The conservation-welfare nexus in reintroduction programmes: a role for sensory ecology

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Abstract

Since reintroduction programmes involve moving animals from captive or wild environments and releasing them into novel environments, there are sure to be a number of challenges to the welfare of the individuals involved. Behavioural theory can help us develop reintroductions that are better for both the welfare of the individual and the conservation of populations. In addition to modifying captive environments to prepare animals for release to the wild, it is possible to modify the animals' experience in the post-release environment. For releases to be more successful, they need to better accommodate the ecological and psychological needs of individuals. A better understanding of sensory ecology — how animals acquire and respond to information in their environment — is needed to develop new, more successful management strategies for reintroductions. Sensory ecology integrates ecological and psychological processes, calling for better synergy among researchers with divergent backgrounds in conservation and animal welfare science. This integrative approach leads to new topics of investigation in reintroduction biology, including more careful consideration of post-release stress and the role of social support. Reintroductions are essentially exercises in 'forced' dispersal; thus, an especially promising avenue of research is the role of proximate mechanisms governing dispersal and habitat selection decisions. Reintroduction biologists have much to gain from the study of mechanism because mechanisms, unlike function or adaptive value, can be manipulated to enhance conservation and welfare goals.

Keywords: *animal welfare, conservation breeding, habitat selection, reintroduction, sensory ecology, stress*

What is reintroduction and how does it relate to conservation and animal welfare?

The goal of most conservation-minded reintroduction programmes is the recovery of a species of conservation concern (eg threatened and endangered species). In cases where a species range is reduced to one or a few extant populations, there is a critical need to establish new viable populations to spread the risk over several areas so that a single catastrophic event cannot cause species extinction. Animals may be brought in from the wild for conservation breeding programmes designed to provide candidates for release back to the wild, or they may be captured and transferred directly to a new site without an intervening stint in captivity. Much effort is expended in the care of these animals, but only rarely does the welfare of individual animals figure prominently in strategic planning. From an animal welfare perspective, the fate of individuals matters most. In addition to the ultimate fate of released animals (life or death), animal welfare advocates are concerned with subjective experience of the animal throughout the reintroduction process. The International Union for the Conservation for Nature (IUCN) does mention welfare once in the guidelines: "The welfare of animals for release is of paramount concern through all these stages" of reintroduction (IUCN 1998). However, few wildlife managers and conservation biologists are equipped with the scientific tools of applied ethology and animal welfare science.

In preparing captive-living animals for life in the wild, concerns for welfare and conservation may collide. Beck (1995) and others have pointed out that providing for good welfare in captivity is often incompatible with the goals of reintroduction. Animals reared in captivity are 'softened' by a life relatively free of disease, predation, starvation, injurious conflict, and extremes of temperature. In fact, animals are likely to suffer after release if they are protected from the vagaries of nature in their captive environments. Hence, environments for reintroduction candidates should include some of the challenges they will face in the wild, even those which cause poor welfare in the short term, in order to promote good welfare — and survival — post-release.

Taken one step further, many have argued that captive environments need to maintain the selection pressures prevalent in the wild to prevent loss of genetic diversity, retain heritable survival skills, and avoid disruption of co-adapted gene complexes (Vrijenhoek & Leberg 1991; McPhee & Silverman 2004). The more generations spent

in captivity, the more profound the evolutionary consequences of relaxed (or altered) selection. Temperament appears to be one of the most evolutionary labile behavioural characters. Rapid change or loss of temperament types in captivity could compromise both welfare and conservation goals if release groups are composed of individuals with maladaptive temperaments or lacking the complete suite of behavioural types needed for the new population to thrive (McDougall *et al* 2006; Watters & Meehan 2007). Given that selection in captive environments involves differential survival and reproduction, a selection regime that maintains wild genotypes will undoubtedly compromise the welfare of some individuals. Thus, judicious decisions must balance the overall goal of the programme (species recovery) with the welfare concerns for individuals both in captivity and after release.

For these various reasons, reintroduction programmes will entail some welfare costs to individuals, but how can the gap between conservation and welfare goals be minimised? Recent calls for better integration of the distinct skill sets of welfare scientists and conservationists argue that this new synthesis promises strong returns for the investment, both for welfare and conservation (Swaisgood 2007; Teixeira *et al* 2007). Such a synthesis can be found in the emerging discipline of sensory ecology which aims to integrate Tinbergen's levels of explanation: causation, development, adaptive value, and evolutionary history (Tinbergen 1963). Sensory ecologists are interested in how animals acquire and respond to information in their environment and how this information acquisition contributes to population- and ecosystem-level processes (Dusenbury 1992). Examples of research in sensory ecology include prey detection (Goerlitz & Siemers 2007), signaling behaviour (Endler 1992), and assessment of predators (Swaisgood *et al* 1999), mates (Andersson 1994; Rich & Hurst 1999), competitors (Parker & Rubenstein 1981; Gosling & Roberts 2001), and habitat (Stamps 2001). By integrating ecological and psychological processes, researchers have made new inroads into important issues in behavioural ecology and, more recently, into conservation (Reed 2004; Lim *et al* 2008), captive breeding (Swaisgood 2007; Swaisgood & Schulte, in press), and enrichment strategies (Swaisgood *et al* 2005). A better understanding of sensory ecology is also needed to develop new, more relevant management strategies for reintroductions. Reintroduction biologists have much to gain from the study of mechanism because mechanisms, unlike function or adaptive value, can be manipulated to enhance conservation and welfare goals.

