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

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Abstract

Coming soon

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

Introduction

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

The term *reintroduction* is unfortunately characterized by confusion. The World Union for the Conservation for Nature (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 does not stipulate the animal’s origin and refers to both captive and wild animals, but confines reintroduction to those areas where the species no longer exists. A sister term, *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’s use to wild-to-wild animal relocations, but does not indicate whether 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” but again does not specify the origin of the released animals. The IUCN guidelines do not provide specific terminology for release of animals whose origin is from captive stock. In more general parlance, and especially among zoo biologists, reintroduction is 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 program*” has been proposed as a less confusing term (Fischer and Lindenmayer 2000), but it has not caught on, perhaps because it is unwieldy, lacks historical significance, or subtly implies wild-to-wild relocations (translocations) more than releases from captivity. 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. Much of my discourse on reintroduction here will focus on the captive-field interface and therefore on “*captive-release programs*.”

The goal of most conservation-minded reintroduction programs is the recovery of a species of conservation concern (e.g., 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, spreading the risk over several areas so that a single catastrophic event cannot decimate the remaining population(s). For the most part, the conservation community treats reintroduced animals as chess pieces employed in a larger strategy to “save the species.” Animals may be brought in from the wild for conservation breeding programs 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. Of course, a great deal of effort is expended in the care of these animals, but only rarely does the welfare of individual animals figure prominently in strategic planning. To be fair, the 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) P9. The fact remains, however, that few wildlife managers and conservation biologists are equipped with the scientific tools that applied ethologists and others working in welfare disciplines have at their disposal. Recent calls for better integration of the distinct skillsets 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). Among other things, welfare scientists bring to the table a better understanding of proximate mechanisms related to stress, perception, and motivation.

From a welfarist perspective the fate of individuals matters most. In addition to the ultimate fate of released animals (life or death), welfarists are concerned with subjective experience of the animal throughout the reintroduction process. One perspective is that an animal's subjective experience is *ipso facto* better when the animal is "free" in nature than when "confined to captivity" REFERENCE. However, one does not have to dig deep to dispel the myth of idyllic life for free-living animals, who must face predators, starvation, pathogens, and so forth without the benefit of modern medical care (Veasy et al. 1996). Life in nature often entails struggle, and animals regularly sacrifice one aspect of their welfare to accommodate competing priorities. Take the case of elk that are willing to forgo foraging opportunities, suffering health consequences, to avoid areas where the threat of wolf predation is higher (Creel et al. 2007). In humans good health, a reliable supply of food, and security are considered to be among the most important prerequisites to psychological wellbeing (e.g., Maslowe's hierarchy of needs), yet this fact seems to resonate little with animal rightists that consider freedom the ultimate factor fostering good welfare. My intent is not to become submerged in a philosophical quagmire, but only to point out that any *a priori* claims for superior welfare in nature are highly debatable. Of immediate concern here are the welfare and conservation goals in reintroduction programs.

In preparing captive-living animals for life in the wild, concerns for welfare and conservation often collide. Ben Beck (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. How can we expect them to fare once released from this protected and controlled environment and exposed to the vagaries of nature? For captive individuals destined for reintroduction we do no service to their welfare by our well-intentioned coddling. Enriched environments for reintroduction candidates, then, should include some of the challenges they will face in the wild, even those which cause suffering, poor welfare and perhaps death. Thus, welfare sacrifices must be made to maximize 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 and Leberg 1991; McPhee and 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 behavioral characters and rapid change or loss of temperament types in captivity could compromise both welfare and conservation goals if release groups are comprised of individuals with maladaptive temperaments or lacking in the complete suite of behavioral types needed for the new population to thrive (McDougall et al. 2006; Watters and Meehan 2007). When considering the impact of selection operating in captive environments, we are—by definition—speaking of differential survival and reproduction. It's hard to imagine a selective regime with the goal of maintaining wild genotypes that does not compromise welfare of individuals. Judicious decisions must balance the overall goal of the program (species recovery) with the welfare concerns for individuals both in captivity and after release.

Reintroduction vs. rehabilitation and nuisance animal relocations

There is a subcategory of reintroductions motivated primarily by welfare concerns. These reintroductions typically involve the relocation of nuisance wildlife or rehabilitation of orphaned, sick or injured wildlife. Among the conservation community there has been considerable debate regarding whether these relocations are beneficial to conservation, some arguing that they may be detrimental to conservation by shifting the focus and funding away from real conservation issues and/or negative impacts of released animals on the existing wild population. For example, in the minutes of a recent workshop on bear reintroductions the participants endorsed a position stating that “from a conservation point of view it is advisable to recommend against releases of rehabilitated bears*”* (Kolter and van Dijk 2005) PAGE105. Several reasons are given, including: (1) because of the notoriously poor post-release monitoring in the majority of these programs it is difficult to determine whether the releases are successful from conservation or welfare perspectives; (2) rehabilitated bears often become “problem” bears for people, which has repercussions not only for the released bear but changes human attitudes towards bears, exacerbating human-bear conflict; and (3) cultural transmission of “bad” behaviors from releasees may have a ripple effect through a larger number of wild bears. While these participants clearly have legitimate concerns with rehabilitation programs, they hope to find solutions by encouraging “animal welfare organisations and bear conservationists… to increase the dialogue and strengthen knowledge on bear rehabilitation and releases, practices and impacts” (Kolter and van Dijk 2005) PAGE4.

