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Biological and technical considerations of carnivore translocation: a review

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Abstract

Carnivore translocations are usually risky and expensive, and a number of biological and non-biological factors can influence success. Biological considerations include knowledge of genetics, demographics, behavior, disease, and habitat requirements. This information is critical for determining if the translocation should be attempted, if it could be successful, and how it could be implemented in an efficient and effective manner. We stress that individual species will vary in their responses, and ideas should be tested scientifically. The technical considerations of translocation are closely related to the biological questions. They include legal framework, fiscal and intellectual resources, monitoring capacity, goals of the translocation, logistic challenges, and organizational structure of decision-making. We do not discuss socio-economic aspects of translocation because those challenges require detailed discussion in a separate paper. We suggest that because large carnivores often play key roles in regulating ecological interactions between trophic levels, restoring them is more than a single-species activity. By restoring carnivores in viable numbers, we can take a large step toward recovering ecological integrity of geographically extensive landscapes.

INTRODUCTION

While this paper draws specific attention to carnivores, most of the issues discussed apply to many, if not all, translocation efforts. We focus on carnivores in this paper for four basic reasons.

First, humans have drastically changed most of the Earth's ecosystems (Vitousek *et al*., 1997). As a result of these ecosystem changes, and direct persecution, carnivores have been eliminated from most areas in a manner disproportionate to species of other trophic levels. The consequences of habitat fragmentation, such as area effect, edge effect, distance effect, rarity effect, age effect, and disturbance dynamics, have been well documented (e.g. Frankel & Soulé, 1981; Wilcox & Murphy, 1985; Wilcove, McLellan, & Dobson, 1986; Noss, 1987; Noss & Cooperrider, 1994; Soulé, 1995). Basically, as habitat patch size decreases, more species disappear: larger, wide-ranging, and specialized species are disproportionately represented in those losses (Soulé, 1995).

Second, large carnivores often have disproportionate effects on ecosystem processes (Terborgh, 1988; Estes, 1996; Power *et al*., 1996; Terborgh, Lopez *et al*., 1997; Terborgh, Estes *et al*., 1999). Since the ground-breaking studies by Paine (1966), the effects of predators have been demonstrated in numerous systems, and many of these investigations have been reviewed by Terborgh, Estes *et al*. (1999).

Protecting top carnivore species, therefore, can have positive effects on the entire system. Where carnivores have been eliminated, events such as herbivore release (McShea, Underwood & Rappole, 1997) and mesopredator release (Soulé *et al*., 1988) have produced trophic cascades that have severely disrupted ecological communities and extirpated species (Estes, 1996; Terborgh, Lopez *et al*., 1997; Terborgh, Estes *et al*., 1999). Because many carnivores play umbrella, flagship, indicator, and keystone roles, reintroducing a suite of extirpated carnivores is a step toward restoring the natural integrity to large sections of land (Miller, Reading, Strittholt *et al*., 1999).

Third, in most cases, natural recolonization is no longer an option. Large carnivores have been widely extirpated, and severe habitat disruption poses a barrier to their natural dispersal. Finally, carnivores seem to be disproportionately difficult to re-establish via translocation.

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In this paper, we discuss some of the variables that influence the success of carnivore translocation, or moving organisms from one area to another. We emphasize returning species to areas where their populations have been extirpated (reintroduction) because releasing animals to augment an existing population (restocking) and releasing animals outside their historical range (introduction) are generally inadvisable (IUCN, 1987), although they can be useful under special circumstances (e.g. Gerrodette & Gilmartin, 1990).

Because the focus of this paper is biological, we will not discuss the socio-economic aspects of translocation in great detail. That does not diminish their importance. The social challenges of carnivore reintroduction are even more daunting than the biological ones (Reading & Clark, 1996), and a successful program will need a holistic and truly inter-disciplinary approach that integrates social and biological sciences toward the goal of conservation.

BIOLOGICAL CONSIDERATIONS FOR TRANSLOCATIONS

An array of biological factors affect the success of translocations. Knowledge of genetics, demography, behavior, disease, and habitat requirements can lead to more effective reintroduction methods and provide baseline data against which the results of a translocation program can be evaluated (Kleiman, 1989; Stanley Price, 1989; Miller, Biggins *et al*., 1993; Reading & Clark, 1996). Unfortunately, such information is often lacking, as only 15% of terrestrial carnivore species have been the subject of at least one field investigation, and the status of most remains obscure (Schaller, 1996).

