MAINTAINING BEHAVIOURAL DIVERSITY IN CAPTIVITY FOR CONSERVATION: NATURAL BEHAVIOUR MANAGEMENT

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Abstract *Animal Welfare 2003, **12***: 85-94

Behavioural management in zoos is often practiced within the confines of environmental enrichment, a well-known method which attempts to increase the welfare of captive animals. For the successful conservation and reintroduction of threatened or endangered species, however, it is also important to manage behaviour in such a way as to maintain behavioural diversity. The development of natural behaviour management (NBM) programs is advocated in this paper. These programs will act to maintain behavioural diversity in captivity and will encourage behaviour to be displayed in appropriate contexts through exposure of captive animals to naturalistic stimuli. The importance of developing appropriate antipredator and predation behaviours will be discussed in order to demonstrate how NBM strategies differ from, and can even conflict with, environmental enrichment strategies undertaken for welfare reasons.

Keywords: *animal welfare, antipredator and predation behaviour, captive breeding, ex situ conservation, predator/prey recognition, environmental enrichment*

Introduction

The importance of preserving the natural behaviours of animals in captivity, for the purposes of conservation and reintroduction into the wild, has been addressed in the past with regards to foraging, courtship, parental and antipredator behaviours (Burghardt & Milostan 1995; Gittleman & McMillan 1995; Hutchins *et al* 1995; Miller *et al* 1999). It is clear, at least conceptually, that preserving behaviour in captive populations is a matter of great importance. Indeed, many of the better zoos and their managers have acknowledged that behavioural loss or alteration in captivity is a problem and have also recognised the need to preserve behaviour in captive populations of wild animals (Hartmann & Schiess 1997). However, when zoos have focussed attention on the behavioural needs of animals, they have often done so within the framework of animal welfare and not with the intent to preserve behaviour in appropriate contexts. Under those circumstances, zoo managers' attention to behaviour has focussed on environmental enrichment, which has formally been described as enriching "elements of the environment that measurably increase the animal's well-being" (Markowitz & Gavazzi 1996). As part of this enrichment, some zoos have commonly allowed captive animals to interact with man-made toys including basketballs, cardboard boxes, telephone books or Kong toys, which scarcely resemble stimuli that animals would encounter in the wild (Maple & Perkins 1996; Markowitz & Gavazzi 1996). These toys do reduce stereotypies, alleviate boredom, and definitely entertain zoo patrons. Yet, they do little to teach captive animals how to forage for food in the wild; nor do they elicit many other behaviours in contexts necessary for survival in the wild. Although some have already begun to address the need to preserve behaviour in captivity (eg Law *et al* 1990; Law 1993; Hartmann & Schiess 1997), greater attention is still warranted toward preserving behaviours in their appropriate contexts. As zoological institutions continue their active role in conservation, zoos should begin to emphasise more greatly the maintenance of behavioural diversity in captivity.

Many zoos currently contribute to the conservation of natural ecosystems through public education, scientific research and fundraising to support field conservation programs (Hutchins & Conway 1995; Wiese & Hutchins 1997). For example, the Wildlife Conservation Society has implemented an educational program in the Yunan Province of China that has attempted to modify local attitudes regarding the use of animal products in traditional Chinese medicine (Berkovits & Naiman 1994). Researchers at the National Zoological Park in the United States have spearheaded efforts to protect and restore habitat in Brazil through the establishment of the Poco das Antas Reserve (Kleiman *et al* 1991). Additionally, zoos have assisted in previous ecosystem restoration attempts through the reintroduction of captive animals to the wild (see Stanley Price 1989; Kleiman *et al* 1991; Miller *et al* 1994 for examples). However, reintroduction can only be an effective management tool if behaviours crucial to survival in the wild are maintained in captivity. For example, the inability to migrate effectively and find nests has contributed largely to the failure of a bald ibis reintroduction attempt (Akcakaya 1990), while a lack of aversive behaviour towards humans has generated problems in the California condor reintroduction program (Snyder & Snyder 2000). Thus, the loss or alteration of important behaviours in captivity will make reintroduction difficult and may result in the failure of reintroduction attempts (Beissinger 1997).

