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REVIEW

The importance of behavioural studies in conservation biology

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ABSTRACT

The exciting research developments in animal behaviour over the last two decades have had a negligible impact on conservation. I list 20 subjects in which the study of animal behaviour can make a significant contribution to conservation. Behaviour may in itself be worth conserving. I also suggest how behavioural ecologists could become more involved in conservation.

Conservation is an excellent subject for research by those interested in behaviour. As well as obviously being important in its own right, the solving of conservation problems is often intellectually stimulating and conservation helps ensure the persistence of subjects for future behavioural research.

In view of the exciting research developments in animal behaviour, it is surprising that this subject has made a negligible contribution to conservation biology. In Table 1, I have summarized the subjects of 229 papers from the 1996 volume of *Animal Behaviour* and 97 from *Conservation Biology*. There is a complete lack of papers in *Animal Behaviour* that directly relate to conservation. Although nine papers in *Conservation Biology* include an aspect of behaviour in the title, most of the behavioural papers in that journal are descriptive (but still useful) studies of subjects such as the use of corridors and changes in time budgets in response to human disturbance. It is remarkable that current conservation seems to make so little use of the revolution in behavioural ecology of the last 20 years. There is little use of modern developments in subjects such as game theory, sperm competition, cultural evolution, learning or breeding systems.

Similarly, at the latest (1997) International Ethological Conference there was little evidence from the talks or poster sessions of a real interest in answering conservation problems (1.6%: nine out of 577 of the papers related to conservation). Students seem keen to study conservation, there are increasing amounts of money available to study conservation, there are books and there have been conferences linking the two subjects (Ulfstrand 1996; Clemmons & Buchholz 1997; Caro, in press; Gosling & Sutherland, in press), I doubt that editors and conference organizers show a prejudice against conservation papers or talks, yet there is a clear gap between the two subjects.

It is remarkable that the animal behaviour community seems to have shown so little interest in conservation, unlike the population biology or genetics community. I think one problem is that those studying animal behaviour do not believe they have an important role to play in conservation biology. I also suspect that the priorities are to remove the prejudice amongst those studying animal behaviour that conservation is dull and not intellectually challenging and remove the prejudice amongst conservation biologists that animal behaviour is of little relevance and, if really necessary, can be studied without any background in the subject.

Table 1. Classification of subjects of research papers in the journals *Animal Behaviour* and *Conservation Biology* in 1996

	Journal	
Subject	*Animal Behaviour*	*Conservation Biology*
Conservation	0	88
Behaviour	229	0
Conservation and behaviour	0	9

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If most animal behaviour research were directed at applied problems, such as conservation biology, the subject could well be less exciting and develop more slowly conceptually. It would, however, seem appropriate that a reasonable percentage (say 10%) of papers in journals and talks at meetings should have applied implications. Furthermore, there are likely to be increasing calls to justify our research funding and it would be useful to be able to point to practical applications.

HOW BEHAVIOURAL STUDIES CAN HELP CONSERVATION

I list 20 areas in which I believe that the study of animal behaviour should be providing a major contribution to solving conservation problems. This is not intended to be an exhaustive list: I have concentrated on those areas in which behavioural studies could make a substantial contribution to a subject area.

Small Population Extinctions

Small populations decline and go extinct for many reasons, some of which are behavioural. For example, there may be members of each sex present in the population yet they fail to breed successfully. The Allee effect (Allee 1931) describes such a decline in population growth rate at low population sizes, but the behavioural component of this has attracted little research. For example, it would be useful to know if species with communal displays, such as leks, are most susceptible to small population extinctions. Small populations of plants could also experience reduced pollination as a result of changes in the behaviour of pollinators. Very small populations may experience greater predation as a result of reduced vigilance or group defence. Some species are more likely to breed in the presence of conspecifics (Reed & Dobson 1993). The obvious implication of this research is that it may then be possible to find ways of reducing extinction risk and to identify the risks of allowing a population to become small.

The fate of small populations may also be linked to sexual selection. Studies of the fate of populations of introduced birds in Tahiti and Oatu (McLain et al. 1995) and in New Zealand (Sorci et al., in press) showed that the probability of extinction was higher if the species was sexually dichromatic. This can be interpreted in terms of exaggerated ornamentation or coloration that promotes reproductive success also reducing survival (Lande 1980; Sutherland & De Jong 1991) thus potentially reducing the population size or growth rate.

An understanding of the manner in which the sex ratio changes with population density and environmental conditions will also have implications. For example, Komdeur et al. (1997) showed considerable distortions of the sex ratio of Seychelles warblers, *Acrocephalus seychellensis*, in response to differences in habitat. Helpers are usually females. On good quality territories, helpers increase the reproductive success of their parents and 87% of young are females. On poor territories helpers reduce their parents' success and only 23% are females. Phenomena such as these must greatly alter the extinction probabilities.

Mating Systems and Inbreeding Depression

The level of inbreeding depression will depend upon the level of homozygosity, which is in turn related to the effective population size, which in turn is related to the mating system (Seal 1985). Understanding the relationship between breeding system and inbreeding depression will help us to understand when inbreeding depression is likely to be a problem. There is also the possibility of manipulating the social system to alter effective population size.

Species Isolation

Species diversity obviously depends upon species remaining genetically isolated and whether this happens often depends upon the details of the behaviour. Seehaussen et al. (1997) showed that in Lake Victoria recently increased turbidity, as a result of deforestation and agricultural practices, constrains the colour vision of cichlid fish, thus interferes with mate choice and so blocks reproductive isolation. Eutrophication leads to a community of low species diversity, few colour morphs and dull-coloured fish.

