Opinion

The ethics of intervening in animal behaviour for conservation

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Conservation behaviour is a growing field that applies insights from the study of animal behaviour to address challenges in wildlife conservation and management. Conservation behaviour interventions often aim to manage specific behaviours of a species to solve conservation challenges. The field is often viewed as offering approaches that are less intrusive or harmful to animals than, for example, managing the impact of a problematic species by reducing its population size (frequently through lethal control). However, intervening in animal behaviour, even for conservation purposes, may still raise important ethical considerations. We discuss these issues and develop a framework and a decision support tool, to aid managers and researchers in evaluating the ethical considerations of conservation behaviour interventions against other options.

The goals of conservation behaviour

Conservation behaviour is a growing field that applies insights and knowledge from the study of animal behaviour to address conservation challenges [1]. In comparison to traditional approaches, including lethal management, behavioural interventions can offer novel opportunities or outcomes and are generally viewed as being less intrusive and less harmful (Box 2). However, modifying and manipulating animal behaviour (Box 1), even for conservation and management purposes, can raise important ethical considerations that must be understood so they can be evaluated relative to alternate options when determining appropriate management practices. Ongoing biodiversity decline [2] makes addressing these questions increasingly urgent.

Berger-Tal *et al.* [3] describe the field of conservation behaviour as consisting of three core activities: understanding and quantifying anthropogenic impacts on animal behaviour; developing tools for **behaviour-based management** (see Glossary); and using behaviour as an indicator of environmental change or population viability or health. While each of these areas may raise ethical questions, our focus is on behaviour-based management, which raises underexplored issues pertaining to animal welfare, interference in the expression of animals' normal behaviours, impacts on nontarget species, and impacts on local human communities (Figure 1).

Animal welfare

Inflicting harms on other (sentient) beings is widely considered to be morally undesirable [4]. An ethical dilemma can arise when some animals are harmed for their own or others'

Highlights

Conservation scientists often modify or take advantage of existing animal behaviour to achieve management outcomes.

To date, there has been little analysis of the ethical issues potentially raised by modifying animal behaviours in this way.

These ethical issues include animal welfare, interference in the expression of animals' normal behaviours, impacts on nontarget species, and impacts on local human communities.

Assessing the goals of a behaviour intervention against a set of explicit values is an essential step in the development of ethical approaches to conservation.

We provide a framework for considering the relationship between values, goals and conservation actions, and a decision support tool for comparing and contrasting the ethical dimensions of possible conservation behaviour interventions against alternative options.

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> **Box 1. What is behaviour?**
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> Behaviour can be defined in various ways. At the simplest level, it is a quantifiable change in motor response to a stimulus. These changes may ultimately result from changes in gene expression and physiology; conventionally, behavioural changes are externally detectable. Behavioural responses can be described by their structure or consequences (what an animal does – foraging behaviour, reproductive behaviour, antipredator behaviour, habitat selection), or it can also define what an animal is (i.e., its location on a personality spectrum which can be viewed as a trait). Focusing on how behaviour is defined is essential to frame a discussion of the ethics of intervening to change behaviour.
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> For example, when we view behaviour as a trait – essentially who animals are – we may select individuals with particular personality traits to translocate because they do better once released. A suite of behavioural outcomes follows as a result of this intervention, because what animals 'do' in part depends on what they 'are', behaviourally. Alternatively, when we think about behaviours as what animals do, we may intervene and attempt to teach them not to do something (like eating a specific prey). Such interventions can be done irrespective of underlying behavioural traits. However, these interventions may be more likely to succeed if we can identify the trait and intervene in a way that best caters for that. For instance, shy animals may need a different form of intervention than bold ones to alter their predatory behaviour. It is important to realise that changing what animals do may ultimately change their underlying behavioural traits (e.g., through social learning and ecological inheritance).

conservation. Behavioural interventions may significantly reduce the need for some forms of harm and killing. Indeed, one of the core elements of conservation behaviour is that it can shift the focus, for example, from reducing the population size of a problematic species (often through lethal control), to managing the specific problematic behaviours of the species, or even of a subset of individuals. However, even if behavioural approaches lead to a net reduction in harm, it is important to acknowledge that these approaches may also create other ethical considerations such as those listed in the following section (Figures 1 and 2).

Trauma and distress

Lethal control might be avoided in some cases of human–wildlife conflict by using aversive stimuli to alter animal behaviour and teach animals to associate unpleasant experiences, such as fear, physical discomfort, and pain, with contexts humans want them to avoid [5]. Such techniques, however, impose distress and potential trauma [6,7]. There are no perfect solutions here. In some cases, this distress will be what keeps the animals alive, encouraging them to avoid potentially deadly interactions with local communities [8]. However, the fact that the alternative to distress is often death – either at the hands of managers or local people – does not negate the need to consider, and ideally minimise, this form of harm. This situation is complex because distress is less amenable to observation and quantification than physical harm and mortality but may be required for the behavioural intervention to be effective.