The term 'reintroduction' is unfortunately characterised by confusion. The IUCN defines reintroduction as "an attempt to establish a species in an area which was once part of its historical range, but from which it has been extirpated or become extinct" (IUCN 1998). The term refers to the release of both captive-bred and wild-caught animals, and confines reintroduction to those areas where the species no longer exists. 'Translocation' is defined as "the deliberate and mediated movement of wild animals or populations from one part of their range to another" thereby reserving the term for wild-to-wild animal relocations, whether or not a resident population is present at the release site. Finally, 're-inforcement/supplementation' refers to the "addition of individuals to an existing population of conspecifics" and can involve captive-bred or wild-caught animals. Among zoo biologists, reintroduction is usually taken to mean the release of captive-born individuals 'back to the wild' (Beck *et al* 1994) or simply as an umbrella term to refer to all types of intentional human-mediated animal movements. 'Animal relocation programme' has been proposed as a less-confusing term (Fischer & Lindenmayer 2000), but it has not caught on. Here, I will use 'reintroduction' as an umbrella term referring to the release of animals from wild or captive origins to areas with or without conspecifics.

What welfare problems do reintroduced animals face?

To understand the welfare impacts of reintroduction it is heuristic to take the perspective of an individual animal undergoing the reintroduction process. In the case of translocation, first the animal may suddenly find itself confined in a trap, experiencing frustrated motivation to escape. Then, the trapped animal is approached by humans (likely perceived as predators), handled, transported to a novel environment, and either held in a human-constructed enclosure or released immediately (Griffith *et al* 1989). In its home area it had invested considerable time and energy learning how best to exploit local resources (Stamps & Krishnan 1999; Inglis *et al* 2001). It had learned where to find food resources, including those that are seasonally limiting. It knows where predators lurk, how to avoid them, and where to find cover or refuge (Lima & Dill 1990). It knows its place in the social group and is able to maintain its position with minimal escalated aggression (Huntingford & Turner 1987; Archer 1988). If territorial, it has established beneficial relationships with its neighbours that reduce conflict and defence costs (Temeles 1994; López & Martín 2002). Forced to forego a lifetime of such graduallly acquired, situation-specific knowledge, the animal must deal with its post-release environment without many of the advantages it retained at home. Under stress and cognitively impaired (Teixeira *et al* 2007), the animal ventures into a dramatically novel and dangerous environment. Now consider this scenario for a captive-bred animal. While some of the stressors associated with capture and transport may be alleviated by prior exposure to humans and human-altered environments, the post-release challenges must be much greater because a captive-bred animal has less generaliseable knowledge of how to cope in the wild, to the extent that its captive environment differs from nature.

Given this scenario, an animal welfarist might argue that reintroduction involves unacceptable welfare costs. But one must also consider the alternative. Conservation goals aside, animals may need to be translocated for a variety of reasons, including increasing anthropogenic change making the environment no longer suitable for the source population (Teixeira *et al* 2007). In some cases, animals may need to be

pulled from the wild to remove them from (typically) anthropogenic threats, reared in captivity, and released back to the wild after they have 'outgrown' the threat. Such 'headstarting' programmes are a common tactic used to rescue endangered herpetofauna from invasive predators (Alberts 2007). Here, the welfare costs of captivity and reintroduction may outweigh the welfare costs (and risk of death) if headstarting was not attempted.

More commonly, however, source animals are captured from an area where they are doing well — that is, from a stable or growing population with surplus animals that can be used to establish a new population elsewhere. The goal is not individual welfare, but reducing the long-term risk of extinction of the species. Here, and in the majority of conservation-driven reintroduction programmes, there are clear welfare costs to individuals, which need to be balanced against conservation goals and, where possible, minimised.

Are reintroductions successful?

Are reintroductions successful from a conservation perspective? So far, documented successes are few and far between. Most reintroductions are judged by the outcome of establishing a viable population, and the failure rate may approach 75–90% (Beck *et al* 1994; Wolf *et al* 1998). Successful or not by this definition, many released animals — whether captive-bred or translocated from another wild population — die within days or weeks (Beck *et al* 1994; Stamps & Swaisgood 2007; Teixeira *et al* 2007), and there has been little to no improvement over the past twenty years (Fischer & Lindenmayer 2000). Reintroductions often fail for one of several reasons: limited understanding of the species' basic ecology and behaviour, poor planning for the release, and lack of post-release monitoring to determine success and identify problem areas for improvement. Virtually all reviews of reintroductions conclude with a plea for more rigorous evaluation and testing of the factors involved in success and failure, but progress continues to be slow (Armstrong & Seddon 2008).

Nonetheless, a number of lessons have been learned. We know, for example, that: (i) translocated wild animals fare better than released captive-reared animals; (ii) the quality of habitat at the release site matters; (iii) it is better to release animals near the core than the periphery of their historical range; and (iv) releasing more animals increases the chances of long-term success (Griffith *et al* 1989; Beck *et al* 1994; Wolf *et al* 1998; Fischer & Lindenmayer 2000). Other factors, such as using soft-release vs hard-release methods (defined below), do not significantly improve success in these meta-analyses. We can also reasonably assume that it is important to first eliminate the threat that originally caused species decline, that local community and government buy-in is essential, that captive environments should mimic nature, and that better post-release monitoring is needed (Kleiman 1989).