A translocation program should include a feasibility study, a preparation phase, a release phase, and a monitoring phase (IUCN, 1987). Several biological questions should be addressed during the feasibility study (Reading, Clark, & Kellert, 1991; Kleiman, Stanley Price & Beck, 1993). These include: is there a need to reintroduce or restock a wild population? Did the species occur as a viable population in the proposed release area? If restocking is a possibility, would it pose a threat to the existing wild population? Have the causes of the population decline or extirpation been eliminated? Is there sufficient protected habitat for the translocated animals to survive? Are there suitable animals available that are surplus to the genetic and demographic needs of the source population? Is there sufficient knowledge to formulate a plan of action and evaluate its success?

If a reintroduction is deemed feasible, a myriad of additional biological considerations should be addressed. We explore several of these considerations in more detail.

Selecting animals for translocations

Taxonomy

Animals chosen for reintroduction should be as similar as possible to those that originally inhabited the release site. However, existing subspecific frameworks should be examined critically because they may not reflect the true distribution of genetic variation and phylogenetic discontinuities within species (Ryder, 1986; Avise, 1989; Avise & Nelson, 1989). Early mammalogists described and named large numbers of subspecies within most species of carnivores, and they often based their subspecific classifications on a small number of morphological characters from a small number of specimens. These subspecies are still listed in many reference works: for example, Hall & Kelson (1959) name 24 subspecies of gray wolves (*Canis lupus*). This probably overestimates the number of wolf subspecies because minor differences between clinal distributions of neighboring populations are unlikely to merit subspecific status (Carbyn, 1987). Wolves can disperse over long distances, and 'the vast expanses of boreal areas on the North American continent resulted in a wide-spread unrestricted gene flow from one area to another during the period prior to European settlement' (Carbyn, 1987).

Molecular genetic data

Descriptive genetic studies using modern molecular techniques can help to define appropriate genetic subdivisions. In large North American canids, patterns of mitochondrial DNA variation suggest 'that gene flow may occur across the continent and suppress genetic differentiation among even widely separated populations' (Mercure *et al*., 1993). For example, widely separated populations of coyotes (*Canis latrans*) show little mitochondrial DNA differentiation (Lehman *et al*., 1991). However, in kit foxes (*Vulpes macrotis*), a small canid with limited dispersal capabilities, there are significant genetic differences between populations that reflect geographical barriers (Mercure *et al*., 1993). Molecular genetic differentiation among populations must be interpreted critically because it does not always reflect historical barriers to gene flow. For example, Wayne *et al*. (1992) believed that apparent genetic differences among extant gray wolf populations reflect population declines and habitat fragmentation rather than a long history of genetic isolation.

In summary, spatial heterogeneity in population genetic structure is probably not a relevant concern for large carnivores that range widely, but it can be for smaller carnivores with limited dispersal capability. We emphasize, however, that each species be weighed individually. For example, grizzly bears (*Ursus arctos*) have more limited dispersal patterns than expected for an animal of their size.

Maximizing genetic diversity among release animals is probably the best strategy for most species. Haig, Ballou & Derrickson (1990) suggested selection of animals for release based on maximizing founder genome equivalents as a good compromise between maximizing founder contributions and allelic diversity. However, this strategy should not jeopardize the genetic integrity of the source population (Kleiman, 1989). Greater genetic diversity among release animals would reduce the chances for founder effects and inbreeding depression, which may be important in a small population struggling to become established. Greater diversity may also enable the population to better adapt to its habitat.

Wild versus captive animals

Wild-born animals are preferable to captive-born animals for translocations (Griffith *et al*., 1989), and we recommend releasing captive carnivores only when there are no other alternatives. Captive breeding is a strategy in conservation, and captive breeding and reintroduction of black-footed ferrets (*Mustela nigripes*) has saved that species from extinction (Miller, Reading & Forrest, 1996). In addition, captive animals can be used for education and research whether or not they are ever translocated to the wild. For example, some questions important to conservation, such as understanding energetic needs or reproductive habits, can be difficult to answer from wild animals.