Incidental harms

Animals that are not explicitly considered are sometimes harmed or killed in conservation behaviour interventions. For example, sandhill cranes (*Grus canadensis*) were injured and killed when used as surrogates in the development of techniques to teach whooping cranes (*Grus americana*) to migrate with ultralight aircraft [9]. Even some approaches labelled as 'nonlethal' can involve the killing of nontarget species to produce necessary inputs, for example, in the production of baits for taste aversion conditioning [10].

Approaches to learning

Sometimes the specific learning requirements of target species require approaches that would otherwise be avoided to support animal welfare. For example (Box 2), efforts to condition yellow-

spotted monitor lizards (*Varanus panoptes*) not to consume toxic cane toads (*Rhinella marina*) are far more effective when carried out with live toads [10], whereas blue-tongued lizards (*Tiliqua scincoides*) can be deterred from eating toads through encounters with dead animals [11]. Conservationists must attend to how animals perceive and learn, and modify their approaches accordingly, balancing effectiveness of the intervention against the harm that it produces for all animals involved. Doing so may lead to counterintuitive approaches. For example, **aversive conditioning** of elk (*Cervus canadensis*) appears to be more effective if it subjects animals to isolation, which is stress-inducing for herding species, and might also reduce **habituation** to subsequent human encounters [12].

Impacts on human communities

It is important to consider the perceptions, needs, and values of human communities when planning behavioural interventions [13]. Biodiversity conservation projects can have significant negative impacts on local communities, including on livelihoods, traditional cultural practices, and access to land [14]. For example, farmers might be asked to replace traditional management practices with novel and unfamiliar behaviour-based approaches to protect crops or livestock such as **biofences** or coloured flags as deterrents, and benefit from but also bear much of the risk of these methods in terms of impacts on lives and livelihoods [15–17]. These interventions can also have positive impacts on human communities and human/wildlife relations (Box 2).

Valuing behaviours

It is important to identify which kinds of behavioural changes are ethically acceptable, and under what contexts. While animals regularly modify their behaviour in response to novel environmental factors [18], including anthropogenic impacts, managers should still critically scrutinise efforts to deliberately alter the behaviour of wild animals. Doing so requires them to consider how and why specific animal behaviours might be valued.

One of the core arguments offered for conserving animal behaviours is their functional ecological role in maintaining biodiversity [19]. Other **instrumental values** associated with conserving specific behaviours include their aesthetic, scientific, and cultural values to human communities (e.g., altering migratory routes or summering locations of birds [20]). Some animal behaviours may also be viewed as intrinsically valuable natural phenomena that ought to be conserved irrespective of any other values they may hold to others, including unique cultural practices like the use of sponges for foraging by some bottlenose dolphins (*Tursiops sp.*) [21]. Of course, some animal behaviours can also conflict with important values, for example, by undermining the integrity of ecosystems or human safety and livelihoods. In these cases, as discussed further in the following section, it is necessary to find ways to maximise desired values.

What is acceptable behavioural change?

When considering deliberately altering animal behaviours for conservation, managers should consider the behavioural autonomy of individual organisms, that is, the extent to which wild animals ought to be allowed to express their natural behavioural repertoires without human interference. This is particularly pertinent in case where altered behaviours may become self-perpetuating such as through social learning. For example, habituating the critically endangered Hawaiian crow (*Corvus hawaiiensis*), a frugivorous forest bird, to human presence and introducing them to anthropogenic food sources was dismissed as a conservation option, in part because this change was considered an unacceptable modification to 'naturalness' [22].

Glossary

Aversive conditioning: a form of operant conditioning where animals learn to associate a naturally feared unconditioned stimulus (e.g., pain) with a conditioned stimulus that is not feared (e.g., the appearance of a person) to avoid future conflict.

Behaviour-based management: management actions that are aligned with valued behaviours (e.g., corridor planning that matches a species home range or migratory path), or that change behaviours (e.g., by reducing the frequency of a problem behaviour or by inculcating antipredator behaviour in predator-naive individuals) or that exploit normal behaviours (e.g., attractants or deterrents that work with normal foraging and/or risk avoidance behaviours).

Behavioural bycatch: the observed and unobserved welfare and fitness costs on nontarget individuals (conspecific or heterospecific) as a result of interaction with a behaviour-based management action.

Behavioural diversity: the total number of behavioural variants observed within and among species, populations, and individuals.

Biofence: the use of scent or other biologically relevant cues to communicate information, such as a territorial boundary, that restricts animal movement.

Habituation: a nonassociative form of learning in which, after repeated exposures to a stimulus that lacks positive or negative consequences, an animal reduces its behavioural response to its occurrence.

Instrumental value: possessing value for someone or something other than itself, generally as a means to another end.

Intrinsic value: possessing value in and of itself, irrespective of its potential utility or value to others.

Olfactory misinformation: can work to either camouflage or mask olfactory cues of a species or resource or devalue food odours to trick foragers into dismissing the food as unavailable.