Hybridization between native and nonindigenous species is becoming a widespread problem (Simberloff 1998). Two species may hybridize such that the native species disappears through introgression, as is the case with the introduced ruddy duck, *Oxyura jamaicensis*, in Europe mating with the native white-headed duck, *Oxyura leucophela*. Alternatively the hybrid fetus may abort or the resulting offspring may be infertile resulting in a reduction in fertility. For example, the introduced American mink, *Mustela vison*, is greatly affecting the reproduction of the European mink, *Mustela lutreola*, as the hybrid fetus aborts and the female loses a breeding season (Rozhnov 1993).

If a pair of species will hybridize, then the consequence for each species will greatly depend upon the details of mating behaviour and mate choice. In the cases described above, the white-headed duck females seem to prefer males of ruddy ducks to conspecifics and because the American mink males reproduce earlier the female European mink mates disproportionately with them (Simberloff 1998). Thus the behavioural details determine the severity of the problem.

Dispersal in Fragmented Populations

Habitat fragmentation is a major conservation issue. As a habitat becomes more fragmented, it becomes increasingly unlikely that a patch will be recolonized after local extinction. A major issue in understanding the consequences of fragmenting habitats on populations or metapopulations is the behaviour of dispersing individuals. If an individual can search an infinite area then any patch can be located, but with a more realistic assumption of restricted search, patches will be left unoccupied even though there are also individuals that fail to find patches. In the heated debate about northern spotted owls, *Strix occidentalis caurina*, between foresters and conservationists, the crucial issue was the dispersal behaviour of young owls and how they find patches (Harrison et al. 1993).

There is a clear need for more work on how dispersing animals search, sample and select patches. The need for corridors is widely argued (e.g. Hobbs 1992; Simberloff et al. 1992) but it may also be important to discourage individuals from dispersing (see Minimum Area Necessary for Reserves below) by understanding the factors that influence dispersal in that particular species (e.g. Kuussaari et al. 1996; Sutcliffe & Thomas 1996).

Dispersal behaviour is also likely to determine the rate and direction of spread of diseases. Diseases may persist as metapopulations with local extinction within small host populations followed by recolonization (Finkenstadt & Grenfell 1998), or may spread through populations that may be too small to retain them, as in the morbillivirus that swept through the seals in European waters and then disappeared (Swinton et al. 1998). In both cases the dynamics depend upon the rate with which susceptible individuals come into contact with infected individuals which will depend greatly upon dispersal.

Predicting the Consequences of Environmental Change

It is clearly important to be able to predict what will happen to animal populations as a result of current or future environmental changes. An advantage of understanding the behavioural decisions made by individuals is that it is possible to predict their behaviour in novel environments such as those resulting from environmental change. If the ecological response is simply measured, then if the environment changes it has to be remeasured. With models based on behavioural decisions, it is then possible to examine the consequences of habitat loss, habitat fragmentation or changes in mortality (Goss-Custard & Sutherland 1997).

Predicting the consequences of environmental change is best understood in relation to the pattern of density dependence (Sutherland 1996a). Understanding the negative feedback occurring on the feeding grounds, such as that resulting from depletion or interference (Goss-Custard et al. 1995a, b), or within breeding behaviour, resulting from territorial behaviour or social rank (Kokko & Sutherland, in press) makes it possible to understand the response to environmental change (Sutherland 1996a, b).

Understanding the breeding system and social behaviour may also improve predictions of environmental change; for example, a rapid turnover of pride male lions, *Panthera leo*, as a result of shooting or disease, will result in increased infanticide as the new males join the pride (Packer et al. 1988) and thus may depress reproductive output and even stop recruitment (Caro & Durant 1995).

Reducing Predation

Introduced predators have led to many extinctions and native predators may create local problems. Conservationists are thus often keen to reduce the effects of predation. One solution is simply to reduce the numbers of predators but this is often ineffective (Côté & Sutherland 1997) and for native predators there may also be conservation implications of such measures. There are also often ethical and welfare problems with killing predators. There are thus calls for nonlethal means of reducing predation.

The suggested solutions include manipulating the behaviour of the predators (for example by aversive conditioning) or manipulating the behaviour of victims (for example by training them to change nest sites). Simple approaches include understanding the predator's behaviour and then manipulating the habitat, for example by creating barriers of habitat that it dislikes crossing or making predation less easy by changing the vegetation height or placing feeders near to cover (Hinsley et al. 1995). Another approach is to find deterrents such as high-frequency sounds or distasteful chemicals. Avery & Decker (1994) showed that once fish crows, *Corvus ossifragus*, had eaten eggs treated with distasteful chemicals they then avoided other treated eggs. A more subtle approach is to train animals to associate the unpleasant response with the prey itself. Aversive conditioning using electrified human dummies has been successful in reducing predation by tigers, *Panthera tigris*, on humans (Sanyal 1987). Four captive red foxes, *Vulpes vulpes*, were given pheasant, *Phasianus colchicus*, meat treated with 17α ethinyloestradiol: all four ate their familiar food when this was provided a few hours later but all avoided untreated pheasant meat each time they were tested over the subsequent year (Cowan et al., in press). Field testing of such methods has produced mixed results, however (Cowan et al., in press) and there is even the possibility that introducing the predator to the prey could increase predation risks. Should not the research on learning behaviour be having a greater input here?