Yet, captive breeding for purposes of translocation is expensive in time, space, and money and can be risky (e.g. see Scott & Carpenter, 1987; Leader-Williams, 1990; Derrickson & Snyder, 1992; Hutchins, Willis & Weise, 1995; Miller, Reading & Forest, 1996; and Snyder *et al*., 1996). The captive environment may erode the genetic basis for important morphological, physiological, and behavioral traits via artificial selection. For example, while captive-born animals may still exhibit the correct behavior in a given situation, they may not perform at the level of efficiency needed for survival in the wild.

Indeed, during a captive-breeding program, learned behavioral traits can degenerate much more rapidly than genetic diversity (May, 1991). Some examples of behavioral traits that may be adversely affected by the captive environment include: searching for food, killing, predator avoidance, recognition of home sites, movement patterns (such as seasonal migrations), methods of raising young, ability of young to follow mothers to kill sites, and negative response to human presence (Derrickson & Snyder, 1992; Miller, Biggins *et al*., 1993; Beldon & McCown, 1996; Miller, Reading & Forest, 1996; Snyder *et al*., 1996). As a result, when captive-born animals are reintroduced, mortality rates are often high. Reducing the impact of these problems during reintroduction of captive-raised black-footed ferrets was time-consuming and expensive (see Miller, Reading & Forest, 1996; Biggins, Godbey, Hanebury *et al*., 1998).

Different species respond variably to captive conditions, but more generations in captivity will likely increase the degeneration of survival skills. Pre-release preparation and post-release training may not be able to restore survival traits to full efficiency. Effective development of adaptive behaviors requires the correct environment for learning (including a skilled parent) or, in the case of critical periods, the correct stimulus at the proper time during development (Gossow, 1970). Captive conditions can make it difficult to provide these requirements. Furthermore, selection for tameness and other genetic adaptations to the captive environment are likely to become increasingly serious as populations are maintained in captivity for many generations, reducing the probability of a successful reintroduction (Frankham, 1995; Snyder *et al*., 1996). Frankham (1995) provides suggestions for minimizing genetic adaptations to the captive environment.

When captive-raised and wild-born individuals of the same species have been released experimentally, captive-raised animals exhibited different behaviors and lower survival times than their wild-born counterparts (Schadweiler & Tester, 1972; Cade, Redig & Tordoff, 1989; Griffith *et al*., 1989; Beck, Kleiman *et al*., 1991; Biggins, Hanebury, *et al*., 1991; Wiley, Snyder & Gnam, 1992; Beldon & McCown, 1996; Miller, Reading & Forest, 1996). Important to the release of large predators, are their interactions with humans and livestock. Captive-raised pumas (*Puma concolor*) in Florida had less fear of humans and were more likely to engage in puma–human and puma–livestock encounters than wild-caught animals (Beldon & McCown, 1996). Similarly, orphan sea otter (*Enhydra lutris*) pups raised in captivity and released into the wild often approach people, and two such animals attacked humans (C. Benz, pers. comm.; J. Estes, pers. obs.).

Age-sex categories

Individuals in different age-sex classes vary in reproductive value and often exhibit different behaviors. It is usually advisable to release animals in sex ratios similar to that exhibited by wild populations to ensure reproductive encounters (Erickson & Hamilton, 1988). This often entails releasing more females (Short *et al*., 1992). Differences between male and female behavior may influence release considerations, and age is also crucial. Young animals often display greater behavioral plasticity than adults and are less important to the source population (Gordon, 1991; Logan *et al*., 1996; Miller, Reading & Forest, 1996). Some translocations use releases of mixed sexes and ages that replicate natural social groups, such as wolf packs (Moore & Smith, 1991; Bangs & Fritts, 1996).

In many cases, both genetic and demographic considerations are constrained by the availability of animals from the source population (i.e. some translocations must take whatever animals they can get). This is especially true when the source population is a captive-breeding program. In many such situations managers are concerned with the genetic and demographic management of the source population rather than the translocated population (Gordon, 1991; Moore & Smith, 1991; Miller, Reading & Forest, 1996). This is a tactic we support, especially in the initial stages of release, when the translocated population is just getting established and experiencing high mortality.

