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A Review of Management Problems Arising From Reintroductions of Large Carnivores

Mark Edwards[1]

Large carnivores are often apex predators and are important in ecosystems as their behaviour promotes biodiversity. They frequently fall victim to anthropogenic causes of local extinction and subsequently, have often been the subjects of conservation efforts involving reintroduction programs. As land-use changes restrict ranges and reduce prey for large carnivores, the trend towards local extinction is set to increase; therefore ex-situ conservation is likely to be increasingly prevalent. Reintroduction programmes are divided into two distinct parts. The first part is pre-release, which includes selection, breeding, and preparation of animals. The second part runs from the time the animals are ready for release through the actual release process and may include post-release monitoring and the release of further, supplementary, animals where this is necessary and feasible. This study identifies and discusses a number of potential problems involved in the use of captive animals to seed reintroductions including welfare as well as ethical and political issues. Other challenges include the genetic and behavioural integrity of founder animals and disease control, both in captivity and post release. This study also identifies a number of points for consideration during and after release, including the involvement and motivation of stakeholders. The potential ecological ramifications of reintroductions are discussed as is the role of zoos in future programmes. Recommendations are made regarding the involvement of social scientists and conservationists in future release programmes.

INTRODUCTION

Large carnivores are important ecosystem engineers, dynamically changing ecosystems and increasing both habitat heterogeneity and biodiversity (Ritchie et al., 2012). The term “large carnivores” is used here to indicate predators who are often at the apex of their food webs. As such they will often be large bodied but may actually be smaller than some other species within their ecological communities. For example, wolves (*Canis lupus*) are considered large carnivores but are smaller than some ungulates, such as elk (*Cervus canadensis*). As apex predators these animals initiate trophic cascades that promote biodiversity in both aquatic and terrestrial ecosystems (for a review see Ritchie & Johnson, 2009). A trophic cascade is a series of interactions over more than one trophic level where apex predators supress mesopredators or prey, leading to an increase in number and/or diversity of primary producers. Depression of other species may occur through direct predation or through behavioural change within those species, which (temporally or spatially) affects their foraging ability (Ritchie & Johnson, 2009). In a high profile example of this, Estes and Duggins (1995) showed that the presence of sea otters (*Enhydra lustris*) depressed populations of sea urchins, which, in turn, allowed the proliferation of kelp forests, subsequently increasing biodiversity. In sites where otters were not present, kelp was significantly denuded or completely absent. Long term monitoring showed that, in areas where otters were introduced or where their range expanded, urchin biomass was reduced by between 50 and 100% and biodiversity increased. In contrast, in areas where otters were constantly present or absent, urchin biomass was unchanged. It should be noted though that trophic cascade effects are not always predictable or even desirable from a management perspective. For example, when killer whales (*Orcinus orca*) suddenly began to prey on the sea otters the numbers of urchins increased and kelp decreased (Estes, Tinker, Williams, & Doak, 1998).

As apex predators, large carnivores often reproduce slowly, require relatively large home ranges, and occur at relatively low densities (Primack, 2006). This makes them vulnerable to changes within the ecosystem. Climate change, anthropogenic land use, and degradation or destruction of habitat have decreased biodiversity (Primack, 2006; Samways, 2005). Changes in land use coupled with climate change are predicted to have the largest influence on biodiversity between now and the end of this century (Sala et al., 2000). It is likely that many large carnivores will lack sufficient space and/or prey and will need conservation attention. Therefore, ex-situ conservation programmes may become increasingly common (Snyder et al., 1996).

Reintroduction programmes are split into two phases. The first phase consists of the selection, breeding, rearing and keeping of suitable captive stock to seed the reintroduction. Problems encountered in this phase include ethical and welfare issues, such as keeping animals in relatively confined and sub-optimal conditions (for a review see Norton, Hutchins, Stevens, & Maple, 1995). Stress management is also classified as a welfare issue. In a literature review, Teixeira, de Azevedo, Mendl, Cipreste, and Young (2007) found that different types of stress can produce additive effects that may profoundly affect an animal’s performance, particularly in regard to cognitive functions such as memory. This

[1]School of Life Sciences, University of Lincoln, Brayford Campus, Lincoln LN6 7TS, UK.