By contrast, conservation practices may inadvertently increase predation. There is evidence that removing the horns from black rhinos, *Diceros bicornis*, in an attempt to reduce poaching results in increased predation of their calves (Berger 1993; but see Loutit & Montgomery 1994 and Berger & Cunningham 1994).

Retaining Cultural Skills

The success of release programmes of captive-bred or translocated animals depends to a large extent upon their behavioural skills. Thus captive-bred golden lion tamarins, *Leontopithecus rosalia rosalia*, lacked the ability to recognize food or predators in the wild and even lacked basic locomotory skills (Beck et al. 1991). There is a clear need to ensure that introduced animals acquire these skills. One example involved training rufous hare-wallabies, *Lagorchestes hirsutus*, to recognize predators by squirting them with a water pistol whenever a stuffed predator on a trolley was pulled across the cage from a box (McLean et al. 1994). Whooping cranes, *Grus americana*, have been fed using human hand puppets and when older taken out in the cranes' environment with humans in crane costumes. The humans also had a tape recorder with contact calls and also alarm calls which were played in response to dangers. The release programme was a success with the birds joining their wild relatives and migrating (Horwich 1989).

Cultural evolution seems to be a great, largely unexplored area in animal behaviour despite the pioneering work of Cavalli-Svorza & Feldman (1981). There are clearly considerable opportunities for theoretical, field and laboratory studies on how ideas originate, are transmitted and are subject to selection. A better understanding of cultural evolution would have considerable consequences for conservation

Behavioural Manipulations

Many conservation projects involve trying to manipulate behaviour. The world population of black robins, *Petroica traversi*, was once reduced to five individuals including just one breeding pair. A key aspect of the success of the project to retrieve the population was the realization that it was possible to transfer the eggs to Chatham Island tits, *Petroica macrocephala chatemensis*, who would then rear them (Butler & Merton 1992).

There is a scheme to alter the migration route of the lesser white-fronted goose, *Anser erythropus*, so that it winters in the Netherlands rather than southeastern Europe, where they tend to get shot (Essen 1991). This scheme involves a population of captive barnacle geese, *Branta leucopsis*, which breed in Stockholm Zoo but winter in the Netherlands. The barnacle geese are taken to Lapland where they nest and are then given lesser white-fronted geese eggs. The lesser white-fronted geese then fly with the barnacle geese foster parents to the Netherlands. Next spring the barnacle geese return to Stockholm Zoo and the lesser white-fronted geese return to Lapland where they have paired with conspecifics and bred.

My third example illustrates how behaviour can hinder manipulations. A reserve was created and managed on the island of Islay, Scotland, with a major aim of attracting barnacle geese. Although the reserve was managed in a manner attractive to the geese, they increased in number faster elsewhere on the island than inside the reserve! The answer to this paradox is that young geese return with the adults to the wintering area and are site faithful with the result that those in a wintering area tend to be related and from a similar breeding location (Percival 1991). It just so happened that the breeding area from which the birds wintering on the reserve came had a series of years with poor breeding success.

The success or failure of many conservation schemes thus depends upon a detailed understanding of the animals' behaviour.

Release Schemes

Many release schemes fail for behavioural reasons in addition to the problem of losing cultural skills outlined above. For example, Soderquist (1994) studied release programmes of the bush-tailed phascogale, *Phascogale tapoatafa*, and showed that if males and females were released together, the males dispersed and so the females could not find a mate. Release schemes in which females were released first, so they could create a home range, followed by the release of males who joined the females, were much more successful. An understanding of social systems and dispersal behaviour should allow animal behaviourists to provide recommendations as to how release schemes should be organized.

Rufous hare-wallabies kept in cages 10–15 m long tend to run for a similar distance after disturbance once released in the wild (McLean 1997). Identifying and rectifying such behavioural problems is clearly important if release schemes are to be a success.

Habitat Requirements of Species of Conservation Concern

Conservationists need far more information on the habitat requirements of species of conservation concern. Much of this is behavioural in terms of diet choice, home range, social system and breeding behaviour. For example, altitudinal migrations can be important (Powell & Bork 1995) and these need to be understood when designing reserves or conservation policies. Many species rest in a habitat of low predation risk or their habitat use is constrained by the threat of predation.

Understanding the behaviour of seed dispersers and pollinators is also important to predicting the consequences of their decline on plant populations. For example, there are considerable concerns about the over-exploitation of fruit bats (Cox et al. 1991) and the declines in pollinators (Buchmann & Nabhan 1996).

Minimum Area Necessary for Reserves

Small areas obviously usually contain small populations and these are more likely to go extinct through genetic, stochastic or demographic processes. This will depend upon home range, social behaviour and dispersal. For example, Thomas & Hanski (1997) quantified the extent to which butterflies disperse and thus wander out of areas. Small areas are unlikely to sustain populations because of the high emigration rate resulting from the high perimeter relative to the area. The silver-studded blue, *Plebejus argus*, is a weak disperser and the minimum area for survival was calculated at 0.05 ha while the silver-spotted skipper, *Hesperis comma*, disperses more readily and was estimated to require about 0.7 ha (Thomas et al., in press).

