Review

Research Priorities from Animal Behaviour for Maximising Conservation Progress

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Poor communication between academic researchers and wildlife managers limits conservation progress and innovation. As a result, input from overlapping fields, such as animal behaviour, is underused in conservation management despite its demonstrated utility as a conservation tool and countless papers advocating its use. Communication and collaboration across these two disciplines are unlikely to improve without clearly identified management needs and demonstrable impacts of behavioural-based conservation management. To facilitate this process, a team of wildlife managers and animal behaviour researchers conducted a research prioritisation exercise, identifying 50 key questions that have great potential to resolve critical conservation and management problems. The resulting agenda highlights the diversity and extent of advances that both fields could achieve through collaboration.

Who Should Be Involved in Conservation Research Decisions?

The successful conservation of biodiversity requires collective decision-making among multiple stakeholders with diverse viewpoints, including scientific researchers and applied wildlife managers. While the ultimate goals of academics and wildlife managers can be similar, the means by which they tackle conservation problems differ. Academics often focus on mechanisms or overarching principles, while pursuing questions that attract grants and publications. By contrast, managers require detailed and feasible solutions for handling specific situations and need evidence for the cost and effectiveness of their proposed projects, while competing for resources devoted to other species or habitats in need (Box 1). Such different approaches lead to conflicting research priorities. Conservation science and management crucially need both of these complementary perspectives, but collaboration between them is often weak [1–3]. The following research agenda represents the outcome of a collaborative process between

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Trends
Conservation progress relies on communication between researchers and managers.

Ethologists and wildlife managers determined 50 conservation research priorities.

The list shows tremendous breadth and potential for conservation gain.

We identify routes for developing efficient and cost-effective interventions.
managers and researchers that developed priority areas for animal behaviour research with the aim of increasing its use in conservation biology. This process can be fine-tuned in the future as greater numbers of stakeholders engage in defining research priorities, and could become established as a way to stimulate conservation action more broadly in related fields. For such agendas to ultimately contribute to solving real-world problems, their subsequent research outputs must be made readily available to managers. Thus, research prioritisation exercises must go hand in hand with providing access to evidence about the effectiveness of new versus traditional techniques, similar to what has been championed in other conservation areas [4].

Why Animal Behaviour?
Animal behaviour research can influence conservation outcomes [5,6] and serve as an indicator of anthropogenic impact [7]. Perhaps more importantly, it can be used as a powerful management tool to modify the trajectory of crisis scenarios [8], such as halting the spread of invasive species [9], or mitigating human–wildlife conflict [10] (Box 2). Some applications of animal behaviour research have been recognised as having urgent conservation management functions, such as preventing the collapse of top predator populations [11]. However, evidence for the effectiveness of animal behaviour as a conservation tool is not widely available, especially to managers. Therefore, it is important to determine not whether behaviour is valuable, but rather how behavioural research can be made more specifically relevant and available for conservation practitioners and wildlife managers to address current threats.

Animal behaviour and conservation biology are vast disciplines, and a lack of communication between academics and applied practitioners has stalled their integration [12,13]. The bulk of behavioural research can therefore seem irrelevant in conservation contexts [14]. Accordingly, a clear link between research and management applications is often missing in academic discourse [13,15]. Here, we begin the process of bridging this gap by prioritising behavioural questions that are most relevant to conservation actions, evaluating their efficacy, and stimulating future research [16,17] (Box 1).
Box 2. The Links between Animal Behaviour and Conservation.

There are three main ways in which behavioural research can be of use to conservation biologists and wildlife managers [8,76]:

(i) The behaviour of animals is, in most cases, their first line of defence in the face of a changing environment, and the type and speed of the behavioural response will determine the impact of environmental change [77]. Understanding these behavioural responses could therefore allow us to recognise the mechanisms through which anthropogenic disturbances impact population dynamics and predict population trends (e.g., in creating ecological traps [78]).

(ii) Knowledge of behavioural responses to natural and anthropogenic cues can allow us to design more effective mitigation strategies, and can play a crucial role in the successful implementation of conservation translocations, reserve and corridor design, invasive species control, and other conservation interventions (e.g., exploiting natural nonassociative learning processes to reduce impacts of alien predators [79]).