What more can be done to increase reintroduction success for the benefit of both conservation and the welfare of the animal post-release? For the remainder of this paper I focus on new ways to tackle problems with reintroductions based on concepts in behavioural ecological theory that yield promising hypothesis-testing approaches and an 'adaptive management' paradigm wherein the animal and its pre- and post-release environments are systematically manipulated, with intensive monitoring to provide feedback and guide changes in reintroduction protocols (Armstrong *et al* 2007; Armstrong & Seddon 2008). I propose that some of the most readily manipulable aspects of reintroductions relate to the species-specific sensory ecology of individuals.

Preparing captive-bred reintroduction candidates for life in the wild

A number of reintroduction programmes have involved extensive modifications and enrichment of the captive environment to prepare captive-bred animals for life in the wild (Kleiman 1989, 1996). Captivity has a variety of effects on behavioural development, some of them detrimental to reintroduction (Carlstead 1996). Not only are specific survival skills absent in the behavioural repertoire of many captive-reared animals (Beck *et al* 1994), but there can be general effects that compromise behavioural competence, effects that can be offset with enrichment programmes.

Several studies have demonstrated positive developmental effects on brain and cognitive function. Animals reared in more enriched environments have a heavier cerebral cortex, more glial cells, enhanced synaptic connectivity, increased acetylcholinesterase, and increased levels of RNA in the brain, which are thought to reflect memory consolidation (Greenough 1976; Renner & Rosenzweig 1987). These animals also demonstrate improved learning ability, as evidenced by better performance on discrimination and maze tests, are less emotionally reactive, and are more exploratory and less hesitant with novel objects and places (see also, Meehan & Mench 2002). In addition, some captive animals, particularly those with high rates of stereotypy, as may result from impoverished environments, may find it difficult to unlearn what has been learned (Garner *et al* 2003; Vickery & Mason 2004; Mason *et al* 2007). Clearly, reintroduced animals need all their cognitive and learning skills intact if they are to adapt to new challenges they will face in the wild (Teixeira *et al* 2007).

Several case studies provide model reintroduction programmes. The golden lion tamarin (*Leontopithecus rosalia*) programme has used an adaptive management approach, with several iterations before an acceptable level of success was realised (Beck *et al* 1991; Castro *et al* 1998). Several types of pre-release training — such as locomotor training, food-search tasks, and other forms of enrichment — had no effect on post-release survival. The method found to work best was pre-release, free-ranging experience on the zoo grounds combined with extensive post-release support. In another model programme, researchers manipulated and tested a number of variables in the captive environment of black-footed ferrets (*Mustela nigripes*) designated for release (Miller *et al* 1998; Vargas & Anderson 1998, 1999; Biggins *et al* 1999). Variables manipulated included pen size, various forms of naturalistic enrichment, opportunities for digging burrows, experience

with live native prey, and anti-predator training. Close post-release monitoring allowed them to determine the effects of these variables on behaviour, settlement, survival, and reproduction, and ultimately devise a more effective reintroduction programme for the species.

Captive-bred prey species are particularly vulnerable, as predation is one of the most significant threats to reintroduction of predator-naïve animals (Griffin *et al* 2000). Consequently, anti-predator training has become one of the most common behavioural manipulations in captive-release programmes (Bunin & Jamieson 1996; McLean *et al* 1999, 2000; van Heezik *et al* 1999; Blumstein *et al* 2001, 2002). These programmes require significant study to determine what kinds of experiences promote the development of effective antipredator behaviour. For example, Shier and Owings (2006, 2007) demonstrated that experience with predators improves antipredator behaviour and post-release survival, but providing a wild-caught conspecific as a demonstrator of appropriate antipredator behaviour markedly enhanced the effect. These studies show how application of behavioural theory, matched with rigorous hypothesis-testing, can improve reintroduction success. Although antipredator training likely evokes a stress response in captive animals, the long-term welfare is presumably better for animals equipped with realistic expectations of predation threat.

The recent application of the concept of temperament to reintroduction programmes is an emerging and promising development. Although temperament has long played a role in the literature of psychology (Koolhaas *et al* 1999; Gosling 2001) and applied ethology (Grandin 1998; Price 1999), the concept is relatively new to ecology and evolution (Sih *et al* 2004; Réale *et al* 2007), apart from recognising a shy-bold continuum in antipredator behaviour (eg Wilson *et al* 1993). In both the psychological traditions and the emerging interest in 'behavioural types' among ecologists, a major focus is on how temperament affects perceptual processes such as: responsiveness to novel environments and potential stressors; cues used to assess predators, mates, competitors, or habitat; risk assessment across a variety of situations; and other information-acquisition activities. A greater understanding of these processes — and inter-individual variation in their expression — can be useful when applied to reintroduction programmes.

