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Introduction

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Linking behaviour to dynamics of populations and communities: application of novel approaches in behavioural ecology to conservation

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The impact of environmental change on the reproduction and survival of wildlife is often behaviourally mediated, placing behavioural ecology in a central position to quantify population- and community-level consequences of anthropogenic threats to biodiversity. This theme issue demonstrates how recent conceptual and methodological advances in the discipline are applied to inform conservation. The issue highlights how the focus in behavioural ecology on understanding variation in behaviour between individuals, rather than just measuring the population mean, is critical to explaining demographic stochasticity and thereby reducing fuzziness of population models. The contributions also show the importance of knowing the mechanisms by which behaviour is achieved, i.e. the role of learning, reasoning and instincts, in order to understand how behaviours change in human-modified environments, where their function is less likely to be adaptive. More recent work has thus abandoned the 'adaptationist' paradigm of early behavioural ecology and increasingly measures evolutionary processes directly by quantifying selection gradients and phenotypic plasticity. To support quantitative predictions at the population and community levels, a rich arsenal of modelling techniques has developed, and interdisciplinary approaches show promising prospects for predicting the effectiveness of alternative management options, with the social sciences, movement ecology and epidemiology particularly pertinent. The theme issue furthermore explores the relevance of behaviour for global threat assessment, and practical advice is given as to how behavioural ecologists can augment their conservation impact by carefully selecting and promoting their study systems, and increasing their engagement with local communities, natural resource managers and policy-makers. Its aim to uncover the nuts and bolts of how natural systems work positions behavioural ecology squarely in the heart of conservation biology, where its perspective offers an all-important complement to more descriptive 'big-picture' approaches to priority setting.

This article is part of the theme issue 'Linking behaviour to dynamics of populations and communities: application of novel approaches in behavioural ecology to conservation'.

1. Introduction

Human activities have significantly altered three-quarters of the terrestrial and two-thirds of the marine environment [1] and are rapidly decimating the world's biodiversity with an estimated 60% drop in vertebrate population sizes between 1970 and 2014 [2] (figure 1). Reversing this trend is a tremendous, costly task, and if funds available for biodiversity research are limited, one may ask to what extent studying the behavioural ecology of animals should be a

Figure 1. Biodiversity under threat. (*a*) Plains zebra (*Equus quagga*) and blue wildebeest (*Connochaetes taurinus*) by Nairobi, Kenya (© Jakob Bro-Jørgensen). (*b*) Carcass of a Peter's duiker (*Cephalophus callipygus*) for sale in Makokou, Gabon (© Natalie van Vliet). (*c*) South American sea lions (*Otaria flavescens*) in Valdivia, Chile (© Kristine Meise). (Online version in colour.)

priority. This theme issue is motivated by the conviction that the most cost-effective way to obtain conservation impact indeed often involves behavioural ecological study [3–5]. The fact that the most immediate response of animals to environmental change typically is behavioural puts behavioural ecology in a central position to inform natural resource management [6]: not only can behaviour serve as an early warning system of environmental deterioration, behavioural changes also directly or indirectly affect vital rates, i.e. survival and reproduction, the very key parameters determining the dynamics of populations and their aggregate, communities. It is the links between behavioural ecology via population and community ecology to conservation on which this theme issue concentrates.

2. A framework linking animal behaviour to community level processes and conservation

Since its emergence half a century ago, behavioural ecology has proven its worth as a rigorous scientific discipline uncovering the principles by which animal behaviour shapes—and is shaped by—ecology and evolution. Behavioural ecology's aim of identifying predictors of fitness has much in common with conservation biology's aim of securing viable wildlife populations for the future. Yet it was pointed out some 20 years ago that integration of the two disciplines had met with only limited success [7]. This was attributed partly to lack of time for the two, then relatively recently established, disciplines to connect and, perhaps related to that, technical difficulties in linking individual behaviour, the focus of behavioural ecology, to population-level processes, the focus of conservation. However, since then, significant conceptual and methodological advances in behavioural ecology have been paving the way for increasingly sophisticated modelling of population and community responses to environmental change and the likely outcomes of alternative management options.