Personality: consistent behavioural differences among individuals within a species over time and context. Often defined in ecology by axes (traits) such as the bold-shy continuum, exploration, activity; and may exist as correlated traits in a behavioural syndrome.

In contrast to valuing past behaviours, it might be argued that organisms and species are constantly changing, with or without human involvement, and that in this context it does not make sense to prioritise stasis, especially when a given behaviour is threatening the survival of a species (e.g., [23]). Navigating these competing perspectives may require managers and the public to find new ways to characterise and value different forms of behavioural continuity and change that may occur from conservation interventions [22,24].

In some contexts, modifying a species' behaviour may even give rise to the question of whether a species has genuinely been 'conserved' or has actually been 'lost'. An example of this comes from the polarised debate surrounding the conservation of the California condor (*Gymnogyps californianus*), in which some conservationists were so strongly opposed to the possible behavioural impacts of bringing the birds into captivity that they viewed the extinction of the species as a preferable outcome, arguing that the condor was 'better dead than bred' [25]. Here too, there is arguably a need to move beyond static notions of animal behaviour and identity to value both continuity and change.

Relational values: cultural and other values and responsibilities that emerge from the relationships between people and species or ecosystems.
Translocation: the capture, transport, and release of animals into a new environment or an environment where they previously occurred. It may include animals sourced from the wild or from a captive-breeding environment.
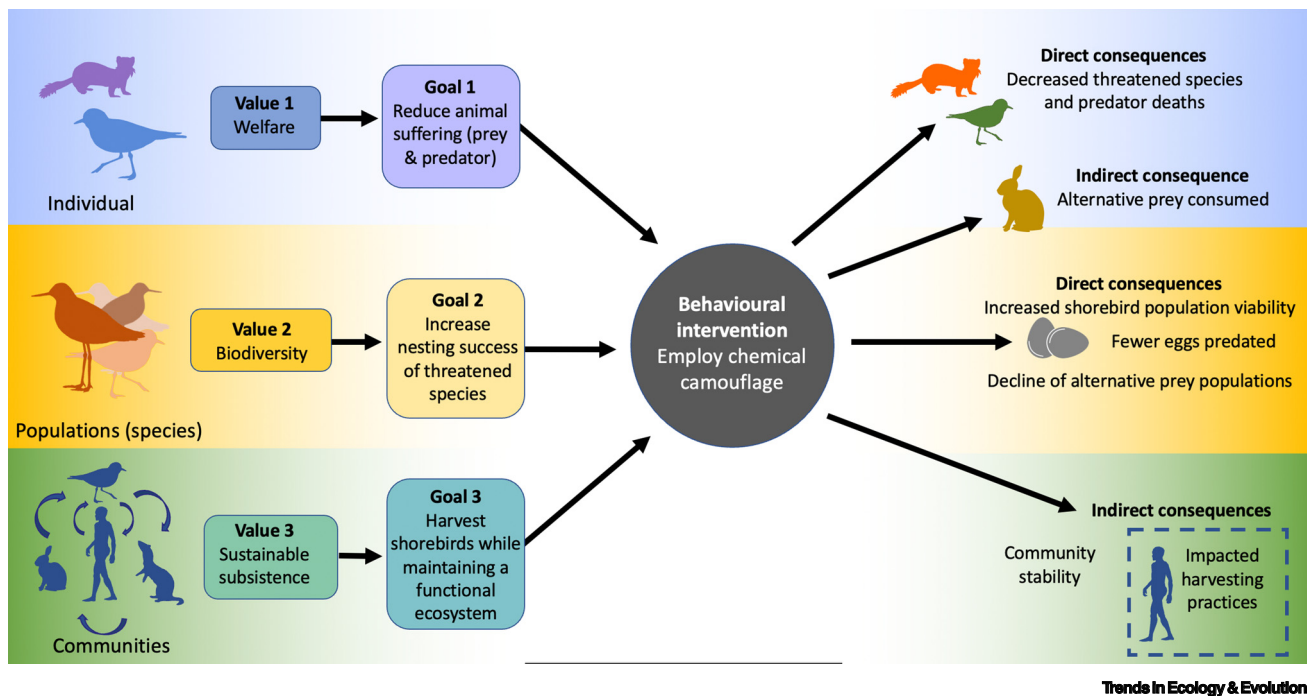