Carnivores often go extinct even in very large protected reserves. This can be attributed to persecution along the perimeter. As a result, the calculated minimum reserve size for persistence is correlated with the home range (Woodroffe & Ginsberg, in press). Some species with large home ranges, such as wild dogs, *Lycaon pictus*, require huge reserves, estimated at about 3600 km^2. Although the mechanism differs between the silver-studded blue and the wild dog and the scale is enormously different (0.05 ha versus 3600 km^2), the principle that individuals wandering from the area are likely to be lost to the population is the same.

Captive Breeding

Captive breeding often fails as a result of behavioural problems (Synder et al. 1996) and behavioural issues are accepted as important in the management of captive species (Gibbons et al. 1995). Can all the work on mate choice, sperm competition and social behaviour provide more of an input? For example, how important is it to allow mate choice? Grahn et al. (in press) suggest that male animals in zoos should be allowed to display within arenas and their popularity to females used as one criterion for selecting which males should be used for mating. Domestic pigeons, *Columba livia*, produce more eggs, earlier eggs, and a higher proportion of fertile eggs if allowed choice (Klint & Enquist 1981) and pairs of Mauritius kestrels, *Falco punctatus*, paired in captivity are less successful than those with free choice in the wild (Jones et al. 1995). Although there are a number of possible interpretations of these results it suggests that it is worth considering the benefits of choice. The combination of free mate choice and strong preferences, however, may conflict with the goals of genetic management.

Reproductive Behaviour and Reproductive Physiology

Zoos have for some time monitored and manipulated reproductive behaviour and physiology (Durrant 1995). The opportunity for using such techniques for wild populations under extreme risks of extinction seems underexplored.

Trade-offs in Habitat Preferences

The trade-off between predation risk and food supply is well known (e.g. Milinski 1985). A similar approach can be used to evaluate the importance of human disturbance by assessing the level of food depletion in relation to the disturbance (Gill et al. 1996). Pink-footed geese, *Anser brachyrhynchus*, eat a lower percentage of their food, sugar beet, in fields close to a road. By measuring this trade-off between depletion of the food supply and disturbance it is also possible to quantify the consequences of the disturbance on the population (Gill & Sutherland, in press). Such behavioural titrations could be used for other conservation issues such as the response to pollution.

Measuring Deteriorating or Stressful Conditions

Environmental conditions may seem poor to us, for example as a result of pollution or human interactions, but it is useful to have independent measures of the effect these conditions actually have. These measures may involve developmental asymmetry, hormonal, physiological or behavioural studies. Developmental asymmetry has been shown to occur in the presence of deviant climatic conditions, food deficiency, pesticides and parasitism and is related to growth, fecundity and survival (Møller 1997). The issue as to whether red deer, *Cervus elaphus*, find it stressful to be chased by dogs for up to 30 km before being killed was resolved by hormonal and physiological studies (Bradshaw & Bateson, in press). Studies of behaviour can be used as a biomonitor for degradation such as pollution in the case of fish, yet only a tiny percentage of papers on pollution and behaviour use this approach (Jones & Reynolds, in press).

Census Techniques

The majority of census techniques make assumptions about the behaviour of the animals. The extent to which individuals call, variation in likelihood of being seen or caught, and the movement pattern all greatly influence the accuracy of census techniques (Greenwood 1996). McGregor et al. (in press) have shown that the standard method of censusing corncrakes, *Crex crex*, on the basis of the location of calls underestimated the population by 20–25% as a result of the birds moving shorter distances in better habitats. In addition, birds on average called less frequently than the radiotracked birds on which the technique was based, but the technique assumes their calling frequency is the norm. This may be because these individuals were caught by being attracted to tapes. Hofer & East (1991) recalculated population estimates for the spotted hyaena, *Crocuta crocuta*, from earlier data but adjusted for the proportion visible and on the home range in relation to season and commuting behaviour outside the home range. They showed that allowing for this behaviour is important in providing realistic estimates.

Exploitation

The pattern of exploitation is influenced by the behaviour of both the hunters and the prey. Thus Cree Indians showed greater selectivity with increasing encounter rates, owing to their acquisition of snowmobiles, in accordance with optimal foraging theory (Winterhalder 1981) and the distribution of fishing and whaling boats has been explained in terms of the ideal free distribution (Abrahams & Healy 1990; Whitehead & Hope 1991).

Probably the most spectacular recent case of overexploitation is the Atlantic cod, *Gadus morhua*, off eastern Canada. This was the world's largest cod stock yet was closed to commercial fishing in 1992 causing considerable unemployment. The explanation of this process given by Hutchings (1996) closely resembles the buffer effect, that at low densities individuals concentrate in the best site but at higher densities they are more widely distributed (Brown 1969). Hutchings showed that as the total cod population declined, the fish aggregated in the preferred areas and the density there changed little owing to movement from the less preferred areas. The persistent ease of capture in these restricted areas of high density gave the fishing community confidence in continuing to exploit the stock at a high rate and confidence to criticize the predictions of total population collapse being produced by the scientists.

Increase in Human Population

The overwhelmingly important problem to humanity and biodiversity is the increase in human population. This is partly related to the reproductive decisions made by individuals, which is, of course a central issue in behavioural ecology. For example, as expected from life history theory, humans have fewer children only when the mortality risks are low, variation in economic conditions is low but the cost of each child is high (Mace, in press). These factors thus greatly influence when the demographic transition takes place.

Discounting

Discounting is the widespread preference for benefits now rather than in the future (it is different from inflation, which is the change in the value of money). Discounting explains why we have to pay the bank extra if we spend money before we earn it or why the bank will pay us if we defer spending.

