategies and morphology.

The field of behavioural ecology emerged in the 1960s and 1970s from a synthesis of evolutionary theory and ecology into the field of animal behaviour². The last 50 years has seen an explosion of research in this area, to tackle a diversity of topics, from foraging and host-parasite interactions to sexual selection and cooperation. This research has included applying the behavioural ecology approach to a diversity of traits that might not typically be thought of as ‘behaviour’, such as parasite virulence, genomic imprinting and immunology.

The rapid expansion of behavioural ecology and its fundamentally interdisciplinary / integrative nature can make it hard to see where the field is, what it has contributed, and where it is going. How does behavioural ecology link to other areas that study adaptation or ecology? Are there broader implications from the field of behavioural ecology? Is research expanding in scope or focusing on increasingly narrower questions? Is it a ‘softer’ or less rigorous relative to other areas of evolutionary research³? How do we define behavioural ecology in 2025? What are the important future directions for behavioural ecologists?

Our aim is to answer these questions in a way that captures the enduring excitement of behavioural ecology, while also highlighting how insights from behavioural ecology have contributed broadly to our understanding of organisms and the natural world. Rather than list a series of precise questions that behavioural ecologists should answer, our goal is to instead step back and ask what behavioural ecology has contributed and why it is still needed. Put

simply, what have we gained from and why does the world still need behavioural ecologists? We answer this by examining some major contributions that behavioural ecology makes to fundamental science and global challenges.

Contributions 1-7: Fundamental Science

1. Natural selection and adaptation. Behavioural ecology has provided some of the greatest examples of how natural selection leads to adaptation^{1,4,5}. Organisms can appear to be adapted or ‘designed’ for the environments in which they live (Fig. 1). Echidnas have sharp pointy spines to protect against predators. Maleos bury their eggs in volcanic sand to incubate them. Bald eagles have extremely sharp vision, allowing them to see prey from 1-2 miles away. Weaver ants work together, using the silk produced by larvae to turn leaves into hanging nests.

Darwin’s theory of natural selection explained how adaptation could have arisen without a creator, or how you can get the appearance of design without a designer⁶. Heritable traits that are associated with increased survival and reproduction (fitness) will accumulate in a population. This improving process will lead, over time, to organisms that appear *as if* they were designed (adapted) for the environments in which they live^{7,8}. The qualification ‘as if’ is key here – natural selection leads to the appearance of design (adaptation), without a designer⁹.

While Darwin’s theory provided a general explanation for how organisms become adapted to their environment, it didn’t aim to explain particular adaptations. The adaptive benefit of our above examples, such as spines and sharp eyesight, are relatively obvious, but many other features of living organisms can be harder to explain. For example, animals sometimes fight to the death or parents allow their young to die. The primary aim of behavioural ecology is to pose and answer questions about such harder to explain features of living organisms.

It is useful here to give some specific examples of the kind of questions that behavioural ecologists ask, especially those that don’t seem to make sense at first glance¹⁰⁻¹⁸. Why do male redback spiders catapult themselves into the mouths of females? Why do male dung beetles have two very different forms (called morphs)? Why do some female bluehead wrasse change sex to become a male? Why do female chimpanzees advertise their sexual receptivity with sexual swellings? Why is male parental care more common in fish, but female parental care more common in mammals? Why do social insect workers become sterile helpers, unable to breed? Why do some bacteria kill themselves (cell lysis) to release toxins? Why do rhizobia bacteria provide nitrogen to their host plants?

Similar questions about the adaptive (selective) benefit can be asked about any aspect of any organism. Time and time again, behavioural ecology research has answered such questions, by examining the underlying costs and benefits^{1,4,5}. While useful for understanding behaviours, this approach can be applied to any type of biological adaptation.

To focus on one gruesome example from our list, why do male redback spiders somersault themselves into the jaws of the female during copulation (Fig. 2)? On the surface, this seems like a maladaptive option for the male. Yet, females often eat these males, which increases the mating time with that male and reduces the likelihood that the female mates with another male^{10,19}. Consequently, the benefit of being eaten for a male is that it reduces competition for fertilizations with other males (sperm competition) - an eaten male fertilises a larger fraction of the eggs produced by the eating female. In contrast, the cost of being eaten is relatively low for males, because they are unlikely to be able to find another receptive female^{20,21}. The benefit outweighs the cost and so somersaulting to death is favoured. Other

possible hypotheses, such as the nutritional benefit of eating a male leading to more eggs for that male to fertilize, were rejected in redback spiders.

As with any behavioural ecology research, answering one question led to new questions (Box 2). In the case of redback spiders, new questions included why females only eat some males, why males do not throw themselves into the jaws of immature females, and whether any nutritional benefits of eating a male are passed to offspring²¹⁻²³. Questions can also be asked about differences across species. Males of some spider species curl up and die during copulation, whereas males of other species will go to great lengths to avoid being eaten, by first wrapping females in silk²³⁻²⁵. How can we explain such variation?

