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Behavioural biology: an effective and relevant conservation tool

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'Conservation behaviour' is a young discipline that investigates how proximate and ultimate aspects of the behaviour of an animal can be of value in preventing the loss of biodiversity. Rumours of its demise are unfounded. Conservation behaviour is quickly building a capacity to positively influence environmental decision making. The theoretical framework used by animal behaviourists is uniquely valuable to elucidating integrative solutions to human-wildlife conflicts, efforts to reintroduce endangered species and reducing the deleterious effects of ecotourism. Conservation behaviourists must join with other scientists under the multidisciplinary umbrella of conservation biology without giving up on their focus: the mechanisms, development, function and evolutionary history of individual differences in behaviour. Conservation behaviour is an increasingly relevant tool in the preservation of nature.

The origins of conservation behaviour

Behavioural biology did not rank among the fields included under the multidisciplinary umbrella of conservation biology when this new science was created in 1985 [1]. Perhaps as a consequence, behavioural study was not incorporated into the first conservation biology textbooks and conservation was not mentioned in the animal behaviour texts of the era [2]. It required another decade for the nascent field of 'conservation behaviour' to coalesce from symposia, workshops and the resulting multi-authored volumes that appeared after the mid-1990s (citations in [3]). Some have suggested that behavioural biologists became interested in conservation only because they anticipated a new source of research funding [3,4], but those of us who were graduate students at the time know the real reason that conservation behaviour arose: in the face of biodiversity loss and widespread habitat destruction, we wanted our science to be relevant to saving the natural world.

Wishing for behavioural biology to be useful to conservation, however, is not evidence that it is. Indeed, some early proponents of conservation behaviour recently seem to have lost their faith in the discipline*. Likewise, I have observed that some aspiring conservation behaviourists are questioning the success of conservation behaviour at integrating with mainstream conservation efforts. Their pessimism is in sharp contrast to my own view: a decade after I co-edited the first book on the subject [5], I am pleased with recent developments in the adolescence of conservation behaviour. After only a decade of existence, it is premature to dismiss the relevancy of the conservation behaviourist to saving biodiversity. Here, I show evidence of the vibrancy of this growing field (Box 1) and then recount how the theoretical framework of conservation behaviourists is already positioning them to help solve the types of conservation issues that will be especially vexing in the coming decades.

Defining conservation behaviour

It is obvious that species-typical patterns of animal movement, feeding and mating must be considered in conservation planning. Thus, the debate over the role of modern animal behaviour studies in conservation is not a question of whether major differences in species comportment (e.g. seasonal migration versus year-round residency) are important to conservation planning. Instead, it is a disagreement over whether the discipline-specific training of animal behaviourists, *sensu stricto*, is a valuable addition to conservation action teams [6]. I have observed two possible reasons why conservation behaviour has not made major in-roads in traditional conservation biology circles: conservation ecologists believe that they already 'do' behaviour, and many think that animal behaviourists work at scales of minor value to protecting entire landscapes, the most cost-effective means of conservation.

Behaviour thinking

On the surface, 'doing' behaviour seems relatively easy. For example, conservation biologists might walk through a forest quantifying territorial vocalizations to census a population of songbirds. Such superficial uses of behavioural biology are no doubt useful, but they, like species-typical behavioural descriptions by natural historians [7], are not conservation behaviour. Conservation behaviour takes advantage of an investigatory framework implicit to all modern animal behaviour studies. This framework is commonly referred to as Tinbergen's 'four questions', because it was first proposed by Nobel-Prize-winning ethologist Niko Tinbergen as a way to guide behavioural research [8]. Tinbergen suggested that we can ask four mutually exclusive questions about any one behaviour by considering both proximate and ultimate explanations for the cause and origin of that behaviour pattern (see Table I in Box 2). Some refer to this use of Tinbergen's framework as 'behaviour thinking', and to

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Box 1. The influence of conservation behaviour is growing

This tenth anniversary of the publication of the first books on conservation behaviour [5,44] is an arbitrary date on which to assess this young discipline's success at integrating with conservation biology. Rather than expecting conservation behaviour to be fully fledged at this point, we should look for signs that it continues to strengthen in terms of training resources, pervasiveness in the published literature, and acceptance by grant-awarding agencies and career mentors. Supportive evidence includes the following.