Discounting has considerable consequences for conservation. In considering the choice between a long-term gain, such as reduced soil erosion or the capacity to exploit a population sustainably for long periods, or a short-term gain such as deforestation, high discount rates will favour short-term considerations. It will also favour the overexploitation of long-lived species as the long-term benefits of a sustainable yield, once discounted, may be less than the short-term benefit of overexploiting (Clarke 1990).

Both animal behaviourists and economists study discounting (Henderson & Sutherland 1996). Animal behaviourists tend to study the choice between rewards associated with different delays and show that the discounting is hyperbolic. This is true for studies of humans and other animals. By contrast, economists rightly argue that if the discounting rate is constant each year then discounting must be exponential. With exponential discounting, the current value of benefits in the long term, such as sustainable use of slow-growing species, is negligible. Under hyperbolic discounting these current values are considerably higher. There is, however, some evidence that economists, while claiming to use exponential discount rates, adjust them to fit hyperbolic discounting by using lower rates for longer time periods (Henderson & Sutherland 1996).

Increasing Conservation Concern

Many of the huge number of television programmes and magazine articles on wildlife are based on research on behavioural ecology, although this is not usually acknowledged. Such popular interest in behavioural ecology must have had a considerable role in encouraging interest in conservation thus producing concern and a further generation of biologists.

CONSERVING BEHAVIOUR

In some cases the behaviour itself is of interest and worthy of conservation (Dingle et al. 1997). Famous examples include the migration of birds and wildebeest, the winter roosts of monarch butterflies, *Danaus plexippus*, Japanese macaques, *Macaca fuscata*, bathing in the snow in hot springs or tree-dwelling lions in Uganda and Tanzania.

The importance of conserving genetic variation is well accepted. Perhaps we should also consider the importance of conserving cultural variation such as the variation in bower design within a single species of bowerbird and the variation in tool use between populations of chimpanzee, *Pan troglodytes* (Boesch 1996).

CONSEQUENCES OF ENVIRONMENTAL CHANGES ON BEHAVIOUR

I have concentrated upon the implications of behaviour for conservation. This may also be turned on its head to consider the implications of environmental change on behaviour itself. An example is the Arcto-Norwegian population of cod, which spawn in the Lofoten Islands, where they have been fished for at least 1000 years, and winter in the Barents Sea. One probable consequence of this traditional fishery on the breeding individuals is that they bred at an unusually high age. This population has experienced considerable increased mortality prior to breeding as a result of a new trawler fishery in the Barents Sea. As a result very few individuals now survive to the age at which they used to breed. This selection pressure has no doubt been responsible for the change in behaviour such that they now migrate to the Lofoten Islands at a much younger age (Law & Grey 1989).

Blackcaps, *Sylvia atricapilla*, in central Europe used to migrate to southwest Europe but as a result of global warming and feeding at bird tables in Britain there have been genetic changes so that 7–11% of the birds now migrate northwest to Britain (Berthold et al. 1992). Elsewhere (Sutherland, in press) I list 43 examples of species that have altered their migration routes, usually apparently as a response to environmental change. I also give 14 examples of species that appear to take a nonoptional route. If this interpretation is correct then it supports the results of genetic models that populations may sometimes fail to respond to environmental change and whether or not they evolve may depend upon the details of the genetics for that particular system (Dolman & Sutherland 1995).

WHAT SHOULD BEHAVIOURAL ECOLOGISTS DO?

I would like to encourage some of those involved in animal behaviour research to become involved in conservation biology. My concern is that this plea could be deleterious to the conservation cause. Using conservation money for behavioural studies with little feedback to conservation is worse than doing nothing. Similarly, it is not helpful to carry out studies on rare species on the justification that the information is useful, if in reality it is of little use, especially if the study causes disturbance. I suggest that those interested in applying behaviour to conservation talk to practising conservation biologists to ensure that their proposed work is useful.

Useful conservation work does not have to involve studying rare species. One option is to study the behaviour of species that are closely related to those of conservation concern, for example, methods for transferring and releasing the fluttering shearwater, *Puffinus gavia*, were studied in order to gain the experience necessary to release much rarer species (Bell 1994). A second possibility, if one is interested in studying the consequences of rarity, is to study those species that are globally common but rare in the study area. A third option is to seek generalities that will be of wide application to conservation problems, such as how dispersing individuals select patches, how cultural traits are retained or how the behaviour of predators can be manipulated.

As a by-product of their field studies, ethologists often become the expert in the habitat requirements, ecology and status of a species. They also often have expertise on the ecology and changes in land use of an area. This information is often of great use for conservation biologists and should be provided to those that will use it.

Finally, we should not get carried away with self-importance. Many conservation problems require simple nonbehavioural solutions. I believe we have a moral obligation to contribute to effective conservation using whatever approach is most appropriate.

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References

Abrahams, M. V. & Healy, M. C. 1990. Variation in the competitive abilities of fishermen and its influence on the spatial distribution of the British Columbian salmon troll fleet. *Canadian Journal of Fisheries and Aquatic Sciences*, **6,** 1116–1121.

Allee, W. C. 1931. *Animal Aggregations: A Study in General Sociology*. Chicago: Chicago University Press.

Avery, M. L. & Decker, D. E. 1994. Responses of captive fish crows to eggs treated with chemical repellents. *Journal of Wildlife Management*, **58,** 261–266.

