Suitability of Amphibians and Reptiles for Translocation

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Abstract: Translocations are important tools in the field of conservation. Despite increased use over the last few decades, the appropriateness of translocations for amphibians and reptiles has been debated widely over the past 20 years. To provide a comprehensive evaluation of the suitability of amphibians and reptiles for translocation, we reviewed the results of amphibian and reptile translocation projects published between 1991 and 2006. The success rate of amphibian and reptile translocations reported over this period was twice that reported in an earlier review in 1991. Success and failure rates were independent of the taxonomic class (Amphibia or Reptilia) released. Reptile translocations driven by buman-wildlife conflict mitigation bad a bigher failure rate than those motivated by conservation, and more recent projects of reptile translocations bad unknown outcomes. The outcomes of amphibian translocations were significantly related to the number of animals released, with projects releasing over 1000 individuals being most successful. The most common reported causes of translocation failure were boming and migration of introduced individuals out of release sites and poor babitat. The increased success of amphibian and reptile translocations reviewed in this study compared with the 1991 review is encouraging for future conservation projects. Nevertheless, more preparation, monitoring, reporting of results, and experimental testing of techniques and reintroduction questions need to occur to improve translocations of amphibians and reptiles as a whole.

Keywords: herpetofauna, population supplementation, reintroduction, relocation, repatriation, translocation

Aptitud de Anfibios y Reptiles para la Translocación

Resumen: Las translocaciones son berramientas importantes en el campo de la conservación. No obstante el incremento de su uso en las últimas décadas, la efectividad de las translocaciones de anfibios y reptiles se ba debatido ampliamente en los últimos 20 años. Para proporcionar una evaluación integral de la aptitud de anfibios y reptiles para la translocación, revisamos los resultados de proyectos de translocación de anfibios y reptiles publicados entre 1991 y 2006. La tasa de éxito de las translocaciones de anfibios y reptiles reportada en ese período fue el doble de la reportada en una revisión previa en 1991. Las tasas de éxito y fracaso fueron independientes de la clase taxonómica (Amphibia o Reptilia) liberada. Las translocaciones de reptiles dirigidas por la mitigación de conflictos humanos-vida silvestre tuvieron una mayor tasa de fracaso que las motivadas por la conservación, y los proyectos más recientes de translocación de reptiles no tienen resultados conocidos. Los resultados de translocaciones de anfibios estuvieron relacionados significativamente con el número de animales liberados, los proyectos que liberaron más de 1,000 individuos fueron más exitosos. Las causas más comunes de fracasos de translocación fueron el regreso al hogar y la migración de individuos introducidos fuera de los sitios de liberación y bábitat inadecuado. En comparación con 1991, el incremento del éxito de las translocaciones de anfibios y reptiles revisadas en este estudio es alentador para futuros proyectos de conservación. Sin embargo, se requiere mayor preparación, monitoreo, reporte de resultados y experimentación de técnicas y preguntas de reintroducción para mejorar las translocaciones de anfibios y reptiles en conjunto.

Palabras Clave: herpetofauna, reacomodo, reintroducción, repatriación, suplemento de la población, translocación

Introduction

Translocations are an important tool in wildlife conservation (Griffith et al. 1989; Dodd & Seigel 1991; Fischer & Lindenmayer 2000). Thousands of translocations have occurred worldwide, although most of these have been taxonomically biased toward vertebrates, especially mammals and birds (Seddon et al. 2005). One group that has been overlooked in larger reviews of translocation programs, but which stands to reap substantial benefits from such techniques, is herpetofauna.

With further documentation of the worldwide amphibian decline and the extinction of a number of amphibian and reptile species, it is clear that proactive conservation is needed (Gibbons et al. 2000; Stuart et al. 2004; Mendelson et al. 2006). As a part of this, both translocations of wild individuals and projects coupled with captive-breeding programs appear to be growing in popularity. Furthermore, the recent Amphibian Conservation Summit listed translocations as one of 3 long-term conservation programs requiring development and implementation in the Amphibian Conservation Action Plan (Gascon et al. 2007). In addition to conservation-related motives, many other herpetofaunal translocations are being conducted to deal with human-wildlife conflicts, such as "problem" animals or building and development mitigation.