More generally, by answering questions such as those in our above list, behavioural ecology research has explained both the details of what happens in particular species, and variation across species^{1,4}. This work has explained a diversity of traits, including many that previously didn't make sense. If you want clear examples of adaptation for an evolutionary textbook, you turn to behavioural ecology. This research has contributed to our general understanding of how evolution can lead to adaptation and the role the environment plays in shaping these adaptations.

In many cases, successful explanations of adaptation have flowed from a tight integration between theory and data, to test both qualitative and quantitative predictions (Box 2). One of the key contributions of behavioural ecology is the example it provides of how mathematical theory can be combined with rigorous quantitative tests of theory to provide empirical understanding.

2. Broad generalisations across the tree of life. In some cases, behavioural ecology has taken research on adaptation a step further by producing broad generalisations where the same factors appear to play analogous roles across the tree of life. For example, altruistic cooperation can be favoured by kin selection (indirect fitness benefits) if it is directed towards relatives who share the gene for cooperation²⁶. Research has shown that how groups form can lead to a high genetic relatedness between interacting individuals that favours cooperation in analogous ways across all levels of biology, from vertebrates and insects to bacteria and viruses²⁷.

This generalisation has been possible even though the form of cooperation and underlying proximate mechanisms vary hugely. Cooperation across different taxa involves the independent evolution of diverse traits such as the blocking of immune signals by viruses, the production of iron scavenging molecules in bacteria (siderophores) and the feeding of siblings by birds²⁸⁻³⁰. Indeed, the identification of broad generalization has been facilitated by focusing on individual costs and benefits, while choosing to deliberately ignore the underlying physiological or genetic mechanisms.

Broad generalisations make things pleasingly simpler for those of us studying adaptation. Rather than having a different explanation for every species, we can have a single explanatory framework. Similarly successful unifying frameworks exist for other traits, from foraging and parental care to sex allocation and group living^{1,31-34}.

3. Why there are limits to adaptation. As described above, natural selection favours traits that increase fitness, leading to organisms that appear as if they were designed to maximise their fitness. But this doesn't mean that organisms will be perfect fitness-maximising machines or perfectly adapted to their current environment. Natural selection is subject to physiological, informational, and other constraints^{31,35,36}. Behavioural ecologists have been able to study these constraints, and how they limit adaptation.

Mechanisms can constrain adaptation and even lead to individuals making mistakes. In many species, female conditionally adjust their offspring sex ratio, to produce less female

biased sex ratios when more females are laying eggs in a patch³¹. A female biased sex ratio is favoured to reduce competition between sons and provide more mates for those sons – usually termed ‘local mate competition’. An examination of the underlying mechanism in the parasitoid *Nasonia vitripennis* found that females detect the presence of other females by the eggs that they lay, rather than the actual presence of the females³⁷. Consequently, the ability to correctly count females will be constrained by factors such as order of arrival at the patch and egg laying rates. We discuss another example in Box 2, examining how the underlying mechanism can lead to worker ants miscounting the number of males that their queen has mated.

Another issue is that the strength of selection or ‘evolutionary importance’ of a trait can vary. In fig wasps, females of different species show variation in the extent to which they adjust their offspring sex ratio in response to the number of females laying eggs in a fruit. But this variation across species is not random. Females are less good at producing the optimal sex ratio in situations that their species encounters rarely in nature^{38,39}. This illustrates how the precision of adaptation can be greater in situations that organisms encounter more frequently.

4. An approach that informs all branches of biology. If you were to attend a behavioural ecology conference or glance at a textbook, you might get the impression that behavioural ecology is just about animal behaviour, with a heavy bias towards birds. In reality, the last 40 years has seen behavioural ecologists apply their methods to an increasing diversity of issues across the entire tree of life and at many levels of biological organisation.

An illustrative but far from exhaustive list of examples includes: the damage caused by parasites to their hosts (virulence); how parasites respond to intervention strategies such as chemotherapy or vaccines; signaling and cooperation in bacteria; antibiotic resistance; the evolution of multicellular groups; trading of resources between plants and fungi; immunology and immunopathology; hormone production; cancer; genetic variation between bacterial genomes of the same species (pangenome); genomic imprinting; human language; stress; genome fragmentation in viruses^{40–59}.

Anyone could be forgiven for not having noticed this expansion, as it has largely happened by stealth. Behavioural ecologists have spotted areas where *why questions* were not being asked and then applied the behavioural ecology approach to ask them. Rather than bringing these different fields into behavioural ecology, the aim has been to take behavioural ecology into other fields, such as parasitology, microbiology or immunology. If you want to stimulate microbiological research, you need to publish in a microbiological not a behavioural ecology journal.