- Eighty percent of recently published animal behaviour texts address conservation in some fashion [2]. Page content that contains reference to conservation now averages 2% for texts published during the past five years, compared with 0% in the decades before that.
- Conservation behaviour training resources are readily available on the Internet (http://www.animalbehavior.org/Committees/Conservation). It is now easier for aspiring conservation behaviourists (and their mentors) to access background information, including a general bibliography, funding sources and graduate programs. Also available for download is '*The Conservation Behaviorist*', a journal written for both behaviourists and non-scientist decision makers.
- The use of behavioural biology in published conservation studies is not uncommon; in fact, it is growing. Linklater [45] discovered that the percentage of conservation publications that mention behaviour has increased nearly threefold since the conception of conservation behaviour in the early 1990s.
- The EO Wilson Student Conservation Research Grant Award of the Animal Behavior Society (ABS) was created to provide an annual small grant to foster the career development of conservation behaviourists. Conservation grant awardees have studied logging effects on tree shrew mating systems, stream pollution interference with fish communication and dragonfly oviposition requirements as bioindicators of wetland quality. Perhaps more significant than these new conservation behaviour research funds are the types of research that 'regular' student behaviourists are doing. In 2006, 15% of the standard Student Research Awards from the ABS were for projects with conservation themes.

The 'father' of conservation biology, Michael Soulé, said that the new discipline: "should attract and penetrate every field that could possibly benefit and protect the diversity of life" [46]. These demographics suggest that the population of conservation behaviourists is indeed growing.

proximate and ultimate explanations as 'how' and 'why' questions.

Proximate questions about behaviour consider how an individual is able to perform an activity. They ask about the mechanisms within an organism that make it possible for it to behave in a certain way. The proximate causes of behaviour include the sensory and endocrine mechanisms that regulate behaviour. However, we know that these mechanisms can be modified by individual experience; thus, we must consider the proximate origins of behaviour as well (i.e. how learning modifies behaviour).

Ultimate questions about behaviour, on the other hand, ask why animal species have evolved the proximate systems that enable them to behave the way they do. The ultimate cause of a behaviour must explain how it helps the individual survive and reproduce. If we ponder the ultimate origin of that same behaviour pattern, we are examining its evolutionary history by comparing how that behaviour differs across a group of related species. Tinbergen's framework is most easily explained by applying it to a behavioural example (Box 2).

Box 2. Understanding Tinbergen's framework for studying behaviour

Tinbergen's four complementary approaches to studying a behaviour pattern are implicit to modern animal behaviour studies (see Table I). This framework is most easily explained by applying it to an example of human behaviour: automobile drivers stop their cars when a traffic light turns red.

Mechanisms

We can ask how automobile drivers are able to perceive the red colour of the traffic light, the pattern of neural depolarization that allows a decision to be made in the central nervous system and how that decision is conveyed to the muscles that control the placement of the foot on the brake. The problem of 'road rage' suggests that latency to apply the brake may be affected by the hormonal milieu of the driver.

Ontogeny

Humans are not born knowing how to drive an automobile. We can ask questions about how humans go about learning to stop at a red light and how it is that development affects the ability to learn. For example, accident statistics suggest that teenagers and senior citizens may have greater difficulty stopping at red lights than other drivers.

Function

We can investigate why stopping at red lights allows drivers to live longer and reproduce successfully. The legal and financial costs and benefits that contribute to the individual fitness of drivers are worthy of study. We might also consider why some individuals are more likely to cooperate with other drivers in their society.

Phylogeny

An investigation of the history of traffic signals might tell us how responses to red lights have changed over time. In humans, we can look at how populations have independently developed means of making intersections safer. If we compare humans to other species, we might ask how the colour red has evolved as a warning signal.

Table I. Tinbergen's framework for organizing the study of behaviour proposes that any behaviour pattern should be investigated from four complementary perspectives

	Cause	Origin
Proximate	Mechanisms	Ontogeny
Ultimate	Function	Phylogeny

The beauty of Tinbergen's four questions is that they force us to consider multiple, complementary explanations for the same behaviour [9]. In terms of saving biodiversity, this framework is especially effective in situations in which the behavioural adaptations of wildlife are at odds with anthropogenic landscapes [10]. Conservationists might eventually stumble upon the need for knowing both the 'how' and the 'why' of animal behaviour (Box 3), but it would be much more cost effective and time efficient if Tinbergen's framework was applied at the onset of conservation research.