Beck, B. B., Rapaport, L. G. & Wilson, A. C. 1994. Reintroduction of captive-born animals. In: *Creative Conservation: Interactive Management of Wild and Captive Animals* (Ed. by P. J. S. Olney, G. M. Mace & A. T. C. Feister), pp. 265–286. London: Chapman & Hall.

Bell, B. 1994. Translocation of fluttering shearwaters: developing a method to re-establish seabird populations. In: *Reintroduction Biology of Australian and New Zealand Fauna* (Ed. by M. Serena), pp. 143–148. Chipping Norton: Surrey Beatty & Sons.

Berger, J. 1993. 'Costs' and short-term survivorship of hornless black rhinos. *Conservation Biology*, **7,** 920–924.

Berger, J. & Cunningham, C. 1994. Phenotypic alterations, evolutionary significant structures and rhino conservation. *Conservation Biology*, **8,** 833–840.

Berthold, P., Helbig, A. J., Mohr, G. & Querner, U. 1992. Rapid microevolution of migratory behaviour in a wild bird species. *Nature*, **360,** 668–670.

Boesch, C. 1996. Three approaches for assessing chimpanzee culture. In: *Reading into Thought* (Ed. by A. Russon, K. Bard & S. Parker), pp. 404–429. Cambridge: Cambridge University Press.

Bradshaw, E. & Bateson, P. P. G. In press. Animal welfare and wildlife conservation. In: *Behaviour and Conservation* (Ed. by L. M. Gosling & W. J. Sutherland). Cambridge: Cambridge University Press.

Brown, J. L. 1969. The buffer effect and population regulation in tit populations. *American Naturalist*, **103,** 347–354.

Butler, D. & Merton, D. 1992. *The Black Robin: Saving the World's Most Endangered Bird*. Oxford: Oxford University Press.

Buchmann, S. L. & Nabhan, G. P. 1996. *The Forgotten Pollinators*. Washington Island Press.

Caro, T. In press. *Behavioural Ecology and Conservation Biology*. Oxford: Oxford University Press.

Caro, T. & Durant, S. 1995. The importance of behavioural ecology for conservation biology: examples from Serengeti carnivores. In: *Serengeti II* (Ed. by A. R. E. Sinclair & P. Arcese), pp. 451–472. Chicago: University of Chicago Press.

Cavalli-Svorza, L. L. & Feldman, M. W. 1981. *Cultural Transmission and Evolution*. Princeton, New Jersey: Princeton University Press.

Clarke, C. W. 1990. *Mathematical Bioeconomics*. New York: J. Wiley.

Clemmons, J. R. & Buchholz, R. (Eds) 1997. *Behavioural Approaches to Conservation in the Wild*. Cambridge: Cambridge University Press.

Côté, I. M. & Sutherland, W. J. 1997. Removing predators to protect bird populations: does it work? *Conservation Biology*, **11,** 395–405.

Cowan, D. P., Reynolds, J. C. & Gill, E. L. In press. Manipulating predatory behaviour through conditioned taste aversion: can it help endangered species. In: *Behaviour and Conservation* (Ed. by L. M. Gosling & W. J. Sutherland). Cambridge: Cambridge University Press.

Cox, P. A., Elmguist, T., Pierson, E. D. & Rainey, W. E. 1991. Flying foxes as strong interactors in South Pacific island ecosystems: a conservation hypothesis. *Conservation Biology*, **5,** 448–454.

Dingle, H., Carroll, S. P. & Loye, J. E. 1997. Conservation, behaviour, and 99% of the world's biodiversity: is our ignorance really bliss. In: *Behavioural Approaches to Conservation in the Wild* (Ed. by J. R. Clemmons & R. Buchholz), pp. 72–92. Cambridge: Cambridge University Press.

Dolman, P. M. & Sutherland, W. J. 1995. The response of bird populations to habitat loss. *Ibis*, **137,** 538–546.

Durrant, B. S. 1995. Reproduction in mammals: captive perspectives In: *Conservation of Endangered Species in Captivity* (Ed. by E. F. Gibbons Jr, B. S. Durrant & J. Demarest), pp. 331–354. Albany, New York: State University of New York Press.

Essen, L. V. 1991. A note on the lesser white-fronted goose *Anser erythropus* in Sweden and the result of a re-introduction scheme. *Ardea*, **79,** 305–306.

Finkenstadt, B. & Grenfell, B. 1998. Empirical determinants of measles metapopulation dynamics in England and Wales. *Proceedings of the Royal Society of London, Series B*, **265,** 211–220.

Gibbons, E. F., Jr, Durrant, B. S. & Demarest, J. 1995. *Conservation of Endangered Species in Captivity*. Albany, New York: State University of New York Press.

Gill, J. A. & Sutherland, W. J. In press. Role of behavioural decision making in predicting the consequences of human disturbance. In: *Behaviour and Conservation* (Ed. by L. M. Gosling & W. J. Sutherland). Cambridge: Cambridge University Press.

Gill, J. A., Sutherland, W. J. & Watkinson, A. R. 1996. A method to quantify the effects of human disturbance on animal populations. *Journal of Applied Ecology*, **33,** 786–792.

Gosling, L. M. & Sutherland, W. J. In press. *Behaviour and Conservation*. Cambridge: Cambridge University Press.

Goss-Custard, J. D. & Sutherland, W. J. 1997. Individual behaviour, populations and conservation In: *Behavioural Ecology* (Ed. by J. R. Krebs & N. B. Davies), pp. 373–395. Oxford: Blackwells.