The gathering momentum in this area of inquiry holds great promise for application to conservation (McDougall *et al* 2006; Watters & Meehan 2007). For example, captive-reared weasels (*Mustela nivalis nivalis*) are less timid than their wild-caught counterparts, and are therefore more visible — and susceptible — to predators (Hellstedt & Kallio 2006). In whooping cranes (*Grus americana*) vigilance levels in captivity predict vigilance levels post-release, and rearing techniques strongly influence both vigilance levels and tendency to group with conspecifics (Kreger *et al* 2005). Vigilance behaviour also significantly affected post-release survival (Kreger *et al* 2006). Bremmer-Harrison *et al* (2004) measured levels of boldness in captive

swift foxes (*Vulpes velox*). They found that individuals that more readily approached novel objects and behaved less cautiously in their presence were significantly more likely to die within six months post-release. In most cases, the cause of death was unknown, but the fact that bold individuals ranged farther probably exposed them to more risks, such as road traffic and predators. These examples underscore the important effects of captivity on temperament-mediated, post-release survival. Solutions to these problems include careful screening of reintroduction candidates for temperament traits, or modification of captive environments to regulate the development of at-risk behavioural types.

However, elimination of certain behavioural types from reintroduction programmes may be counterproductive to conservation goals. Watters and Meehan (2007) argue convincingly that release groups should be composed of the whole suite of behavioural types present in a species. The post-release environment varies temporally and spatially and it is quite possible that different behavioural types will perform better in different environments. Behavioural type is heritable, but also influenced by the environment. The implication for reintroduction is that individuals representing the full genetic variability for behavioural types should be included in releases. Equally important is providing the appropriate developmental influences to increase the expression of multiple behavioural types. This means that reintroduction candidates will need to be reared using different husbandry and enrichment protocols, rather than using a single 'optimal' method. Thus, to create the best release strategy, it will be necessary to expose individuals to different environments that will, undoubtedly, be associated with different levels of welfare and, moreover, to knowingly risk the lives of some behavioural types that are ill-equipped to deal with a particular post-release environment. Consideration of behavioural types may be equally important for translocations. Animals rescued from small habitat fragments or animals captured may not be representative of the whole population of behavioural types. Indeed, any time the site of capture has only a limited array of habitat types — especially if they differ from the release site — the right behavioural types may not be translocated. Also, the method of capture may be important; for example, bold ('trap-happy') individuals may be better represented than 'trap-shy' individuals.

Management of the post-release environment

Management strategies for the post-release environment are less well developed. 'Hard release' entails little more than transport and release with few if any efforts to support the animal after release. 'Soft release' protocols typically include a period of acclimation at the release site to adjust to local conditions and perhaps learn something about the environment outside the enclosure (Griffith *et al* 1989; Kleiman 1989; Beck *et al* 1994). Reintroduction managers may also make efforts to reduce stress during transport or provide supplemental food or water for a short transitional period. The rationale for supplemental food is straightforward: it may reduce weight loss often experienced by rein-

troduced animals (eg Bright & Morris 1994), buying time for the animal to explore and adapt to its new environment without facing the challenge of finding food resources. Intervention to rescue or assist releasees at risk is also made possible by post-release monitoring.

It is surprising how infrequently these methods develop from behavioural and ecological theories and how few releases involve comparing different methods to move the technique forward. When such methods are tested, the results are sometimes surprising. For example, expensive and labour-intensive soft-release techniques may sometimes confer little or no advantage, despite their intuitive appeal (Wolf *et al* 1998). Soft-release programmes may fail for several reasons, but a prominent one is that many released animals simply do not remain near the release site long enough to benefit from the support system that managers provide (Bright & Morris 1994; Seddon 1999; Stamps & Swaisgood 2007). Thus, it is time to move beyond simple concepts of soft release and find more guidance from the behavioural and ecological phenomena that influence how animals respond to the challenges of relocation.

The use of social support shows how the application of behavioural knowledge can improve post-release success. While the number of animals released is often carefully considered in reintroduction programmes (Griffith *et al* 1989; Beck *et al* 1994; Taylor *et al* 2005), the composition of the release group is rarely taken into consideration beyond age and sex categories of releasees. In social species, conspecifics form relationships that confer fitness advantages (eg Dugatkin 1997). These relationships are particularly important in a challenging post-release environment. Recent studies with black-tailed prairie dogs (*Cynomys ludovicianus*) (Shier 2006) show that animals translocated in family groups were less likely to be killed by predators, had five-fold higher survival, and higher reproductive rates than animals released in groups of unfamiliar individuals. Familiar conspecifics are important for welfare, and disruption of these social relationships is a potent source of stress (Moberg & Mench 2000). Even more importantly, social companions can buffer animals from other external stressors such as novel environments; that is, animals perceive novelty differently when in the company of familiar conspecifics (Sachser *et al* 1998; DeVries 2002).

In stable populations, even territorial species have negotiated relationships with their neighbours and interact differently with them than with strangers, where aggression is prone to escalate (Huntingford & Turner 1987). For example, in black rhinoceros (*Diceros bicornis*) aggression levels are moderate and serious injury rare in stable source populations, but following translocations into unoccupied reserves aggression levels are unacceptably high, leading to high rates of injury and death (Linklater & Swaisgood 2008). Rhinos released into larger reserves are able to avoid one another successfully, whereas in smaller reserves rhinos encounter each other more frequently. Not only does this result in higher fight-related injuries and deaths, but rhinos also are more likely to injure themselves

attempting to escape through the boundary fences. Social instability and stress from frequent conspecific encounters contribute to this behaviour. Thus, xenophobic tendencies can interact with other factors, such as reserve size and release density, to exacerbate conservation and welfare problems in reintroduction programmes. Clearly, choosing the right number of animals and sufficient space to accommodate space- and familiarity-mediated aggressive behaviour can counteract these problems. In the modern landscape, reserves are increasingly bounded by fences or other barriers to animal movements, so this issue will likely become more important in the future.