The claim that rehabilitation programs are typically beneficial to the welfare of individual animals has also been seriously challenged. In their guidelines to reintroduction, the Association for Zoos and Aquariums (Anon 1992) states: "In view of the considerable mortality inherent in even the best planned and managed reintroduction programs, the reintroduction of orphans should not be represented as "humanitarian."" It is indeed likely that most such rehabilitation programs, while well-intentioned, have a net negative effect on welfare. However, after considerable effort, research and intensive post-release monitoring "compassionate releases" can be successful from a welfare perspective. For example, a rehabilitation program for orphaned chimpanzees eventually achieved a modicum of success, but required intensive monitoring and frequent intervention to prevent the deaths of nearly half of all released males that would have died from fight-related injuries (Goosens et al. 2005). In the United Kingdom hedgehogs often find their way into animal rehabilitation programs, where they are treated for injuries and released. Molony and colleagues (Molony et al. 2006) show that with sufficient planning, research, and understanding of the species, these reintroductions can be successful, but these successes rest on the shoulders of many failures. By careful evaluation of potential factors affecting success they are able to demonstrate statistically that protocols where animals are held in captivity for longer periods of time before release are superior to direct translocations involving brief stays in captivity. At first counterintuitive, this result may reflect the benefits of allowing more recovery time between successive stressors associated with handling or—alternatively—time to build up fat reserves to sustain them during the transition period post-release.

Wildlife managers face similar challenges in nuisance wildlife relocation programs. In response to human-wildlife conflicts ranging from minor property damage to disease transmission to human mortalities, wildlife managers are asked to remove animals from human-inhabited landscapes (VanDruff et al. 1994). In these situations the animals are not relocated for the benefit of their welfare, but as a nonlethal means to rid themselves of problem animals. Thus, concern for welfare governs the method but not the motivation for relocation. Virtually all of the same concerns for rehabilitated animals apply here, including poor post-release monitoring to document outcome and an unknown but probable period of poor welfare, which may often lead to mortality anyhow (Craven et al. 1998). Again, research is sorely needed to document outcomes and develop optimal relocation strategies. Raccoons, for example, are one of the primary “beneficiaries” of nuisance relocation programs in North America, yet they suffer high mortality (Mosillo et al. 1999) and most often end up making a nuisance of themselves again following translocation (O'Donnel and DeNicola 2006). The fate of translocated urban grey squirrels may be even more dire, with 97% dying or disappearing within three months of release (Adams et al. 2004).

The take-home message from these case studies is that welfare-motivated animal relocations, while well-intentioned, can cause considerable pain, suffering, and mortality if they are not based soundly in a scientific approach. Moreover, even if successful from the perspective of the released individual’s welfare, their conservation value may be nil or even negative. The greatest opportunity for conservation application of rehabilitation programs lies in the potential to develop techniques and refine general concepts that are transferable to other reintroduction programs.

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. (Such frustrated highly motivated behavior, if sustained, is perhaps the most reliable motivational substrate leading to stereotypy development (Mason and Rushen 2007).) Then the trapped animal is approached by a group of two-legged animals likely perceived as predators, handled, and transported to a completely novel environment. Perhaps it is held for a while in a human-constructed enclosure or perhaps it is released immediately (Griffith et al. 1989). Back in its home area it has invested considerable time and energy learning how best to exploit local resources (Stamps and Krishnan 1999; Inglis et al. 2001). It has 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 and Dill 1990). It knows its place in the social group and is able to maintain its position with minimal escalated aggression (Huntingford and Turner 1987; Archer 1988). If territorial, it has established beneficial relationships with its neighbors that reduce conflict and defense costs (Temeles 1994; López and Martín 2002). Forced to forego a lifetime of such gradually 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 out into a dramatically novel and dangerous environment to fend for itself against all odds. 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 (less so for animals reared with minimal human contact as is usually optimal reintroduction), the post-release challenges must be greater by an order of magnitude. Not only does a captive-bred animal lose any situation-specific knowledge gained in its captive environment, it also has much less generalizeable knowledge regarding how to cope in the wild—to the extent that its captive environment differs from nature.

Given this scenario, an animal welfarist might justly argue that such a conservation tactic is never admissible from a welfare perspective. 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 at 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" programs are a common tactic used to rescue endangered herpetofauna from invasive predators (Alberts 2007). Under this scenario one risks compromising the welfare of individuals first by subjecting them to the stressors of captivity, then again by the reintroduction process. Does the possible suffering caused by elevated predation threat, as well as the real risk of death, offset these stressors associated with headstarting? Here the "unmanipulated" animals suffer at the expense of human activities (introduction of predators), so—as is increasingly true—we must decide whether to use more "invasive" methods to partially undo what we have done. (One may also notice that I are ignoring the other elephant in the room—predator control, an issue of great interest to many welfarists.)

More commonly, however, source animals are captured from an area where they are doing well, that is, 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 by “spreading the eggs over many baskets.” Here, and in the majority of conservation-driven reintroduction programs, there are clear and explicit costs to individuals, who suffer or pay with their lives in the greater interest of the conservation of their species. Of course, they have no choice in the matter and it is left to humans to decide whether these sacrifices are offset by the benefits for conservation. Should we risk the welfare and lives of individuals in order to preserve the species? To many conservationists, including ourselves, the answer is affirmative. To make such a statement, by default, makes one a suscriber of the more pragmatic utilitarian philosophies and forsakes the more utopian philosophies professed by many welfarists, particularly those at the rights end of the spectrum. Adopting this approach, however, allows us to pursue further the development of new approaches that can move forward the goals of conservation while also remaining sensitive to the goals of better welfare.