Studies of puma translocations illustrate several of these points. In the Florida puma release, wild-caught females with kittens did not move far from their release site, and the kittens behaved normally; however, wild-caught and released males covered large areas until they located females (Beldon & McCown, 1996). Logan *et al*. (1996) translocated wild-caught pumas in New Mexico, and they found success was affected by sex, age, and social status. The best results came with translocated pumas between 12 and 27 months of age (Logan *et al*., 1996). They moved the shortest distance from the release site and quickly established areas of use. Pumas of this age group may settle more quickly because, being at dispersal age, they may be predisposed to accept an unfamiliar area (Logan *et al*., 1996). In addition, the females of this age group moved less and had higher survival rates than males. The removal of pumas less than 27 months of age from a self-sustaining population would probably not jeopardize the source population genetically or demographically (Logan *et al*., 1996), an important consideration in selecting animals for translocation (Kleiman, 1989; Stanley Price, 1989).

Adult translocated pumas (28–96 months of age) taken from established territories traveled the farthest from their release site, often showing homing tendencies (Logan *et al*., 1996). Indeed, two pumas in this age class returned to their original home territories, over 400 km away. Older pumas (over 96 months of age) showed high, immediate risk of death (Logan *et al*., 1996). Similarly, adult male sea otters had a greater risk of death during capture and translocation than individuals in other age-sex classes (T. Williams, pers. comm.).

In general, puma translocation increased mortality over that observed in the source population (Logan *et al*., 1996). The risks were long-term, and a number of deaths occurred in the second year after release. Chronic stress may have been a factor, particularly for adults. Combining suggestions for puma translocation from Logan *et al*. (1996) and Beldon & McCown (1996), it may be preferable to first release dispersal age females. After the female pumas establish areas of use, young males could be released in the presence of those females to keep them from wandering long distances. We caution, however, that it can sometimes be difficult to determine optimum ages for translocation. For example, in some species, juveniles may have higher survival rates after translocation, but their future reproductive potential must be balanced against the immediate reproductive capacity of any adults that establish in the release area. Even after years of data on sea otters, there is still some disagreement as to the optimum sex and age composition for translocation.

Homing behavior and excessive movement from the release site has been a major problem in translocation of ursids, canids, felids, and mustelids (Linnell *et al*., 1997). For example, when 139 California sea otters were translocated to San Nicolas Island, the majority dispersed away from the island, and a minimum of 30 individuals, including both juvenile and adult females, returned to their capture location (G. Rathbun, pers. comm.). Excessive movement from the release site is a major reason for low survival and poor reproductive rates of translocated carnivores. There is often a correlation between movement distances after release and mortality (Biggins, Godbey & Vargas 1993a; Logan *et al*., 1996). Linnell *et al*. (1997) suggest holding animals on a release site for a time prior to release to reduce post-release movements, and moving large carnivores far from their capture site to reduce homing.

Genetics

Understanding genetic considerations is important to translocation, yet genetic screening was performed in only 37% of the reintroduction projects using captive-raised animals (Beck, Rapaport *et al*., 1993). As discussed above, translocated animals should be as genetically diverse as possible because of the potential for founder effects and inbreeding depression within the small populations typical of translocation programs (Templeton, 1990). This is especially true in the early stages.

Inbreeding depression (reduced reproductive fitness due to matings between close relatives) has been documented in a large number of mammals (Ralls, Ballou & Templeton, 1988; Lacy, Petric & Warneke, 1993; Lacy, 1997), including wolves (Laikre & Ryman, 1991) and Florida panthers (Roelke, Martenson & O'Brien, 1993; O'Brien, 1994). Inbreeding depression is a potential problem in small, reintroduced populations of large mammals because these species probably had low inbreeding rates prior to European settlement (Ralls, Harvey & Lyles, 1986; Frankham, 1995).