*To whom correspondence should be addressed: maedwards@lincoln.ac.uk

same study also found that many conservation practitioners involved in reintroductions were not fully aware of these additive effects. There are also problems with releasing individuals into the wild who may not be fully adapted (either phenotypically or behaviourally) to wild environments. For instance, captive-reared Californian condors (*Gymnogyps californianus*) released into the wild were shown to be behaviourally maladapted, which compromised their chances of survival (Meretsky, Snyder, Beissinger, Clendenen, & Wiley, 2000). Management issues during the captive phase may also include challenges to the promotion of natural behaviours for mating, hunting and feeding. The issue of live feeding of vertebrate prey is especially contentious. Many countries have welfare laws that forbid this practice, yet without it is difficult for captive carnivores to learn and maintain a full suite of natural behaviours.

The second phase of the reintroduction programme begins with the release of animals into a wild environment and may continue through post-release monitoring and any subsequent action which may be required until the programme is deemed to have been either a success or to have failed. Problems here may include the attitudes of various stakeholders with human/carnivore conflicts being particularly important. For instance, one study analysed questionnaire data and showed that the distance to the nearest wolf territory significantly affected the respondent's attitude to wolf reintroductions, with those most distant from reintroduction sites being least concerned about them (Karlsson & Sjostrom, 2007). Another study analysed data from people living in conservation areas and showed that compensation schemes for livestock losses can mitigate the negative effects of human/carnivore conflicts in relation to reintroduction programmes (Mishra, 1997). The sequestration of land to form parks and other land-use changes may present further obstacles (Brandon, 1997).

The issue of disease control is relevant during both the captive phase and during and after release. In a review of captive breeding for endangered species, Snyder et al. (1996) list a number of incidents where disease has caused conservation programmes to fail.

Recent reintroductions of large carnivores include the wolf (*Canis lupus*) into Yellowstone National Park. This is generally held as an example of how re-introducing large carnivores can bring balance to an ecosystem and increase biodiversity. Smith, Peterson, and Houston (2003) describe this re-introduction and compare its effects to those that occurred when wolves naturally repopulated Isle Royale National Park in Michigan. African lions (*Panthera leo*) have been successfully reintroduced to several sites in the Eastern Cape province of South Africa through a system of soft release (A system whereby animals are acclimatised in large pens which are eventually left open to allow them to access the wider environment. At this stage supplementary food is often provided and this will be gradually withdrawn until the release subjects are self-sufficient). Although there were initial problems with the availability of prey and some males were removed to prevent excessive predation on other species, lions have successfully bred at six sites (Hayward et al., 2007). This same study details re-introductions for African hunting dogs (*Lycaon pictus*), spotted hyenas (*Crocuta crocuta*) and cheetah (*Acinonyx jubatus*), also in the Eastern Cape. Although all of these reintroductions were eventually classified as successful (recruitment has exceeded adult death rate), the cheetah programme suffered due to predation by lions.

Although this topic is well represented within the literature, it lacks synchronicity. Therefore, the aim of this review is to synthesize research from several different areas of zoology, ecology and conservation biology and to highlight the issues facing practitioners, We aim to thereby provide a point of reference for those seeking to use re-introduction as a method of conservation.

Potential problems during the captive breeding phase

One of the first problems when considering a reintroduction programme is identifying a population of animals that is suitable for use as founder stock. Large carnivores are often charismatic species and so are frequently found in zoological collections. However, not all captive individuals are necessarily suited for captive breeding programmes. The African lion is listed by the International Union for Conservation of Nature (UICN) as in decline and threatened (Nowell, Breitenmoser-Wursten, Breitenmoser, & Hoffmann, 2012). Many lions are in captivity at zoos and therefore have the potential for use in conservation breeding programmes. However the UICN lists six genetically distinct sub species of P. leo and many of the lions in collections have either been captive bred without regard to genetic background or insufficient records have been kept (J. Minnion, personal communication, 21 May, 2011) so that the specimens involved are of little conservation value. The purpose of, and justification for, zoos is a broad topic and beyond the remit of this work but there should be a clear demarcation between animals kept in collections as candidates for reintroduction programmes and those kept for aesthetic, research or other purposes.