(iii) Since behavioural responses to environmental changes will almost always precede demographic responses, behaviour can be used as a leading indicator for a variety of disturbances before demographic responses are evident [80] and to monitor the effectiveness of management interventions (e.g., early indication of chemical pollution [86]).

These three themes – understanding behavioural responses to anthropogenic disturbances, employing behaviour-based interventions, and identifying behavioural indicators – are complementary. Consequently, while most of the questions on our list are framed within one of these themes, they can be easily modified to fit the other two (Table I). Systematic reviews that tackle one of the questions on the list would do best to explore each of these themes in gathering evidence for the utility of a particular application of behaviour for conservationists.

<table>
<thead>
<tr>
<th>Theme</th>
<th>Sample Question</th>
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<tbody>
<tr>
<td>Measuring behavioural responses to understand mechanisms of impact</td>
<td>What demographically important behaviours are affected by harvest?</td>
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<tr>
<td>Develop behavioural interventions</td>
<td>How can knowledge of behaviour allow us to harvest populations in a more efficient and sustainable way?</td>
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<tr>
<td>Use behaviour as conservation indicator</td>
<td>Which behaviours alert us to the presence of poachers or overharvesting?</td>
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We conducted a research prioritisation exercise, employing a horizon scanning technique [18], to identify key questions in animal behaviour research that have the greatest potential to influence conservation outcomes. As a tool, such exercises are essential to translate research questions into policy and funding priorities [18]. Ideally, they encourage researchers to explore understudied topics and help policy makers and practitioners respond to key issues [19].

Idenfication and Ranking of Questions

The process we followed, from the initial generation of questions to their final ranking, was an application of the Delphi technique [20], using similar protocols to what has been advocated before [21]. This collective decision-making process downplays the input of any single individual’s research bias, and has been applied in determining research priorities in other fields, for example, [22]. We first recruited 85 experts in conservation biology or animal behaviour through an online survey that was distributed worldwide via email requests, personal networks, and Twitter sharing. Respondents were kept anonymous, but information was collected on their area of expertise, level of knowledge about animal behaviour, and their country of work and research.

The survey asked people to identify the top areas of overlap between animal behaviour and conservation biology, and determine which research questions would have the greatest impact if they were to be answered. Respondents submitted 238 questions. The organisers removed redundancies and reformatted responses submitted as statements into 209 questions.

Each of the 20 workshop participants (the authors) was then assigned a subset of the questions to further research with existing literature and define what concrete problems could be solved if they were to be answered. Participants came from a range of academic and applied conservation disciplines, representing research institutions or government agencies from Europe, Asia, Africa, the Americas, and Australia. We gathered at the San Diego Zoo’s Institute for Conservation
Research to generate a priority list of 50 questions. The full question list was reduced to 50 through discussion, rewording, and voting (via a process similar to the question selection criteria set forth in [11]). Each question had to be achievable in one or two research grants (2–3 years) when applied to a specific species or system, and to have clear conservation applications if answered.

We reduced the original 209 questions to 50 in two steps. First, we grouped questions within eight topics of anthropogenic threat or conservation action and discussed them in four sessions of two parallel groups. After discussion, each group rated questions as ‘gold’ (top 40%), ‘silver’ (20%), or ‘neither’ (the rest). This step reduced the 209 original questions to 109 (listed in the Supplemental Information online). In a second step, the best silver questions were identified and then these and the gold questions were pruned by voting to a total of 55 gold and 25 silver questions. In a series of additional discussions and votes, the group eliminated the bottom gold questions and added the top silver ones to produce a final list of exactly 50 questions. The questions could be reworded for clarity at each stage.

In the following sections, we present the final 50 questions, assigned to six categories of conservation topics. The questions are not ranked within or between sections; all should be viewed with equal potential to impact the field.