Behavioural ecology has now accumulated a rich toolbox for quantifying how the main behaviours of animals relating to foraging, predation, mating, parental care, communication and sociality are affected by the current threats to biodiversity, notably habitat loss and fragmentation, overexploitation, climate change, pollution, disease, and invasive species. This provides a firm foundation for a bottom-up approach to understanding human impacts on the natural world (figure 2). Still, many systems under threat remain poorly understood from a behavioural ecological perspective owing to lack of data and research attention, and the framework presented in figure 2 outlines how conceptual and technical advances at various levels can all strengthen the application of behavioural ecology in conservation. Conceptually, new insights into individual variation in behavioural responses to environmental change come i.e. from recent studies of animal personalities [8–10], pace-of-life syndromes (POLS) [11,12], gene-by-environment interactions (GEI) [13,14] and definitions of fitness [15,16], while higher-order drivers of population responses are revealed by research into collective behaviour [17,18] and multi-species interactions [19–21], with spatial variation in fitness explicated by the field of movement ecology [22,23] and related concepts such as 'landscapes of fear' [24]. Technologically, the quantity and quality of data available have been revolutionized with major breakthroughs in animal tracking and remote-sensing [25], the omics [26] and the processing of Big Data [27]. Methodologically, innovative approaches to modelling and analysis include new developments in agent-based modelling (ABM) [28], social network analysis (SNA) [29–31], metapopulation modelling [32,33], landscape genetics [34] and other spatially explicit landscape-based models.

This progress has huge potential for adding precision to predictive models of population and community dynamics for the benefit of conservation, and the applicability of such models can be enhanced by further integrating the feedback

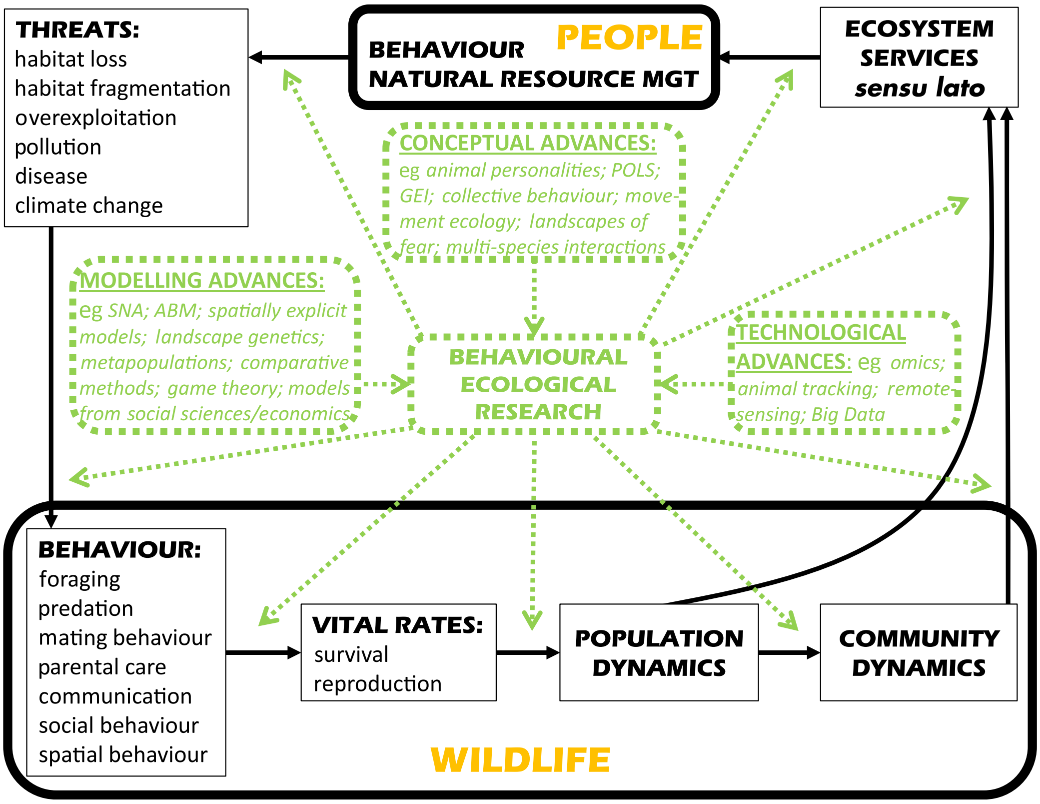

Figure 2. A framework for the contribution of behavioural ecology to population and community ecology and conservation. Behavioural ecological research can inform conservation policy and practice both directly by discoveries that advance our qualitative understanding of relationships in the system and by quantifying links that allow models of populations, communities and human–wildlife interactions to be constructed (GEI: gene-by-environment interactions; POLS: pace-of-life syndromes; SNA: social network analysis; ABM: agent-based models). (Online version in colour.)