In a review of amphibian and reptile translocations, Dodd and Seigel (1991) found that amphibian and reptile projects have very low success rates, especially compared with translocations of other taxa, and they suggest that amphibian and reptile species are not suitable for translocation. Since the publication of their review, there has been wide debate in the literature (Burke 1991; Dodd & Seigel 1991; Reinert 1991; Seigel & Dodd 2002; Trenham & Marsh 2002). Despite their questionable suitability for translocation and that many amphibian and reptile species continue to undergo translocation, there has been no comprehensive review of amphibian and reptile translocations since 1991.

To improve management decisions, successes and failures of past programs need to be considered. We reviewed the results of programs published in scientific journals from 1991 to 2006 to reevaluate the suitability of amphibians and reptiles for translocation. In addition, we examined trends that may indicate key factors leading to the success or failure of projects.

Definition of Terms

Several terms have been used to refer to the release of animals into former areas within their range, including *reintroductions*, *translocations*, *relocations*, and *repatriations* (Griffith et al. 1989; Reinert 1991; Dodd & Seigel 1991; IUCN 1987, 1998). Because these terms have been used inconsistently in the literature, a recent call has been made to return to the original International Union for Conservation of Nature (IUCN) definitions outlined in the 1987 IUCN translocation position statement (Armstrong & Seddon 2008). We followed these IUCN definitions and use the term *translocation* to mean any movement of living organisms from one area to another. This includes deliberate movements of animals to establish a new population, reestablish an extirpated population, augment a critically small population, or mitigate for conflicts between animals and humans (Griffith et al. 1989; Wolf et al. 1996; Wolf et al. 1998). For the purpose of this review, we did not include releases and introductions of animals outside their natural range.

Although many projects report success, often what is being reported is only a short-term success. The ability of released animals to successfully overwinter, create burrows, or remain within a protected area does not, by itself, constitute a successful translocation program. A successful program produces a viable, self-sustaining population in the wild (Griffith et al. 1989; Dodd & Seigel 1991; IUCN 1998), and the population must be monitored for a sufficient amount of time to determine that it is selfsustaining. The amount of time necessary to do this may vary from several years for short-lived species to several decades for long-lived species (Dodd & Seigel 1991).

Here, we considered a translocation project a success if it met 2 criteria: there was evidence of a substantial addition of new recruits to the adult population due to successful reproduction at the translocation site, and the site had to have been monitored, at the very least, for the amount of time it takes that species to reach maturity. The outcome of a program was considered uncertain if monitoring time was inadequate or if there were too few data to classify it as a success or failure. We ranked projects as failures if they did not establish self-sustaining populations.

Methods

We reviewed amphibian and reptile translocation projects published in the scientific literature from 1991 to 2006, although some of the actual projects were carried out as early as the 1970s. Reports published before 1991 have been reviewed elsewhere (Dodd & Seigel 1991). We used electronic databases, reference lists, and personal contacts to find articles. Sea turtles were deliberately excluded because of the large number of projects concerning head-starting and release programs and the difficulty in relating the issues involved with their release to terrestrial and freshwater herpetofauna.

We attempted to determine the following factors for each project: species or taxonomic group being relocated; geographic region (North America, South America, Africa, Europe, Asia/Oceania) of the translocation; reason for translocation; date of release; whether founder individuals were from the wild or captivity; number of animals released; life stage of released animals (eggs, larvae, metamorphs, juveniles, subadults, adults); success of the project (as determined on the basis of our criteria); and cause of project failure.