Goss-Custard, J. D., Caldow, R. G., Clarke, R. T., Durell, S. E. A. le V dit & Sutherland, W. J. 1995a. Deriving population parameters from individual variations in foraging behaviour I. Empirical game theory distribution model of oystercatchers *Haematopus ostralegus* feeding on mussels *Mytilus edulis*. *Journal of Animal Ecology*, **64,** 265–276.

Goss-Custard, J. D., Clarke, R. T., Durell, S. E. A. Le V. dit., Caldow, R. W. G. & Ens, B. J. 1995b. Population consequences of winter habitat loss in a migratory shorebird. I. Estimating model parameters. *Journal of Applied Ecology*, **32,** 337–351.

Grahn, M., Langefors, Å & von Schantz, T. In press. The importance of mate choice in improving viability in captive populations. In: *Behavioural Ecology and Conservation Biology* (Ed. by T. Caro). Oxford: Oxford University Press.

Greenwood, J. J. D. 1996. Basic techniques. In: *Ecological Census Techniques* (Ed. by W. J. Sutherland), pp. 11–110. Cambridge: Cambridge University Press.

Harrison, S., Stahl, A. & Doak, D. 1993. Spatial models and spotted owls: exploring some biological issues behind recent events. *Conservation Biology*, **7,** 950–953.

Henderson, N. & Sutherland, W. J. 1996. Two truths about discounting and their environmental consequences. *Trends in Ecology and Evolution*, **11,** 527–528.

Hinsley, S. A., Bellamy, P. E. & Moss, D. 1995. Sparrowhawk *Accipiter nisus* predation and feeding site selectivity by tits. *Ibis*, **137,** 418–420.

Hobbs, R. J. 1992. The role of corridors in conservation: solution or bandwagon. *Trends in Ecology and Evolution*, **7,** 389–392.

Hofer, H. & East, M. L. 1991. Population dynamics, population size, and the commuting system of Serengeti spotted hyenas. In: *Serengeti II* (Ed. by A. R. E. Sinclair & P. Arcese), pp. 332–363. Chicago: University of Chicago Press.

Horwich, R. H. 1989. Use of surrogate parental models and ager periods in a successful release of hand-reared sandhill cranes. *Zoo Biology*, **8,** 379–390.

Hutchings, J. A. 1996. Spatial and temporal variation in the density of northern cod and a review of hypotheses for the stock's collapse. *Canadian Journal of Fisheries and Aquatic Sciences*, **53,** 943–962.

Jones, C. G., Heck, W., Lewis, R. E., Mungroo, Y., Slade, G. & Cade, T. 1995. The restoration of the Mauritius kestrel *Falco punctatus* population. *Ibis*, **137,** 173–180.

Jones, J. C. & Reynolds, J. D. In press. Effects of pollution on reproductive behaviour of fishes. *Reviews in Fish Biology and Fisheries*, **7,** 1–29.

Klint, T. & Enquist, M. 1981. Pair formation and reproductive output in domestic pigeons. *Behavioral Processes*, **6,** 57–62.

Kokko, H. & Sutherland, W. J. In press. Optimal floating strategies: consequences for density dependence and habitat loss. *American Naturalist*.

Komdeur, J., Daan, S., Tinbergen, J. & Mateman, C. 1997. Extreme adaptive modification in sex ratio of the Seychelles warbler's eggs. *Nature*, **385,** 522–525.

Kuussaari, M., Nieminen, M. & Hanski, I. 1996. An experimental study of migration in the Glanville fritillary butterfly. *Journal of Animal Ecology*, **85,** 791–801.

Lande, R. 1980. Sexual dimorphism, sexual selection and adaptation in polygenic characters. *Evolution*, **34,** 292–307.

Law, R. & Grey, D. R. 1989. Evolution of yields from populations with age-specific cropping. *Evolutionary Ecology*, **3,** 343–359.

Loutit, B. & Montgomery, S. 1994. The efficacy of rhino dehorning: too early to tell. *Conservation Biology*, **8,** 923–924.

Mace, R. In press. Human populations and behaviour. In: *Behaviour and Conservation* (Ed. by L. M. Gosling & W. J. Sutherland). Cambridge: Cambridge University Press.

McGregor, P. K., Peake, T. M. & Gilbert, G. In press. Communication behaviour and conservation: the application of sound science. In: *Behaviour and Conservation* (Ed. by L. M. Gosling & W. J. Sutherland). Cambridge: Cambridge University Press.

McLain, D. K., Moulton, M. P. & Redfearn, T. P. 1995. Sexual selection and the risk of extinction of introduced birds on oceanic islands. *Oikos*, **74,** 27–34.

McLean, I. G. 1997. Conservation and the ontogeny of behaviour. In: *Behavioural Approaches to Conservation in the Wild* (Ed. by J. R. Clemmons & R. Buchholz), pp. 132–156. Cambridge: Cambridge University Press.

McLean, I. G., Lundie-Jenkins, G., Jarman, P. J. 1994. Training rufous hare-wallabies to recognise predators. In: *Reintroduction Biology of Australian and New Zealand Fauna* (Ed. by M. Serena), pp. 177–182. Chipping Norton: Surrey Beatty & Sons.

Milinski, M. 1985. Risk of predation taken by parasitised fish under competition for food. *Behaviour*, **93,** 203–216.

Møller, A. P. 1997. Developmental stability and fitness: a review. *American Naturalist*, **149,** 916–932.