**Conservation Topics**

**Habitat Loss and Fragmentation**

Habitat loss is a primary threat to global biodiversity [23,24], and concurrent fragmentation severs landscape connectivity, a key consideration in reserve design and protected area management [25]. Knowledge of animal behaviour is fundamental in understanding and mitigating the effects of habitat loss and fragmentation. For example, functional landscape connectivity, defined as the degree to which the landscape impedes or facilitates animal movement, explicitly concerns animal behaviour [26]. Behavioural traits are also key determinants in the ability of animals to colonise or persist within habitat patches [27], or to tolerate edge effects within protected areas [28]. Moreover, habitat fragmentation interacts with and intensifies the effects of other agents of global environmental change, including limiting the ability of organisms to maintain migrations or shift distributions in response to climate change [29,30].

- Which cues impede or facilitate animal movement, and hence functional connectivity, through altered landscapes from the sensory perspectives of different species?
- What are the behavioural traits that facilitate the colonisation of restored or recovering habitat?
- How can social interactions and social learning be manipulated to attract animals to habitat patches or to drive them away?
- How can sensory perception and behavioural responses to human disturbances be used to better estimate the optimal size and configuration of protected areas (e.g., edge effects)?
- How can behavioural traits (e.g., space use or responses to human disturbance) inform the design and mitigation of infrastructure associated with transportation, resource extraction, or energy production?
- Which habitat features are essential functional platforms for animal communication and reproduction?
- Which behavioural traits predict the risk of hybridisation when geographic barriers break down?
- Which behavioural traits predict the resilience and vulnerability of species to climate change?
- How do we facilitate the colonisation of more suitable habitats as animals shift distributions in response to climate change?

**Habitat Degradation**

Habitats can be degraded by human activity and the co-occurring introduction of noise, light, and chemical pollution, with potential impacts on animal behaviour that scale up to affect...
populations and communities. For example, human disturbance and pollution can disrupt critical behaviours, including those associated with signal transmission and the accurate assessment of predation risk and habitat quality [31–34]. Understanding the effects of habitat degradation on behaviour is essential to inform management decisions on levels of human activity allowed in protected areas [35]. It can also guide the development of tools to manipulate perceived predation risk and habitat quality for attracting animals to certain habitats or repelling them from others [32]. Furthermore, understanding the effects of pollutants on behaviour can aid in the development of behavioural indicators as measures of environmental pollution [36].

- How do resource extraction practices disrupt critical behaviours, and how can these impacts be minimised?
- How can an improved understanding of behavioural responses to varying levels of human recreation activity inform protected area management?
- When does human presence drive away predators (i.e., create a predator shield), thereby reducing perceived risk by prey species, and can we use that information to manipulate predator and prey behaviour?
- Which are the most frequent causes of mismatches between actual and perceived habitat quality and how can this knowledge be used to overcome ecological and perceptual traps? (Box 3)
- How does noise, light, and chemical pollution alter settlement decisions?
- How does noise, light, and chemical pollution interfere with communication in ways that affect survival and reproduction?
- How do chemical (e.g., pharmacological, petrochemical) pollutants modify behaviour, and can these behaviours be used as indicators of the presence or magnitude of chemical pollution?

**Human–Wildlife Conflict and Overexploitation**

Species are under increasing pressure to adapt to human activities, such as hunting, tourism, transportation, resource extraction, energy development, and intensive agriculture, which frequently produce conflict. By strict definition, human–wildlife conflict occurs whenever an action by wildlife or humans has a detrimental effect on the other, but the term usually refers to the negative effects of wildlife on human lives or property [37]. We combined the topics of human–wildlife conflict and overexploitation of wildlife (a primary conservation threat across taxa and continents [38,39]) because they are often inter-related and invoke lethal effects. Ironically, human–wildlife conflict can be worsened by conservation efforts that alter the abundance, movement, or distribution of wildlife populations [40,41]. Human behaviour is readily acknowledged as a contributor to conflict, but animal behaviour is equally paramount to developing solutions. Considering ecosystems holistically, while acknowledging trophic interactions that include people, might allow for better predictions of conflict and the advancement of more comprehensive solutions [6].