Because of the nature of the data collected, we present the results with descriptive statistics in histograms to help illustrate trends. If a project fits into more than one category for a variable (i.e., if a project released both juvenile and adult animals), then it was counted twice. Therefore, total *n* may be greater than the total number of projects reviewed. Percentages are of the total *n*, which included projects of known (successes and failures) and uncertain outcomes.

We tested for the independence of outcomes in relation to variables with chi-square tests. For chi-square tests, we compared only projects with known outcomes (success or failure). The exception to this rule was in our evaluation of the time period (decade) during which translocations took place, for which we compared projects that succeeded, failed, and had unknown outcomes. When a contingency table had at least one expected cell frequency <5 and a chi-square test could not be used, we used a Fisher's exact test to compute a probability. Significance levels were set at $\alpha = 0.05$.

Results

We reviewed 91 translocation projects that covered 25 amphibian species and 39 reptile species. A complete table of all projects reviewed together with appropriate references is available from www.otago.ac.nz/zoology/ staff/academic/bishop.html. Six of the 91 projects involved restocking into existing populations (also known as augmentation) and were not included in the main analyses, but are discussed separately. Of the 85 amphibian and reptile translocations, 38 projects (45%) consisted of translocations of amphibians and 47 projects (55%) involved reptiles. Thirty-six of these combined projects (42%) were successful. For 25 projects (29%), the longterm success was still uncertain, whereas 24 projects (28%) failed. Success and failure rates were independent of the taxonomic class (Amphibia or Reptilia) released $(\chi^2 = 0.545, df = 1, p = 0.460; Fig. 1).$

To determine whether there were any differences over time in the known and unknown outcomes of programs (success, failure, and uncertain) published since 1991, we sorted the projects into decades on the basis of when the translocation occurred. For amphibians, program outcome was independent of the decade during which the translocation was carried out (p = 0.204). Project results for reptiles, however, were tied to the decade in which they were carried out (p = 0.009), with projects carried

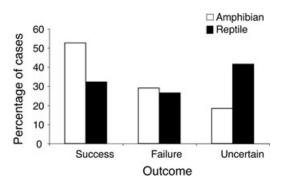


Figure 1. Outcomes of translocation projects for 38 amphibian and 47 reptile projects.

out in recent years having higher proportions of uncertain outcomes (Fig. 2).

The specific reasons for translocating a species varied greatly, but could generally be grouped into one of the following: conservation, research, or human-wildlife conflict (which included development mitigation and dealing with problem animals). For amphibians, the majority of translocations were carried out for conservation reasons (89.5%), and human-wildlife conflict motivations (7.9%) and research (2.6%) made up only a small proportion of the overall reasons for carrying out a release. In the case of amphibians, the success or failure of translocations was unrelated to the reasons for conducting the release (p = 0.480). For reptiles, although conservation was still the leading motivation for translocation projects (74%), research projects and projects motivated by human-wildlife conflict made up 10 and 16% of the projects reviewed, respectively. Furthermore, for reptile translocations with known results, the project outcome was correlated with the program motivation (p = 0.006). Reptile projects carried out to deal with

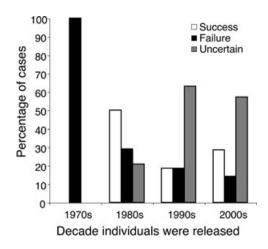


Figure 2. Outcomes of reptile translocations on the basis of the decade of animal release (1 project from 1970s, 23 from 1980s, 22 from 1990s, and 7 from 2000s).

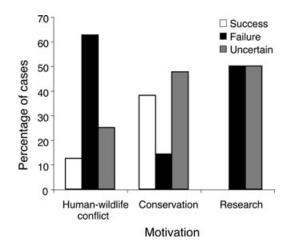


Figure 3. Outcomes of reptile translocations on the basis of motivation for the translocation (38 projects motivated by conservation reasons, 5 by research, and 8 by human-wildlife conflicts).

human-wildlife conflicts had the highest failure rates of the 3 motivations, whereas conservation-driven projects had the highest success rates (Fig. 3).