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Figure 1. The motivations and consequences of conservation behaviour interventions illustrated with the behavioural intervention of **olfactory misinformation** (chemical camouflage) to reduce invasive species predation on threatened native shorebirds (e.g., see [46]). This technique has the potential to avoid suffering associated with traditional lethal control methods such as 1080 poisoning and trapping. Decision-makers must identify the set of stakeholder values, for example, animal welfare, conserving biodiversity, and maintaining or restoring ecosystem functioning, which are relevant at different spatial scales (individual, populations, species, community). These values inform the goals which might include reducing suffering of both predators and threatened prey species, increasing nesting success of a threatened shorebird, and maintaining a functional ecosystem. In other contexts, this might include the conservation of an apex predator that consumes endangered prey. These goals might be achieved using the behavioural intervention of chemical camouflage. The behavioural intervention has direct and indirect, long-term and short-term effects at varying spatial scales. For example, a direct short-term effect is that fewer eggs are predated, and a direct long-term effect is increased nest survival. An indirect short-term effect could conceivably be that more individuals of the predators' primary prey (rabbits) could be consumed if predators ignore the camouflaged threatened species, an instance of behavioural bycatch. In other contexts, where the endangered or predatory species has a cultural and/or livelihood significance for local people, this conservation intervention would also impact on their relationships with those species. For example, culturally significant nesting birds and their predators (e.g., pigs) might become available for harvesting/hunting (in accordance with traditional knowledge practices that could maintain ecosystem functioning [47]). This hypothetical addition to the use of olfactory misinformation is represented in the bottom right corner of Figure 1. In these cases, value 3 and goal 3 might also be suitably revised to include sustainable harvest. Icon images courtesy of Phylopic 2.0.
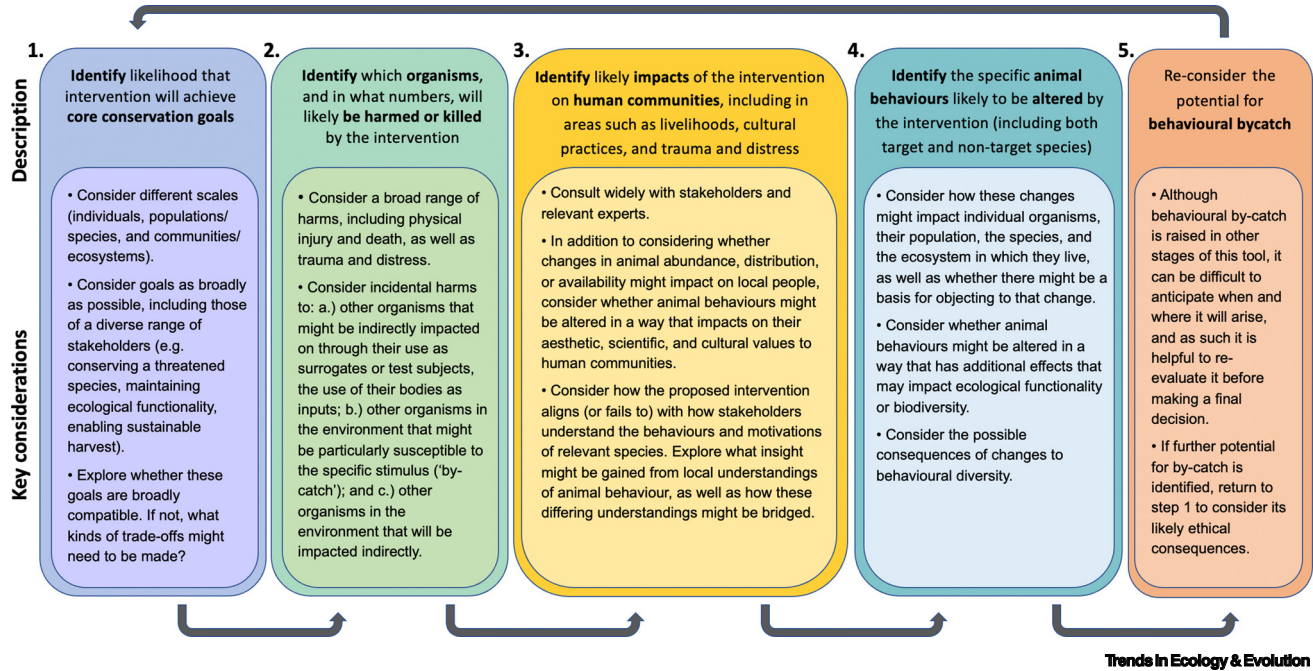
Figure 2. A decision support tool for evaluating the ethics of behavioural interventions relative to other options. This tool could aid researchers and managers in contrasting the ethics and efficacy of actions that include a behavioural intervention to address a conservation issue. This tool does not aim to rank possibilities, instead supporting critical and inclusive analysis of potential ethical considerations with the practical and pragmatic limitations of available resources, expertise, timeframes, and so forth. Prior to using the tool, it is necessary to consider the values the intervention should protect/maximise and identify the conservation goals that allow this to be achieved. Doing so will generally require consultation with stakeholders. The tool can then help users to identify the specific conservation interventions (behavioural and otherwise) that will achieve all or most of these core goals. Each intervention (or group of interventions) can be assessed against the five general categories of ethical considerations: 'core conservation goals', 'animal welfare', 'human communities', 'valuing behaviours', 'Behavioural bycatch.' Users should also evaluate the scenario in which no intervention occurs.

The cultural perspective through which we approach conservation challenges may also influence whether it is deemed appropriate to modify animal behaviours. For example, many Indigenous communities view animals as kin and have intimate knowledge of behavioural idiosyncrasies, which can be bound up with cultural practices and traditional ecological knowledge [26,27]. What some cultures may view as positive human–wildlife interactions, others view as negative forms of conflict [28]. In this context, some people may be averse to changing animal behaviours that are important to the identity of a species or a related cultural association.