A behavioural ecology background facilitates expansion into new areas of research. The first step in any behavioural ecology course or textbook is to explain Tinbergen’s four questions and especially the distinction between evolutionary (ultimate) versus mechanistic (proximate) questions⁶⁰. Behavioural ecologists know that you can’t give a mechanistic answer to an evolutionary question, but also that understanding one can help understand the other. In contrast, most biologists primarily ask mechanistic questions, making it easy for misunderstandings to arise about adaptive value questions or how to answer them⁶¹. Consequently, a key task when moving to these different research areas has been to outline the importance of different kinds of questions and to explain how the behavioural ecology approach can be used to help answer them^{49,53,62–68}.

In addition, behavioural ecology is by definition interdisciplinary and integrative. It is about the questions, and so researchers use whatever method will help them. Advances in any area from DNA fingerprinting to microchip identification to robotics can be and are used by behavioural ecologists^{69–71}. Single studies integrate behaviour with methods such as

genomics, neuroendocrine manipulation, across-species comparisons and experimental evolution⁷²⁻⁷⁴. In many cases, to solve the puzzles raised by evolutionary questions about behaviour, researchers must draw on multiple ways of thinking and diverse methodologies.

5. The game theory poster child. The productivity and success of behavioural ecology has relied on a close integration between mathematical theory and empirical testing (Box 2). The development of competing hypotheses and their mathematical formulation is what makes behavioural ecology a hard science and not just story telling (Box 3). Furthermore, the integration between theory and empirical testing is often iterative, gradually producing increasingly refined answers to why questions.

In some cases, the success has been remarkably quantitative. For example, we can quantitatively explain why: (a) only some pied wagtails share their winter feeding territories, depending upon food availability; (b) great tits lay 8-9 eggs when reproducing; (c) male dung flies copulate with females for 36 minutes; (d) some ant colonies produce only male reproductive offspring, while others produce only female reproductive offspring (split sex ratios), depending upon how many times their queen has mated (Box 2); (e) the proportion of females varies across years in a sex-changing shrimp⁷⁵⁻⁸⁰.

This work has provided the most successful application of game theory in any of the natural or social sciences. Game theory was originally developed by economists to explain interactions between humans but was imported into behavioural ecology and evolutionary biology in the 1970s^{81,82}.

Three factors have been key to the success of game theory in behavioural ecology. First, when applying game theory to humans, a guess must be made about what matters to humans (preferences) and what they can be assumed to be trying to maximise (the utility function). That can be hard, and often the aim is to determine the utility function or preferences. In contrast, we know the utility function for adaptation – natural selection leads to organism that will behave *as if* they are trying to maximise their fitness. And we have a general quantitative definition of fitness at the individual level - inclusive fitness^{26,83-85}.

Second, behavioural ecology has long moved on from stylized games such as the prisoner's dilemma and hawk-dove game. These games were incredibly useful in the 1970s and 1980s for illustrating points such as the problem of cooperation⁸⁶. However, these games and their extensions make restrictive assumptions that will often not match real biological scenarios. Behavioural ecologists have developed much more general, powerful and often simpler methods for analysing a diversity of traits. Crucially, these methods allow the biology to lead to mathematics, rather than contorting real systems into the form of an artificial game^{82,84,87-89}. Consequently, when studying specific traits, such as cooperation, we have a diversity of models developed for different systems from pathogenic bacteria and wasps to viruses and birds, as well as 'meta-models' for a more general overview^{52,90-95}. Third, working with non-humans allows unrivalled opportunities to test theory via both observation and experimental manipulation, as well as broad across species comparative studies (Contribution 1).

In addition to this quantitative success, behavioural ecology has taken game theory in surprising directions. Who would have guessed when game theory was first being developed that: bacteria play public goods games; sperm allocation can depend upon whether egg fertilisation is a fair raffle or not; tropical fish interact in 'cleaning markets'; foraging games can lead to juvenile ravens marauding in gangs; fungi trade in 'biological markets' with plants; or that the snowdrift game can lead to genomic fragmentation in viruses^{28,48,52,96,97}.

6. Scientific Methodology. Behavioural ecology research has provided numerous case studies in how to integrate mathematical theory with empirical hypothesis testing, and how

the strategic choice of simplifying assumptions can facilitate the illumination of broad generalisations (Contributions 1-5). In addition, behavioural ecologists have contributed to fundamental scientific methodology, especially with respect to transparency, replicability and self-correction.