In Wyoming, translocated big horn sheep (*Ovis canadensis*) have been living in small isolated populations, and genetic changes (including shifts in allele frequencies, decreases in number of alleles, and changes in heterozygosity) in those animals were detected within 10 to 20 years after release (Fitzsimmons, Buskirk & Smith, 1997). Genetic problems may be contributing to declining numbers in the translocated herds (Berger, 1990; Fitzsimmons *et al*., 1997). Wildt *et al*. (1995) demonstrated that felid populations with reduced genetic diversity ejaculate lower total sperm counts and extraordinarily high numbers of malformed spermatozoa, than do populations of the same species with high levels of genetic diversity. They also showed homozygous populations are plagued with an array of physiological defects, including cardiac and immune-system problems.

Outbreeding depression (reduced reproductive fitness due to matings between individuals that are genetically dissimilar) is much less likely to be a problem than inbreeding depression (Ballou, 1995; Frankham, 1995). Evidence for outbreeding depression comes primarily from plants and animals with extremely limited dispersal (Ballou, 1995). Serious outbreeding depression in mammals appears to result mainly from crosses between individuals with significant genetic (e.g. chromosomal) differences resulting in sterility in the F1 generation (Ballou, 1995).

Furthermore, several studies of captive animals failed to find evidence of outbreeding depression in mammals. Smith *et al*. (1987) observed no adverse effects of crossing rhesus macaques (*Macaca mulatta*) from India and China. Jaquish (1994) found no outbreeding depression from crosses between subspecies of saddle-back tamarins (*Saguinus fuscicollis*). Ballou (1995) found no evidence for outbreeding depression in captive mammals, including orangutan (*Pongo pymaeus*) subspecies from Borneo and Sumatra. Finally, Lacy has conducted extensive crosses between several subspecies of *Peromycus polionotus* and found that all crosses display heterosis, with respect to percent of pairs breeding, litter size, juvenile survival, and growth rates, at the F1 and subsequent generations (R. C. Lacy, pers. comm.). Importantly, these studies were all conducted in captivity. Theoretically, outbreeding to genetically dissimilar reintroduced animals could have repercussions, such as birthing at inappropriate times and reduced fitness with a particular, more restricted, habitat (Leberg, 1990; May, 1991). However, such effects have not yet been documented in large mammals such as carnivores.

Many conservationists caution against simply trying to bolster numbers or to maximize genetic heterogeneity by translocating animals into an area with a remnant population. The result could be 'contamination', or even swamping, of unique, remnant genetic stocks by the translocated animals (Berg, 1982; Betram & Moltu, 1986; Sale, 1986; Stanley Price, 1989; R. R. Johnson, 1990). This effect has been documented when hatchery fish are released into wild waters and is one of the arguments against restocking (IUCN, 1987). For example, native breeding populations of coho salmon (*Oncorhynchus kisutch*) have been replaced in the lower Columbia River basin by feral hatchery fish (O. W. Johnson *et al*., 1991). For a mammalian example, red wolves interbreeding with congeneric species living at the release site could lead to genetic contamination or swamping (Phillips, 1990; Moore & Smith, 1991).

In addition, it is problematic to use translocation of animals between isolated patches of habitat as an alternative to restoring the historical connections between those isolated patches. While animals may be captured and moved between fragments, there may be no functional benefit from those efforts. Homing behavior and excessive movement from release site have been a major problem in carnivore translocations (Linnel *et al*., 1997). As mentioned above, several translocated pumas traveled over 400 km to return to their original territories (Local *et al*., 1996), and a young male tiger (*Panthera tigris*) translocated to a new area was quickly killed by a resident male (Seidensticker, 1976).

Most importantly, simply moving animals between fragments is not a viable attempt to restore wilderness or expanses of habitat similar to those that existed prior to extensive human development. Indeed, relying on such half-way technology can preserve existing patterns of habitat fragmentation. So, even if genetic material can be successfully exchanged, the small fragments would still be susceptible to demographic events, environmental events, and poaching. Even if large animals persist over the short-term in these fragments, important ecological processes such as fire, nutrient cycling, grazing, and flooding would remain altered by isolation and reduced scale. Following the same logic, translocating 'problem animals' as a cure for livestock depredation will probably have more cosmetic value than conservation substance, and it may only deflect attention from the deeper questions about existing ecological conditions that encourage predation on livestock.

