Endangered species and a threatened discipline: behavioural ecology

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Behavioural ecologists often see little connection between the current conservation crisis and the future of their discipline. This view is myopic because our abilities to investigate and interpret the adaptive significance and evolutionary histories of behaviours are increasingly being compromised in human-dominated landscapes because of species extinctions, habitat destruction, invasive species, pollution, and climate change. In this review, we argue that many central issues in behavioural ecology will soon become prohibitively difficult to investigate and interpret, thus impeding the rapid progress that characterizes the field. To address these challenges, behavioural ecologists should design studies not only to answer basic scientific questions but also to provide ancillary information for protection and management of their study organisms and habitats, and then share their biological insights with the applied conservation community.

Behavioural ecology under threat

Most biologists realize that we are living in an extraordinary period, a time of mass extinction caused by humans. Population growth and increased per capita demands on resources are the root causes, resulting in over-exploitation, habitat alterations, climate change, invasions by non-native species, and pollution [1,2]. Biologists from many different subdisciplines have recently sought to link these changes to their own scientific specialties, including life histories [3,4], migration patterns [5], morphologies [6], and epidemiology [7].

Behavioural ecologists have been slower to realize how their disciplinary focus and abilities to conduct business as usual will be affected by novel environmental changes. Although some behavioural ecologists are committed conservationists, and certainly theories, methods, and results from studies of behavioural ecology have been usefully applied to conservation and management [e.g. references in 8–12], many behavioural ecologists have yet to appreciate the dangers that the current conservation crisis poses for their own research programmes and their discipline. Loss of species, anthropogenic habitat alterations, and invasive species stymie experimental, observational and comparative approaches to infer both the adaptive significance and evolutionary history of social and reproductive behaviours, primary foci of behavioural ecologists (Box 1). Here we provide a novel justification for linking behavioural ecology and conservation biology by forecasting how anthropogenic ecological changes are liable to reshape specific aspects of behavioural ecology during the 21st Century. We believe that the outlook is grim, and that it would be prudent for behavioural ecologists to make greater individual and concerted efforts to conserve species and habitats to continue making exciting discoveries. Our purpose is not to encourage more ‘conservation behaviour’ (i.e. the application of knowledge of animal behaviour to solve conservation problems [12]), although we regard that as an important endeavour. Instead we argue that behavioural ecology itself is under threat, and that it is in the self-interest of all behavioural ecologists to get more involved in preserving their study organisms and habitats.

Species loss

Loss of species is particularly significant for behavioural ecologists because behaviour leaves no fossil record. When a species goes extinct, its behaviour can be inferred only indirectly. We will never know how the dodo Raphus cucullatus foraged, the significance of the remarkable sexual dimorphism in bill structure of the New Zealand huia Heteralocha acutirostris, whether golden toads Bufo periglenes exhibited behavioural syndromes, or if Tasmanian wolves Thylacinus cynocephalus had helpers-at-the-den. Fossils of extinct species can yield information about morphology, physiology, and even genetic structure (through studies of ancient DNA), but fossils generally reveal nothing about mate choice, parental care, reciprocity, reproductive skew, diseases, kin recognition, communication, personality differences, or UV reflectance (i.e. topics at the forefront of behavioural ecology).

Overall reduction in number of species

Loss of species stymies testing hypotheses about how behavioural traits map onto environmental variables. For example, if the naked mole-rat Heterocephalus glaber had been extinct, we would have thought that eusociality occurred only in termites, ants, some bees, wasps, aphids, and shrimp. We would have been unable to understand that eusociality is not associated exclusively with the genetics, physiology or phylogenetic history of arthropods. The behaviour of naked mole-rats reveals that cooperative breeding and eusociality are convergent social systems
that occur in mammals, birds and arthropods when ecological pressures preclude independent dispersal and reproduction, groups cooperate to forage and defend themselves, and individuals can raise their inclusive fitness sufficiently by helping to rear siblings to compensate forgoing personal reproduction [20].