between wildlife dynamics and the behaviour of people. Behavioural ecologists are increasingly engaging in multi-disciplinary research, just as conservation biologists have always done, realizing that compartmentalized research is counterproductive to finding solutions to complex real-life issues [35]. Changes in wildlife population sizes affect ecosystem services and thereby people's behaviour including how they manage their natural resources, and this in turn feeds back on the intensity of the threats to biodiversity (figure 2). Hence by incorporating the behaviour of people in the modelling framework, the loop back to the anthropogenic drivers of behavioural change in animals is completed. Interdisciplinary approaches building on ties with the social sciences can here identify integrated solutions taking into account both human livelihoods and conservation priorities. Social psychology in particular offers useful models for incorporating drivers of human behaviour, allowing the effectiveness of alternative management interventions to be assessed [36].

3. Setting priorities in conservation—behavioural ecology and the evolutionary perspective

The bottom-up understanding of ecoevolutionary processes provided by behavioural ecology is indispensable as a counterpoint to the top-down, broad–brush analyses which are currently taking centre stage in conservation biology. Macroecological studies, which are dominating the high-impact-factor journals, are indeed important to guide priority setting (e.g. [37]); however, they are not a replacement for a thorough understanding of how the constituents of ecosystems work, and behavioural ecology should have a far more instrumental role in shaping approaches to conservation than is the case at the moment. Hence, a dominant framing of conservation in current conservation biology sees people and nature as one system, and under this paradigm, conservation scientists have increasingly shifted to recognize an all-pervasive impact of humans ('People and Nature'; [38]). One of the key concepts has become 'adaptability', a central question being to what extent nature is able to persist by modifying itself in a human-dominated world. Behavioural ecologists have a crucial contribution to make here! The growing acceptance of anthropogenic change to the natural environment as inevitable brings us into a grey zone where it is critical that we are fully aware of how ecological systems, shaped by evolution, are being modified, and it raises serious questions about exactly what it is that we are trying to preserve: how do we define concepts such as species integrity, and what do we require for natural systems to be considered 'wild' [39]? As the ultimate goal of conservation is to preserve natural ecological and evolutionary processes, behavioural ecology—with its emphasis on both the process of adaptation and purely ecological responses—can provide vital insights.

Consider, for example, the debate about whether conservation objectives are best achieved by promoting coexistence between humans and wildlife in the same area ('land-sharing'), or rather by maximizing the (non-conservation) use of areas already under human land use and thereby avoiding conversion of more natural habitats elsewhere ('land-sparing') [40]. Support for the land-sparing argument comes from broadscale studies reporting higher densities and larger population sizes when strategies involve high-yield farming, as long as linking mechanisms are in place to ensure that the area used for food production thereby is minimized [41,42]. However, while such information is highly valuable, conventional biodiversity metrics do not capture what is happening to ecoevolutionary processes well, and therefore tell only part of the story. To properly understand the full consequences of integrating land use at the local level, the complementary, bottom-up approach of behavioural ecology is needed to shed light on ecosystem functioning. As a case in point, more behavioural ecological input would refine the current 'half-Earth' argument that natural systems must be preserved as such across half the globe to ensure adequate conservation of biodiversity [43].

The behavioural ecological perspective is highly relevant also to the current, controversial, push for 'compassionate conservation', which aims to integrate principles of animal welfare and conservation [44,45]. Although setting both conservation and welfare priorities will always entail moral judgement, a thorough scientific understanding is essential to inform decisions on how the two value systems involved are best integrated. Behavioural ecology is in a primary position to provide guidance as it offers both the ecoevolutionary understanding needed to weight conservation priorities, and a fundamental insight into animal cognition which is central to assess emotional states and suffering in animals and hence to weight welfare priorities. In fact, the behavioural ecological approach is likely to resolve current disagreements as welfare issues will often be addressed most effectively by maintaining or re-establishing the natural systems under which animals have evolved to function, providing an additional argument for land-sparing.