Demography

Colonies of reintroduced animals must become large enough, as quickly as possible, to withstand fluctuations in both the environment and population size, because vacillations in either can drastically increase the chance of extinction in small populations (Gilpin & Soulé, 1986). To understand these population dynamics, biologists must analyze demographic parameters such as fecundity, mortality, population growth rate, age structure, sex ratio, and life expectancy in natural populations (Stanley Price, 1989; Reading & Clark, 1996). Comparing demographic traits of reintroduced populations with wild populations will help managers determine when a reintroduced population has become an established, viable population.

Demographic characteristics are also important for defining habitat quality, which is the foundation of any management plan. Van Horne (1983) discussed misleading conclusions about habitat quality when simple density estimates (and presence/absence data) were used without knowledge of age structure or social structure. For example, density surveys can be taken in the warm months when winter habitat may be the critical factor for mortality (Van Horne, 1983). Additionally, social interactions can push juvenile, dispersing animals into poorer quality habitat, or even habitat sinks, because all good habitat is occupied by a stable population of territorial adults. Even though numbers of individuals can be temporarily high in the poor habitat, very few of those animals will survive to reproduce (Van Horne, 1983).

In polygynous carnivores, adult females with young will center their activities where critical resources are concentrated and easiest to obtain. When caring for offspring, females are restricted to optimal habitat as they need to satisfy elevated energetic requirements with minimum time away from the young (Lindstedt, Miller & Buskirk, 1986). Male carnivores, on the other hand, wander over extensive areas searching for females. Their movements are highly variable and often more related to reproductive needs and social status than habitat quality (Ewer, 1973; Powell, 1979). For that reason, adult females, which form the demographic base of a population, will often best represent the habitat needs of a species. Without attention to demographic factors (such as age structure, mortality, and reproduction) and behavioral information (such as social structure) one can not truly differentiate the quality of habitat types.

Behavior

Behavioral traits must be performed efficiently in a variety of situations. The expression of a given trait is also influenced by a host of simultaneous behaviors that are also necessary for survival. Indeed, several authors have suggested using behavior as a measure of reintroduction success (Kleiman, Beck, Dietz *et al*., 1986; Miller, Kleiman, Beck, Baker *et al*., 1990; Miller, Biggins *et al*., 1993; Miller, Reading & Forest, 1996). Box (1991) suggests using expression of behavioral traits in the selection of individuals for release. Knowledge of hunting, killing, caching, predator avoidance, reproduction, parenting, imprinting periods, social organization, communication, territoriality, locomotion, daily movements, seasonal movements, and habitat choices will affect the demographic selection of individuals for release, timing of reintroductions, method of release, and choice of sites. We have discussed many of these factors in previous sections.

As mentioned earlier, site fidelity and homing behavior, are important behavioral traits affecting large carnivore reintroduction success (Linnell *et al*., 1997). Habituating animals to release sites appears to help reduce dispersal following reintroduction for many species (Berg, 1982; Jacuart *et al*., 1986; Stanley Price, 1989; Linnell *et al*., 1997). Permitting animals to become habituated to release sites also permits them to hone behavioral skills, such as locomotion, social skills, and foraging (Bangs & Fritts, 1996).

Health and disease

The health and physical condition of animals selected for release should be carefully assessed. Despite the fact that Griffith *et al*. (1989) found no correlation between success and physical condition of animals at time of release, we believe only animals in good physical condition should be used in translocations. In addition, translocation should not introduce diseases to the release site, yet only 46% of the translocation programs using captive-born animals conducted any kind of medical screening before release (Beck, Rapaport *et al*., 1993). In a survey including captive-raised and wild-born animals for translocation, 24% utilized medical screening (Griffith *et al*., 1989) while about 25% of the programs had data that was inadequate for calculating the proportion of translocated animals lost as a result of disease (Griffith *et al*., 1993). These figures are shockingly low. Many of these translocation programs used animals that were housed in multi-species facilities, and that increases the possibility of contacting an exotic disease. Risks can be minimized by veterinary intervention at the founder site, screening at the proposed release site, through vaccination if necessary, and by post-release monitoring (Woodford & Rossiter, 1993). A paper by Ballou & Wildt (1991) provides a vehicle to assess the risk of disease. The ultimate success of black-footed ferret reintroductions will probably depend on a better understanding of the dynamics of both canine distemper and plague (Williams, Thorne *et al*., 1988; Williams, Mills *et al*., 1994; Reading, Clark, Vargas *et al*., 1996).