Are reintroductions successful?

Given the myriad problems outlined thus far, one might fairly ask, *Are reintroductions successful from a conservation perspective?* The answer, so far, is that documented successes are few and far between. Most reintroductions are judged by their ultimate outcome relating to the likelihood that a viable population is established, and the failure rate may approach 75-90% (Beck et al. 1994; Wolf et al. 1998). Successful or not by this definition, most released animals—whether captive-bred or translocated from another wild population—can expect to die within days or weeks (Beck et al. 1994; Stamps and Swaisgood 2007; Teixeira et al. 2007). More surprisingly, there has been little to no improvement over the past twenty years (Fischer and Lindenmayer 2000). Reintroductions often fail for one of several reasons: limited understanding of the species' basic ecology and behavior; poor planning for the release strategy; 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.

This is not to say that little has been done to increase the success rate of reintroductions. On the contrary, much has been learned. We know, for example, that (1) wild-born fare better than captive-reared animals; (2) that the quality of habitat matters; (3) that it is better to release animals near the core than the periphery of their historical range; and (4) releasing more animals increases the chances of long-term success (Griffith et al. 1989; Beck et al. 1994; Wolf et al. 1998; Fischer and Lindenmayer 2000). Other factors, such as using soft vs. hard-release methods, do not reliably attain significance in these meta-analyses. We also know, without statistical support, 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).

This brings us to a central premise of my essay—what more can be done to increase reintroduction success? My focus is on success in conservation terms, but I also find a great deal of compatibility between conservation and welfare goals in this domain; improving survival and reproduction post-release also, as a consequence, often enhances welfare. For the remainder of this paper I focus on new ways to tackle problems with reintroductions. I do so by examining concepts in behavioral ecological theory that yield promising hypothesis-testing approaches that address both conservation and welfare concerns. I promote an adaptive management paradigm wherein the animal and its pre- and post-release environments are systematically manipulated, with intensive monitoring to provide critical feedback that is used to effect change in reintroduction protocols (Armstrong et al. 2007). I find 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

As I discussed above, a great deal of effort has been expended trying to improve the welfare of individuals in conservation breeding programs, but preparation of reintroduction candidates has required a different approach designed to maximize post-release survival. In this endeavor much headway has been made, which I review briefly here, focusing on recent developments.

A number of reintroduction programs have involved extensive modifications of the captive environment to prepare captive-bred animals for life in the wild (Kleiman 1989; Kleiman 1996). Enrichment programs, modified explicitly to prepare animals for the wild, have figured prominently in many reintroduction programs (Shepherdson 1994). Captivity has a variety of effects on behavioral development, some of them detrimental to reintroduction (Carlstead 1996). Not only are specific survival skills absent in the behavioral repertoire of many captive-reared animals (Beck et al. 1994), but there can be general effects that compromise behavioral competence, effects that can be offset with enrichment programs. Several studies have demonstrated a variety of positive developmental effects on brain function. Animals reared in more enriched environments have higher cortical weight, more glial cells, enhanced synaptic connectivity, increased acetyl cholinesterase, and increased levels of RNA present in the brain (thought to reflect memory consolidation; (Greenough 1976; Renner and 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 and Mench 2002). In addition, recent evidence suggests that some captive animals, particularly those with high rates of stereotypy, may find it difficult to unlearn what has been learned (Garner et al. 2003; Vickery and 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 programs. The golden lion tamarin program is well known for its use of an adaptive management approach, with several iterations before an acceptable level of success was realized (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 effects on post-release survival. The method found to work best is pre-release free-ranging experience on the zoo grounds combined with extensive post-release support. In another model program, researchers manipulated and tested a number of variables in the captive environment of black-footed ferrets designated for release (Miller et al. 1998; Vargas and Anderson 1998; Biggins et al. 1999; Vargas and Anderson 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 behavior, settlement, survival, and reproduction, and ultimately devise a more effective reintroduction program for the species.

Captive-released 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 behavioral manipulations in captive-release programs (Bunin and Jamieson 1996; McLean et al. 1999a; McLean et al. 1999b; van Heezik et al. 1999; McLean et al. 2000; Blumstein et al. 2001; Blumstein et al. 2002). These programs are rarely simple and require significant study to determine what kinds of experiences promote the development of effective antipredator behavior. Shier and Owings (Shier and Owings 2006; Shier and Owings 2007), for example, demonstrated that experience with predators produces a measurable improvement in antipredator behavior and post-release survival, but providing a wild-caught conspecific as a demonstrator of appropriate antipredator behavior markedly enhanced the effect. These studies show how application of behavioral theory matched with rigorous hypothesis-testing can make a good reintroduction program even better.

While it is clear that manipulations such as these make for good conservation, their effects on welfare are less clear. The antipredator training regime exposes prey species to predators or predatory models. Sometimes predator models are paired with aversive stimuli to condition avoidance behavior. Real predators may likewise evoke stress responses in prey species and housing and handling predator species used in these experiments may also compromise welfare.