From a conservation perspective, reproduction post-release is all-important to establish a self-sustaining population in nature (IUCN 1998). Animal welfarists also include opportunities to mate and rear offspring among the goals for establishing good psychological well-being. How can release strategies be managed to maximise the probability of rapid and successful reproduction? For monogamous species, releasing pair-bonded and behaviourally compatible pairs can increase success (Munkwitz *et al* 2005). For species dependent on refuges, such as nesting cavities or burrows, the distribution of these important resources may affect access to mating partners (Gerber *et al* 2003) in addition to their more obvious effects on survival. Thus, post-release environments should be surveyed for such security areas to ensure sufficient availability and appropriate spacing for both survival and reproduction. If availability is inadequate, construction of artificial nests (Piper *et al* 2002; Bolton *et al* 2004), burrows (Souter *et al* 2004), or dens (Zhang *et al* 2007) may be warranted and cost-effective. Adequate security is a prerequisite to both conservation and welfare objectives.

Ensuring reproduction, even for all released females, however, does not ensure a self-sustaining population. Mating systems can dramatically affect effective population size (Ne). Reproductive skew — in which some individuals have higher reproductive success than others — reduces Ne, resulting in loss of genetic diversity and evolutionary potential to adapt to changing environments (Anthony & Blumstein 2000; Wedekind 2002). The distribution of resources on the landscape can determine whether a few males can monopolise reproductive access to females. The sequence in which males are released can also influence establishment of site-specific dominance and access to females (Saltz *et al* 2000).

There are also a number of ways to manipulate mate-choice signals to counteract reproductive skew driven by female choice (reviews in Swaisgood 2007; Swaisgood & Schulte, in press). This application of sensory ecology involves: (i) research to understand the production of mate-choice signals and their impacts on the receiver's mate-choice decisions; (ii) collection or synthesis of preferred versions of these signals; and (iii) manipulation of these signals to alter female mate choice to favour unrepresented males. While there are only two empirical conservation-relevant examples in the literature (Fisher *et al* 2003a,b; Roberts & Gosling 2004),

this approach is fairly widespread among behavioural ecologists interested in sexual selection (Andersson 1994) and in some cases can be relatively simple and cost-effective (for example, supplementing male diets to promote the development of condition-dependent signals).

The role of sensory ecology in reintroduction programmes

Other aspects of sensory ecology offer opportunities for reintroduction programmes. Surprisingly, two of the primary issues in this arena are quite well established elsewhere in the literature, but only recently have researchers begun to realise their potential in reintroduction programmes. The first is the potential importance of the stress response — a topic central to animal welfare but largely ignored in reintroduction research (Teixeira *et al* 2007). The second is dispersal, which may turn out to be one of the most important behavioural ecological concepts in reintroduction programmes.

How does post-release stress impact performance?

'Stress' is a complex concept, subject to considerable debate on definition and even the usefulness of the concept itself (Hofer & East 1998; Moberg & Mench 2000; Sapolsky *et al* 2000). Most researchers, however, are in general agreement that stress is the outcome of the animal's perception of a threat that challenges homeostasis or fitness, and the behavioural and physiological adjustments that the organism undergoes to avoid or adapt to the threat. 'Stressors' are the external threats, and the behavioural and physiological reactions are the 'stress responses'. Here, I will use the term 'stress' loosely as a descriptive concept to refer to these processes. Thus defined, stress has important consequences for conservation and welfare. Partly because the stress response diverts mobilisable energy away from some basic functions, such as digestion, immune response and reproduction, it can have negative effects on health and reproduction. Signs of stress are also correlated with other measures of poor welfare, and excessive or chronic stress is considered detrimental to welfare (Broom & Johnson 1993; Moberg & Mench 2000). In consequence, research on stress has long played a major role in animal welfare science and is becoming an important tool in conservation programmes. What constitutes a stressor varies widely among species and even among individuals. These characteristics make stress a challenging topic for research.

Systematic research to understand the implications of stress in conservation programmes involves identifying how animals perceive environmental change and challenge. Animals may detect sources of stress that are not detected by humans (Morgan & Tromborg 2007). For example, polar bear (*Ursus maritimus*) biologists are concerned about the impacts of noise pollution from industrial activities in the arctic, such as petroleum exploration and development, which include very high and very low frequency sounds. Recent findings demonstrate that polar bears can indeed hear better at lower frequencies than other carnivores studied, increasing concern for this class of noise (Owen & Swaisgood 2008). The potential for such disturbance must be considered when determining appropriate release sites in reintroduction programmes.

Captive-held animals are especially susceptible to stress, in part because small enclosures may not allow animals to execute normal escape and avoidance responses to aversive stimuli, and other coping mechanisms may be similarly constrained. Researchers in zoo settings have borrowed many of the stress research tools from psychologists and applied ethologists to enhance breeding and welfare in zoo animals (Carlstead 1996; Carlstead & Shepherdson 2000; Shepherdson *et al* 2004; Morgan & Tromborg 2007). Working with small sample sizes, endangered species, and limited experimental control makes statistically robust studies a challenge, but has also increased efforts to understand individual variation and to work closely with animal caretakers to provide direct, rapid feedback to benefit animals (eg Owen *et al* 2004; Swaisgood *et al* 2006). Thus, carefully controlled research, even with small numbers, can have important consequences for individual animals and provide a model for others to utilise. Escalating contact — and conflict — between humans and animals is drawing increasing interest from conservation biologists, who have documented a number of stress-mediated negative consequences for populations of wild animals (Hofer & East 1998; Tarlow & Blumstein 2007).