- Which demographically important behaviours are affected by harvesting individuals from the population?
- Which behavioural characteristics predict conflict with people?
- Which behavioural measures are most reliable and valid for quantifying habituation and sensitisation of wildlife to human activities?
- Which sensory abilities, decision rules, and levels of experience determine whether animals avoid collisions or areas of potential collision danger?
- Which impacts do deterrents have on the behaviour of nontarget species and individuals?
- How can we facilitate the effectiveness of buffer zones, the use of corridors, and other habitat features to reduce conflict?
- How can knowledge about social relationships and information transmission be used to reduce the acquisition and spread of ‘problem’ behaviours?
- How does learning reduce the effectiveness of control or deterrent strategies?

Understanding the behaviours underlying demographic processes can be fundamental to reversing population decline. The management of the Be‘er Sheva fringe-fingered lizard Acanthodactylus beershebensis serves as an prime example (Figure I). A. beershebensis is endemic to loess scrublands of the northern Negev Desert, Israel. The species has nonoverlapping generations; adults die after eggs are laid in the late fall, and hatching occurs synchronously in May [81]. In the late 20th century, the Forestry Department of the Jewish National Fund began an afforestation project in these scrub lands, creating a mosaic landscape (i.e., savannisation). As the project proceeded, A. beershebensis declined and was listed as critically endangered [81]. Since A. beershebensis declined in both natural and altered habitats, land managers argued that the population decline could not be attributed to the savannisation project and the project was designated for expansion to other areas in the region. However, Hawlena and Bouskila [82] argued that the afforested areas generated an ecological trap by providing perches for birds of prey, a threat not recognised by the dispersing subadult lizards. The high predation in the afforested patches would result in vacant areas that attract dispersing juveniles from nearby loess scrubland, generating an ecological trap and a resulting source and sink population [83], which explained the decline in both habitat areas. Hawlena et al. [81] designed a controlled experiment where plots with artificial trees were established within the loess scrubland. The results demonstrated that habitats with the artificial structures favoured predator activity, which created a population sink for the lizards. The following season these unoccupied patches attracted dispersing lizards because of the apparent reduced intraspecific competition. This supported Hawlena and Bouskila’s hypothesis that a mismatch between perceived and realised habitat quality explained the decline of the species in the mosaic landscape of the savannisation project. These findings were sufficient to convince land managers of the Jewish National Fund and other agencies to abandon the savannisation plans for the remaining A. beershebensis habitats and to establish a large sanctuary surrounded by sufficient buffer zones to protect the lizard.

Figure I. Be‘er Sheva Fringe-fingered Lizard, Acanthodactylus beershebensis.

- How can we use learning theory, such as reinforcement schedules, or stimulus intensity, to improve aversive conditioning in the wild in order to train animals to avoid people, livestock, or infrastructure?
- How effective are different means of hunting or trapping of conflict species in increasing fear of humans to reduce conflict?

Disease and Invasive Species

The processes that influence the population dynamics of disease and invasive species involve establishment, spread, and impact [42]. Many of the challenges managers face in controlling disease and invasive species can be linked to understanding the behavioural parameters affecting movement and reproduction. Managers can use behavioural information to increase detection probability [43,44], to understand how density dependence influences patterns of spread, and to focus control efforts (e.g., [45,46]). Additionally, behavioural traits could be used to identify the individuals that are most susceptible to disease, more likely to colonise new areas, or otherwise disproportionately important to the dynamics of disease and invasion.
• Which interspecific and intraspecific behavioural interactions increase cross-species disease transmission?
• Which are the anthropogenic habitat changes and management strategies that inflate movement or contact rates and drive disease spread?
• How can we incorporate knowledge of social network structure and ‘super-spreaders’ to better model disease spread, and optimise disease control and prevention?
• To what extent can invasion and disease transmission be slowed by focusing control efforts on behavioural phenotypes that are more likely to move or spread disease?
• How can we incorporate knowledge of species’ and individuals’ movement patterns to optimise the control and prevention of invasive species and disease spread?
• Which behavioural traits predict the establishment of non-native species?
• Which behavioural traits predict the impacts of non-native species on native species?
• How does the behaviour of introduced organisms influence the efficiency of detecting them?
• How does the behaviour of introduced organisms influence how easy they are to control?