One might argue that equipping animals with skills making them more competent at avoiding predation is good for welfare, but one could equally counter that ill-equipped naïve animals may enter the wild unburdened by the fear of predation. One hopes, however, that few would take the “ignorance is bliss” stance in this circumstance. It seems clear that the long-term welfare is better for animals equipped with realistic expectations of predation threat.

The recent application of the concept of temperament to reintroduction programs is an emerging and promising development. Although temperament has long played a role in the psychological (Koolhaas et al. 1999; Gosling 2001) and applied ethology (Grandin 1998; Price 1999) literature, the concept is a relative newcomer to ecology and evolution (Sih et al. 2004; Réale et al. 2007). Although the importance of temperament has been recognized in the ecology of antipredator behavior for longer, this application has mostly been limited to the dimensions along the shy-bold continuum (e.g., Wilson et al. 1993). In both the psychological traditions and the emerging interest in “behavioral types” among ecologists, a major focus is on how temperament affects perceptual processes such as: responsiveness to novel environments and potential stressors; cues used for predator, mate, competitor, or habitat assessment; risk assessment across a variety of situations; and other information acquisition activities. As will become clear below, a greater understanding of these processes—and inter-individual variation in their expression—can be useful when applied to reintroduction programs.

The gathering momentum in this area of inquiry holds great promise for application to conservation (McDougall et al. 2006; Watters and Meehan 2007). Perhaps benefiting from a closer association with the intellectual tools of applied ethology, researchers in captive breeding programs have been quicker to realize the importance of such inter-individual differences for managing welfare and breeding (Carlstead et al. 1999; Zhang et al. 2004). Recently, a growing number of empirical studies have documented the importance of temperament in reintroduction programs. For example, captive-reared weasels are less timid than their wild-caught counterparts, making them more visible—and susceptible—to predators (Hellstedt and Kallio 2006). In whooping cranes 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 behavior also significantly affected post-release survival (Kreger et al. 2006). Bremmer-Harrison and colleagues (Bremmer-Harrison et al. 2004) measured levels of boldness in captive swift foxes. 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 also ranged farther probably exposed them to more risks such as road traffic and predators. These examples underscore the importance of the effects that captivity can have 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 behavioral types.

While this conclusion may seem straightforward, there is reason for caution. Elimination of some behavioral types from reintroduction programs may be counterproductive to conservation goals. Watters and Meehan (Watters and Meehan 2007) argue convincingly that release groups should be comprised of the whole suite of behavioral types present in a species. The post-release environment varies temporally and spatially and it is quite possible that different behavioral types will perform better in differing environments. Behavioral type is heritable, but also influenced by the environment. The implication for reintroduction is that individuals representing the full genetic variability for behavioral types should be included in releases. Equally important, however, is providing the appropriate developmental influences to increase the expression of multiple behavioral 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 individuals that will have behavioral types that are ill equipped to deal with a particular post-release environment. Consideration of behavioral types may be equally important for translocations. Animals rescued from small habitat fragments or animals trapped or otherwise captured may not be representative of the whole population of behavioral types. Indeed, any time the site of capture is comprised of limited array of habitat types—especially if they differ from the release site—the right behavioral types may not be translocated. Also, the method of capture may be important; for example, “trap-happy” individuals may be better represented than “trap-shy” individuals.

Management of the post-release environment

In contrast to the increasingly sophisticated approaches to modify captive environments to prepare animals for release to the wild, less consideration is given to the possibility of modifying the post-release environment. By far the most common tools to aid releasees’ transition to a new environment are the techniques associated with soft release. Hard release entails little more than transport and release, with few if any efforts made 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 reintroduced animals (e.g., Bright and 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 behavioral and ecological theories and how few releases involve trialing different methods and ideas against one another to move the technique forward. When such methods are tested, the results are sometimes surprising. For example, these expensive and labor-intensive soft-release techniques may sometimes confer little or no advantage, despite their intuitive appeal (Wolf et al. 1998). Soft-release programs may fail for several reasons, but a prominent one is that many releasees simply do not remain near the release site long enough to benefit from the support system that managers provide (Bright and Morris 1994; Seddon 1999; Stamps and Swaisgood 2007). These observations argue that it is time to move beyond simple concepts of soft release and find more guidance from the behavioral and ecological phenomena that influence how animals respond to the challenges of relocation.

The role of social support offers an excellent example of the application of behavioral knowledge that can bring about tangible improvements in post-release success. While the number of animals released is often carefully considered in reintroduction programs (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 important fitness advantages (e.g., Dugatkin 1997). If these relationships are advantageous in stable source-population environments, one can imagine that they will be even more important when animals face the challenge of novel post-release environments. Recent studies with black-tailed prairie dogs provide unequivocal support (Shier 2006): animals translocated in family groups were less likely to be killed by predators, had fivefold higher survival, and higher reproductive rates than animals released in groups of unfamiliar individuals. Numerous studies also show that familiar conspecifics are important for welfare, and disruption of these social relationships is a potent source of stress REFS. Even more importantly, social companions can buffer animals from other external stressors such as novel environments REFS; that is, animals *perceive* novelty differently when in the company of familiar conspecifics.