The integrative and iterative hypothesis-testing nature of behavioural ecology research (Box 2), with its inherent “constructive replication” means that p-hacking and other ‘replication crisis’ problems, though present, have been less common, compared to some other behavioural sciences (<https://sortee.org>)^{98–100}. Behavioural ecologists have a long history of actively identifying and solving problems that can arise in the analysis of noisy data. Examples include statistical power; statistical versus biological significance; different forms of pseudoreplication; phylogenetic non-independence and disentangling causality from correlation^{66,99,101–107}. These methods have also been applied to test data integrity and identify scientific fraud^{108–111}. The study of “fluctuating asymmetry” provides a striking example of how to retreat from and abandon a topic where there was initially high enthusiasm for a theoretically appealing hypothesis, but where improved empirical testing and increased data transparency showed that enthusiasm to be overblown^{109,112,113}. Though the field of behavioural ecology has not been immune to challenges, the emphasis on testing alternative or quantitative hypotheses has required scientists to consider their own biases and develop methods to address them rigorously.

7. Understanding humans. Human behavioural ecology has helped us understand many aspects of human behaviour⁶⁸. Work in this area initially focused on behaviours such as foraging in hunting and gathering populations but has since expanded to other societies¹¹⁴, including industrial, and a diversity of behaviours, from cooperation to homicide^{68,115,116}. The behavioural ecology approach has provided a conceptual coherence across several areas of human research, from anthropology to behavioural economics and evolutionary psychology^{68,117}. A limitation is that this research is sometimes relatively isolated from other areas of behavioural ecology. Consequently, there are clear opportunities for greater integration, which also offers a unique chance to build bridges between the biological and social sciences. Possible applied implications include the potential to provide new insights into problems such as resource management, environmental change, morality, the consequences of inequality and the manipulation (‘nudging’) of human behaviour^{68,118}. Behavioural ecology can also be applied to help understand factors of medical importance such as the complications that can occur during pregnancy or brain development^{116,119–121}.

Contributions 8-10: Global Challenges

8. Helping humans. Behavioural ecology has and will continue to help humans deal with pests and pathogens, as well as increase the efficiency of biotechnology.

Pest management. Integrated pest management (IPM) relies implicitly on the application of behavioural ecology, combining sustainable tools to control insect pests, whilst reducing use of chemical pesticides¹²². Olfactory behaviour is exploited to produce lures for monitoring and predicting pest populations, prevent and delay mating, and “attract and kill (mass trapping)”^{123–125}. Knowledge of non-crop host plants can be applied as trap crops or intercrops to control pests¹²⁶. An understanding of mating frequency, mating sites, and mate selection have informed the release of infertile (irradiated) males to prevent wild females from mating with viable males, and sexually transmitted immune contraceptives^{127,128}.

Behavioural ecology helps find solutions for the containment, management and eradication of novel invasive pests. From a behavioural ecology perspective, invasive insects

are no different from any species that finds itself in a new environment, armed with the behaviours that shaped survival and reproduction in its ancestral habitats. Behavioural ecology can provide information on new crops that may be susceptible to invasive species and identify non-crop plants where pest populations may breed, as well as predict how rapidly the invasive pest is likely to spread, and how best to track it^{129–132}.

Biocontrol practices implicitly rely on the application of behavioural ecology to pest and weed management. When exotic biocontrol agents are imported to control an invasive pest, a rigorous process of screening is used to establish host specificity, thereby avoiding the repeat of disasters of the past, such as the introduction of the cane toad to Australia^{133–137}. Behavioural ecology is applied broadly to provide a framework for optimising biological control programmes: for example in providing feeding sites, alternative hosts for reproduction, and refuges for natural enemies, bolstering their effectiveness in the field^{133,138}; and the application of sex ratio theory to produce a female bias in parasitoid mass-rearing and thereby reduce production costs¹³⁹.

Pathogen mitigation. Behavioural ecology research into cooperation has suggested novel methods to deal with microbial parasites. Mouse mortality from *Pseudomonas aeruginosa* infections was reduced 50% by co-infecting with a non-cooperative cheat strain¹⁴⁰. Interventions that disrupt cooperation can offer advantages over the use of antibiotics^{141,142}. The use of cheats to reduce virulence is already being carried out for viruses and the behavioural ecology approach can help design more effective and stable ‘cheat therapies’⁵³. Another possibility is to use cheats as ‘trojan horses’ to invade useful genes into infections, such as antibiotic susceptibility¹⁴³?

Behavioural ecology can anticipate consequences of parasite intervention strategies. The introduction of a vaccine that reduces pathogen growth rate can select for parasites to become more virulent^{42,144}. Subcurative doses of antimalarials can lead to malaria parasites increasing their production of the transmission stage (gametocytes)^{41,145}. The success of strategies aimed at eliminating malaria and other parasites ultimately depends upon an understanding of the behavioural ecology of their vectors^{146,147}. The usefulness of using other microbes as intervention strategies against pathogens can depend critically upon aspects of their behavioural ecology such as cooperation¹⁴⁸.