Behavioural diversity matters

From an ethical perspective, it is also important to note that **behavioural diversity** itself might have animal welfare and ecological values. Behavioural diversity is a form of biodiversity which is gaining increasing attention [29]. Within species, individuals exhibit **personality**-consistent behavioural differences across time and contexts [30]. Such differences can directly bear on the reproductive and survival prospects of individuals and, in so doing, influence the stability, resilience, and adaptive capacity of populations [31]. It is surprising, therefore, that individual-level variation in behaviour – and how this variation can be affected by conservation interventions – is not more widely considered. Behavioural diversity may increase the chances that a population can adapt to future environmental changes, such as changing climates [32]. Populations that are more behaviourally diverse also exhibit higher population growth and persist longer than those that are less diverse [33,34]. Indeed, reduced behavioural diversity within

Box 2. Behavioural interventions can improve conservation outcomes

Behavioural interventions have improved the effectiveness of a broad range of conservation projects. Here, we present several examples where incorporating behavioural techniques has successfully avoided lethal control, reduced mortality, or otherwise changed a focal species' behaviour and led to improved conservation outcomes.

### Improving post-release survival of large carnivores and primates following reintroductions

Large carnivores and primates have historically suffered from high rates of post-release mortality following reintroductions [48–50]. Captive-bred individuals require complex foraging skills to survive in the wild and may be unable to find food, die of starvation, and/or succumb to predation or disease (e.g., the golden lion tamarin (*Leontopithecus rosalia*), Figure IA). Behavioural interventions such as pre-release training that includes foraging enrichment and predator recognition as well as incorporating social behaviour and group dynamics into release protocols has significantly improved the success of translocations for both captive-bred and wild-origin individuals [51].

Reducing mortality of native predators from toxic invasive cane toads

The spread of introduced toxic cane toads (*Rhinella marina*) across northern Australia has led to population declines of native reptilian predators that eat the poison prey, including freshwater crocodiles (*Crocodylus johnsoni*) (Figure IB), yellow-spotted monitor lizards (*Varanus panoptes*), and blue-tongued lizards (*Tiliqua scincoides*; [52]). Toxic baits made of dead (or sometimes small live) cane toads are now deployed ahead of the invasion front to provide a nonlethal but aversive experience and accelerate learning by predators to avoid consuming wild toads [10,53]. Population declines of native species have been reduced because this technique permits native predators to learn to avoid toads. In addition to their **intrinsic value** and important ecological function, native reptiles have cultural value to Aboriginal and other local communities.

Protecting livestock, reducing human–wildlife conflict and improving conservation outcomes for lions

In combination with husbandry practices, use of behavioural techniques, including hazing, has reduced livestock losses and retaliatory killing of lions (*Panthera leo*) in Southern Africa (Figure IC) [54]. Within each pride, at least one lion is fitted with a GPS collar and early warning messages are sent to local communities if the animals approach areas with livestock. Volunteers then chase the lions using horns to move them away. This technique has been shown to be particularly successful when the aversive events are repeated regularly and before animals have developed problematic behaviours [8].
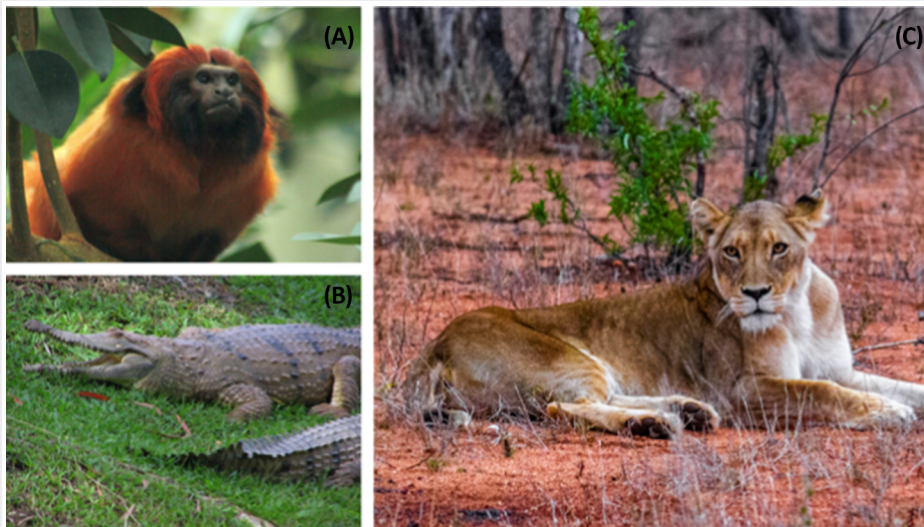
Figure I. Species that have been involved in behavioural interventions. (A) Golden lion tamarin (*Leontopithecus rosalia*) (Source: Daisyree Bakker, CC BY 2.0 via Wikimedia Commons); (B) Freshwater crocodile (*Crocodylus johnsoni*) (Source: Benchill, CC BY 3.0 via Wikimedia Commons); (C) African lion (*Panthera leo*) (Source: https://www.vecteezy.com/free-photos).

populations may even result in higher extinction risk [35]. In the context of reintroduction and **translocation** programmes, a growing number of studies in taxa as diverse as turtles [36] and mammals [37] have reported an important link between different behavioural characteristics and post-release survival (Box 2).

