The behaviour–conservation interface

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In the past four years, there have been several attempts to apply studies of animal behaviour to conservation. Knowledge of individuals’ behaviour has the potential to alter understanding of how populations fare in fragmented habitats, the responses of populations to exploitation and disturbance, disease susceptibility, effective population size, captive breeding and reintroduction efforts, and population monitoring and modelling. It can even be useful in understanding human conservation actions.

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Enormous advances in understanding animal behaviour have yet to penetrate attempts to conserve animal populations. First, conservation biology has successfully emerged from population ecology (incorporating measures of birth, death, immigration and emigration), from population genetics (using genetic variation and genetic population structure) and from systematics (relating on traditional and molecular techniques to reconstruct phylogenies) without incorporating much animal behaviour. Second, any use of behavioural knowledge has never been expounded by the conservation biologist. Third, there is a conceptual divide between the study of variation in behaviour of individuals and the study of the response of populations to deterministic and stochastic events. Finally, there is a view among ethologists and behavioural ecologists that conservation biology lacks theoretical backbone. So, is there any conceptual or practical point in bridging these two disciplines? Three recent edited volumes, five reviews and a special edition of a journal totalling 106 authors think that there is1–3. Although none of them is suggesting that behavioural study has the answer to all conservation problems1, there is a breaking wave of enthusiasm for linking these fields. Here, I discuss this interdisciplinary interface by demonstrating how practical and conceptual issues in conservation biology can benefit from a knowledge of individual behavior and pin-point where future research would be most profitable.

Fragmented habitats

The principal cause of species’ extinctions is habitat loss and fragmentation5. Conservation biologists have developed metapopulation dynamics to predict populations’ responses to fragmentation2 and these require assumptions about ranging behaviour and individual dispersal distances. For instance, colonization of unoccupied habitats, ‘rescue’ effects of low density patches, and source-sink effects depend on factors such as dispersal distance, the influence of landscape on individual movements and conspecific attraction. There are several studies with data on dispersal distances and a few on environmental and social factors affecting movement and settlement patterns that could be fed into metapopulation models or used in practical management plans. In general, however, few empirical data on ranging and dispersal have been collected in fragmented habitats (but see Ref. 13) leaving controversial models, such as those for the spotted owl (Strix occidentalis), open to challenge by opposing interests4. Reserve design has logged conservation biology for years, initially in the form of the ‘single large or several small’ debate, and now in regard to connectivity between reserves or habitat patches5. If we knew more about species’ ranging...
patterns within and between years, we would know how effective reserves of differing size could be in protecting viable populations of different species. Woodroffe and Ginsbergl, for example, have argued that the wide ranging of many large carnivore species results in substantial human-induced mortality, even when such species live in protected areas. In regards to corridors, conservation biologists have developed a list of possible responses that include failing to traverse occupied territories, treating the whole corridor as edge habitat, or ‘settling in’ rather than moving through a corridorl, but these have rarely been evaluated using data on movements and habitat selection in individual animals. Clearly, study of individual movement patterns has an important role here.

Responses to exploitation and disturbance

Conservation biology is also concerned with population responses to exploitationl. Classic economic models of exploitation, particularly of marine species, usually treat individuals as equivalent, but individuals differ in reproductive potential. For example, most mammals are polygynous with many males failing to breed. Modelling shows that the mating system has dramatic effects on population growth rate under certain forms of exploitation. For instance, in monogamous species in which males help rear offspring, a population shows low intrinsic rates of increase if males are removed, and, in inexcitable species, male off take leads to increased rates of offspring mortality when new males move in to fill vacanciesl (but see Ref. 20). Moreover, heavy exploitation of one sex, such as male African elephants (Loxodonta africana) by poachersl, or sperm whales (Physeter macrocephalus) by whalersl, can make it difficult for females to find males, especially if they are choosy about their partners. These sort of ‘Allee effects’ have gained prominence in demographic models but empirical data on how low density affects group-related antipredator behaviour, settlement patterns or mate choice have still to be collected systematically (but see Ref. 8) and put into models. Exploration of one species can also lead to behavioural changes in another. Bergerl investigated antipredator responses of moose (Alces alces) in areas from which wolves (Canis lupus) and grizzly bears (Ursus horribilis) had been removed. He found that moose rapidly reduce their reliance on auditory and olfactory cues associated with these predators, which lead to prey population reductions if managers reintroduce natural predators in the future.