Careful consideration should also be given to the number of animals released at a single site, a determination that should not be made arbitrarily. Knowledge of the how individuals of the species distribute themselves in the landscape (e.g., home range size and overlap) is important (e.g., White et al. 2007), but this information may be misleading without an understanding of underlying behavioral processes. In stable populations even territorial species have negotiated relationships with their neighbors and interact differently with them than with strangers, where aggression is prone to escalate (Huntingford and Turner 1987). Take the case of the black rhinoceros (Linklater and Swaisgood 2008). A mostly solitary species, in stable source populations aggression levels are moderate and serious injury rare, but following translocations into unoccupied reserves aggression levels are unacceptably high, leading to high rates of injury and death. In larger reserves rhinos 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 mortalities, but also rhinos are more likely to injure themselves in apparent attempts to escape through the boundary fences. Presumably, social instability and stress from frequent conspecific encounters contributes to this behavior. Thus, xenophobic tendencies can interact with other factors, such as reserve size and release density, to exacerbate conservation and welfare problems in reintroduction programs. Clearly, choosing the right number of animals and sufficient space to accommodate space- and familiarity-mediated aggressive behavior can counteract these problems. In the modern landscape, reserves are increasingly bounded by fences or other barriers to animal movements, so I predict this issue will become more important in the future.

From a conservation perspective, reproduction post-release is all-important to accomplish the principal aim of establishing a self-sustaining population in nature (IUCN 1998). Welfarists also include opportunities to mate and rear offspring among the goals for establishing good psychological wellbeing REF. How can release strategies be managed to maximize the probability of rapid and successful reproduction? For monogamous species, releasing pair-bonded and behaviorally 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 reproductive goals. 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 that the ultimate goal of a self-sustaining population will be realized. Mating systems can dramatically affect effective population size (N_e). Reproductive skew—in which some individuals secure "more than their fair share" of reproduction—reduces N_e, resulting in loss of genetic diversity and evolutionary potential to adapt to changing environments (Anthony and Blumstein 2000; Wedekind 2002). The distribution of resources on the landscape can determine whether a few males can monopolize reproductive access to females and 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 and Schulte In press). This application of sensory ecology involves (1) research to understand the production of mate choice signals and their impacts on the receiver's mate choice decisions; (2) collection or synthesis of preferred versions of these signals, and (3) manipulation of these signals to alter female mate choice to favor unrepresented males. While there are just two empirical conservation-relevant examples in the literature (Fisher et al. 2003a; Fisher et al. 2003b; Roberts and Gosling 2004), this practice is fairly widespread among behavioral 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 programs

While many of the concepts I have mentioned above relate to aspects of sensory ecology, such as signal-receiver interplay in communication, for the remainder of this essay I focus on some new issues and opportunities in reintroduction programs that are just beginning to gain a foothold. Surprisingly, two of the primary issues in this arena are quite well established elsewhere in the literature, but only recently have researchers begun to realize their potential in reintroduction programs. The first is the potential importance of the stress response and how it might compromise an animal's ability to adapt to challenging post-release environments, a topic I touched upon earlier. By necessity, reintroduction involves a series of successive stressors, which can have additive effects that cumulatively compromise the releasee further (Teixeira et al. 2007). The second is dispersal, which may turn out to be one of the most important behavioral ecological concepts in reintroduction programs. Stress—a concept well-known to psychologists and applied ethologists—is outside the expertise of most researchers and managers involved in reintroduction programs, so it is unsurprising that it has received little systematic attention. However, ecologists, who oversee many reintroduction programs, have a rich and long tradition of research on dispersal. This tradition, however, focuses largely on population-level consequences at the expense of the behavioral processes that determine dispersal patterns. For reintroduction programs, understanding these processes, most of which fall into the domain of sensory ecology, is what matters most. And what is reintroduction if not an exercise in “forced” dispersal?

How does post-release stress impact performance?

The term "stress" delineates a murky concept, subject to considerable debate on definition and even the usefulness of the concept (Hofer and East 1998; Moberg and 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 internal homeostasis and the behavioral and physiological adjustments that the organism undergoes to avoid or adapt to the stressor to return to homeostasis. "Stressors" are the external threats to homeostasis and the behavioral and physiological reactions are the "stress response." Here we 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. Because the stress response diverts mobilizable 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 and Johnson 1993; Moberg and Mench 2000). In consequence, research on stress has long played a major role in welfare science and is becoming an important tool in conservation programs.

Systematic research to understand the implications for stress in conservation programs involves identifying how animals perceive environmental change and challenge. Animals’ perceptual abilities often differ substantially from humans’ and research has demonstrated numerous sources of stress that are undetected in humans (Morgan and Tromborg 2007). Detection, of course, is a prerequisite to stress, but researchers must also determine the biological salience of potential stressors. What constitutes a stressor varies widely among species and even among individuals. These characteristics make stress a challenging topic for research.

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 act upon challenges to breeding and welfare in zoo animals (Carlstead 1996; Carlstead and Shepherdson 2000; Shepherdson et al. 2004; Morgan and 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 so that feedback benefiting animals is direct and rapid (e.g., Owen et al. 2004; Swaisgood et al. 2006). Thus, even when results may not be statistically generalizable to the whole population, carefully controlled research can still have important consequences for individual animals and provide a model for others utilize. Using a different subset of research tools and concepts, field researchers are addressing the increasing challenges faced by many wild animal populations (Hofer and East 1998; Tarlow and Blumstein 2007). Recent years have witnessed escalating contact—and conflict—between humans and animals, causing many conservation biologists to raise the alarm. Ranging from noisy military exercises to the rising wave of ecotourism activities, researchers are discovering detrimental effects of anthropogenic disturbance (see also, Lusseau, this volume).