Is it acceptable to modify an animal's behaviour instead of modifying our own?

As with wildlife management and conservation more generally, the root causes of most issues that conservation behaviour addresses are anthropogenic. One significant category of such issues is human–wildlife conflict as animals adapt their behaviour to exploit new resources in anthropogenic environments. Aversive behavioural interventions seek to make these resources, the landscapes that contain them, or people themselves, less attractive, sometimes through the creation of fear and perhaps trauma [8,38,39]. In these cases, animals are often required to change their behaviours because of an inability or unwillingness to alter human societal practices. While vastly different socio-ecological dynamics underlie these situations in different parts of the world, in developed countries these conflicts are often driven by avoidable and irresponsible human activities (including poor urban planning and waste disposal). It is essential that this dynamic be recognised and addressed wherever possible so that conservation behaviour does not become a band-aid solution that sidesteps more difficult social and economic interventions [40]. This is especially pertinent where there are high costs in animal welfare of the proposed behavioural intervention.

'Behavioural bycatch' should be expected and actively explored

Any intervention occurring within a natural area may have consequences for nontarget individuals, both conspecific and heterospecific. **Behavioural bycatch** refers to these unexpected welfare and fitness costs on nontarget individuals as a result of interactions with a behaviour-based management action. A common objective of nonlethal behavioural interventions is to limit access to a resource (e.g., livestock, rubbish, or a prey species). In these cases, deterrents across modalities, such as the smell, sight, or sound of predators, may impact multiple species in a community. In multi-trophic ecological systems, these nontarget effects can drive apparent competition as well as facilitation [41] cascading beyond the initial intervention target. Understanding the potential for nontarget effects depends on understanding the perceptual abilities and motivations of potential nontarget species. This will be particularly important when stimuli are broadcast widely into the environment. For example, attempts to limit pinniped predation on aquaculture using acoustic seal scaring devices led to unintended impacts on nontarget odontocetes [42]. Odontocetes may be more sensitive to the frequencies of the acoustic devices and less likely to habituate to their sound. Consequently, these nontarget animals may be more prone to abandoning the area than the target animals.

The likelihood of this bycatch is not simply dictated by whether a species can perceive the aversive stimulus, but also how it values the resource. For instance, some subordinate birds are likely to return to forage at a patch sooner after a predator has visited than dominant birds because there will be less competition [43]. Similarly, a resource may have different value to different species and this will influence its cost/benefit trade-offs [44]. The potential for bycatch exists even when the management action exploits species-specific signals, because many species eavesdrop on the cues and signals of others to acquire information about their environment [45].

From an ethical perspective, the potential for bycatch requires adoption of a precautionary approach via adaptive management with more focus on continued exploration of how animals perceive and learn about their environments.

Drawing the strands together: identifying and maximising values in conservation behaviour

Values underlie all conservation goals and drive conservation actions (Figures 1 and 2). These include economic, cultural, heritage and aesthetic values, valuing the welfare and sentience of animals, as well as ecological and evolutionary values. Importantly, once values are identified, we often find that they conflict, and so an ethical inquiry must explore and consider which values ought to take precedence and when. The ethical development of the field of conservation behaviour requires the interrogation of values to guide decision-making about when specific approaches will be utilised and how they might be further developed to maximise desirable values.

Figure 1 is a framework to assist in making values explicit and to illuminate tensions and disagreements within and between stakeholder groups. Considering as many values as possible can allow decision-makers to identify behavioural conservation interventions that align with many values and goals at once. This framework helps decision-makers consider the relationships between values, goals, and the consequences of possible conservation interventions. Figure 2 is a decision support tool that can subsequently be used to compare and contrast the ethical dimensions of a set of possible conservation interventions where at least one of those interventions is behavioural in nature.

Concluding remarks

Conservation behaviour should not be viewed in a vacuum; it provides a useful set of tools to address conservation problems. Like all management interventions, conservation behaviour raises important ethical considerations. To design ethically robust behavioural interventions, we must clearly identify our goals and interrogate their underlying values, as well as any collateral impacts and wider consequences of our actions (Figures 1 and 2). The complexity of these interventions will continue to make this a challenging task, but future research might reduce some of those areas of uncertainty (see Outstanding questions). We hope that this framework, which explores the unique ethical challenges to behavioural interventions, and their relationship to values and goals, will improve ethical applications of behavioural interventions and, more broadly, improve conservation outcomes.

Declaration of interests

No interests are declared.