Stress can have important implications for both captive releases and translocations (Teixeira *et al* 2007). Acclimation techniques, wherein animals are held at a release site to adapt to local conditions, may give animals time to recover from the stress of handling and transport. In some cases, animals have been treated pharmacologically to reduce short-term stress during animal relocation (eg Letty *et al* 2000), but manipulations designed to determine how animals perceive and respond to different activities during reintroductions have rarely been carried out.

Reintroduction managers do not seem to be aware of the plethora of negative influences stress can have on perception, learning, and cognition — all crucial skills that should be intact during the challenge of reintroduction (Teixeira *et al* 2007). Stress can weaken memory consolidation, compromise learning abilities, alter attention mechanisms and threat perception, and impact decision-making and other cognitive processes (Teixeira *et al* 2007). How does an animal with impaired learning abilities adapt to its novel environment, learn the distribution of important resources such as food and cover, and interact with unfamiliar conspecifics? How do attention deficits influence its ability to detect predators and other threats? During a time when every decision can mean life or death, can such an animal be expected to make the best decisions? Stress may also affect how animals move through the environment and expose themselves to risks. If the 'fight-flight' mode of the stress response is activated, their attempt to escape may expose them to greater risk of predation. Alternatively, if they adopt the conservation-withdrawal mode, they may

remain in an area for too long, allowing odours to accumulate that attract odour-guided predators (Banks *et al* 2002). These examples indicate that high post-release predation may result partly from an interaction between stress-induced maladaptive behaviour and the sensory mechanisms that predators use to locate prey.

These observations underscore the importance of understanding and mediating stress during reintroductions. They also bring to the fore the realisation that even short-term stress, lasting a few days, should not be taken lightly, as is often the case (eg Hartup *et al* 2005).

The sensory ecology of animals on the move: dispersal and habitat selection

Translocation and captive-release programmes are essentially exercises in 'forced dispersal' for conservation purposes (review in Stamps & Swaisgood 2007). A widespread problem with animal relocations is that many releasees move away from the release site rapidly, 'dispersing' over long distances (Griffith *et al* 1989; Kleiman 1989; King 1990; Short *et al* 1992; Yalden 1993; Miller *et al* 1999) and sometimes 'homing' back to their capture site (Miller & Ballard 1982; Fritts *et al* 1984). This dispersal post-release may arise because the animal finds itself in a habitat that it perceives, rightly or not, to be unsuitable and searches for one that is more favourable. Dispersal is a dangerous life-history stage even for naturally dispersing animals, more so for animals forced to disperse into unfamiliar environments. It is unsurprising, then, that mortality is highest during the immediate post-release period (Brittas *et al* 1992; Sjöåsen 1996; Castro *et al* 1998; Kenward & Hodder 1998; Sarrazin & Legendre 2000) and that a large proportion of these deaths is attributed to the perils of long-distance dispersal (King 1990; Bright & Morris 1994; Linnell *et al* 1997; Biggins *et al* 1999). To the extent that delayed habitat selection and settlement exacerbate these dangers, efforts to understand and manage these behavioural processes promise to improve the success of animal relocations. Reducing post-release dispersal distances is important not only because of these risks, but also because keeping animals close to the release site improves the ability of conservation managers to monitor, provision, and otherwise intervene to assist releasees during this critical period as they adapt to the novel environment (Stamps & Swaisgood 2007). Reducing early mortality is especially important in light of the small number of founders generally used to 'seed' an area in reintroductions where the local population has been extirpated. High losses at this time can greatly compromise genetic diversity. Conservation managers already recognise these risks, and sometimes use acclimation techniques to attempt to reduce post-release dispersal movements (Bright & Morris 1994; Linnell *et al* 1997; Miller *et al* 1999; Letty *et al* 2000; Moehrenschlager & Macdonald 2003).

Ecologists have recently come to appreciate how perception and decision-making by dispersers determine the distribution and abundance of animals on the landscape (Lima 1996; Stamps 2001). Perceptual constraints, for example, limit the distance at which preferred habitats may be detected by dispersers, preventing animals from meeting predictions (or in some cases assumptions) laid out in optimality-based models (Lima 1996). Dispersers must balance energy available for further dispersal, search costs, search time, all the while relying on poor information about the distribution and quality of habitat patches (Davis 2007). Since direct assessment of each patch encountered is not cost-effective, dispersers must rely on indirect cues that correlate with habitat quality (Stamps 1988; Davis & Stamps 2004). Cue use and decision-making rules can change over the course of a dispersal event as energy reserves are depleted or as the animal learns about habitats encountered and adjusts its expectations of the quality of habitat it is likely to find. These assessments, along with the starting condition of dispersers upon leaving their natal habitat, can dramatically affect acceptance thresholds for habitats encountered during dispersal (Stamps *et al* 2005, 2007; Stamps 2006; Davis 2007). To reduce the costs of dispersal — such as high probability of death — reliance on cues can be so important that relatively poor quality habitat may be selected just because it is easily detected by the sensory apparatus of the disperser (Stamps & Krishnan 2005).