4. Overview of contributions

The series of papers in this theme issue includes reviews, theoretical models and field studies, which showcase the conservation relevance of current behavioural ecological research in addressing the major threats to biodiversity. In doing so, they cover a broad range of concepts, approaches and behaviours in a diverse set of taxa. In the first paper, Sæther & Engen emphasize the importance of among-individual variation in behaviour as a key determinant of demographic stochasticity and thus population viability, in particular of small populations, which are the focus of most conservation efforts [16]. Maspons & Sol then show how population performance further depends on the behavioural mechanisms by which animals respond to environmental change, specifically their decision-making ability and their capacity for learning, with the advantage of the alternative mechanisms depending on life-history characteristics [12].

Turning the focus to how animals behave within their landscapes, Wittemyer *et al.* review how recent innovations in movement ecology invite behavioural ecological analysis to understand the structure, function and fitness consequences of animal movement [23]. Investigating migration in shorebirds, Gill *et al.* show how long-term study of individual variation in movement patterns can bring insights into the mechanisms underlying population-level responses to climate change, in this case by revealing the importance of generational rather than an individual change in behaviour [46]. By contrast, St Clair *et al.* propose that behavioural flexibility and rapid learning account for pronounced individual variation in the response to railroads in a case study of grizzly bears (*Ursus arctos*), and on this basis, they advocate learning-based approaches to reduce mortality [47]. Tamburello *et al.* then show how viewing landscapes as structuring metapopulations within which individuals behave can be useful to manage invasive species, in this case, to eliminate invasive fish populations most effectively; the study thus presents an alternative conservation application of metapopulation models to their well-established use in the management of threatened species [33]. In the following paper, Berger-Tal & Saltz introduce the concept of landscape-independent fragmentation to capture how it is not only physical alterations but sometimes also purely behavioural mechanisms, that reduce connectivity between populations in response to human presence in a landscape [48].

Examining social networks, Meise *et al.* show how climatic changes, and the presence of migrants, can affect social relationships between species, and thereby community structure, in a case study of African savannah herbivores [21]. Staying on the African savannah, but focusing on the predator community, Green *et al.* then point out how monitoring changes in the behaviour of a key species, the spotted hyaena (*Crocuta crocuta*), can predict the population dynamics, not only of the species itself but also of other predators [49]. Next, Dobson *et al.* turn their attention to predicting the behaviour of people and demonstrate how innovative integration of SNA and ABM can elucidate the effectiveness of conservation interventions that depend on social relationships, in this case, sharing of information on sanctions for rule-breaking [35]. Zooming in on disease transmission, Silk *et al.* follow on by reviewing how recent epidemiological modelling using SNA integrates demography and information on social behaviour to further our understanding of the spread of infections and thereby inform management interventions [31]. Herrera & Nunn in the subsequent paper expand to a general review of how the mutual effects between behaviour and disease transmission scale up from the individual level to the population and community levels [50].

The following two papers focus on applying behavioural ecology in the context of conservation translocations. First, Blumstein *et al.* make a case for the practical relevance of understanding the mechanisms guiding antipredator responses to ensure the persistence of reintroduced populations, in this case of Australian marsupials [51]. Next, Richardson *et al.* find links between personality and development and survival in a threatened, reintroduced bird, the hihi (*Notiomystis cincta*) and discuss the option of developmentally targeted management interventions. Hereafter, Candolin & Wong illustrate the conservation relevance of another major research field in classical behavioural ecology, reproductive behaviour, by reviewing how mate choice is affected by pollution and the consequences for population and community dynamics [52].

Moving to the macroecological scale, Tobias & Pigot consider the value of behaviour to identify threatened taxa and

Box 1. Behavioural ecological research priorities from a conservation perspective.

Questions emerging from this issue include:

How far can demographic stochasticity, currently dismissed as 'random noise', be explained from behavioural ecological principles?
To what extent do learning and genetic adaptation allow adjustment to human-induced environmental changes? How fundamentally are natural ecoevolutionary processes altered hereby?
Can behavioural mechanisms be linked to wider pace-of-life syndromes by general principles, and can such links be used to predict responses to rapid environmental changes?
How do depauperate environments alter antipredator behaviours? When does this have a detrimental impact on survival following conservation translocation, and how can this be mitigated to improve the success of reintroductions?
How do environmental and genotypic variations interact to shape animal personalities, and what are the implications for survival and reproduction in the wild, particularly in the context of reintroduction?
How can a mechanistic understanding of space use within landscapes be linked to fitness to identify spatial conservation priorities?
How wide-spread is landscape-independent fragmentation of populations?
When do behavioural responses of collectives, such as groups, populations and generations, show properties not apparent from individual-level analysis?
How do repercussions through interspecific networks affect population dynamics in multi-species systems?
How can the effect of social behaviour on disease transmission, and the reverse effect of disease on social behaviour, be incorporated into demographic models to predict the spread of infections and inform management interventions?
How are behavioural ecological and social science approaches best integrated to support adaptive management?
Under what circumstances can behavioural monitoring effectively predict population and community changes?
How can we incorporate threats to behavioural diversity into threat assessment of biodiversity, which is currently focused on taxonomic diversity? What is the optimal classification system for behaviour to predict extinction risk?
Can innovations in the funding system promote the uptake of behavioural ecology in conservation?
see also Greggor *et al*. [5].

latent extinction risk, and the usefulness of global datasets to identify threatened behaviours [53]. From a pragmatic viewpoint, Caro & Berger next point out how behavioural ecologists can add conservation value to their research by choosing their study systems strategically and engaging opportunistically with conservation issues [54]. Closing the theme issue, Durant *et al*. draw on long-term field experience from Africa to provide clear recommendations for best practice that will maximize the conservation impact of behavioural ecological field research [55].

As a whole, the contributions demonstrate how a behavioural ecological approach, which links the individual level to the population and community levels, can lead to a holistic understanding that is all-important in practical conservation. Two particular strengths of behavioural research emerge: (i) its power to boost population and community models by explaining what is generally dismissed as random, stochastic variation in individual fitness, or 'noise', including the distinction between heritable and environmentally induced components; and (ii) its capacity to identify proximate mechanisms underlying behavioural responses and their genetic basis, which is necessary to (a) predict when environmental change is likely to result in ecological traps owing to maladaptive responses and when animals have the flexibility to adjust, either because of phenotypic plasticity in behaviour or because behavioural traits are evolvable and allow evolutionary rescue, and (b) select the most effective targets for management interventions, e.g. when considering translocation, learning- or developmentally focused mitigation, or culling. The studies show how these strengths are used to build more reliable models of ecosystem processes and highlight several exciting areas for multidisciplinary research, in particular, with the social sciences, and disease and movement ecology. In box 1, we present research priorities coming to the fore in the contributions.

By mapping out the tremendous potential of behavioural ecology when it comes to informing conservation policy and practice, we hope that this theme issue will promote the mainstreaming of behavioural ecological research into conservation. We particularly hope that the publication will further galvanize the behavioural ecological community by inspiring the many behavioural ecologists in whom a desire to contribute to solving real-world conservation challenges has been sparked, as their excitement from gaining new insights into the principles governing the behaviour of animals in the wild increasingly manifests itself against the sombre background of alarming declines in the species under study.

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Jakob Bro-Jørgensen (PhD University College London) is a senior lecturer at the University of Liverpool where he is a member of the Mammalian Behaviour and Evolution Group. His research focuses on social behaviour and conservation using ungulates as model systems, with key topics including reproductive and communicative strategies, interspecific interactions and climate change impacts. Since 1998, he has been a research affiliate of Kenya Wildlife Service and Director of the Masai Mara Herbivore Research Project in Kenya. He is a member of the IUCN Antelope Specialist Group and former Programme manager for the Bushmeat & Forest Conservation programme of the Zoological Society of London.

Daniel W. Franks (PhD University of Leeds) is a reader at the University of York in a joint appointment between the departments of Biology and Computer Science. His research focuses on social behaviour and life-history evolution, with key topics including reproductive strategies, helping and harming behaviour, and animal social networks. His work often combines both theory and empirical studies, often combining agent-based modelling with long-term field data.

Kristine Meise (PhD University of Bielefeld) studied social relationships among male Galapagos sea lions (*Zalophus wollebaeki*) for her thesis and then moved on to a postdoctoral project on the drivers of mixed-species groups in the African herbivore community with Jakob and Dan. Focusing primarily on interactions between individuals and between species, her research aims to understand how environmental processes shape animal social behaviour and how behavioural changes relate to fitness benefits and costs, thereby assessing the resilience of populations to anthropogenic disturbances.

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