Packer, C., Herbst, L., Pusey, A. E., Bygott, J. D., Hanby, J. P., Cairns, E. J. & Borgerhoff Mulder, M. 1988. Reproductive success of lions. In: *Reproductive Success: Studies of Individual Variation in Contrasting Breeding Systems* (Ed. by T. H. Clutton-Brock), pp. 363–383. Chicago: University of Chicago Press.

Percival, S. M. 1991. The population structure of Greenland barnacle geese *Branta leucopsis* on the wintering grounds on Islay. *Ibis*, **133,** 357–364.

Powell, G. V. N. & Bork, R. 1995. Implications of intratropical migration on reserve design: a case study using *Pharomachrus mocinno*. *Conservation Biology*, **9,** 354–362.

Reed, J. M. & Dobson, A. P. 1993. Behavioural constraints and conservation biology: conspecific attraction and recruitment. *Trends in Ecology and Evolution*, **8,** 253–256.

Rozhnov, V. V. 1993. Extinction of the European mink: ecological catastrophe or a natural process? *Lutreola*, **1,** 10–16.

Sanyal, P. 1987. Managing the man-eaters in the Sundarbans Tiger Reserve of India: case study. In: *Tigers of the World: The Biology, Biopolitics, Management, and Conservation of an Endangered Species* (Ed. by R. L. Tilson & U. S. Seal), pp. 427–434. Park Ridge, New Jersey: Noyes Publications.

Seal, U. S. 1985. The realities of preserving species in captivity. In: *Animal Extinctions: What Everyone Should Know* (Ed. by R. J. Hodge), pp. 71–95. Washington D.C.: Smithsonian University Press.

Seehausen, O., va Alpen, J. J. M. & Witte, F. 1997. Cichlid fish diversity threatened by eutrophication that curbs sexual selection. *Science*, **277,** 1808–1811.

Simberloff, D. 1998. Small and declining populations In: *Conservation Science and Action* (Ed. by W. J. Sutherland), pp. 116–134. Oxford: Blackwells.

Simberloff, D., Farr, J. A., Cox, J. & Wehlman, D. W. 1992. Movement corridors: conservation bargains or poor investments. *Conservation Biology*, **6,** 493–504.

Soderquist, T. R. 1994. The importance of hypothesis testing in reintroduction biology: examples from the reintroduction of the carnivorous marsupial *Phascogale tapoatafa*. In: *Reintroduction Biology of Australian and New Zealand Fauna* (Ed. by M. Serena), pp. 156–164. Surrey Beaty & Sons.

Sorci, G., Møller, A. P. & Clobert, J. In press. Plumage dichromatism of birds predicts introduction success to New Zealand. *Journal of Animal Ecology*.

Sutcliffe, O.L. & Thomas, C. D. 1996. Open corridors appear to facilitate dispersal by ringlet butterflies (*Aphantopus hyperantus*) between woodland clearings. *Conservation Biology*, **10,** 1359–1365.

Sutherland, W. J. 1996a. Predicting the consequences of habitat loss for migratory populations. *Proceedings of the Royal Society Series B*, **263,** 1325–1327.

Sutherland, W. J. 1996b. *From Individual Behaviour to Population Ecology*. Oxford: Oxford University Press.

Sutherland, W. J. In press. Evidence for flexibility and constraint in migration systems. *Journal of Avian Biology*.

Sutherland, W. J. & De Jong, M. C. M. 1991. The evolutionary stable strategy for secondary sexual characters. *Behavioral Ecology*, **2,** 16–20.

Swinton, J., Harwood, J., Grenfell, B. T. & Gilligan, C. A. 1998. Persistence thresholds for phocine distemper virus infection in harbour seal *Phoca vitulina* metapopulations. *Journal of Animal Ecology*, **67,** 54–68.

Synder, N. F. R., Derrickson, S. R., Beissinger, S. R., Wiley, J. W., Smith, T. M., Toone, W. D. & Miller, B. 1996. Limitations of captive breeding in endangered species recovery. *Conservation Biology*, **10,** 338–348.

Thomas, C. J. & Hanski, I. A. 1997. Butterfly metapopulations. In: *Metapopulation Biology* (Ed. by I. A. Hanski & M. E. Gilpin), pp. 359–386. London: Academic Press.

Thomas, C. J., Baguette, M. & Lewis, O. T. In press. Butterfly movement and conservation in patchy landscapes. In: *Behaviour and Conservation* (Ed. by L. M. Gosling & W. J. Sutherland). Cambridge: Cambridge University Press.

Whitehead, H. & Hope, P. L. 1991. Sperm whalers off the Galapagos Islands and in the Western North Pacific, 1830–1850. *Ethology and Sociobiology*, **12,** 147–161.

Winterhalder, B. 1981. Foraging strategies in the boreal forest: an analysis of Cree hunting and gathering. In: *Hunter-gatherer Foraging Strategies* (Ed. by B. Winterhalder & E. A. Smith), pp. 66–98. Chicago: University of Chicago Press.

Woodroffe, R. & Ginsberg, J. R. In press. Ranging behaviour and extinction in carnivores: how behaviour affects species vulnerability. In: *Behaviour and Conservation* (Ed. by L. M. Gosling & W. J. Sutherland). Cambridge: Cambridge University Press.

Ulfstrand, S. 1996. Behavioural ecology and conservation biology. *Oikos*, **77,** 183.