A further problem is that of animal behaviour; in order for reintroductions to be successful the subjects should not be at any competitive disadvantage. Sufficient consideration must be given to promoting natural behaviours whilst in captivity to ensure that individuals are able to display near natural behaviours in the wild. Captive animals in zoological collections are often denied the opportunity to engage in normal courtship and mating behaviours, and hunting behaviour is often restricted by laws which ban the live feeding of vertebrate prey (Bashaw, Bloomsmith, Marr, & Maple, 2003).

Captive rearing of avian predators may seem more straightforward than that of their mammalian counterparts as eggs can be removed from wild bird nests and incubated to ensure a high degree of hatching success. However, there are potential risks to developing behavioural problems here. Birds may imprint upon or become accustomed to their keepers, as the reintroduction programme for the Californian condor demonstrated. In order to keep captive bred birds naïve to humans, the condors were hand fed by keepers who hid themselves from view and wore glove puppets to make it appear as though adult condors were presenting the food. Despite these efforts, one study that analysed the population dynamics of Californian condors during the reintroduction programme found that released birds only lived to an average age of about four years (less than the age of sexual maturity) and that behavioural issues, which stemmed from captive rearing, had contributed to a large number of deaths (Meretsky et al., 2000).

For reintroductions to be successful, individuals must be both genetically and physiologically true to type, but animals will quickly begin to adapt to life in captivity. Belyeav (1979) noticed considerable changes in just a few generations of silver fox (*Vulpes fulva*) while Boice (1981) demonstrated that wolves and jackals (*Canis* spp.) showed changes in bone structure and tail carriage in as little as one generation of captive breeding. Such changes would render canids released into the wild at a considerable behavioural or physical disadvantage. Tail carriage is important for intra-species communication and can affect acceptance by wild conspecifics. These rapid changes have been defined as "contemporary evolution." Stockwell, Hendry and Kinnison (2003) give several examples of such evolution in captive breeding situations and post release. In changing environments, relatively rapid evolutionary change may not be exceptional (Hendry & Kinnison, 1999).

In general, less active individuals with lower aggression are better suited to captivity (Boice, 1981; Stockwell et al., 2003) and anthropogenic selection for traits better suited to captivity may mean that heterogeneity is reduced as the actions of natural selection are reduced (McDougall, Réale, Sol, & Reader, 2006). This leads to inbreeding depression, which may affect the fitness of released animals and possibly the wild population into which they are released. In contrast, some animals subject to conservation efforts, including the Mauritius kestrel (*Falco punctatus*) and Florida panther (*Puma concolor coryi*), have gone through quite severe genetic bottlenecks but still remain viable (Pullin, 2002). The genetic purity of the Florida panther may, however, be questioned since Pullin (2002) states that another subspecies of panther was temporarily used to introduce vigour during its recovery programme.

In order to prevent the evolutionary changes that affect behaviour, McDougall et al. (2006) say that temperamental traits must be measured and monitored. However, whilst monitoring will alert practitioners to problems, such an alert may come too late to prevent changes in behaviour, producing individuals that are not behaviourally suited to life in the wild.

Competitive disadvantages may extend beyond the first generation of released individuals. Studies have shown that the offspring of captive bred individuals may be at a competitive disadvantage compared to those with purely wild ancestors (Ford, 2002; Araki et al., 2007). Araki et al. (2009) showed that salmonids from captive parents had less than half the reproductive fitness of those from entirely wild stock.