With stress expertise on both the captive and wild side of conservation research, it is indeed surprising that so few have addressed stress systematically at the captive-wild interface—captive-release reintroductions. However, as reviewed extensively in a timely paper, this appears to be the case for both captive-releases and translocations (Teixeira et al. 2007). On some level reintroduction managers and researchers have been aware of the potential adverse effects of stress on released animals. Indeed a primary motivation for the use of acclimation techniques is to give animals time to settle in and recover from the stress of handling and transport. In some cases animals have been treated pharmacologically to reduce short-term stress during animal relocation (e.g., Letty et al. 2000), but manipulations designed to determine how animals perceive and respond to different activities during reintroductions have rarely been carried out. “Common sense” is arguably the best way to characterize reintroduction managers’ approach to stress.

Reintroduction specialists do not seem to be aware of the plethora of negative influences stress can have on perception, learning, and cognition—all crucial skills to have intact during the challenge of reintroduction (Teixeira et al. 2007). Most mortality occurs within a few days or weeks post-release (Stamps and Swaisgood 2007), so releasing stress-impaired animals can amplify the effect. Stress can weaken memory consolidation, compromise learning abilities, alter attention mechanism 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 they 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 at greater predation risk. Alternatively, if they adopt the conservation-withdrawal mode, they may stay put for too long, allowing odors to accumulate that attract odor-guided predators (Banks et al. 2002). These examples indicate that high post-release predation may result not only from poor antipredator skills, but also from an interaction between release-induced maladaptive behavior 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 realization that even short-term stress, lasting a few days, should not be taken lightly, as is often the case (e.g., Hartup et al. 2005). More research is needed to determine the extent to which stress contributes to the high mortality rate in the period immediately following release. Greater synergy between those working in the areas of conservation and welfare will advance our ability to tackle stress in the reintroduction context.

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

Translocation and captive-release programs are essentially exercises in “forced dispersal” for conservation purposes (review in Stamps and 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 and Ballard 1982; Fritts et al. 1984). This second voluntary dispersal post-release may arise because the animal finds itself placed in a habitat that it perceives, rightly or not, to be unsuitable. A reasonable response of an animal finding itself in a non-preferred habitat is to begin searching for one that is more favorable, that is, dispersing. 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 and Hodder 1998; Sarrazin and Legendre 2000) and that a large proportion of these deaths is attributed to the perils of long-distance dispersal (King 1990; Bright and Morris 1994; Linnell et al. 1997; Biggins et al. 1999). To the extent that delayed habitat selection and settlement exacerbates these dangers, efforts to understand and manage these behavioral 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. 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 recognize these risks, as shown in the common use of acclimation procedures prior to release. Also termed “soft release,” this technique—used in up to three-quarters of captive-release programs (Beck et al. 1994)—involves enclosing animals at the release site for a period of time before release. Acclimation is sometimes explicitly used or recommended to reduce post-release dispersal movements (Bright and Morris 1994; Linnell et al. 1997; Miller et al. 1999; Letty et al. 2000; Moehrenschlager and Macdonald 2003).

Ecologists initially overlooked the importance of perception and decision-making by dispersers, but more recently have come to appreciate how these processes determine the distribution and abundance of members of a species 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, and often relatively poor information about the distribution and quality of habitat patches (Stamps 1988; Davis 2007. Direct assessment of each patch encountered is not cost-effective, forcing dispersers to rely on indirect cues that correlate with habitat quality [Davis, 2004 #3577). Cue use and decision-making rules can change over the course of a dispersal event as energy reserves are depleted, but also to accommodate changing expectations of available habitat as the disperser learns from previous encounter rates with patches of varying quality. 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; Stamps 2006; Davis 2007; Stamps et al. 2007). To reduce the costs of dispersal—such as high probability of mortality—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 and Krishnan 2005).

The influence of perception on habitat selection behavior is of increasing importance in today's fragmented landscape (Lima 1996; Bélisle 2005). The functional connectivity of the landscape is determined by the animal's perception of gaps in the landscape more than by their physical ability to cross such gaps. This realization introduces other concepts unfamiliar to most ecologists, such as motivation and risk assessment, which influences an animal's willingness to move through a landscape. In fact, McDonald and St. Clair (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 programs. In the sections that follow I focus on two hypotheses that have been advanced to explain how natural dispersers select and settle in habitat: conspecific cueing and natal habitat preference induction. These hypotheses show great, but largely unrealized, promise for application to reintroduction management.

Conspecific cueing. The conspecific cueing (also called conspecfic 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 equally well to relatively solitary, territorial species. Ecologists had long believed in the "ideal free distribution" of animals on the landscape, wherein population density directly reflected habitat quality (Fretwell and Lucas 1970). Dispersing individuals were envisioned to settle in the most suitable habitat and to avoid settling in close proximity to conspecifics, which were thought of as competitors for resources. Territories should clump close together only where density of resources was high.

Controling for habitat quality, Stamps (Stamps 1987) found that *Anolis* lizards actively preferred to settle adjacent to conspecifics and proposed that dispersers used the presence of conspecifics as cues to territory quality. Taking a more behavioral perspective than that of ecologists, Stamps suggested that dispersing individuals lack knowledge of habitat suitability, and could most easily assess habitat quality by its correlation with the presence of other conspecifics. Thus, dispersers may follow the rule-of-thumb that if other conspecifics are present, then the area must be relatively safe and contain appropriate resources. This cost-saving mechanism for habitat selection has the advantage of integrating multiple components of habitat quality—ranging from foraging resources to security areas to predation—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 behavioral phenomenon even in relatively asocial species [Stamps, 2001 #2238; Dobson, 1998 #2141; Reed, 1993 #2142; Smith, 1990 #2171].