Loss of species obfuscates attempts to understand the behaviour of remaining organisms. If an important food plant goes extinct, for example, the foraging and territorial behaviour of herbivores and frugivores that depended on it will fail to make adaptive sense. In another example, we can never be sure if the exceptional speed and flight behaviour of pronghorn antelopes Antilocapra americana was a defense against extinct North American cheetahs [21]. The magnitude of this problem will depend on the extent to which the behaviour of the surviving species is flexible. Those that are plastic in their responses to new environments will adapt more rapidly than species whose responses are canalized and in which adaptation depends on the rate of evolutionary change [22,23].

Loss of species precludes use of comparative methods to infer both the adaptive significance and evolutionary history of behaviours. Studies of behavioural adaptations typically include comparisons among phylogenetically related species that differ in aspects of their biology relevant to the questions being asked (e.g. studies of social behaviours of prairie dogs [24] and African mole-rats [25]) or of more distantly related species that share similar ecological niches (e.g. bank swallows Riparia riparia and rough-winged swallows Stelgidopteryx serripennis [26] or rock-dwelling rodents [27]). Extinctions of species deprive such analyses of power and perspective. Reconstructing ancestral characters, tracking phylogenetic signals, and analyzing correlated trait evolution [28] also require comprehensive knowledge of behaviour and morphology of related species. Omission of such species strongly affects outcomes of these analyses unless many variables are examined concurrently. To take one example, the extinction of the quagga Equus quagga (a partially striped equid) and lack of knowledge about its behaviour cloud attempts to understand the adaptive significance of black-and-white striping in equids generally. Studies of sensory bias require inferring female preferences of ancestral species: if clades are depauperate because of extinctions, we might never know if there were latent female preferences that went unexploited, whether new male traits arose via this process [29], or how the coevolution that results from males exploiting female biases and females responding to male exploitation proceeds [30].

Loss of species will be selective not random. Proportions of endangered species differ among animal taxa (Figure 1), with amphibians, mammals and reptiles being disproportionately affected. Numerous path-breaking studies in behavioural ecology were conducted on these taxa, and their accelerating losses will negatively impact the discipline. Consider the following:

Larger species live at lower population densities and are thus more prone to extinction than smaller species [32,33]. Extinctions in the 21st Century will curtail long-term studies of some large mammals and birds [34], jeopardizing our
understanding of patterns of cooperation and competition, life histories and senescence, dispersal, and social cognition. Large-bodied herbivores will encounter novel balances of selection pressures as predators disappear and competition becomes ascendant.

Apex predators are disappearing, and insights derived from studying them are jeopardized. How wild dogs *Lycaon pictus*, lions *Panthera leo*, wolves *Canis lupus*, and killer whales *Orcinus orca* cooperate in hunting and reproduction will no longer be tractable topics of research. Predator avoidance by prey species could be modified or even lost when selection is relaxed [35]. Mechanisms of predator recognition and avoidance disappear at different rates according to modality and species once predators are extirpated, obfuscating attempts to understand behavioural syndromes or trait complexes. Moreover, effects of extinction of one species can ripple through an ecosystem, eventually affecting the behavioural ecology of species far removed trophically and even physically from the species that has been extinguished [36]. The phenomenon of mesopredator release, whereby mid-sized predators flourish in the absence of a top predator, puts increased demands on antipredator defenses of species eaten by mesocarnivores. Once again, this makes inferring the adaptive significance of the behaviour of remaining species problematic.

Primates are in jeopardy. Almost half of the 634 primate species in the world are classified as threatened or endangered on the IUCN Red List [37]. For example, the chimpanzee *Pan troglodytes* population in Gombe Stream National Park has been progressively declining for 40 years [38]. Studies of primate communication [39], cooperation and conflict [40,41], warfare [42,43], infanticide [44], tool use [45] and culture [46,47] have yielded insights into the ecological and social forces that moulded their behaviours. Losses of our closest phylogenetic relatives chip away at our ability to broaden the perspectives that have already been obtained, and to use comparative approaches to investigate the adaptive significance and evolutionary history of our own behaviour.