Where does conservation behaviour fit?

It would be preposterous to claim that behavioural biology is the conservation 'cure all'. Behavioural study is neither appropriate nor a priority at all levels of conservation action (Table 1 and [11]). The need for behaviourists will be greatest when we are confronted with the challenge of maintaining animals marooned in protected islands of habitat, isolated in a sea of humanity, and managing

Box 3. Harbour porpoises and gill nets: application of Tinbergen's framework

In 1994[†], Marquez and I used the example of a 'real-world' conservation problem, the drowning of harbour porpoises *Phocoena phocoena* following entanglement in the gill nets of commercial fisherman, to explain how Tinbergen's four questions could guide conservation research. Read and colleagues [47] had called for improved understanding of the behaviour of harbour porpoises around gill nets. Incidental bycatch of harbour porpoises in the US Gulf of Maine groundfish gill net fishery alone averaged over 2000 individuals per year in the early 1990s, more than twice the allowable take rate.

For heuristic purposes, we suggested that behavioural aspects of gill net bycatch research could be approached simultaneously from mechanistic, ontogenetic, functional and phylogenetic perspectives. Revisiting the problem now, it is rewarding to see that anti-entanglement research evolved within Tinbergen's framework.

Harbour porpoises appear to be in the vicinity of nets because nets are placed where porpoise prey are abundant [48]. Making nets from material that is more reflective of porpoise sonar did reduce bycatch significantly, but perhaps only because the nets were stiffer and less likely to entangle the porpoises [49]. Adding acoustic alarms, called 'pingers', to gill nets reduces the bycatch mortality of harbour porpoises [50]. Harbour porpoises show aversive reactions to pinging, including spatial avoidance and increasing respiration rate [51].

Other small cetaceans, however, do not necessarily react the same way [51]. In a field experiment, bottlenose dolphins *Tursiops truncatus* (Figure I) appeared to use fish caught in the gill net as a food source, but dolphin groups were less likely to approach the net's 'zone of vulnerability' when the pingers were activated [50]. There is considerable interest in investigating how these species will react to long-term use of acoustic alarms. Will cetaceans become sensitized to pingers and avoid them more often, or will pingers become a 'dinner bell' of sorts, attracting porpoises and dolphins to pre-caught fish?

Although the gill net responses of relatively few cetaceans have been studied so far, some researchers have hypothesized that vulnerability to natural predators, such as sharks and killer whales *Orcinus orca*, might explain species differences in the efficacy of using acoustic alarms to reduce incidental bycatch mortality.

I do not mean to suggest that these studies are the result of our Society for Conservation Biology poster; these works developed organically from the need to solve the gill net entanglement problem. Nevertheless, this conservation problem demonstrates how *a priori* use of a conservation behaviour framework would foster an efficient conservation research plan [52].

Figure I. Bottlenose dolphins are attracted to the fish caught in commercial gill nets (photo by Jill Frank).

[†]Marquez, M. and Buchholz, R. (1994) An Ethological Framework for Conservation Biology. Poster at the annual meeting of the Society for Conservation Biology, University of Guadalajara, Jalisco, Mexico.

the inevitable conflicts between the daily needs of humans and other animals. It is not pleasant to think of a future in which most of nature is drastically altered by humans, but the reality is undeniable [12].

Global warming

Conservation behaviourists are developing predictive tools for understanding which species in pristine communities will need behavioural management when their habitats are altered by direct and indirect human disturbance. Paz y Miño [13] has termed these circumstances 'behavioural unknowns' (after Myers 'environmental unknowns' [14]). The most pressing of these, perhaps, is the need to understand how the mechanisms, ontogeny, adaptiveness and phylogenetic diversity of animal behaviour will respond to climate change due to global warming. Conservation behaviourists have already begun to develop a body of literature that addresses behavioural responses to rapid climatic alterations (Box 4).