These observations pose a problem for conservation managers attempting to recruit animals into suitable habitat, such as newly created protected areas (Reed and Dobson 1993; Dobson and Poole 1998). If the species has been eradicated in the area, animals may not recolonize it through natural dispersal. If animals are reintroduced there, they may not settle, instead choosing to disperse to another area in search of conspecifics. Conspecific cueing may explain why reintroduced animals often colonize occupied area first and then gradually expand their range from a seed population (Newton et al. 1994). Conspecific cueing may also help explain why so many reintroduction programs fail: released animals following simple behavioral rules-of-thumb for habitat selection and settlement may choose not to stay in habitat that is perfectly suitable.

A promising strategy for addressing this problem is for conservation behaviorists to conduct research to understand the behavioral mechanisms underlying habitat settlement rules (Reed 2004). The key is to understand which cues animals use to identify the presence of conspecifics and find ways to manipulate these cues to encourage settlement. Recent research is beginning to tap into this realization and settlement patterns have been managed for conservation purposes in several species. Playback of conspecific bird song promotes settlement in unoccupied habitat (Ward and Schlossberg 2004). Decoy models capitalizing on visual cues have been used to attract colonially nesting seabirds to safe places (Jeffries and Brunton 2001). In some cases simpler visual cues can be used. For example, reintroduced Griffon vultures can be attracted to new breeding sites by painting cliffs with white paint imitating the accumulation of feces (Sarrazin et al. 1996) . Grouse can be induced to establish new lek sites using acoustic playbacks of vocalizations. The role of olfactory signals in habitat settlement is less explored, as is the usefulness of this technique in manipulating the behavior of mammals. Recent research however shows that translocated black rhino can be induced to settle next to “virtual scent territories” by spreading conspecific dung in a way that mimics natural dung-marking patterns (Linklater and Swaisgood 2007). For denning species, such as bears, olfactory cues may prove useful for attracting animals to safe denning sites in the same way that visual cues have worked to attract birds to nesting sites. However, caution is warranted when manipulating cues for reintroduction programs. Selection of cues must proceed only after careful study of how animals respond to these cues because some conspecific cues, for example, indicating dominance, could deter settlement (Linklater and Swaisgood 2007). Such and effect has been found in laboratory experiments with common lizards ARAGON.

Recent research has uncovered several other variations on conspecific cueing, raising other 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). 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 (Danchin et al. 2001; Sergio and Penteriani 2005). Potential manipulations for reintroduction capitalizing 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 and 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 an array of vertebrate and invertebrate taxa. The outcome of NHPI also has been shown to drive genetic structuring of populations, providing an example of how behavior can drive evolution. For example, wolves of two different ecotypes, based on prey specialization, 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 and Swaisgood 2007). Experience in a particular habitat may increase performance in that habitat. For example, predators may learn the skills needed to capture a prey species native to that habitat, prey may learn more effective antipredator behavior for predators specific to a habitat, and herbivores may develop modified foraging skills or digestive systems to deal with local plant defenses. Thus, an animal developing in natal habitat type A incurs 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 because the animal possess a specific natal habitat-induced skillset that allows it to thrive in habitat similar to its natal habitat. The second way dispersers may benefit from settling someplace like home relates again to the significant time, energy and fitness costs associated with the searching and sampling phase of dispersal. A disperser has limited time for direct contact with and assessment of habitats along its path of dispersal, but has a great deal of information about its natal habitat. After all, the fact that it has reached the age of dispersal in its natal habitat provides direct experience-based information on the quality of its natal habitat. This information greatly improves its chances of finding suitable habitat with minimal risks and energy costs. All it needs to do is learn the characteristics of a few conspicuous cues in its natal habitat and keep dispersing until it finds someplace with these same cues.

For reintroduction programs 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

(Stamps and Swaisgood 2007). If the manager fails to take into consideration the habitat the releasees experienced during development, 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 the proposition that NHPI plays a key role in the poor outcomes of many reintroductions.

NOTE: A FAIR AMOUNT OF THE REMAINING TEXT BELOW IS PLAGIARIZED FROM STAMPS AND SWAISGOOD (2007); I WILL MODIFY AND REDUCE THIS BEFORE PUBLICATION.

Long-distance post-release movement is de facto evidence for rejection of the habitat at the release site in favor of searching elsewhere for suitable habitat in which to settle (Stamps and Swaisgood 2007). The phenomenon of homing might be thought of as the ultimate case of habitat preference induction, where the animal the animal's search for someplace like home takes it back to its natal habitat. When the animal eventually settles--presuming it lives long enough--it makes this decision because either it has found preferable habitat or because it has exhausted resources available for searching and settles for what is available following the habitat sampling period during dispersal. It may also take considerable time for reintroduced animals to settle into a stable home range; for example the settlement phase in swift foxes occurs more than 50 days post-release (Moehrenschlager and Macdonald 2003). Animals reared in captive environments more similar to the natural environment at release sites often have shorter dispersal distances post-release. For example, black-footed ferrets raised in semi-naturalistic enclosures with burrows and live prairie dogs (their primary prey) dispersed shorter distance and higher survival rates than those reared in more traditional cages (Miller et al. 1998; Biggins et al. 1999). Enrichment programs that increase the number of stimuli shared by captive and release environment may enhance the success of captive-release programs.