Most herpetofaunal translocation projects were carried out with wild individuals, with 76% of amphibian translocations and 93% of reptile translocations carried out with only wild animals. Most reptile translocations in which captive animals were used had, at present, uncertain outcomes; thus, it was not possible to determine whether the source of animals translocated had an impact on the success of the project. Nevertheless, in the case of amphibians, the source of animals reintroduced (wild, captive, or a combination) was independent of the project outcome (p = 0.310).

Translocation outcome was independent of life-stage category of released animals for both amphibians (p = 0.683) and reptiles (p = 0.312). Nevertheless, amphibian and reptile translocation projects used different age groups for release. For amphibians, 71% of the projects included the release of eggs, larvae, and metamorphs and 45% included the release of adults. Only 21% of amphibian translocations released juveniles. For reptile translocations, 64% of the projects incorporated the release of juveniles and subadults and 75% released adults. Only 4% of reptile translocations included the relocation of eggs.

Location had no effect on the outcome of translocations in both amphibians (p = 0.141) and reptiles (p = 0.10). The greatest number of publications on translocations were from North America for both amphibians (23 projects) and reptiles (32 projects). Australasia had the second-greatest number of publications on reptile translocations (9 projects) and Europe was second in the number of publications on amphibian translocations (9 projects).

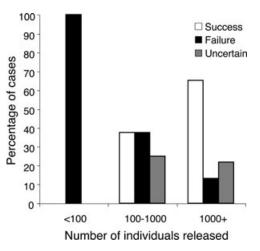


Figure 4. Outcomes of amphibian translocations on the basis of the number of individuals released (3 projects for <100 individuals, 8 projects for 100-1000 individuals, 23 projects for over 1000 individuals).

For amphibian translocations, the number of animals released significantly affected success rates (p = 0.008); projects releasing over 1000 individuals were more successful than those releasing less than 100 or 101-1000 individuals (Fig. 4). The number of individuals released in reptile translocations (0-50, 51-100, or >100 individuals) was independent of project outcome (p = 0.639).

Of the reported causes of failure, the most common for amphibians and reptiles were homing, large movements, and migration away from the release site. Other factors, such as insufficient numbers and poaching or human collection, were evident in both failed amphibian and reptile translocations (Fig. 5). In many projects, however, the cause of failure was unknown or not reported.

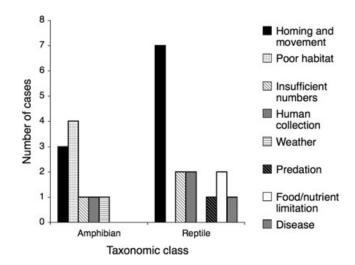


Figure 5. Reported causes of failure of amphibian and reptile translocation projects.

Of the 6 cases of restocking, 4 were carried out for conservation and 2 for research purposes. Of the conservation-motivated projects, 2 were successful and 2 had uncertain outcomes.

Discussion

Overall Review of Amphibian and Reptile Translocation Results

The proportion of successful amphibian and reptile translocation projects (41%) we reviewed from the past 15 years is double that previously reported for herpetofaunal translocations (19%; Dodd & Seigel 1991). This increase in positive results is an encouraging sign for the management and conservation of amphibians and reptiles. Nevertheless, this figure is within a similar range of reported success rates from reviews of translocations across all animal taxa (Griffith et al. 1989; Wolf et al. 1998; Fischer & Lindenmayer 2000). Even with the increase in success rates of amphibian and reptile translocations, the current figures demonstrate that room for improvement remains.

Publication bias and the reluctance of authors to report failed translocations may have caused an overestimation of true success rates (Dickerson & Min 1993; Scargle 2000). Without access to information on failed translocations, conservation managers and researchers cannot make informed decisions about the techniques to be used in future translocations.