Biotechnology. Many microbial biotechnological processes rely on cooperation to either break things down or to produce things^{149,150}. For example, the recycling of organic matter, the breakdown of plastic or agricultural waste and the production of some biofuels. Behavioural ecology tells us how to optimise and maintain that cooperation. Other technological applications of behavioural ecology include how communication in ants is inspiring the development of internet protocols^{151–153}.

9. Mitigating humans. If we want to conserve species, or predict how they will respond to climate change, then we need to understand their behavioural ecology^{154–156}. Our understanding of behaviour also contributes to effective management of commercially and recreationally important species^{157–159}. How is reproduction influenced by conservation actions or fishing? For example, designing a supplementary feeding programme that allowed for sex ratio adjustment doubled the rate of kakapo population growth¹⁶⁰. The likelihood that all the females in a population will be mated depends upon the mating system, which can be influenced by patterns of poaching^{161,162}. How can we mitigate the effects of artificial light or pollutants for animal migration and breeding^{163–167}? Similarly, if we want to understand how climate change will influence species, or how to mitigate those influences, then we need to understand migration, reproduction and other aspects of behavioural ecology^{168,169}.

10. Inspiration and awareness. Modern nature documentaries, such as those produced by the BBC Natural History Unit, are heavily based on behavioural ecology research. Behavioural ecology provides a framework to understand the lives, loves and troubles of living organisms, in a way that is accessible to a wide audience. It makes for exciting and illuminating viewing, that is helping inspire the next generation of biologists, as well as making the public care about conservation^{170,171}. Many other factors can matter for the evolutionary process such as linkage disequilibrium and effective population size, but they just don't make for exciting viewing. This is about more than entertainment. Public interest in animal behaviour leads to engagement with research and science in ways that matter for awareness, funding, and the preservation of the natural world.

A key factor in the success of behavioural ecology research has been active choices about what to focus on and what to ignore. For example, behavioural ecologists often make simplifying assumptions (black boxing) about other aspects of behaviour, such as the underlying genetics and physiological mechanism, because this better enables them to focus on and understand adaptive value^{84,172} (Box 4). However,

Strategically choosing assumptions

A key factor for all the contributions from behavioural ecology has been active choices about what to focus on and what to ignore. All scientific studies involve trade-offs between different approaches or questions¹⁷³. Behavioural ecologists usually choose to focus at the phenotypic level, examining the fitness consequences of phenotypic variation, in response to the ecological conditions. They deliberately ignore factors such as the underlying genetics (the 'phenotypic gambit'), using approaches such as game theory to model the outcome of evolution, and black box the underlying mechanisms that control behaviour¹⁷².

Behavioural ecologists make these active choices because time and time again because their use has facilitated the interplay between theory and data, helping them understand adaptation in natural populations (Contribution 1). Indeed, broad across species generalisations have generally only been possible by assuming the phenotypic gambit, while ignoring the underlying proximate mechanisms (Contribution 2). Of course, not all studies are equally useful, but that is trivially the same in any field.

Behavioural ecologists do not think that genetics or mechanism are uninteresting – it is just that they have been able to make better progress on the questions that they are interested in by relaxing assumptions that are usually made in other fields (i.e. they choose what details to focus on). Any scientist could try to argue that another field is narrow because it ignores the complications they examine in their field, but this mainly just tells us about that scientist's interest, not the usefulness of the underlying science¹⁷³.

The utility of these simplifying assumptions are not just philosophical choices – the last 50 years of research has empirically tested whether they are useful. Has the behavioural ecology approach, with the assumptions usually made, advanced our understanding of adaptation? Even just a cursory look at a textbook, let alone the primary literature, shows that the answer is a huge yes¹. Furthermore, because simplifying assumptions are active choices they can be relaxed at any time when doing so is useful. For example, there are numerous cases where behavioural ecologists have expanded from their initial *why* questions to also ask questions about mechanism or genetics, to better understand adaptation^{174–182} (Contribution 3; Box 2).

Conclusions

Behavioural ecology is a thriving and growing field, both conceptually and taxonomically, focused on question- and theory-driven science. It helps explain biodiversity at all levels, both within and between species. Our aim was to be illustrative, not comprehensive. So, we focused on a small number of key reasons why the world benefits from having behavioural ecologists. Indeed, behavioural ecology is rapidly expanding into so many new areas that it would be very unwise to claim that we could be comprehensive. It is however possible to identify some broad patterns in terms of future directions and outstanding challenges.