References

1. Blumstein, D.T. and Fernandez-Juricic, E. (2010) *A Primer of Conservation Behavior*, Sinauer Associates
2. IPBES (2019) In *Global assessment report on biodiversity and ecosystem services of the Intergovernmental Science-Policy Platform on Biodiversity and Ecosystem Services (Version 1)* (Brondizio, E.S. *et al.*, eds), pp. 1148, IPBES Secretariat
3. Berger-Tal, O. *et al.* (2011) Integrating animal behavior and conservation biology: a conceptual framework. *Behav. Ecol.* 22, 236–239
4. Palmer, C. (2010) *Animal Ethics in Context*, Columbia University Press
5. Shivik, J.A. (2006) Tools for the edge: what's new for conserving carnivores. *BioScience* 56, 253–259
6. Beckmann, J.P. *et al.* (2004) Evaluation of deterrent techniques and dogs to alter behavior of "nuisance" black bears. *Wildl. Soc. Bull. (1973-2006)* 32, 1141–1146
7. Kidd-Weaver, A.D. *et al.* (2022) Evaluating the efficacy of capture as aversive conditioning for American alligators in human-dominated landscapes. *J. Wildl. Manag.* 86, e22259
8. Petracca, L.S. *et al.* (2019) The effectiveness of hazing African lions as a conflict mitigation tool: implications for carnivore management. *Ecosphere* 10, e02967
9. van Dooren, T. (2016) *Flight Ways: Life and Loss at the Edge of Extinction*, Columbia University Press
10. Ward-Fear, G. *et al.* (2017) Eliciting conditioned taste aversion in lizards: live toxic prey are more effective than scent and taste cues alone. *Integr. Zool.* 12, 112–120

Outstanding questions

What is the likely scale and scope of behavioural bycatch, and how can it be accurately assessed before undertaking a behavioural intervention?

How do differences in individual behavioural phenotypes affect success of behavioural interventions?

How should stakeholders be defined and what is an inclusive framework to negotiate competing and **relational values** among them?

How/do costs and benefits shift over time (short to long term) and do these raise unique ethical issues (e.g., by trading-off short-term costs for long-term benefits)?

11. Price-Rees, S.J. *et al.* (2011) School for skinks: can conditioned taste aversion enable bluetongue lizards (*Tiliqua scincoides*) to avoid toxic cane toads (*Rhinella marina*) as prey? *Ethology* 117, 749–757

12. Found, R.O.B. and St. Clair, C.C. (2018) Personality influences wildlife responses to aversive conditioning. *J. Wildl. Manag.* 82, 747–755

13. Dickman, A.J. (2010) Complexities of conflict: the importance of considering social factors for effectively resolving human–wildlife conflict. *Anim. Conserv.* 13, 458–466

14. West, P. *et al.* (2006) Parks and peoples: the social impact of protected areas. *Annu. Rev. Anthropol.* 35, 251–277

15. Littlewood, N.A. *et al.* (2020) *Terrestrial Mammal Conservation: Global Evidence for the Effects of Interventions for Terrestrial Mammals excluding Bats and Primates*, Open Book Publishers

16. Morizot, B. (2022) *Wild Diplomacy: Cohabiting with Wolves on a New Ontological Map*, SUNY Press

17. King, L.E. *et al.* (2017) Beehive fences as a multidimensional conflict-mitigation tool for farmers coexisting with elephants. *Conserv. Biol.* 31, 743–752

18. Klump, B.C. *et al.* (2022) Is bin-opening in cockatoos leading to an innovation arms race with humans? *Curr. Biol.* 32, R910–R911

19. Tobias, J.A. and Pigot, A.L. (2019) Integrating behaviour and ecology into global biodiversity conservation strategies. *Philos. Trans. R. Soc. Lond. Ser. B Biol. Sci.* 374, 20190012

20. Parsons, M.H. *et al.* (2018) Biologically meaningful scents: a framework for understanding predator–prey research across disciplines. *Biol. Rev.* 93, 98–114

21. Krützen, M. *et al.* (2005) Cultural transmission of tool use in bottlenose dolphins. *Proc. Natl. Acad. Sci. U. S. A.* 102, 8939–8943

22. van Dooren, T. (2016) Authentic crows: identity, captivity and emergent forms of life. *Theory Cult. Soc.* 33, 29–52

23. Merkle, J.A. *et al.* (2022) Site fidelity as a maladaptive behavior in the Anthropocene. *Front. Ecol. Environ.* 20, 187–194

24. Chrulew, M. (2020) Reconstructing the worlds of wildlife: Uexküll, Hediger, and beyond. *Biosemiotics* 13, 137–149

25. Braverman, I. (2014) Captive for life: conserving extinct in the wild species through ex situ breeding. In *The Ethics of Captivity* (Gruen, L., ed.), pp. 193–212, Oxford University Press

26. Ens, E.J. *et al.* (2012) Australian approaches for managing 'country' using Indigenous and non-Indigenous knowledge. *Ecol. Manage. Rest.* 13, 100–107