Restoring balance to ecosystems

Other behavioural unknowns may have less to do with how we are destroying habitat and more to do with our attempts to restore ecological integrity to human-altered landscapes. The reintroduction of large carnivores appears to enhance ecosystem biodiversity and stability [15]. Nonetheless, game managers fear that huntable (by humans) prey species will be decimated because of their naiveté after generations without non-human predation. By experimentally investigating the anti-predator responses of ungulates to predator cues before and after carnivore reintroduction, Berger [16] found that prey typically return to 'normal' anti-predator strategies within one generation of carnivore return. If politically feasible, conservation behaviour data such as these will be used to support the repatriation of carnivores so that balanced ecosystems are restored.

Ecological prediction is a mainstay of traditional conservationists [17]. Game theory, and other skills in the behaviourist's toolbox that take advantage of individual differences in behaviour, are currently being used to anticipate the population consequences of management options [18]. In addition to predicting how animals will respond to anthropogenic disturbances, animal behaviourists are influencing conservation management directly.

Conservation behaviourists in action

To date, the contributions of conservation behaviourists are much more than theoretical. Conservation behaviourists are already involved in hands-on efforts to restore and protect animal species. Here, I briefly review some recent contributions of note.

Species reintroduction

Although the future of biodiversity is in the wild, captive breeding of endangered species is sometimes an irreplaceable component of the conservationist's toolbox [11,19]. Conservation behaviourists have concentrated on two important aspects of captive propagation of endangered species: preventing 'captive selection' (i.e. maladaptive heritable changes in behaviour), and behavioural training

Table 1. Behavioural biology is relevant to multiple conservation contexts

Conservation context	Conservation tool	Example of use
Preventing biodiversity loss	Reserve design[a]	[37]
	Ecosystem management[b]	[15]
	Population viability analysis[b]	[43]
Compromises with economic development	Sustainable use[b]	[29]
Species and habitat restoration	Field recovery of endangered species[a]	[23]
	Captive breeding and reintroduction[a]	[20]
	Ecosystem restoration[a]	[16]

[a]Tools with current behaviour usage.
[b]Tools that will need more behaviourist input as habitat degradation continues (after Beissinger [11]).

Box 4. Etho-conservation tackles global warming

The weather systems of the Earth are expected to become more extreme, perhaps suddenly and with great spatial heterogeneity, owing to the atmospheric retention of heat energy from anthropogenic 'greenhouse gas' production. How animals might react to climate change is one of the many 'behavioural unknowns' caused by environmental degradation [13] that is being investigated using Tinbergen's four questions.

Mechanisms

Cactus-living *Drosophila* species might respond to climate change via selection on the timing of their active period in the circadian clock mechanism [53]. By becoming active at cooler times of the day, they are able to avoid deleterious exposure to heat extremes. The physiological stress responses of vertebrate organisms are likely to be dependent on individual differences in social status and the social function of dominance in that species [31,54].

Ontogeny

Culturally determined foraging movements of sperm whale *Physeter macrocephalus* clans might make some song clans predictably susceptible to changes in ocean-current-dependent food sources [55]. For species with temperature-mediated sex determination, such as turtles and crocodilians, behavioural commitment to reusing traditional nest sites will impede adaptive population-level responses in these long-lived animals. For example, if global warming occurs as forecast, modelling suggests that natal site philopatry by egg-laying painted turtles will condemn them to producing such biased sex ratios that the population becomes inviable [43].

Function

Species with poor mobility might experience rapid evolutionary behavioural adaptation in response to micro-climatic divergence. For example, wood frog tadpoles in shaded, cool ponds appear to evolve adaptive thermal preferences quickly [56]. Populations in warmer sun-lit ponds, however, seem to lack growth-benefiting thermal preferences, suggesting that global warming would cause meta-population sinks with predictable localized patterns of species extirpation. Hawksbill turtle *Eretmochelys imbricata* females might be able to adjust to a hotter climate through existing preferences for tree-shaded beach nesting sites. Unfortunately, beach deforestation may prevent this endangered species from avoiding climate-induced biased sex ratios [57].