It should be remembered that acts of capture and holding until release will likely stress the animals, particularly wild-born animals, and that can increase susceptibility to new or latent infectious diseases (Woodford & Kock, 1991; Woodford & Rossiter, 1993). Logan *et al*. (1996) speculated that stress was an agent in the death of some translocated wild-born pumas, particularly adults older than 27 months of age.

Habitat

Among the most important points in assessing a release site are determining the amount and type of habitat required and the cause of decline for the species to be translocated. If sufficient habitat is not available or the cause of decline has not been eliminated, it is nearly impossible to justify a translocation (Kleiman, 1989; Stanley Price, 1989; Short *et al*., 1992; Reading & Clark, 1996). For many large carnivores (e.g. gray wolves), effectively halting harvest or control of the species may be enough, but other species (e.g. jaguars) may be much more sensitive to human presence and disturbance. A baseline study before translocation could determine the impact of the translocation on prey and competitors (Reading & Clark, 1996).

Translocation sites shold be evaluated in terms of habitat requirements, spatial characteristics, and management considerations (Reading & Clark, 1996). We caution, however, that *a priori* it is relatively easy to determine if habitat is inadequate (demonstrating that one or more critical elements are missing) but nearly impossible to demonstrate that habitat is adequate (determining that all critical elements are present).

Sites should be compared quantitatively during the selection process (e.g. Biggins, Miller *et al*., 1993b). Some obvious examples are prey, cover, denning sites, water sources, competitors, predators, and the presence of exotics. More difficult to assess are ecosystem resilience and the effects of disturbance such as fires, droughts, catastrophic storms, etc (Kleiman, 1989; Stanley Price, 1989; Reading & Clark 1996). Such disturbances will have effects that are scale dependent, and issues of scale are some of the most difficult to understand (Soulé, 1996). But the presence of large carnivores, with their extensive movements, allows managers to evaluate conservation issues across a landscape. Because the landscape level is important to regional biodiversity, and habitat fragmentation has its most drastic effects at that level of scale, large carnivores can be a good indicator of wilderness quality (Miller, Reading, Strittholt *et al*., 1999).

The degree of isolation, size, shape, and site location (in the context of historical range) are important spatial considerations (Kleiman, 1989; Reading & Clark, 1996). In North America, many of the native ecosystems are unrepresented or underrepresented in protected areas and only a small fraction of the reserves are large enough to maintain a full range of ecological processes or viable populations of middle-sized or large carnivores (Newmark, 1985; Caicco *et al*., 1995; Davis *et al*., 1995).

Habitat area is especially important for large carnivores. They exist at the top of the food chain and their densities are lower than species living at other trophic levels. So, when the average area of habitat patches declines through fragmentation and alteration, carnivore populations are among the first to disappear. Conflict with people on reserve borders is the major cause of mortality of large carnivores living in reserves, and it represents roughly 89% of the mortality for grizzly bears (Woodroffe & Ginsberg, 1998). Therefore, wide-ranging carnivores in small reserves are most vulnerable because they are more often exposed to the population sink that exists at the reserve boundary (Woodroffe & Ginsberg, 1998).

For that reason, sufficient prey is also a critical habitat trait (Sharps & Whitcher, 1982; Scott-Brown, Herrero & Mamo, 1986). With an adequate and constant prey base, carnivores will have smaller home ranges and wander over less territory. Fewer animals will therefore be exposed to the high mortality associated with reserve boundaries. Adequate prey densities also reduce the amount of livestock depredation and its consequent conflicts (Ravi Chellam & Saberwal, in press).

Even if large animals survive in fragmented habitats for long periods of time, their evolutionary potential is diminished. The forces of natural selection in small, isolated populations will be eventually overwhelmed by the randomized effects of genetic drift (Soulé, 1980, 1995, 1996). Evolutionary potential of large carnivores is necessary if they are to play a long-term role in ecosystem processes. Maintaining evolutionary potential in large animals will be impossible unless we can protect and restore large, and geographically extensive, populations (Soulé, 1995, 1996). By geographically extensive we mean for example, a system of core areas, linked by wildlife corridors, forming habitat connections throughout North America (Soulé, 1991, 1995; Noss & Cooperrider, 1994).