The influence of perception on habitat selection behaviour is of increasing importance in today's fragmented landscape (Lima 1996; Bélisle 2005). The functional connectivity of the landscape is determined by the animals' perception of gaps in the landscape more than by their physical ability to cross such gaps. This realisation introduces other concepts unfamiliar to most ecologists, such as motivation and risk assessment, which influence an animal's willingness to move through a landscape. In fact, McDonald and St Clair (2004) conclude that the "nature of barrier types (artificial or natural) may be less important in determining barrier permeability than are differences in perception among species…".

These same perceptual and decision-making processes undoubtedly influence the movement of releasees in reintroduction programmes. Several hypotheses, including 'conspecific cueing' and 'natal habitat preference induction', have been advanced to explain how natural dispersers select and settle in habitat. These hypotheses show great, but largely unrealised, promise for application to reintroduction management.

Conspecific cueing

The conspecific cueing (or conspecific attraction) hypothesis posits that in many species dispersers rely on the presence of conspecifics to assess habitat suitability (Stamps 1988). Somewhat counter-intuitively, this hypothesis applies to relatively solitary, territorial species, as well as to social species. Ecologists had long believed in the 'ideal free distribution' of animals on the landscape, wherein population density directly reflected habitat quality (Fretwell & Lucas 1970). Dispersers were predicted to settle in the most suitable habitat and to avoid settling in close proximity to conspecific competitors. Turning this prediction on its head, Stamps (1987) found that *Anolis* spp lizards preferred to settle adjacent to conspecifics.

As Stamps (1988) proposed, conspecifics may be a cue to habitat quality, providing valuable information to risk-prone dispersers looking to settle quickly. To dispersers, the presence of conspecifics integrates multiple components of habitat quality — including foraging resources, security areas, and predation risk — into one simple, conspicuous cue. Since the hypothesis was proposed, tests in a variety of vertebrate species support the notion that conspecific cueing is a widely distributed behavioural phenomenon even in relatively asocial species (Smith & Peacock 1990; Reed & Dobson 1993; Dobson & Poole 1998; Stamps 2001).

These observations pose a problem for conservation managers attempting to recruit animals into suitable but unoccupied habitat, such as newly created protected areas (Reed & Dobson 1993; Dobson & Poole 1998). If the species has been eradicated in the area, animals may not recolonise it through natural dispersal, or — as is the case for red kites (*Milvus milvus*) — recolonisation may proceed slowly with initial dispersers settling in one area and subsequent dispersers settling next to them, gradually radiating out (Newton *et al* 1994). Conspecific cueing may also help explain why so many reintroduction programmes fail: released animals may not settle in suitable habitat at the release site, choosing instead to disperse to another area in search of conspecifics.

Reintroduced griffon vultures (*Gyps fulvus*) appear to do just that, settling in the closest habitat with the largest existing population of conspecifics (Le Gouar *et al* 2008).

Could the behavioural mechanisms underlying conspecific cueing be manipulated to achieve conservation goals (Reed 2004; Swaisgood 2007)? The key is to understand, through research, which cues animals use to identify the presence of conspecifics and find ways to manipulate these cues to encourage settlement. Acoustic cues, such as song playback, promote settlement into unoccupied habitat (eg black-capped vireos [*Vireo atricapilla*]; Ward & Schlossberg 2004). Visual cues (decoy models of conspecifics) will attract colonially nesting fairy terns (*Sterna nereis*) to safe breeding sites (Jeffries & Brunton 2001). Reintroduced griffon vultures can be attracted to new breeding sites by painting cliffs with white paint mimicking the accumulation of faeces (Sarrazin *et al* 1996). For many mammals, the appropriate cue may be olfactory. Translocated black rhinoceros can be induced to settle next to 'virtual scent territories' by spreading conspecific dung in a way that mimics natural dung-marking patterns (Linklater & Swaisgood 2007). However, selection of cues must proceed only after careful study of how animals respond to these cues because some conspecific cues (eg dominance signals) could deter settlement (Swaisgood *et al* 2004). In laboratory experiments, common lizard (*Zootoca vivipara*) 'dispersers' showed behaviour indicating willingness to settle when exposed to the scent of solitary conspecifics, but showed avoidance to communal scents indicative of higher social density (Aragón *et al* 2006).

Other variations on conspecific cueing raise additional possibilities for cue manipulation in reintroduction contexts. In some cases heterospecific cues from animals with similar habitat preferences have been used to encourage settlement (Parejo *et al* 2004; Fletcher 2007). Heterospecific cues may be easier to obtain than those from endangered species typically used in reintroductions. According to the 'public information hypothesis', animals may use performance-based cues. For example, there is evidence that animals use breeding success of conspecifics to assess habitat quality, which guides decisions in selecting breeding sites (Danchin *et al* 2001; Sergio & Penteriani 2005). Performance cues may be more effective than cues indicating presence but not reproductive success. Potential manipulations for reintroduction capitalising on these findings include planting artificial conspecific nests with eggs, playbacks of chick begging calls, or scent from multiple young animals.