Phylogeny

Sexual selection may have an impact on the response of animals to climate change. The degree of advancement of spring migration in birds is associated with the strength of female choice across species [58]. Colonizing warmer habitats appears to release energetic constraints on sexual selection in dark-eyed juncos *Junco hyemalis* [59]. The relaxation of cold climate extremes might select against isolating mechanisms, such as reproductive diapause in mustelids [60].

and management to maximize post-release survival of reintroduced individuals.

Often, captive conditions impose different selection pressures on animal genomes than natural selection, resulting in behaviour that is advantageous to the survival and reproduction of individuals in captivity, but maladaptive should they be reintroduced to the wild. For example, captivity selects for aggressive behaviour in place of foraging behaviour in breeding colonies of the endangered butterfly splitfin fish *Ameca splendens* [20]. Behaviourists are helping to modify aquaculture programs to produce fish that will forage rather than fight when released to their restored habitat.

In other cases, the protected nature of captive environments might allow genetic release from directional selection. The escape behaviour of captive-bred oldfield mice *Peromyscus polionotus*, for example, is never subjected to selection by owls, stoats, snakes or any of the predators that normally threaten the survival of free-living rodents. As a result, they have long escape latencies that would make them highly susceptible to predators in the wild [21]. By considering the genetic mechanisms underlying variation in behaviour, McPhee and Silverman [22] conclude that we need not abandon reintroduction of such individuals. Their solution is to simply use the variance in escape behaviour to recalculate the number of released animals sufficient to ensure a surviving nucleus of breeders. By understanding the genetic mechanisms underlying behaviour, conservation behaviourists are able to provide release and survival estimates that are more realistic. This would thus engender more reasonable expectations and cost planning by wildlife managers and political decision-makers, and more patience for success from the general public.

Similarly careful behavioural preparation of captive-raised animals will lessen animal welfare concerns over the poor survival of individuals released to the wild for conservation purposes. Anti-predator training of captive-reared prairie dogs *Cynomys ludovicianus* appears to increase survival upon reintroduction [23]. But the value of behavioural manipulation is not limited to potential prey species. Poor attention to the social management of African wild dog *Lycaon pictus* groups during 'soft' releases to the wild might explain several costly reintroduction failures [24]. If individuals are chosen to minimize dominance conflicts among members of the released wild dog pack, the reintroduced animals are more likely to behave cooperatively and hopefully survive to reproduce.

Conservation behaviour and natural populations

There are two major areas of inquiry in which 'behaviour thinking' is already being applied to the conservation of wild populations: improving population viability by adaptively managing individual survival and reproductive success in isolated populations, and identifying and managing deleterious effects of ecotourism.

Managing survival and reproduction

Re-establishing prairie dog populations in protected areas is important to ecosystem functioning [25], and is crucial to efforts to establish a prey base to grow viable populations of the highly endangered black-footed ferret *Mustela nigripes*. Behaviourist Debra Shier took advantage of existing behavioural information on the adaptive nature of kin groups to demonstrate experimentally that translocating entire wild prairie dog families achieves conservation goals more successfully and efficiently than moving unrelated animals [26]. The red-cockaded woodpecker *Picoides borealis* is another endangered US species that has benefited from a behaviourist's understanding of kin recognition mechanisms. Wallace and I showed that, by exchanging nestlings between nesting cavities at an age young enough that parents had not yet learned to identify their offspring, we could overcome genetic isolation in a fragmented habitat without reducing survivorship of translocated individuals [27].

Behaviourists have shown how evolutionary conflicts among individual animals can give us insight into management methods that would not be apparent to a traditionally trained wildlife ecologist or conservation geneticist. When it comes to population viability, larger population size is usually better. Unfortunately, small populations do not always have room to grow. A case in point is the threatened Cuban iguana *Cyclura nubile* population confined to the US Naval base at Guantanamo Bay, Cuba. In the absence of opportunities to increase the overall lizard population, Alberts *et al.* [28] showed how the negative impact of male dominance on population-wide genetic variation (N_e) could be overcome through behavioural management. Temporarily removing dominant males allowed other adult males to obtain mates.