Preserving behaviour through natural behaviour management

Although environmental enrichment does encourage animals to express species-typical behaviour, enrichment techniques have seldom emphasised the performance and preservation of these behaviours in their appropriate contexts. Zoos that house captive carnivores, for instance, have hung meat from swinging poles, which in turn elicits behavioural components of hunting (Law 1991). Although this practice does allow animals to engage in hunting behaviour, it is highly doubtful that the expression of such behaviour in response to a swinging pole can sufficiently teach an animal to complete the complicated task of stalking, hunting, capturing and killing live prey in the wild. Therefore, it is important for us to develop a management program that specifically addresses the need to preserve animal behaviour in appropriate contexts at zoos and captive breeding facilities. I propose the implementation of natural behaviour management (NBM) programs. NBM programs will be defined as programs that act to maintain behavioural diversity in captivity and encourage behaviour to be elicited in appropriate contexts through the presence of naturalistic stimuli. NBM programs will emphasise the preservation of learned or socially transmitted suites of behaviour, as these behaviours have the potential to be lost or altered in a captive population if they are not expressed in every generation. Behaviours that commonly involve the learning of a complex sequence of motor actions, and those that are dependent on context or are influenced by the social environment, include parental care (Baker *et al* 1996), hunting

(Leyhausen 1973; Polsky 1975b), reaction to predators (Seyfarth & Cheney 1980; McLean *et al* 1996) and mate choice (Dugatkin & Godin 1992; Galef & White 1998). NBM programs need not emphasise those behaviours that are more 'hard-wired', as these will probably persist in a captive population for many generations irrespective of experience. NBM programs might be incorporated into captive management programs at zoos and wildlife facilities so as to increase the survivorship and viability of captive populations in the future and allow for more successful reintroduction attempts.

Zoos have previously attempted to encourage the development of behavioural diversity in reintroduced animals through pre- and post-release training (Kleiman 1989). However, behavioural management should not be ignored until the time just prior to release. Behavioural management would be more effective if it occurred regularly at all stages of a population's tenure in captivity, so as to elicit the expression of those behaviours that require releasing mechanisms during sensitive periods of development. For such behaviours to develop, animals may need to be surrounded by the appropriate stimuli early in development. Zoos might immerse captive individuals of threatened or endangered species in NBM programs throughout their lives so that natural behaviour will be more likely to be expressed in captive-born animals, pre-release training can be minimised, and survivorship of reintroduced animals increased.

In the development of NBM programs, a variety of stimuli will be included that mimic the selective pressures encountered in the wild. Management of this nature is not traditional, and will sometimes run counter to environmental enrichment procedures, where welfare is the primary goal. In an effective NBM program, animals may actually be exposed to stimuli that compromise their welfare in order to maintain their behavioural diversity. For example, by exposing animals to predatory stimuli in captivity, animals will be encouraged to display behaviours indicative of disturbance, fear, or acute stress, such as escape and avoidance behaviours. These behaviours are normally considered indicators of short-term reductions in animal welfare (Mench & Mason 1997). Exposure to aversive stimuli will reduce the short-term welfare of the captive individual. However, during these experiences, animals will have the ability to learn how to avoid such stimuli. This will probably maximise post-release welfare, because encountering unpleasant stimuli in captivity will allow animals to survive and cope with selective pressures more easily in the wild. Exposure to aversive stimuli will also positively contribute to the welfare of the post-release population by lowering mortality of reintroduced animals and increasing population sizes in the wild.