We recognize that while, in theory, corridors are a solution to habitat fragmentation, they are still a complex and controversial issue. Nevertheless, different types of connections could benefit carnivores. One involves connecting habitat patches within a protected area or the immediate region. Some large carnivores, like pumas, can negotiate through intra-reserve corridors even if there is an occasional bottleneck in the connection (Beier, 1993; B. Miller, pers. obs.). On the other hand, corridors to facilitate long-distance interchange between populations of a metapopulation may need to support residents of the focal species (Noss & Cooperrider, 1994). Even though there are records of dispersing large mammalian carnivores covering hundreds of kilometers, those individuals are usually juvenile males; conversely, the juvenile females establish territories relatively close to their area of birth (Greenwood, 1980). If we wish to maintain the capacity to naturally reestablish populations that have winked-out, we must create habitat connections that allow the movement of females.

Non-biological considerations

Technical considerations are closely related to the biological factors, and difficult management issues should be considered during the feasibility study (Reading & Clark, 1996). Questions posed by Kleiman, Stanley-Price & Beck (1993) include: what legal framework exists, and does the program comply with laws? Is there an active research program to devise tactics? Are there sufficient fiscal and intellectual resources to maintain the program? Will the program be adequately monitored? To these questions we might add: what are the goals of the reintroduction? What logistic challenges must be overcome? Is there an appropriate organizational structure for making decisions?

The reintroduction should be carefully monitored to determine causes of mortality, movements and behaviors of released animals, life history attributes, and changes in habitat. The results of monitoring can guide future releases; therefore, records need to be detailed and should extend to offspring of the released animals (Miller, Biggins *et al*., 1993). Unfortunately, monitoring is one of the first things many organizations eliminate in an effort to reduce expenses (Noss & Cooperrider, 1994).

Goals should be defined carefully to provide accurate evaluation. Defining success solely by survival can be misleading because mortality is likely to be high during early releases; alternatively, analysis of behavioral traits during early releases many provide clues as to how animals respond to their new environment and that can result in improved techniques (Kleiman, Beck, Dietz *et al*., 1986; Kleiman, Beck, Baker *et al*., 1990; Miller, Biggins *et al*., 1993). Knowledge gained toward improved translocation methodology may be the most important goal of early releases. High mortality is not a failure unless biologists do not learn enough to increase survival in future reintroductions. For that reason, careful planning with a sound scientific approach, and effective monitoring, will offer the most efficient path toward recovery (Miller, Biggins *et al*., 1993).

Funding and physical resources are always a problem in biology, and reintroduction programs are expensive. As we have discussed, reintroduction can involve a variable amount of pre-release conditioning and training. Different techniques require different resources, and since resources are always limited, cost–benefit analyses can be important. We suggest comparing techniques on the basis of cost per successfully reproducing female released.

A well-trained and dedicated staff with the appropriate expertise is crucial to program success. We contend that reintroduction programs may be even more vulnerable to staff changes than other biological programs because reintroduction programs are long-lived, require many difficult decisions made in near-crisis situations, and mistakes with small populations can be hard to reverse (Snyder *et al*., 1996). For that reason, careful attention to the organizational structure of the decision-making body is crucial to maintaining an efficient and effective program (Miller, Reading & Forest, 1996; Clark, 1997).

In conclusion, we have discussed some general guidelines for reintroducing carnivores, and included issues of taxonomy, age and sex, genetics, demographics, behavior, health, habitat, and some general non-biological considerations. Many of these issues apply to all types of translocation efforts, but we have concentrated on carnivores for several reasons. Carnivores often play a strong role in top-down interactions among trophic levels, they have been disproportionately extirpated from most of the world's ecosystems, fragmentation has rendered natural colonization difficult, and carnivores are disproportionately harder to reestablish via translocation. For additional 'how to' information on reintroduction issues please refer to the IUCN guidelines for reintroduction (IUCN, 1987) supplemented by Beck, Rapaport *et al*. (1993) and Kleiman, Stanley Price & Beck (1993).

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