There is also a growing interest in behavioural responses to anthropogenic disturbance in the form of agricultural practice, traffic or tourism, and even management programmes themselves (Box 1). Rather than direct exploitation, Sutherlandl has spearheaded the idea that a population’s growth rate is intrinsically linked to animal movements and the strengths of density-dependent breeding and mortality in those patches. Depending on the species, very high levels of disturbance can lead to large population declines within disturbed sites but need not affect the total population size much if density dependence is weak. If density dependence is strong, total population size can decline at slight levels of disturbance. When high levels of displacement occur with little disturbance, survival rates must be weakly density dependent because the reproductive costs of movement are small; paradoxically, managers often characterize such species as flighty and believe their populations to be most sensitive to disturbance. Conversely, species in which individuals remain despite heavy disturbance are doing so to avoid costs of competition in heavily populated undis turbed sites elsewhere; their populations could be most affected by disturbance. Although there is a huge wildlife management literature on behavioural responses to humans, consequences on population growth rates are almost completely unknown and need attention. Sutherlandl provides formal behaviourally based models on which to predict these responses.

Spread of disease

Disease has potentially devastating consequences because it can reduce large or small populations to just a few individuals, leaving them vulnerable to other forms of stochasticity. Recent examples of disease spreading quickly through mammal populations include canine distemper in black-footed ferrets (Mustela nigripes), morbilliviruses in Serengeti lions (Panthera leo) and phocine distemper in grey seals (Halichoerus grypus) and Mediterranean monk seals (Monachus monachus). However, in contrast, disease can be employed as a conservation tool for eliminating populations of damaging exotics because an infected individual is particu larly likely to transmit infection to conspecics if they are aggregatedl as well by individual movements. In addition, the spread of disease is likely to be slower in those species in which individuals avoid mating with unhealthy males because physical contact with infected individuals will be reduced and disease is less likely to be transmitted to offspring. Spread of disease is also likely to be influenced by dispersal between patches and across landscapes. Unfortunately, such behavioural factors have received little attention from modellers working on populations suffering from disease.

Effective population size

Effective population size (Ne), which approximates the number of breeding individuals, can be used to determine the rate of loss of genetic heterozygosity from a population. The number of breeding individuals is strongly influenced by mating system, population and age structure,
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and depends on paternity and maternity certainty. For example, the magnitude of extrapair copulations, manifest in so many bird species, must affect $N_e$. The challenge is to see how extrapair copulation rates change at low densities, where concerns about $N_e$ are greatest. In theory, $N_e$ is influenced by the sex ratio of breeding individuals, but extrapair copulation success caused the greatest reduction in $N_e$. For all species, demographic data on reproductive success, behavioural data on dominance, and genetic data on paternity are fundamental to measuring $N_e$.

Captive breeding and reintroductions

Since animals were first bred in zoos, managers and keepers have paid close attention to behavioural factors that promote successful reproduction. Now that zoological institutions play an important role in species conservation, behavioural knowledge is shared through journals such as Zoo Biology and taxon-specific meetings. For instance, enriched environments, access to conspecifics, and even proximity to particular heterospecics are routine concerns of many modern zoos.

Similarly, reintroducing captive animals into the wild relies informally on behavioural knowledge. Early attempts at predicting reintroduction success and failure listed a host of basic behavioural variables, such as group size, feeding niche and activity patterns, but specific loci have recently emerged: anti-predator behaviour and sexual imprinting. First, captive-born individuals of certain species might fail to recognize or escape from predators when released. Considerable work has gone into aversive conditioning of captive individuals using predators, behaviourists to tell conservation biologists how best to census populations. For instance, the assumption that individuals remain on feeding or breeding territories between censuses can be explored using demographic records.