In designing NBM protocols, it is necessary for zoo managers to rethink the way that animal husbandry has been practiced in the past, in order to allocate the time, staffing and funding required to develop and implement the new programs. These resources are scarce, but will be necessary to increase the success of reintroductions by way of behavioural management in captivity. Many traditional forms of husbandry can be incorporated into NBM programs and will help to minimise cost. For example, zoo managers have already addressed the need to provide animals with a more controllable environment through the presence of response-contingent stimuli during early development (Carlstead 1996). Additionally, to stimulate food-finding and food-manipulation behaviours, many zoos have encouraged animals to 'forage' for food (Shepherdson 1998) or to feed on whole animal carcasses (Law 1991) rather than providing animals with food in single large dishes. These husbandry practices are beneficial for preserving behavioural diversity and could be incorporated into any NBM program. In other cases, however, novel husbandry practices will need to be developed in order to maintain learned or socially transmitted suites of behaviours in their appropriate contexts.

Ethical considerations for natural behaviour management

The preservation of two suites of behaviours that are often socially transmitted — predation and antipredator behaviour — requires us to develop unique husbandry techniques within the framework of natural behaviour management. Maintenance of predation and antipredator behaviour will be difficult if we approach behavioural management from the standpoint of environmental enrichment because the preservation of these behaviours will often depend on decreasing the well-being of individuals. Here we must address an important ethical issue. By exposing animals to aversive stimuli, such as the risk of predation, in order to prepare individuals for reintroduction, the welfare of the individuals is necessarily reduced so as to increase the probability that a wild population of animals will be preserved. This ultimately results in a trade-off between holistic and individualistic approaches to wild animals. Kirkwood (2000) has addressed this very trade-off. Those who have a concern for species conservation and the preservation of biodiversity will generally acknowledge that it is permissible to sacrifice individual welfare for the benefit of the species. On the other hand, individualists may find it unacceptable to sacrifice individual animals' welfare in order to preserve biodiversity. In the end, an ethical balance must be maintained which takes the interests of both camps into account. When the benefits for reintroduction outweigh the cost to the individual, then it may be worthwhile to lower the welfare of some individuals in captivity. However, in situations where the conservation benefit appears low and the cost to individual welfare is high, exposure to aversive stimuli for the purpose of behavioural management and eventual reintroduction may not be a feasible conservation strategy.

In situations where reintroduction is to be attempted, suites of aversive or stress-induced behaviours must be preserved. Suggestions about ways of preserving antipredator and predation behaviour will prove controversial and may be criticised by animal-rights activists and welfare advocates. However, we cannot lose sight of the fact that in developing NBM protocols, we are making an effort to simulate as many natural stimuli as possible for the purpose of behavioural maintenance. Attempting to maintain behaviours by reducing individual welfare should in no way be equated with a lack of understanding or a disregard for animal welfare. Instead, management of this sort should be considered as a means to create more effective *ex situ* conservation programs. I will now outline how both antipredator and predation behaviours might be managed effectively in captivity through natural behaviour management.

Development of antipredator behaviour

The most direct way to elicit antipredator behaviour is through the exposure of prey to predation or the risk of predation. Although this method of behavioural maintenance would be beneficial for conservation purposes, zoo managers have been reluctant to expose captive populations to live predators (Markowitz & Aday 1998). Reluctance in the United States probably stems from fear of a potential public backlash, while in parts of Europe predator exposures are prohibited through legislation against cruelty to captive animals. Nevertheless, under circumstances where this is legal, we should explore the possibility of exposing animals to predatory stimuli in order to determine the effect that predator encounters have on the behaviour of captive prey.

We are already aware that exposure to predators, for the purpose of maintaining antipredator behaviour, varies in its importance. In some species of small mammal, antipredator behaviour appears to be robust and can be maintained in a population for many generations irrespective of previous experience with predators (Coss & Biardi 1997).