Natal habitat preference induction (NHPI)

Similar to the concept of habitat imprinting, NHPI occurs when an animal's experience in its natal habitat shapes its post-dispersal preference for habitat settlement (Davis & Stamps 2004). Positive NHPI, where animals prefer to settle 'someplace like home', is more common, but there are also examples of dispersers with poor experience in natal habitat rejecting their natal habitat type. As with other mechanisms guiding dispersal, dispersers appear to use simple, easily detectable cues to guide dispersal decisions. During its development, an animal learns to associate a subset of available stimuli with its natal habitat and search for these relevant stimuli during dispersal. The phenomenon of NHPI is widespread across vertebrate and invertebrate taxa. The outcome of NHPI has also been shown to drive genetic structuring of populations, providing an example of how behaviour can drive evolution. For example, wolves (*Canis lupus*) of two different ecotypes, based on prey specialisation, disperse within their natal habitat type and breed among themselves even though their ranges overlap extensively, driving genetic divergence without barriers to dispersal (Carmichael *et al* 2007).

NHPI strategies may be beneficial to dispersers for two non-exclusive reasons (Stamps & Swaisgood 2007). Experience in a particular habitat may increase performance in that habitat. For example, predators may learn the skills needed to capture prey species native to that habitat, prey may learn more effective antipredator behaviour for predators specific to a habitat, and herbivores may develop modified foraging skills or digestive systems to deal with local plant defences. Thus, an animal developing in natal habitat type A obtains significant fitness payoff if it selects habitat A over habitat B when dispersing. This may be true even when habitat B is more suitable for the species in general. Settling in 'someplace like home' may also make dispersal more efficient. A disperser has limited time for direct assessment of habitats along its path of dispersal, but has a great deal of information about the natal habitat that supported it successfully to the age of dispersal. Thus, to find suitable habitat with minimal risks and energy costs, the animal may simply learn a few

conspicuous cues in its natal habitat and keep dispersing until it finds habitat with these same cues.

For reintroduction programmes, the possibility of NHPI means that managers need to consider more than just the suitability of the post-release environment for 'typical' members of the species (review in Stamps & Swaisgood 2007). Animals released into habitats differing from their natal habitat may fail to remain near the release site and pay higher search costs that compromise conservation and welfare goals. These possible consequences remain largely untested in reintroductions, but several lines of evidence are consistent with NHPI playing a key role in the poor outcomes of many reintroductions. Owen-Smith (2003) suggests that translocated African ungulates often perform poorly even in 'ideal' habitats because they need time to adjust to novel foraging tasks. Translocated elk (*Cervus canadensis*) from natal habitat dissimilar to the release site habitat show more maladaptive behaviour and suffer higher mortality than those from environments that are similar to the release site (Warren *et al* 1996). Translocated red squirrels (*Sciurus vulgaris*) (Kenward & Hodder 1998) and hedgehogs (*Erinaceus europaeus*) (Morris *et al* 1993) settled in habitats similar to their natal habitat, even though many had to traverse other habitat suitable for their species.

Captive-release programmes may also suffer from NHPI-like preferences for the artificial environments of captivity (Stamps & Swaisgood 2007). For example, NHPI may have been responsible for released California condors (*Gymnogyps californianus*) using power lines as perches (much to their detriment), Guam rails (*Gallirallus owstoni*) avoiding their native thick habitat in favour of more open roads, and peregrine falcons (*Falco peregrinus*) invading the cities and nesting on skyscrapers (in this case a successful choice). In each of these cases, stimuli in the captive environment appeared to influence habitat use post-release. Conversely, animals reared in more enriched, naturalistic environments may develop preferences for environments more similar to what they will encounter upon release back to the wild (eg Biggins *et al* 1999). These results underscore that animals need not 'instinctively' know what is good for them. If there is a mismatch between natal and release environments, animals may avoid the unfamiliar and choose the familiar over the unfamiliar, even if the choice is maladaptive.

Stamps and Swaisgood (2007) outlined some possible solutions to NHPI-related problems in reintroduction programmes. The biggest challenge will be identifying those cues that are most biologically salient and easily manipulated in a reintroduction context. Several approaches are worth exploring: (i) select a release site where the habitat is similar to the natal habitat of the source population; (ii) avoid creating preferences for cues in artificial environments in captive-reared animals; (iii) plant cues from the release site habitat in the natal habitat of the source population, (captive or wild) and/or vice-versa; and (iv) plant conspicuous, biologically salient cues in both the natal habitat (captive or wild) and the release habitat. These cues could even be artificial cues (such as flags) if placed in both environments.

Animal welfare implications and conclusion

Welfare goals are focused on the individual whereas conservation goals are focused on the population. However, since populations are composed of individuals there must be a large domain where conservation and welfare goals are compatible. This shared domain can be increased when sound behavioural research is applied to solve real-world conservation and welfare problems in reintroduction programmes. A better understanding of proximate mechanisms, especially those underlying sensory ecology, will play an instrumental role in moving these goals forward. Behavioural ecologists have been slow to shift their focus from adaptive value to a more pluralistic approach involving all four of Tinbergen's levels of explanation, to the detriment of efforts to move conservation behaviour beyond implication to application (Linklater 2004; Swaisgood 2007). Behavioural ecology provides the most compelling theoretical framework for identifying mechanisms that we can manipulate for conservation gains, but a new synthesis including applied ethology's approach to perceptual and cognitive mechanisms could put us on a better, more direct path to achieving conservation and animal welfare goals.

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