Sustainable ecotourism

Ecotourism, the other doyen of sustainable-use advocates, must also consider the behaviourally mediated impact of human disturbance on population viability. Descriptive behavioural studies are likely to find that wildlife change their behaviour in response to human visitors, but that changes in behaviour are not necessarily bad for the animal under observation. For example, although foraging brown bears *Ursus arctos* alter their feeding activities so that they can be vigilant in the presence of tourists, this behavioural change has no apparent effects on body condition [29]. Therefore, human disturbance probably does not translate into reduced survival and lower population viability in this case. Nesting Magellanic penguins *Spheniscus magellanicus* appear to habituate to frequent tourists, but previously undisturbed colonies are markedly stressed by the arrival of human visitors [30]. Because stressed animals are likely to experience tradeoffs in reproductive investment or survival [31], opening new colonies to tourism is not recommended without careful determination of the human activities that cause the most stress to nesting penguins. The complexity of the interspecific and intraspecific responses of wild animals to anthropogenic and natural stressors benefits from being managed in a conservation behaviour framework.

Should conservation behaviour conform to the emphases of conservation biology?

I think the only way that behavioural biology makes sense for conservation is if we retain our unique perspective on animal diversity. The ecologists that helped found the Society for Conservation Biology [32] did not abandon island biogeography theory to work in conservation; they applied the concept to the habitat islands that are nature reserves. Likewise, population geneticists did not ignore Hardy–Weinberg equilibrium to promote the conservation of bottlenecked populations; rather, they found ways to inform us of the practical importance of theoretical genetics. Conservation behaviourists are conservation biologists; we should be constructively critical of endangered species recovery plans [33]. Decisions are often made with very little or faulty evidence. For example, decisions to allow habitat destruction in the dwindling range of the endangered Florida panther *Puma concolor coryi* were based on questionable evidence and the illogical opinion of one researcher that this subspecies is a forest obligate (for a shocking review, see [34]).

It has become a conservation platitude of sorts that conservation behaviourists must "translate behavior into currencies relevant to conservation at large spatial scales" [11]. But conflicts with large carnivores and other species of potential harm to humans attract much popular press and political interest. It is the young panther that disperses 350 miles [34] or the few African elephants *Loxodonta africana* that invade villages or kill rhinos [35,36] that threaten to scuttle goodwill for conservation, not the average behaviour of the population. It is ridiculous to suggest that individualistic responses of animals are unimportant to conservation.

Conservation behaviourists will rise to the challenge of the important discoveries being made at the interface of conservation ecology and genetics. For example, Riley and colleagues [37] recently used microsatellite analysis combined with radiotelemetry to discover that carnivore territories tend to pile up at habitat edges along an automotive freeway in California, USA. The intense social challenges faced by individual bobcats *Lynx rufus* and coyotes *Canis latrans* attempting to disperse through the gauntlet of territories concentrated near large roadways accentuated the limits on gene flow imposed by the physical barrier of the road itself. Populations on either side of the highway show evidence of genetic differentiation as a result. The problem of 'territory piling' [37] along roadways is one well suited to Tinbergen's framework. These crowded carnivores should expect a visit from some local conservation behaviourists [38].

The next step

Caro's [3] charges of irrelevancy levied against conservation behaviour are genuine, but not unique to our field. There are problems with the application of any science to public policy. Academic scientists get caught up in grant writing, hypotheses testing and data collection, whereas conservation practitioners need practical advice today [39]. The reverse is also true; conservation monitoring programs often take on a life of their own and do not achieve conservation objectives [40].

Nearly 100 years ago, conservationist William T Hornaday [41] declared: "We will endeavor to avoid the discussion of academic questions, because the business of conservation is replete with urgent practical demands". I believe that it is this sort of concern, that there is an opportunity cost to the 'theoretical' concerns of conservation behaviour, that has led some of my colleagues to retreat from conservation behaviour. Instead, they must come to realize that we approach a time of desperate need for applied behaviourists. One need only look at costly efforts to recover species listed under the US Endangered Species Act [42] to see that, although all is not lost, all is not well either. Wildlife managers have stopped many endangered species from going extinct, but few species have recovered sufficiently to be de-listed. We can improve conservation management decisions. The behaviour of individual animals matters to conservation. The growing pains of conservation behaviour are not symptoms of dysfunction, but rather positive signs of a thriving adolescence. Conservation behaviour is relevant right now and the time is ripe for the conservation behaviourist to make a difference.

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