Future directions. As with any field, research is expanding at different rates in different areas. It is true that some of the areas that made such rapid progress in the early years are advancing more incrementally now (e.g. foraging and clutch size). But the behavioural ecology approach can be applied to any area of biology and slower progress in one older area doesn't remove the potential for growth in other new and untapped areas (Contribution 4). Behavioural ecology research is like a healthy, growing phylogenetic tree, and even though the speciation rate can slow down in some branches, novel and even basal branches are still sprouting.

While our aim is not to develop a list of specific questions that need answering, many of the most exciting future advances are likely to involve pushing the boundaries of behavioural ecology. This could involve pushing research into new non-model organisms, or new types of traits, or by integrating new methodologies and approaches. For example, how can behavioural ecologists exploit novel sources of 'big data' to generate and test hypotheses about adaptive function? Can machine learning and other AI tools provide new insights into the causes and consequences of how individuals interact with one another? When can understanding mechanism help us understand the precision of adaptation. Another possibility is to identify further areas where behavioural ecology can help tackle global challenges and provide applied benefits to society.

Outstanding challenges. We conclude by raising two issues where efforts are required to ensure the sustainability of behavioural ecology research. First, scientific progress is facilitated by inclusive and diverse research groups that bring multiple perspectives¹⁸³. Researchers from different global areas will bring questions and insights inspired by different biological habitats and experiences. Diversity can be especially important when investigating topics where researchers may have preconceptions that could help lead to biased conclusions such as sexual selection and sex roles¹⁸⁴⁻¹⁸⁶. While much work is needed to identify and tackle existing problems, some key steps are being made on issues such as the barriers faced by non-native English speakers and assessing how terminology can marginalise groups¹⁸⁷⁻¹⁹¹.

Finally, we need to ensure that the world realizes why it needs behavioural ecologists. Funding for pure science is shrinking and so behavioural ecologists face increasing competition for jobs and resources. We hope this paper has made clear why behavioural ecology is more than a niche field – by addressing fundamental biological questions it makes numerous contributions to science and the global challenges faced by humanity. To ensure that behavioural ecology continues to thrive we need to make this clear, at all levels from hiring committees and grant panel members to teachers and science communicators. It will be exciting to see what happens over the next 50 years.

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Author Contributions

All authors contributed to the conceptualisation and writing of the paper.

Box 1. Watching and wondering

Behavioural ecology begins with ‘watching and wondering’^{1,60}. Imagine that you are watching an Australian magpie foraging for food in grass. Why has it chosen this place to forage? Why is it foraging in a group? Why does it select only certain food options? Why does it spend a certain length of time foraging in the grass before dispersing?

Watching and wondering can be carried out on any aspect of biology. Instead of watching a bird with binoculars, you might be watching hormone levels, enzyme production, gene regulation, or genome sequences. And you can do this on any organism from birds and bees to bacteria and viruses. Watching and wondering means observing biology and coming up with questions about that biology.

The key distinction is that behavioural ecology asks *why* questions about the adaptive advantage (function) of behaviours or any other type of trait (Contribution 1)^{1,60}. Why has natural selection favoured that behaviour? This type of evolutionary question contrasts with questions about the underlying mechanisms that control a behaviour. Most of biology is concerned with more mechanistic questions.

Behavioural ecology tackles questions about adaptive value with a mixture of theoretical and empirical approaches. Theory is developed to help specify hypotheses about what matters, based on the potential costs and benefits of different behaviours (trade-offs).

Hypotheses are then tested with observation, experimental manipulations or across species comparative approaches. For example, by examining the costs and benefits of a behaviour or by examining how a behaviour varies in response to environmental conditions, either within or across species. This approach is then iterated, with refined or alternative hypotheses, to produce increasingly deeper understanding (Box 2).

The behavioural ecology approach of asking *why questions* about adaptive function can be applied to any aspect of any organism and not just what people typically think as behaviour (Contribution 4). Consequently, how do we define behavioural ecology? While there is a field of behavioural ecology, it can be defined more broadly and inclusively as an approach or framework for asking why a trait has been favoured by natural selection.

Care is however needed to not overreach bossily. There are other areas of research that examine traits from an evolutionary perspective, but these are often more concerned with questions about evolutionary history and patterns of trait inheritance (phylogeny). In other cases, such as evolutionary ecology and life history theory, questions about adaptive value are asked. Although researchers in these fields could be described as using the behavioural ecology approach, we don't say they have to be rebranded. Nonetheless, behavioural ecology is relatively unique in its emphasis on determining the adaptive value of traits, and its attempts to measure adaptive value in as natural conditions as possible.

Box 2. Integrative science

A tight integration between theory and different types of empirical research has been key to many of the greatest advances made by behavioural ecology. We illustrate this with a summary of the key steps by which research in one area has progressed over the last 50 years - sex allocation in the Hymenopteran social insects, the ants, bees and wasps. We chose this area because while many are familiar with the basics (steps 1 & 2), the various iterations are much less well known (steps 3-10).