Whilst it may be evolutionarily beneficial to keep these animals both physically and behaviourally suited to life in the wild, this could mean they will not be well suited for display at zoos. Animals may experience high levels of stress and the public may not be prepared to pay to see exhibits where animals are allowed to display behaviours that many humans find distasteful or difficult to understand. This adds further weight to the argument for distinct populations of display animals and those bred with the sole intention of keeping them true to type for release. Balmford, Leader-Williams, and Green (1995) collated data for all threatened mammal species, analysing financial implications and reproductive success. They concluded that field based breeding would be more effective than ex-situ programmes that use animals bred in zoos.

Disease exposure and transmission

Endangered species often have low genetic diversity and this may increase susceptibility to disease in individuals or whole populations (Thorne & Williams, 2005). For this reason disease control may be crucial to the success of a programme (Viggers, Lindenmayer, & Spratt, 1993). Keeping animals in collections alongside species that are novel to them may allow exposure to novel pathogens or parasites to which they have no natural defence (Jacobson, 1993). Screening for disease or parasites prior to release will not necessarily be effective in all cases, particularly where diseases develop over long periods or where individuals are carriers without visible symptoms (Snyder et al., 1996).

Several accounts of accidental disease transmission from captive bred individuals to wild populations exist, including respiratory disease in Mojave desert tortoises (*Gopherus agassizii*) and tuberculosis in Arabian oryx (*Oryx leucoryx*) (Woodford & Rossiter, 1994). Conservation organisations act with the best of intentions and will not want to inadvertently expose wild stocks to novel pathogens (Cunningham, 2002), but evidence shows that this does happen, further supporting the argument that distinct populations should be kept for reintroduction breeding and that these should be isolated from species that are exotic to them.

Animals may also be susceptible to infectious disease or parasites after they have been released. For example, koalas (*Phascolarctos cinereus*) were rapidly infected with ticks when translocated from a parasite-free area to one where these parasites were prevalent. Additionally, orangutans (*Pongo* spp.) were infected with tuberculosis and herpes during translocation from Taiwan to Malaysia (Woodford & Rossiter, 1994). A further study which carried out post-mortem examinations on Eurasian lynx (*Lynx lynx*) found in the Swiss Alps revealed that 40% of radio collared individuals died of infectious disease (Schmidt-Posthaus, Breitenmoser-Wursten, Posthaus, Bacciarini, & Breitenmoser, 2002). These examples demonstrate that it is imperative that practitioners carry out screening for pathogens in the environment wherever this is practical.

Considerations for animals ready for reintroduction

In many cases apex predators have been removed from ecosystems directly by, or as a consequence of, human action. Often this is because people fear them or have taken action to protect livestock or other wildlife (Prugh et al., 2009). While it may be perceived that affording the animal protected status will remove the original cause of decline, this will only be effective if it is correctly enforced. The recent case of the reintroduction of grey wolves to Yellowstone National Park in the USA (Fritts et al., 1997) is a case in point. The wolf has been persecuted for the reasons mentioned above and upon reintroduction into the park wolves were afforded protected status, however some stakeholders who are against the reintroduction of wolves have deliberately killed animals despite their protection in law (Moore, 1995).

It may be that in other cases compensation paid to local people for lost livestock will make them more tolerant of released carnivores, but the best course of action must include educating stakeholders about the ecological effects of reintroductions whilst involving local people to make them feel part of any success story. One such example is the case of the Florida panther whose population was less than 50 individuals (Pullin, 2002). These animals were the beneficiaries of an action plan that included the payment of compensation to individual farmers, and which saw the animal adopted as the state emblem and given much positive media coverage (Clucas, McHugh, & Caro, 2008). This has seen the population recover to a viable size (Pimm, Dollar, & Bass, 2006), although work will need to continue to ensure that populations remain viable.