27. Wyllie de Echeverria, V.R. and Thornton, T.F. (2019) Using traditional ecological knowledge to understand and adapt to climate and biodiversity change on the Pacific coast of North America. *Ambio* 48, 1447–1469

28. Fuentes, A. (2010) Natural cultural encounters in Bali: monkeys, temples, tourists, and ethnoprimatology. *Cult. Anthropol.* 25, 600–624

29. Cordero-Rivera, A. (2017) Behavioral diversity (ethodiversity): a neglected level in the study of biodiversity. *Front. Ecol. Evol.* 5, 7

30. Réale, D. *et al.* (2010) Evolutionary and ecological approaches to the study of personality. *Philos. Trans. R. Soc. Lond. B Biol. Sci.* 365, 3937–3946

31. Wolf, M. and Weissing, F.J. (2012) Animal personalities: consequences for ecology and evolution. *Trends Ecol. Evol.* 27, 452–461

32. Lynch, K.E. *et al.* (2018) The effect of captive breeding upon adult thermal preference in the Queensland fruit fly (*Bactrocera tryoni*). *J. Therm. Biol.* 78, 290–297

33. Carlson, S.M. and Satterthwaite, W.H. (2011) Weakened portfolio effect in a collapsed salmon population complex. *Can. J. Fish. Aquat. Sci.* 68, 1579–1589

34. Modlmeier, A.P. *et al.* (2012) Diverse societies are more productive: a lesson from ants. *Proc. R. Soc. B Biol. Sci.* 279, 2142–2150

35. Schindler, D.E. *et al.* (2010) Population diversity and the portfolio effect in an exploited species. *Nature* 465, 609–612

36. Allard, S. *et al.* (2019) Personality in zoo-hatched Blanding's turtles affects behavior and survival after reintroduction into the wild. *Front. Psychol.* 10, 2324

37. West, R.S. *et al.* (2019) Searching for an effective pre-release screening tool for translocations: can trap temperament predict behaviour and survival in the wild? *Biodivers. Conserv.* 28, 229–243

38. Hawley, J.E. *et al.* (2009) Assessment of shock collars as nonlethal management for wolves in Wisconsin. *J. Wildl. Manag.* 73, 518–525

39. Mazur, R.L. (2010) Does aversive conditioning reduce human—black bear conflict? *J. Wildl. Manag.* 74, 48–54

40. van Dooren, T. (2019) *The Wake of Crows: Living and Dying in Shared Worlds*, Columbia University Press

41. Jones, M. *et al.* (2016) A nose for death: integrating trophic and informational networks for conservation and management. *Front. Ecol. Evol.* 4, 124

42. Götz, T. and Janik, V.M. (2013) Acoustic deterrent devices to prevent pinniped depredation: efficiency, conservation concerns and possible solutions. *Mar. Ecol. Prog. Ser.* 492, 285–302

43. Waite, T.A. and Grubb, T.C. (1987) Dominance, foraging and predation risk in the tufted titmouse. *Condor* 89, 936–940

44. Smith, B.P. *et al.* (2022) Deterring and repelling wildlife. In *Wildlife Research in Australia: A Practical Guide* (Smith, B. *et al.*, eds), pp. 210–232, CSIRO Publishing

45. Banks, P.B. *et al.* (2016) Predator odours attract other predators, creating an olfactory web of information. *Biol. Lett.* 12, 1053

46. Norbury, G. *et al.* (2021) Misinformation tactics protect rare birds from problem predators. *Sci. Adv.* 7, eabe4164

47. Lyver, P.O.B. *et al.* (2015) Insights to the functional relationships of Māori harvest practices: customary use of a burrowing seabird. *J. Wildl. Manag.* 79, 969–977

48. Kleiman, D.G. *et al.* (1991) Costs of a re-introduction and criteria for success: accounting and accountability in the golden lion tamarin conservation program. In *Beyond Captive Breeding: Re-introducing Endangered Mammals to the Wild* (Gipps, J.H.W., ed.), pp. 125–142, Clarendon Press

49. Chrulew, M. (2017) Saving the golden lion tamarin. In *Extinction Studies* (Rose, D.B. *et al.*, eds), pp. 49–87, Columbia University Press

50. Jule, K.R. *et al.* (2008) The effects of captive experience on reintroduction survival in carnivores: a review and analysis. *Biol. Conserv.* 141, 355–363

51. Thomas, S. *et al.* (2023) Evaluating the performance of conservation translocations in large carnivores across the world. *Biol. Conserv.* 279, 109909

52. Shine, R. (2010) The ecological impact of invasive cane toads (*Bufo marinus*) in Australia. *Q. Rev. Biol.* 85, 253–291

53. Ward-Fear, G. *et al.* (2020) Predators learning to avoid toxic invasive prey: a study on individual variation among free-ranging lizards. *Behaviour* 157, 1153–1172

54. Sibanda, L. *et al.* (2022) Effectiveness of community-based livestock protection strategies: a case study of human–lion conflict mitigation. *Oryx* 56, 537–545