Amphibians and reptiles are predicted to be lost disproportionately in the 21st Century [48,49; Figure 1], making it more difficult to use the comparative method to study, for example, the evolution of parental care patterns, the trade-off between predation and growth in terrestrial and aquatic environments, how such life history decisions as when to metamorphose and when to begin reproducing are made, and the adaptive significance of environmental versus genetic sex determination.

### Invasive species

Invasive species often prey on or compete with native flora and fauna [50]. Humans have introduced invasive species purposely or inadvertently, and have created opportunities for dispersive invaders to settle by altering native habitats. As a result, native species will progressively live in environments permeated with invasives.

There are many examples of invasive species altering the community structure of native species, such as introduced fishes in California river systems [51], and cane toads *Bufo marinus* and red foxes *Vulpes vulpes* that prey on native species in Australia [52,53]. Plant invasive species can alter habitat structure with ramifications for habitat selection [54] and antipredator behaviour of animals [55]. Invasive species can also cause evolutionary traps [56,57], which...
occur when organisms have behavioural choices, such as between host plants or food sources, but their evolved decision-making rules lead to maladaptive responses in the new environmental circumstance that includes the invader (e.g. native Australian bluetongue lizards *Tiliqua scincoides* that attack cane toads and die from poisoning [58]). Increasingly, behavioural ecologists will be faced with dilemmas about which behaviours are responses to native predators, competitors, parasites or pathogens, which are responses to non-native species, and which are a heterogeneous mix that is not adaptive in either context.

**Habitat loss**

*Loss of habitats generally*

Loss of habitats not only eliminates or confines populations that depend on them, but also affects our ability to understand the breadth of behavioural responses to different environments. This can occur at different spatial scales: across large biomes such as Madagascar, the Hawaiian Islands, and the Caribbean Islands, and also at smaller scales. For example, in some species, helpers-at-the-nest are found only in saturated habitats (e.g. Seychelles warblers *Acrocephalus sechellensis* [59]). If habitat loss results in inflated population densities in remaining habitats, we will be unable to investigate whether cooperative breeding in other birds is facultative, nor will we be able to elucidate the costs and benefits of helping versus dispersal and independent reproduction. Unusually high densities will also alter other behaviours (e.g. territoriality, foraging, extra-pair mating; Box 1), making it difficult to interpret their adaptive significance.

Habitat loss goes hand-in-glove with fragmentation. Increasing fragmentation will alter dispersal behaviours and distances, and favour native species that live in interstices between habitat patches, such as cowbirds *Molothrus ater* and raccoons *Procyon lotor*. In turn, this will select for new and perhaps unexpected behaviours (bizarre movement patterns, foraging, parental, and antipredator behaviours). The importance of these for behavioural ecologists will depend on the extent of habitat fragmentation and the degree to which the crucial behaviour of a study organism is plastic or canalized.

Loss of habitat creates novel combinations of environments in close proximity (e.g. a plowed field where the

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**Figure 2.** Millenium Ecosystem Assessment (2) estimates of the extent of the earth’s biomes that existed prior to significant human impact which were converted by 1950, between 1950 and 1990, and projected losses from 1990 to 2050. Most of the conversion of these biomes is to cultivated systems.
centre of a shrub-steppe community once stood). Formerly adaptive behaviours can become maladaptive in the new setting, another example of an evolutionary trap [60,61]. It is virtually impossible to infer the adaptive significance of the behaviours of a species that is caught in an evolutionary trap and, as habitats are fragmented and lost, more and more species will be affected. Rates at which behaviours realign themselves after being caught in a trap depend on the strength of selection imposed by the trap and the degree to which the behaviours are phenotypically plastic.