Population viability analyses (PVAs) are used to predict the fate of small populations. They require data on age at first breeding, interbirth intervals, sex ratio and age-specific mortalities. PVAs can be constructed using mean values of these life-history variables but are made far more accurate using variances that are principally derived from long-term studies of individuals (e.g. Ref. 39). Spatially explicit PVAs can incorporate habitat preferences, dispersal dynamics and even the behaviour of the exploiters. For example, animals that live in groups, or that have regular movement patterns, will be easier to kill than solitary or nomadic species and this will change the cost-benefit equation for hunters. None-the-less, paucity of knowledge about changes in prey behaviour resulting from human exploitation, and subsequent changes in hunting practice, still constrains the realistic and predictive power of exploitation models.

Human behaviour

Conservation biology differs from much of biology in that it views human influence as a major factor in the fate of animal and plant populations. Until recently, such influence was couched in terms of economic or sociopolitical factors, with economic models treating the resource as changing only numerically. But the propensity of people to exploit resources will depend in part on both the behaviour of the animal resource and the behaviour of the exploiters. For example, animals that live in groups, or that have regular movement patterns, will be easier to kill than solitary or nomadic species and this will change the cost-benefit equation for hunters. None-the-less, paucity of knowledge about changes in prey behaviour resulting from human exploitation, and subsequent changes in hunting practice, still constrains the realistic and predictive power of exploitation models.

Evolutionary anthropologists and psychologists are now looking at the social and ecological circumstances under which people conserve or exploit populations. To do this, behavioural ecologists have to start looking at the social, ecological and economic circumstances under which decisions to conserve or exploit animal and plant populations are made.

Making behavioural studies more relevant

Despite a long list of connections between behaviour and conservation issues, most are still only plausible possibilities rather than links based on empirical data or formal models. As such, they will fail to impress conservation theorists or managers. Behavioural researchers need to start developing these links explicitly, instead of just talking about them. The main impasse they face is the length of time it takes to collect behavioural data on problems that demand rapid attention because of habitat loss or species exploitation; in particular, long-term demographic studies are the richest in conservation data but take years to yield results.

If behavioural research is to become more central to conservation, not only will it need more people working at the interface, but the nature of research will also have to change. Most importantly, it will need to focus on aspects of behaviour that are most likely to influence vital rates or susceptibility to exploitation or perturbation. Any aspect of social behaviour that affects age at first breeding (e.g. reproductive suppression), interbirth intervals (e.g. dominance), offspring and adult sex ratios (e.g. age or dominance), and juvenile and adult survival (e.g. intraspecific competition) will influence population growth rates and therefore PVA models and, to a lesser extent $N_e$, and so be interesting to conservation biologists.

Behavioural comparisons between populations living in pristine and anthropogenically altered habitats will yield data on behavioural flexibility and response to environmental change. In addition, behavioural biologists may need to work on endangered populations more often and perhaps on several species simultaneously because conservation focuses increasingly on communities and habitats rather than single species. Behavioural studies will also have to be conducted over shorter time frames, will need to target conservation questions earlier in the study, and
basic demographic data will need to be published more quickly given that such data are so central to PVA. Finally, re-
search needs to be conducted on the ontogeny of sexual and antipredator behaviour in species that are set to be
reintroduced.

On a personal note, behavioural field-
workers need to work more closely with local people to determine their exploitation practices and their attitudes to species and habitats. More productive ways to foster conservation locally are required. Behavioural fieldworkers will also need to publish in the popular press as well as in scientific journals in order to increase public awareness.

In short, although it is optimistic that behavioural biologists are at last thinking about conservation problems, their role of goodwill must be backed up by empiri-
cal findings on relevant topics if conserva-
tion biologists are going to treat behav-
ior as a useful tool in their attempts to
stem species’ losses.

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