Letters

Behavioural ecology is not an endangered discipline

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In a recent Opinion article in *TREE*, Caro and Sherman [1] attempt to raise awareness of the supposedly devastating effects that the current conservation crisis will have on the future of behavioural ecology. They predict two problems: (i) many animals with interesting adaptations will go extinct; and (ii) understanding the adaptive values of behaviours will be difficult because anthropogenically modified environments are making those behaviours maladaptive. Although we agree that the conservation crisis is a tragedy in general, and a considerable threat to our profession in particular, we disagree with the notion that it puts the entire discipline of behavioural ecology at risk.

It is indeed rather difficult to study the behavioural ecology of extinct species (but see [2]). However, we do not think that environmental change could render adaptations impossible to study because they become anachronisms. In our opinion, this particular idea is misguided by the erroneous assumption that adaptations are static and remain stable over a long time.

Adaptations increase the fitness of the bearer, and are selected for [3]. There is much discourse about the timescale of evolution, but assuming that this selection process only happened in a distant past is too simplistic. During the past few years, studies have provided evidence for contemporary evolution across all biomes [4], strongly suggesting that, especially in changing environments, adaptations should be considered dynamic.

Furthermore, environmental conditions have always been far from stable. For instance, ice ages have drastically changed habitats in intervals of hundreds of thousand years for the past 3 million years. Human expansion from Africa introduced a new dominant top predator in essentially all habitats of the world between 20 000 and 80 000 years ago. Thus, the notion of a 'pristine' habitat is an oversimplification of environments before the modern age.

Irrespective of the existence of a pristine state, however, most behavioural ecological studies have been successfully conducted on species living in far from natural environments. Studies on birds nesting in boxes provided by humans, for instance, significantly furthered the field. A prime example, the Wytham Woods, where David Lack studied the optimality of avian clutch size, is artificial woodland, created and managed by humans [5].

Moreover, apparently maladaptive behaviours can help identify trade-offs and changing selection pressures. To test experimentally whether certain behaviours are adaptive requires exposing a population to a new environment where a suspected adaptive behaviour would be disadvantageous. Such experiments are logistically often impossible and unethical to conduct on endangered species.

The current anthropogenic changes of habitats over all biomes, albeit devastating, are a historically unique situation, providing exactly the tools and natural experiments needed for the study of adaptations in a natural laboratory. Researchers can use such changes to learn about the behavioural ecology of the affected species [6]. This approach has been taken by many studies on the phenotypic and genetic responses of organisms to global changes (e.g. [7–12]), furthering knowledge of the adaptive potential of species [8–12]. Changes in environmental conditions can thus enable behavioural ecology to discover mechanisms affecting demographic parameters that would otherwise be hard to predict. Such discoveries can equip conservation biology with the tools dearly needed to predict a future environmental scenario.

Young behavioural ecologists, including us, are often driven by an innate curiosity and care about the stunning biodiversity of the world. The future generation of behavioural ecologists is more than eager to contribute essential knowledge to conservation biology. Especially in times of economical instability, we should not discourage them with populistic and pessimistic theses.

Therefore, we agree with Caro and Sherman's notion that non-human life on Earth is facing a bleak future, and we strongly second their call for behavioural ecologists to support conservation biology [1]. At the same time, however, we want to encourage behavioural ecologists to keep up the enthusiasm, and to make the best out of a tragic situation, using global change as an opportunity to learn about adaptations and constraints. Such studies will have a crucial role in the future of behavioural ecology, and can ultimately help researchers to find ways to reconcile human and animal requirements and, thus, prevent species extinction.

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Letters Response

Behavioural ecology cannot profit from unstructured environmental change

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Schroeder and colleagues [1] concur with two key points in our recent Opinion piece on the relationship between behavioural ecology and conservation [2]; namely that, in their words, 'the conservation crisis is a tragedy in general and a considerable threat to our profession in particular' and 'we strongly second their call for behavioural ecologists to support conservation biology.'

However, they dispute our argument that human-induced rapid environmental change obfuscates attempts to understand the evolution and adaptive significance of behaviour. They suggest instead that environments are always changing, that most studies in behavioural ecology have been conducted in changing environments, and that the very idea of a pristine environment is fictitious. However, many important field studies in behavioural ecology were conducted in environments that were substantially untouched (i.e. where anthropogenic perturbations or management actions were unlikely to have affected the traits of interest). For example, contemporary management of Wytham Woods, which was established as a 'Site of Special Interest' in 1950 because 'the ancient woodland copses are undoubtedly of greater age (than AD 1544) and were probably present in Saxon times' [3], is unlikely to have changed aspects of the breeding biology of great tits (*Parus major*) studied by Lack and his successors [4].

Schroeder *et al.* [1] cite studies showing that animals have responded to global warming phenotypically or genotypically, and recent evidence indicates that evolutionary change can proceed more quickly than scientists once imagined [5]. However, the implication that many traits will 'keep up' with the rapidity of environmental changes caused by humans themselves resulting from peripatetic market forces, population migrations and soaring birth rates, seems overly optimistic. If environmental changes are sudden and drastic enough (e.g. because of habitat fragmentation, agricultural conversion, introductions of non-native species, etc.), then behaviours might no longer promote the reproductive success of their bearers. Indeed, there is a growing list of behaviours that have led populations into 'evolutionary traps' [6,7] from which there is no rapid escape via phenotypic plasticity or genetic evolution [8–10], and many other examples in which contemporary behaviours have not been able to respond to environmental changes; in both instances populations were impacted negatively or extinguished outright. In altered landscapes, how long it takes behaviours to return to enhancing individual reproduction is an interesting empirical issue, but uncontrolled environmental change *per se* is not the appropriate experimental paradigm for investigating the costs and benefits of behaviours.

Behavioural ecology has profited enormously from carefully controlled experiments in which a small number of social or ecological factors was manipulated and outcomes were matched to theoretical predictions. This does not mean, however, that environmental changes of any ilk will necessarily provide opportunities to gain useful insights into evolutionary processes. For example, if one finds that a particular behaviour enhances reproductive success in a new environment then this can be interpreted as support for an *a priori* hypothesis about the adaptive significance of the behaviour. However, if one finds that the behaviour does not enhance reproductive success, then the interpretation is unclear: is it because of the

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