Habitat loss shifts our perceptual baseline. Humans have a tendency to accept the ecological conditions and environments they experience from birth as being the ‘normal’ situation (i.e. the one that has prevailed in the area over evolutionary time [62]). In turn, it is reasonable to start by assuming that observed behaviours are adaptive in that environment. A problem arises if the present environment is not actually the environment in which the behaviour evolved; indeed some would argue that this might be true for all species nowadays. In fragmented environments and when novel environmental combinations occur, this assumption will be seriously misleading: many behaviours will be maladaptive due to evolutionary traps or disturbances from which there is no escape [63; Box 1].

Loss of particular habitats

Some habitats are being lost more rapidly than others (Figure 2). Tropical and subtropical dry and moist broadleaf forests, coniferous forests, grasslands, savannas, and shrublands are all predicted to suffer badly in the next 40 years, as well as montane shrublands and grasslands and flooded grasslands and savannas. In the marine realm, coral reefs will be particularly hard hit (Figure 1). These habitat losses will affect species endemic to each biome, in some cases eliminating entire taxonomic groups, again impoverishing exploration of behavioural diversity and weakening the comparative approach. It will also affect investigations of the social and reproductive behaviours of species that remain. For example, inferring the adaptive significance of patterns of foraging, sexuality (protandry, hermaphroditism, bisexuality), and parental care in reef fishes requires detailed cost/benefit analyses of behaviours. But results are only interpretable if the reproductive success that is quantified is evolutionarily relevant reproductive success (i.e. the reproductive success in the environment in which the behaviour under study was moulded).

Change of environments to urban, suburban, agricultural or rangeland habitats

Environmental alterations will result in human-dominated landscapes in which only a subset of species flourish [64]. Many native species do not do well in urban, agricultural, or rangeland habitats. As more habitats are converted, the taxonomic breadth of the remaining species contracts; species with specialized feeding or habitat requirements are especially impacted, and only habitat generalists and omnivores will remain.

Pollution

Environmental pollution affects morphology, physiology and behaviour in many ways. For example, chemical pollution feminizes amphibians [65] and affects vertebrate sexual orientation and homosexuality [66]. Environmental disturbance affects signaling and sexual ornamentation. In urban settings behavioural ecologists’ studies of sexual selection in birds will be obfuscated when females are unable to choose mates based on songs because low frequency traffic noise alters sound transmission [67,68]. In lakes muddied by run off, female cichlid fish can no longer use colouration to choose mates [69]. Over time, this will reduce the breadth of signals produced by males, the criteria that females use to choose among them, and attempts by behavioural ecologists to interpret them. More generally, pollution, be it siltation, noise, chemical effluent, or oil spill has widespread ramifications for all animal behaviours especially those associated with habitat selection, growth and reproduction.

Climate change

There is a growing body of literature on the effects of global warming on geographic ranges [70] and aspects of behav-

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**Box 2. Behavioural ecology in 2100: through a crystal ball**

This is what behavioural ecology might resemble at the dawn of the 22nd Century as a result of the conservation crisis:

1. The general concepts and methodological tools of behavioural ecology will still be in place (e.g. levels of selection, levels of analysis, strong inference, optimality and game-theoretic modeling, evolutionary stable strategies, and cost/benefit analyses).
2. Biodiversity will be reduced, distributed more patchily and limited in extent. Fewer species will exist and comparative analyses will be weakened. If there are any ‘pristine’ habitats left, they will be those that are least accessible and thus exploitable by humans, such as high latitudes and altitudes. Field studies will become more time-consuming and costly, as field sites will be located farther from academic institutions.
3. Some habitats will still be protected in preserves such as national parks and land trusts but they will become increasingly insulated, and heightened recreational demands will likely limit scientists’ abilities to work there effectively.
4. Many long-term studies of animal social and reproductive behaviours will be curtailed or compromised, especially in human-overpopulated habitats. Laboratory-based experimental studies and field studies of common, human commensal organisms will be less affected; however, our ability to assess whether specific behaviours are adaptive or nonadaptive in nature will be compromised.
5. In human-dominated landscapes the behaviours of animals cannot be assumed to be adaptive; this will obfuscate cost/benefit analyses of fitness consequences of behavioural variants.
6. Huge cities, agricultural conversion, and rural restructuring will drive faculty-level behavioural ecologists and their students to incur greater costs (time and money) in pursuing long-term studies of animals in the most natural (least-disturbed) habitats; local research and field trips will be jeopardized.
7. Laboratory studies of domesticated and common species will be unaffected but it will be increasingly difficult to obtain permission to take less common species out of the wild for study.
8. As a consequence of these changes of emphasis, modeling exercises and literature reviews will gain ascendancy in behavioural ecology.
bour that include migration [71] and breeding dates [5] of birds and mammals [72]. In addition, changes in the distribution, abundance, and phenology of important plant resources will probably have effects on ranging, grouping behaviour and intra- and interspecific competition. Some of these behavioural characteristics will change faster than others, resulting in a heterogeneous mixture of matches and mismatches (traps) to the environment.

**Increased human contact**
Contact with humans changes the behaviour of wild species. Some show great wariness initially, whereas others are almost naive in their responses; subsequently, some species habituate and others remain fearful. As a consequence, some become commensals such as Virginia opossums *Didelphis virginiana*, raccoons, coyotes *Canis latrans*, striped skunks *Mephitis mephitis*, and white-tailed deer *Odocoileus virginianus*, whereas others become more shy and reclusive, such as spotted skunks *Spilogale gracilis* and pumas *Felis concolor*. We do not know the genetic or ontogenetic bases of such differences. Regardless, these behavioural changes will alter the community structure of carnivores, herbivores, and omnivores in human-dominated landscapes and will affect the extent of behavioural interactions among the animals themselves as well as differential vigilance to humans’ presence. By 2100 it will be difficult (probably impossible) to locate populations of any species that have not experienced human contact.

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**Box 3. Thinking globally and acting locally: what concerned behavioural ecologists can do**