However, for other species, antipredator behaviour is learned socially. Vervet monkey (*Cercopithecus aethiops*) juveniles learn appropriate contexts in which to alarm-call on the basis of observational learning, reinforcement, or some other social process (Seyfarth & Cheney 1980). Similarly, in some small mammals (Yoerg & Shier 1997), marsupials (McLean *et al* 1996), primates (Joslin *et al* 1964; Murray & King 1973; Hayes & Snowdon 1990), birds (McLean *et al* 1999), fish (Huntingford *et al* 1994) and the Siberian ferret (*Mustela eversmanni*) (Miller *et al* 1990), expression of antipredator behaviour as adults may be influenced by past experience with predator-like stimuli. When antipredator behaviour is learned or socially transmitted, we may have to expose captive prey to predation risk in order to effectively manage those species' antipredator behaviour.

Pilot programs might be developed that both explore the utility of predator–prey encounters in different species and assess public reaction to such encounters. From these initial studies, appropriate NBM programs could be developed that attempt to maintain antipredator behaviour in captivity. These NBM programs could also include the development of public education projects that address the welfare concerns of zoo patrons and explain why exposure to predators is important for the conservation of endangered species. Education programs would reduce public criticism of this unconventional management technique in the United States and Europe. This could eventually lead to changes in European legislation that ease restrictions on the feeding of live prey to animals.

If exposing captive prey to actual predators is deemed too controversial a method to use in NBM programs, we might instead be able to use video playbacks or dynamic models of predators in order to simulate predation risk and to elicit antipredator behaviour. Chickens exposed to video playback of hawks respond by giving aerial alarm calls (Evans & Marler 1991; Evans & Marler 1992), and wild populations of California ground squirrels (*Spermophilus beecheyi*) show appropriate antipredator responses to models of avian predators flown overhead (Hanson & Coss 1997). Exposure to similar video images or models in zoos might be sufficient to develop antipredator behaviour in predator-naïve zoo animals.

It is possible, however, that even when antipredator behaviour is a learned response, exposure to predation risk will not always be necessary for the development of antipredator behaviour. Masataka (1993) reports that predator-naïve squirrel monkeys (*Saimiri sciureus*) exposed to live insects during early development show just as strong an aversion to predators as do wild-born animals. In this case, exposure to reactive stimuli during development apparently acts as a releasing mechanism for antipredator behaviour and could be substituted for actual exposure to predators in an NBM program. Other species would possibly respond similarly to reactive stimuli and might not require exposure to actual or simulated predation risk during natural behaviour management.

Development of predation behaviour

For successful reintroduction, the ability of carnivorous animals to hunt and kill prey is just as crucial for their survival as is the ability of prey to engage in effective antipredator behaviour. Like antipredator behaviour, development of complex predation behaviour is often influenced by experience (Leyhausen 1973; Polsky 1977). Kitchener (1999) states that there are generally two aspects of predatory behaviour that require experience during development: first, young carnivores learn from their mothers which prey species are typically eaten in their local area and how to kill those prey; and second, young animals must learn to refine their prey-killing behaviours so that they can hunt effectively once they are independent.

In order to learn which species of prey are appropriate to hunt in the release area, captive animals may have to be exposed to those species during their time in captivity. Complications have occurred during past reintroductions when animals were not exposed to the appropriate prey species prior to release. In a study by Pettifer (1981), captive-reared cheetahs (*Acinonyx jubatus*) were reintroduced to a reserve in South Africa without prior exposure to wild prey. Released animals attempted to hunt large prey species that are atypical for cheetahs. This put the reintroduced animals at an increased risk of injury from the more dangerous large herbivores. A similar problem occurred during reintroduction of the European lynx (*Lynx lynx*) when some individuals were released without sufficient exposure to wild prey species. These individuals began to hunt domestic animals post-release (Boer *et al* 2000). However, once the lynx were recaptured and exposed to wild prey for an extended period of time, they apparently learned which prey species were appropriate to hunt. The majority of the recaptured lynx subsequently began hunting species-typical prey. Although exposure to typical prey may not be required in all situations, this practice should be carefully evaluated because of its potential benefits.