Conservation Breeding and Translocation
Captive conservation breeding and translocation are important tools available to managers to address problems of isolated, declining, or critically endangered populations. They are often invoked when management fails to stop population decline. Conservation breeding has a long history of using behavioural research [47], but genetic management still governs most breeding decisions [48]. By considering behavioural factors, such as social context, breeding success might be greatly improved. For example, understanding mate choice can have major effects on the productivity of breeding programs [49]. Behavioural training and avoiding domestication can be instrumental for producing high-quality candidates for release [50]. Conservation translocations, which include both captive-bred and free-ranging source animals, are used as a tool to rescue genetically limited populations and re-establish extirpated populations, and might become increasingly used to address shifting habitats and fragmentation caused by climate change [51]. Behavioural research on social group composition and habitat selection mechanisms can greatly improve fitness postrelease and assist with the rapid establishment of released populations [52,53].
• Which are the early cues and consequences of domestication or adaptation to captivity and how should they be managed when translocating individuals?
• Which are the social and breeding contexts (e.g., mate choice) that need to be addressed to establish and maintain a successful conservation-breeding program?
• Which features of the captive environment are most important for promoting behaviours that are essential for conservation breeding?
• What is the role of environmentally mediated maternal or epigenetic effects in increasing behavioural competence for translocation?
• How realistic must predatory and antipredator training be to effectively increase fitness of released individuals?
• Which behavioural indices can be measured postrelease to inform management decisions on the efficacy of ongoing programs?
• Are certain behavioural types more likely to survive translocation?
• Which habitat settlement decision rules can be exploited to anchor animals to the release site?
• Can translocation success be increased by maintaining the social structure and relationships of the group and if so, how? (Box 4)

Cross-Over Questions
Several of our questions are relevant across multiple topics. For example, behavioural indicators can be used as a rapid assessment tool [54] to identify overexploitation (e.g., by providing an early warning of illegal harvest [55]), the presence of disease [56], or the successful
Box 4. Unexpected Consequences of the Social Context.

The case of the endangered Stephens’ kangaroo rat Dipodomys stephensi (Figure 1), endemic to southern California, illustrates how behavioural research can help solve conservation problems facing managers, sometimes in a nonintuitive way. Managers attempted to re-establish this species in newly restored areas, but all translocations failed, including one involving more than 500 animals. When consulted, behavioural ecologists constructed a number of hypotheses to explain why translocated kangaroo rats might fail to establish and survive at the release site, along with corresponding solutions. One idea proposed maintaining the network of social relationships established among animals at the source site when relocated to the release site. This idea had not been considered previously, likely because this species is highly territorial, aggressive, and considered ‘asocial’. However, kangaroo rats invest time and energy establishing relationships with neighbours; thus, having to renegotiate relationships with new neighbours can distract them from other important fitness-enhancing behaviour (the ‘clear enemy’ phenomenon [84]). To test this hypothesis, researchers determined the identity of neighbouring conspecifics at the source site and evaluated whether releasing kangaroo rats adjacent to neighbours conferred any advantage [53]. Postrelease monitoring demonstrated profound behavioural differences between neighbour- and control-translocated individuals. The neighbour group spent more time foraging and vigilant and less time fighting. They settled closer to the release site and established burrows more quickly. These behavioural differences had substantive effects on fitness. A combination of higher survival and reproduction in the neighbour-translocated group yielded a 24-fold advantage in the number of pups produced after 1 year. From these results, it is clear why earlier releases that did not consider social context might have failed. By continuing to conduct translocations incorporating these lessons learned, while also testing a new behavioural hypothesis to further improve outcomes, five new populations were established that have reproduced and grown for several generations. This illustrates the power of behavioural research as a tool for conservation interventions.

Figure 1. A Tagged Stephen’s Kangaroo Rat, Dipodomys stephensi, Postrelease.

establishment of a translocated population [57]. Similarly, research on sensory cues that attract or repel animals can be applied to manage the use of fragmented or degraded habitat [26,28], minimise human–wildlife conflict [37], control the spread of invasive species [58], and improve translocation success [47]. In addition, the explicit integration of behavioural knowledge into quantitative conservation biology can result in more accurate descriptions of population dynamics and risk classification [59]. All the following questions can be applied broadly across multiple conservation contexts.