| Research | Contact chapters of national conservation organizations (e.g. Audubon Society, The Nature Conservancy), regional wildlife societies or Land Trusts and offer to give a presentation and lead a field trip to observe the behaviour of your study species and assess some of the imminent threats to it. |
| Activism | Get involved in national and international attempts to save your species or its taxonomic group. Network with other concerned biologists, and form or join a committee that is attempting to develop habitat- or species-level conservation plans. |
| Politics | (1) Specifically gather data to address the conservation and management of your species and its habitat, in addition to data that address your own behavioural ecology questions and hypotheses. Let conservation questions drive a portion of your research agenda. Plan to write at least one technical paper and one semi-popular article that address the conservation status of your study organism, actual and potential threats to it and its habitat, and make management recommendations. Unique insights derived from closely observing your study organisms can provide important new approaches to long-term preservation. |
| Education | (2) Contact local reserve officials in a practical sense, even if it detracts somewhat from data collection. As examples, determine the best place to put an ecotourism facility for wildlife viewing, one that could raise money to provide alternative livelihoods and fund patrols; install open source software on park office computers, give out copies of your pdf library, pay for spare parts for the only patrol car or boat, or help to fight fires around the national park. |
| Education | (1) Contact local middle- or high-school superintendents and biology department chairs (if your study site is located near an academic institution) to see if any of the science teachers would like you to give classroom presentations. This will heighten awareness about the behavioural biology of your organisms and protecting them and their habitats. Hopefully the students will carry your message home and tell their families and friends about what is happening in their own backyards. This could be complimented with a field trip if your study area is not far from the classroom. |
| Activism | (3) Restructure granting incentives to encourage application of behavioural ecology to conservation problems. For example, publically funded research grants and graduate dissertation programmes, reward senior faculty who have achieved conservation successes, and create endowed lecturerships and visiting professorships to encourage people who address these issues. |
| Activism | (3) Help raise funds for scientific training and capacity building for park officials or local NGOs, thereby furthering the education of local people concerned with wildlife conservation. Either start fund raising yourself, or work with professors and university administrators to get wildlife officials from the developing world to North America or Europe to take courses and study for advanced degrees. |
| Activism | (2) Lobby granting organizations for new research grants and post-doctoral fellowship programmes to encourage studies that will provide supporting data for species and habitat preservation, including information necessary to evaluate candidate species for protection, for example under the Endangered Species Act. |
| Education | (1) Use conservation questions to drive a portion of your research agenda. Plan to write at least one technical paper and one semi-popular article that address the conservation status of your study organism, actual and potential threats to it and its habitat, and make management recommendations. Unique insights derived from closely observing your study organisms can provide important new approaches to long-term preservation. |
| Activism | (1) In your position as a knowledgeable wildlife expert, acquaint local politicians with the unique habitats and organisms that live in their home districts, and provide them with information that will enable them to propose legislation to preserve those habitats and organisms. |
| Politics | (3) Help raise funds for scientific training and capacity building for park officials or local NGOs, thereby furthering the education of local people concerned with wildlife conservation. Either start fund raising yourself, or work with professors and university administrators to get wildlife officials from the developing world to North America or Europe to take courses and study for advanced degrees. |
| Politics | (2) Contact local, state and national wildlife officials to offer assistance. Ask what aspects of behavioural or population biology of your study organism they would find most useful, and how you can effectively cooperate with them to gather relevant information. For example, would they prefer you to survey certain areas for the presence or absence of your study animal and census any new populations you discover? Or do they need information on food or microhabitat preferences, sources of mortality, or anthropogenic threats? Then reformulate your study plans to dovetail more effectively with the needs of the local management community. Meet with these officials regularly to apprise them of your progress, results and ideas, and submit ‘annual reports’ that document your progress in answering conservation and management questions that concern them. |
| Politics | (3) Restructure granting incentives to encourage application of behavioural ecology to conservation problems. For example, publically funded research grants and graduate dissertation awards could be required to include a section on ‘conservation impacts.’ Universities could advance junior faculty who have successfully integrated conservation into their research programmes, reward senior faculty who have achieved conservation successes, and create endowed lecturerships and visiting professorships to encourage people who address these issues. |

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contact, and whose behaviour has not somehow been affected by it.

Conclusion
In a world that is patently disturbed, and as pristine environments that could serve as scientific baselines disappear, it will be increasingly difficult for behavioural ecologists to determine which behaviours are adaptive and which anachronistic. This obstructs analyses of the reproductive costs and benefits, and thus the fitness consequences, of behavioural variants: an essential goal of behavioural ecologists. Similar problems have long bedeviled evolutionary anthropology [73] and are being recognized in ecology [74].

We are surprised, therefore, that any behavioural ecologist remains detached from the realities of the conservation crisis. Behavioural ecology graduate students, postdocs and faculty know that biodiversity is in terrible trouble (many work on species of concern or in places where habitat loss is manifest) yet most have yet to confront the consequences for their own research programmes and discipline (Box 2). Maybe behavioural ecologists find it too depressing to face the reality that the organisms they clearly love are going extinct; or perhaps they fear they will not climb the university ladder if they stray outside their discipline. But more likely, species and habitat losses have not yet touched them deeply enough to motivate action.

We believe this situation must change and quickly if behavioural ecology is to continue to flourish. Some behavioural ecologists would like to help, but they do not know where to begin because the problems seem too big to be tackled alone. An attitude of helplessness leads to disin-terest or even dismissal of conservation problems. Therefore we offer some specific suggestions (Box 3) for how practicing behavioural ecologists can use their expertise to forestall the outcomes that all of us fear. We believe it is important for every behavioural ecologist to contribute to postponing species extinctions for a period long enough to see us through the current human population-explosion-resource-demand bottleneck, hopefully taking us to a time when the world population starts to decline and the pressure on wild populations and habitats diminishes.

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