The role of NHPI in reintroduction remains largely untested and more direct evidence is limited to a few telling case studies. In a recent review Owen-Smith (2003) examined evidence suggesting that poor population growth in ungulate translocations may be related to compromised foraging performance in a novel environment. For instance, sable antelope were translocated to a reserve consisting of "ideal" habitat for the species, yet population growth was extremely sluggish for a few years. Citing experimental studies with domestic species, he suggests that many translocated ungulate species suffer through a period of adjustment to a new foraging strategy. Compelling evidence for habitat preferences is detailed in Kenward & Hodder's (Kenward and Hodder 1998) studies of translocated endangered red squirrels in the U.K. Animals originating from two habitats, Scotch pine and Corsican pine, were translocated. Upon release at the same site all but one found its way to and settled in the same habitat type from which it came, showing a significant preference for their habitat of origin. Productivity in these two habitats is not equivalent so some squirrels passed over better quality habitat in favor of familiar habitat. Similar results have also been found for translocated hedgehogs (Morris et al. 1993). In another example, two ecotypes of caribou were translocated (Warren et al. 1996). Individuals of the ecotype originating from a habitat similar to the release site used foraging strategies learned in their natal habitat survived at twice the rate of their counterparts from dissimilar habitat, which attempted to use foraging strategies similar to those learned in their natal habitat.

Another pitfall to avoid in reintroduction programs is creating NHPI-like preferences for the artificial environments of captivity. For example, California condors reared in flight pens develop a strong preference for perching on posts that closely resemble power line posts, a preference which cost many lives when these birds were released to the wild (Wallace 2000). Captive-reared Guam rails showed a strong preference for traveling along roads, apparently because they were seeking more open habitat similar to their former zoo enclosures in the U.S., and were averse to entering the dark dense forests that makes up their native habitat (Witteman et al. 1990). In another strange and unexpected case, captivity-induced habitat preferences enabled Peregrine falcons to exploit an entirely new niche formerly unoccupied by the species—urban environments.

This discussion points to several observations and recommendations relevant to reintroductions (Stamps and Swaisgood 2007). First, animals raised under highly favorable conditions in captivity may learn conspicuous cues (e.g. lights, sounds, structural features, humans) in their natal habitat, associate those cues with favorable experiences in captivity, and then prefer to settle in new habitats that contain those same cues after being released into the wild. Second, the cues that affect habitat selection behavior need not be directly correlated fitness or other biologically relevant factors. Indeed, some of the factors with the strongest effects on fitness (e.g. the presence of particular predators or pathogens in a habitat) may not be detectable by dispersers during the period when they are choosing a new habitat. Third, animals reared in one type of natural habitat and translocated to a different type of natural habitat may be reluctant to settle in an unfamiliar type of habitat, even if humans have evidence that that type of habitat is suitable for the members of that species. Fourth, if animals are forced to settle in unpreferred habitats (e.g., by releasing them into isolated 'islands' of habitat, or by using artificial enclosures), then their success after release is likely to depend on the extent to which habitat-specific experience in their natal habitat affects their performance in the new habitat. If animals trained in one type of natal habitat lack physiological or behavioral traits which are required to perform well in a novel habitat, then artificial support (e.g. in the form of provisioning with familiar foods or shelter sites, predator-protection, protection against habitat-specific pathogens, etc.) may be needed for extensive periods after release. Finally, we need to keep in mind that animals need not 'instinctively' know what is good for them. Individuals may refuse to settle in unfamiliar habitats, even if those habitats would be better for them than any other habitats available in that landscape.

NHPI would not be a problem if it were a simple matter to raise animals in conditions in natal habitats comparable in every respect to the habitats into which they will be released later in life. But we know from existing evidence that all aspects of the natal environment are not important for the development of appropriate habitat preferences. Generally speaking, animals use a few simple cues correlated with the quality of their natal habitat. Our challenge as scientists and conservation managers is to try to tease apart which aspects of the environment are used as cues, and be sure to provision these in the captive environment. This will be a slow process, but a little educated guesswork should expedite our tests of NHPI. Another angle is to turn our attention to the release site and make modifications there that will attract animals of known origin. For example, the temporary addition of a few human-made features to make captive-born animals feel at home may be all that is required.

Conclusions

It is a truism that welfare goals are focused on the individual whereas conservation goals are focused on the population. However, since populations are comprised of individuals there must be a large domain where conservation and welfare goals are compatible. I have shown that this shared domain can be increased when sound behavioral research is applied to solve real-world conservation and welfare problems in reintroduction programs. A better understanding of proximate mechanisms, especially those underlying sensory ecology, will play an instrumental role in moving these goals forward. It is my opinion that behavioral ecologists—and I count myself among them—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 behavior beyond implication to application (Linklater 2004; Swaisgood 2007). Behavioral ecology does provide the most compelling theoretical framework for guiding our quests for mechanisms that we can manipulate for conservation gains, but a new synthesis including applied ethologists' approach to perceptual and cognitive mechanisms could put us on a better, more direct path to the more relevant discipline of conservation behavior we aspire to create.

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