(1) Theory predicted a conflict between queens and their workers over sex allocation when producing reproductives^{15,192}. In the simplest case, where females only mate once (monogamy) then the queen favours equal investment in the two sexes, while the workers favour a 3:1 female bias. These predictions arise because the Hymenoptera have haplodiploid sex determination, where fertilized eggs become female, and unfertilized eggs become male. This leads to females being three times as related to sisters as brothers (sisters: $R=0.75$; brothers: $R=0.25$).

(2) An across species comparative study supported the prediction for worker control, with a trend across many species towards a 3:1 female biased investment ratio¹⁹². In contrast, many 'control' scenarios, such as non-social species, and diploid social species, showed approximately equal investment into males and females¹⁹³.

(3) However, there was also huge variation within species across different colonies that had not been predicted. Some colonies produced all or predominantly males, while other colonies produced all or predominantly females (termed 'split sex ratios').

(4) Theory predicted that split sex ratios would be favoured in response to three factors that reduce the relatedness of workers to their sisters: (i) multiple mating; (ii) multiple queens; or (iii) the replacement of a dead queen by her daughter^{79,194-196}.

(5) Detailed studies of single species have repeatedly provided clear support for all three of these predictions¹⁹⁷. For example, in the wood ant *Formica truncorum*, colonies with singly mated queens produced predominantly female reproductives and colonies with multiply mated queens produced predominantly male reproductives^{78,198}.

(6) This data suggested that workers could do two things: (i) count how many times their queen has mated; (ii) manipulate sex allocation, despite the sex of eggs being determined by queens.

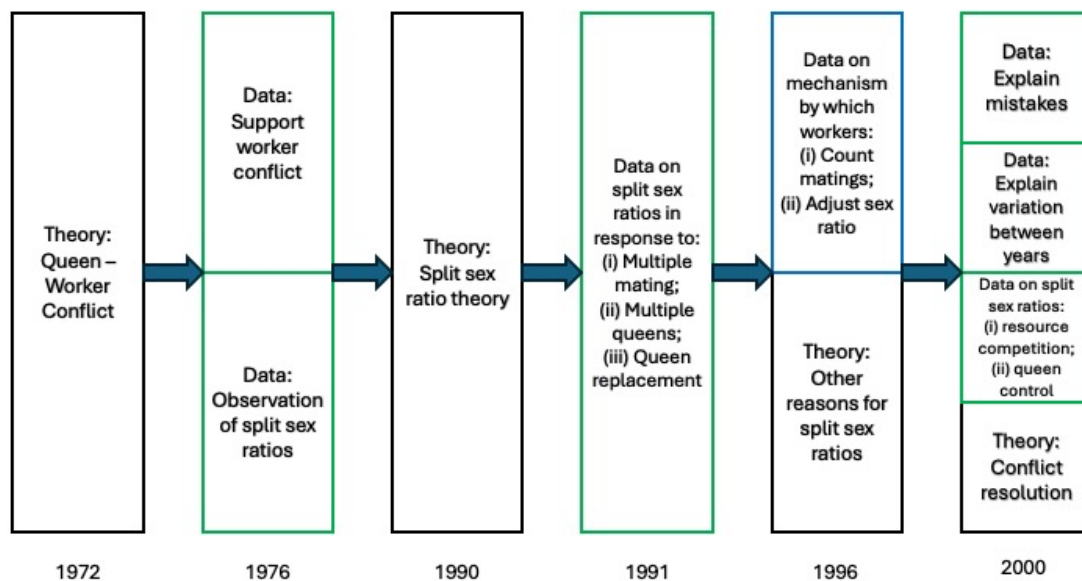
(7) Mechanistic studies showed how workers do these things. Workers count how many times their queen has mated by assessing variation in the hydrocarbon profile ('smell') within the colony¹⁷⁴. Workers of different species appear to manipulate sex allocation in different ways, by either preferentially killing larvae of one sex, or by altering the ratio of females that are reared as reproductives or workers^{199–202}.

(8) This mechanistic work was able to explain when workers make mistakes and produce the 'wrong sex ratio'. If the queen mates two males with similar hydrocarbon profiles, then this leads to low hydrocarbon variation within a colony, and so workers think their queen has only mated one male¹⁷⁴.

(9) The empirical data showed that sex allocation in a colony varied across different years. Further investigation showed that this was because workers adjust sex allocation in response to variation in relatedness²⁰³. For example, if a queen has mated multiple males, but tends to use the sperm of only one male in a certain year, then workers produce a sex allocation appropriate to if their queen had only mated one male.