- How can behavioural indices substitute for more costly, time-consuming, or invasive measures when monitoring populations?
- Which sensory cues (olfactory, acoustic, visual, or multimodal) are most effective in attracting or repelling animals?
- Does habituation to human disturbances reduce animals’ assessment of risk and mortality, and how can such habituation be limited?
• How do the indirect and cumulative effects of stressors impact behaviour and scale to influence population-level dynamics?
• How should management strategies change as a function of density-dependent behaviours?
• How can behavioural attributes and variability be integrated into demographic models for estimating population dynamics and extinction probabilities?

Uniting Over Common Conservation Goals
Interdisciplinary conservation action requires the synthesis and prioritisation of questions and goals that are common to academic-focused researchers and application-focused managers. Although animal behaviour research can help pinpoint conservation problems, and be vital to developing management solutions, progress will not be made unless academics and managers collaborate. This paper represents an effort to forge an interconnected conservation community and foster forward-thinking research.

Our 50 questions highlight the diverse applications of behavioural research that have the greatest potential to solve current and future conservation challenges, while simultaneously advancing basic understanding of animal behaviour. Ultimately, these questions identify key areas for future investment in conservation research, management, and policy behaviour, and thereby fit the scope of questions likely to attract project funding within research programs that would have conservation applications. However, in order for the research generated from these questions to be of use to managers, they need to be tailored to specific species or ecosystems and be properly evaluated alongside traditional methods [60]. Conservation behaviour research must be packaged with practical applications for managers, such as analyses of cost-effectiveness (e.g., [54]), if they are to survive funding struggles and be successfully applied (Box 1).

The specificity of the questions in our list varies partly because animal behaviour has been unevenly researched and applied in conservation management. Well-developed areas where behavioural research has been regularly employed, such as captive breeding and translocations, produced more precisely articulated questions. However, other research topics, including those related to learning theory and sensory ecology, are more broadly applicable or novel to wildlife conservation [61], and therefore produced less specific questions that related to more than one conservation topic. For example, several questions within the human–wildlife conflict section are also applicable to issues associated with disease and invasive species.

Our list of 50 questions is necessarily and intentionally incomplete. It excludes very circumscribed strategies that are already known to be successful. For example, we know that diet and associated maternal condition should theoretically affect the sex ratio of offspring [62] and this mechanism played a key role in management of the endangered Kakapo (Strigops habroptilus) [63]. Additionally, we also excluded novel ideas with potentially limited scope that could still be useful in specific contexts – such as promoting the natural self-medication behaviours that some animals exhibit to combat disease [64].

Concluding Remarks
Since the list we defined represents the output of a democratic process, it would be unrealistic to assume the exact same list would be generated if another group of managers and researchers underwent this exercise. However, we are confident that many of the same questions would arise, given the wide consensus we found across many topics. The ultimate goal of creating a priority list is not to define the exact 50 questions that would have impact above all others, but to help foster the development of credible and generalizable evidence on the effectiveness of animal behaviour for conservation. Therefore, developing the list itself is only one part of the
process. Unless the research generated from the list is made available to managers, any progress made in these priority areas could still fail to have conservation impact.

For managers, having access to scientific evidence on the efficacy of conservation interventions is essential to formulating and enacting sound conservation policies [4,65]. Open access journals and online databases, such as ConservationEvidence.com, narrow the gap between science and conservation management by making systematic reviews of evidence readily available. Despite their success, these reviews are still in their infancy for many important conservation areas [66], including many of the questions within this list. Therefore, by including a systematic review as part of the dedicated research proposal or grant that tackles a question from this list, researchers can increase the likelihood that findings in their field will be adopted in management policy. Such efforts will be instrumental in developing novel, effective, and cost-efficient conservation and wildlife management actions that both researchers and practitioners will be eager to pursue together (see the 50 Outstanding Questions listed in the previous sections).

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Supplemental Information

Supplemental information associated with this article can be found in the online version.

References