Experience with prey during early development is also important in order to refine actual prey-catching and killing behaviour (Polsky 1975a; Langley 1986). As reported in Caro (1994), young cheetah cubs are often taught by their mothers to hunt and kill prey successfully. Once the mother catches prey, she will call her cubs to approach. She will then release the live captured prey so that her young can practice retrieving and killing it. This learning process in cubs is presumably important in developing hunting behaviour. Likewise, when captive Siberian ferrets are released into the wild, only those individuals that have had previous experience with prey and prey burrow systems are successful in hunting and killing prey (Biggins *et al* 1991). In the highly endangered black-footed ferret (*Mustela nigripes*), juvenile ferrets exposed to live prey are found, when they are older, to more effectively kill prey than those ferrets that were fed dead prey (Vargas & Anderson 1999). For the black-footed ferret, where reintroduction is currently being implemented, it is then important to expose captive-born animals to live prey so that they may develop the predatory techniques necessary for post-release survival. With such a suggestion, the obvious ethical, welfare and legal considerations resurface and must again be addressed.

Although, under certain circumstances, staged predator–prey encounters appear to be necessary for the development of hunting behaviour, zoo biologists should attempt to minimise the number of such encounters in captivity. In doing so, zoos will minimise the sacrifice of live animals and maximise individual welfare under conditions that are certainly less than optimal for prey. If possible, domestic animals (eg rats, mice, livestock) might be used in predator–prey encounters so as to reduce the loss of valuable prey from zoo collections. However, as mentioned above, the use of domestic animals as a substitute for natural prey does have risks. Although encounters with live domestic animals would allow captive carnivores to practice and perfect their hunting skills, we must ask whether captive predators would generalise those hunting skills for use with the prey species typically encountered after release into the wild. Because reintroduced animals need to hunt wild species that are abundant in their release area, it will be important to evaluate whether captive carnivores also need experience with typical wild prey species to ensure post-release hunting success. Even if zoos decide that it is unethical to allow each predator in the zoo's collection to be exposed to live prey, permitting certain individuals to hunt and others to observe might still be important for increasing future hunting success (Caro 1980).

In European countries, where legislation prevents feeding live prey to animals, it may prove impossible for zoo managers to teach appropriate hunting skills to captive predators. Instead, zoos in these countries might focus their captive breeding efforts on non-predatory species. At the same time, it would be worthwhile for zoos in countries with fewer legal restrictions to take over carnivore breeding programs and to begin to use NBM techniques that teach captive predators to hunt. Zoos in the United States, for example, have experimented with feeding live prey to captive carnivores (Shepherdson *et al* 1993). Although on a larger scale this would be a complicated and expensive endeavour, it could be a worthwhile method of increasing the success of carnivore reintroduction programs.

Conclusions

In practice, natural behaviour management will not be limited to preserving antipredator and predation behaviours. These two suites of behaviours have been described here as examples of how management practices may differ drastically when approaching captive behavioural maintenance from an environmental enrichment viewpoint or from a NBM viewpoint. NBM programs will require a shift in management practices so as to preserve the diversity of as many suites of learned or socially transmitted behaviours as is possible in captivity. These include those behaviours that are important for foraging, locomotion, navigation, mate choice and social behaviour.

Ultimately, animal behaviour in captivity can be viewed in two ways. We can view behaviour from the environmental enrichment standpoint, with our primary goal being to minimise maladaptive behaviour and increase animal welfare. Alternatively, we can view behaviour from the standpoint of natural behaviour management, attempting to preserve all components of a species' behavioural repertoire in appropriate contexts. If our goal is to reduce maladaptive behaviour, then enrichment programs need not be concerned with promoting natural patterns of behaviour. Once stereotypies or maladaptive behaviours such as hair-pulling have been reduced, enrichment will be viewed as having been a success. However, I hope I have argued convincingly that behavioural programs should set their standards much higher in order to promote education, captive behavioural research, and the possibility for eventual reintroduction. In the end, we must act to maintain populations of captive animals that not only look like their wild conspecifics but behave like them as well.

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