(10) We do not have the space to go into numerous other elaborations, such as how the queen can sometimes gain control of sex allocation, why split sex ratios can be favoured for other reasons, or the consequences of split sex ratios for other aspects of life history evolution^{204–209}.

These steps illustrate the importance of the interplay between theory and data, and between different kinds of data. Data suggested patterns that required a theoretical explanation, and theory then provided new testable predictions. Theory was tested with both across-species comparative studies, and by examining variation within a species. Data suggested underlying mechanisms and then work examining those mechanisms explained variation in the data. There are numerous other areas where similar stories could be told, including decisions about: where to search for food; other aspects of sex allocation; the length of time a male will spend defending a female after mating with her; whether one or both parents care for the offspring^{31–33,210}.



Example theory-data interplay. Research on sex allocation in haplodiploid social insects has involved several iterative steps between theory (black boxes), empirical data testing adaptive hypotheses (green boxes) and empirical data determining the underlying mechanisms (blue boxes). We have represented a simplified summary of some key steps. The

years refer to the publication date of papers which initiated that research – in most cases the research is still ongoing.

Box 3. Just-so stories and other straw men

The behavioural ecology approach is periodically criticized for reasons that appear to stem from a false impression of what behavioural ecologists assume and do¹⁷³. To avoid future confusion, we will briefly consider the three most common misunderstandings.

First, behavioural ecologists do not aim to test if organisms are adapted and behave optimally⁸². They do not assume animals to be ‘perfect’, because natural selection is subject to physiological, informational, and other constraints. Instead, behavioural ecologists ask questions about adaptation, to deduce testable predictions for how traits could increase fitness, and hence how ecology may have shaped adaptation. The assumption of fitness maximization is used as a tool to produce unambiguous theoretical predictions, that allow the role of different factors to be tested, but this is only a starting point. Rather than ignoring constraints, this approach provides a rigorous framework for studying them (Contribution 3 & Box 2).

Second, behavioural ecologists do not assume that natural selection is the only process that leads to evolutionary change^{82,211}. What is special about natural selection is that it is the only process that can lead to adaptation⁷. The other processes of evolutionary change – mutation, migration and drift – provide the variation for evolutionary change, and can add noise, but they cannot create adaptations such as a peacock’s tail or sex ratio adjustment.

Third, behavioural ecologists do not just produce post-hoc “just-so” stories. Behavioural ecology is a hypothesis-driven science. Behavioural ecologists generate testable *a priori* hypotheses, make predictions based on those hypotheses and then test those predictions empirically. Predictions can be quantitative, multiple competing hypotheses are often generated, and this process is repeated iteratively (Boxes 1 & 2).

Criticisms of behavioural ecology or the ‘adaptationist’ approach are often based on a 1979 paper by Gould & Lewontin²¹². Even in 1979 it was clear that the criticisms in that paper were misleading, because they ignored how behavioural ecologists were already using a hypothesis-testing approach, developing quantitative predictions and examining constraints on adaptation^{77,211,213–215}. Indeed, so much progress had already been made that an edited volume had been produced, and a textbook was being written to bring the field together^{2,216}. But, perhaps even more staggeringly, to make such criticisms today is to also ignore the huge research literature which has developed since the 1970s. This literature provides a comprehensive empirical test of the utility of the behavioural ecology approach, with a very clear result (Contributions 1-5; Boxes 1 & 2). And of course, these empirical advances can be compared with those which have since been made using the alternative Baupläne approach suggested by Gould & Lewontin²¹².

Figure Legends



Fig. 1. Examples of relatively obvious adaptation. (a) A short-beaked echidna is protected by its spines (*Tachyglossus aculeatus*; Photo by Gunjan Pandey). **(b)** The maleo (*Macrocephalon maleo*) buries its eggs in warm volcanic sand. **(c)** A bald eagle can see prey from 1-2 miles away (Photo by Andy Morflew). **(d)** Indonesian weaver ants fold and glue a leaf into a nest (Photo by Stuart West with thanks to Sapto 'Itto' Raharjo).



Fig. 2. Copulatory cannibalism in redback spiders (*Latrodectus hasselti*). The photo shows a redback female with two males - one dead following copulatory cannibalism (left) and one courting (bottom right). Photo credit by Ken Jones (©M. Andrade 2005).

Figure sources

Echidna from https://en.wikipedia.org/wiki/Echidna#/media/File:Short-beaked_echidna_in_ANBG.jpg. Maleo purchased from iStock (<https://www.istockphoto.com/photo/maleo-sengkawor-gm466211604-59709674?searchscope=image%2Cfilm>). Bald eagle: [https://commons.wikimedia.org/wiki/File:Bald_eagle_about_to_fly_in_Alaska_\(2016\).jpg](https://commons.wikimedia.org/wiki/File:Bald_eagle_about_to_fly_in_Alaska_(2016).jpg)