Compensation schemes for stakeholders may substantially increase the chances of success for reintroduction programmes. Brandon (1997) recommends the construction of national parks and reserves to conserve biodiversity. However, in the past, conservation programmes for large felids such as the snow leopard (*Panthera uncia*) have been effective at including stakeholders (Mishra et al., 2003). A study that interviewed villagers in the Indian range of the snow leopard found compensation paid to local people to help fence their stock and remunerate them for losses was more effective than declaring areas as national parks (Mishra, 1997). This situation has, however, been complicated by recent canine distemper outbreaks in felids (Deem, Spelman, Yates, & Montali, 2000). Practitioners will now need to model future felid reintroductions to ensure that contact with domestic dogs is minimised.

Ecosystems are dynamic and the removal of an apex predator, especially one that may have been a keystone species, will normally cause a cascade of changes within the system (Ripple & Beschta, 2004). It should be recognised that reintroducing an apex predator may cause further changes and affect different species in ways that may not be fully appreciated. The reintroduction of wolves to Yellowstone again serves as an example. When the apex predators are removed, predators at the next level may proliferate through mesopredator release (Soule et al., 1988). During the 70 years that the wolf was absent from the ecosystem, an alternative predator-prey balance developed between the remaining species. In this particular case, the coyote (*Canis latrans*) proliferated and subsequently, the survival of pronghorn (*Antilocapra americana*) calves was significantly reduced (Berger, Gese, & Berger, 2008). When the wolf was reintroduced it was expected to have a significant effect on elk (*Cervis elaphus*) numbers and behaviour (Ripple & Beschta, 2004). However, less predictable cascade effects included resurgence in beaver (*Castor canadensis*) numbers, as there were fewer elk to browse the willow (*Salix* spp.). Additionally, pronghorn survivorship increased (Berger & Gese, 2007; Ripple & Beschta, 2004) and coyote numbers were initially reduced, due to interference competition from wolves (Berger & Gese, 2007). This final point is not, however, straightforward. Competitive exclusion theory says that similar species should not be able to coexist on the same limiting resource (Hardin, 1960), however, Arjo, Pletscher, and Ream (2002) found that this can be overcome if that limiting resource is prey, provided that the competing species use the prey differentially. In effect, wolves and coyotes now co-exist on the same limiting resource because the wolves hunt, whereas the coyotes act as scavengers.

There is talk of reintroducing large carnivores to Scotland (Wilson, 2004) to control the numbers of large ungulates. Although Scottish ecosystems are different from those in Yellowstone, many of the problems of reintroduction and ecological effects will be similar. For instance, Nilsen et al., (2007) surveyed Scottish stakeholders and found that 43% of respondents favoured the reintroduction of species including wolves; success of the programme would depend on people being kept informed, involved, and motivated.

CONCLUSION

It is apparent that factors requiring consideration during reintroduction programmes are many and multi-faceted, and that various considerations must be addressed well before releasing animals. It is thought that while some of these factors are well managed, others are yet to be addressed effectively. Whilst it is important that conservationists continue to be forward thinking and enterprising in their approach, they must also be sure to heed the lessons of the past. In this respect, Yellowstone provides a rich vein of ecological data that should be used to inform future reintroductions.

It is clear that the curators of animal collections often expend considerable energy keeping their animals healthy and in trying to promote natural behaviours. However, societal attitudes may be a considerable impediment when it comes to maintaining behaviours needed for animals to survive in the wild. There is a place for zoos in the conservation of animals, perhaps as arks for animals that are extinct in the wild and cannot presently be released, or as charities that can raise funds for in-situ conservation programs. Zoo exhibits should be used to inspire the next generation of conservation practitioners, however, zoos are not the ideal place from which to launch reintroductions. Instead, reintroduction programs should be managed from distinct stock in a remote environment where genetic quality, behavioural suitability, and disease status can be best audited. Although there may be occasions where the number of available animals is so limited that zoo stock must be bred from to seed reintroductions, this should become the exception rather than the rule.

The reintroduction of large carnivores may allow ecosystems to return to a semi-natural state, which is important for promoting biodiversity and ecosystem function. For this reason there is a need for further research into the optimal methods of preparing large carnivores for a return to the wild. To facilitate maximum success, further research by social scientists is needed to ensure that human populations are well equipped to live in areas where large carnivores roam free.

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