Another issue to consider is that translocations can take years, if not decades, of monitoring to determine whether or not the project was successful. When looking at the long-term success ratings of projects by decades, the trend is that the proportion of projects with uncertain outcomes has risen dramatically in more recent projects, especially for reptiles, which include a number of longlived and slow-to-mature species. It is nearly impossible to compare the differences in success rates of recent projects when the outcomes of such a great number of projects are unknown. Nevertheless, it does emphasize the importance of long-term monitoring. For many translocation programs, it can take 15–20 years before success can be reliably evaluated (Dodd & Seigel 1991; Nelson et al. 2002; Bell et al. 2004).

Long-term monitoring is necessary for the evaluation of projects and to determine if intervention is needed for the survival of relocated populations (Seddon 1999). Many researchers have advocated for better monitoring (Griffith et al. 1989; Dodd & Seigel 1991; Seddon 1999; Fischer & Lidenmayer 2000), and it is vital that all organizations carrying out translocations commit to the longterm monitoring essential for these projects.

Motivations for Translocation Projects

By far the greatest numbers of translocations for both amphibians and reptiles have been performed for conservation reasons. Although research and the mitigation of human-wildlife conflicts are motivations for a few amphibian projects, in reptiles they make up 16% of projects carried out. In addition, the reason behind reptile translocations was significantly linked to the project's outcome, and reptile projects carried out for conservation had the highest success rates and those driven by human-wildlife conflict were the least likely to meet our criteria for success. This trend was not found in amphibian translocations, perhaps because the sample size of nonconservation-driven projects was small.

Translocations driven by human-wildlife conflicts were usually carried out either as a mitigation effort for development projects or to transfer species that are deemed potentially dangerous to humans. Although these were some of the most unsuccessful projects reviewed, our estimates are probably conservative because it is likely that the results of many of these projects are not being reported. Companies involved in translocations for mitigation purposes may not monitor projects after release and may not report failure rates due to the fear of negative publicity (Edgar et al. 2005; Teixeira et al. 2007). In addition, outside the transfer of a population, factors such as a net loss of habitat or the quality of new habitat created for translocated animals may not currently be taken into consideration by mitigation projects. For instance, a review of great crested newt translocations used for development mitigation in the United Kingdom showed that although new ponds were created to compensate for lost ponds, the overall habitat area available to the newts had decreased (Edgar et al. 2005).

In translocations motivated by human-wildlife conflict, the survival of released animals was poor (Walsh & Whitehead 1993; Hare & McNally 1997; Rathbun & Schneider 2001; Sullivan et al. 2004; Butler et al. 2005*a*, 2005*b*). The majority of translocations of problem carnivore species, most of which were mammals, met with the same poor results for many of the same reasons as in the projects for amphibians and reptiles driven by similar motives (Linnell et al. 1997). Translocations are not an easy solution to these problems and should not be suggested as a first step in dealing with the conflicts between people and animals.

Problem animals and animals whose habitats are to be developed for human use need to be dealt with either through preventative measures or by holding the organizations moving the animals accountable for the results. If animals must be moved for development mitigation, it is essential to consider the strong homing instincts of herpetofauna and the need for appropriate release habitat both in size and quality.

Factors That Influence Translocation Success

Reviews of translocations of other taxa show that several factors often led to more successful programs. One of these has been the source of founding individuals, with translocations of wild animals being more successful than translocations of captive animals (Griffith et al. 1989; Fischer & Lindenmayer 2000). This does not appear to be the case with amphibians because the success rate was similar for wild and captive releases.

A number of traits make amphibians and reptiles good candidates for captive-release programs, including high fecundity, lack of parental care, and that numerous smallsized amphibian and reptile species can be bred in captivity in a very cost-effective manner (Bloxam & Tonge 1995). In addition, captive-bred mammals may lose natural behaviors in captivity, but some amphibians and reptiles seem to retain in captivity behavioral and physiological traits that are genetically programmed. For instance, several tests on captive rattlesnakes showed their strikeinduced chemosensory searching behaviors were similar to those of wild snakes (Chiszar et al. 1993). In addition, approach distances of headstarted West Indian iguanas after release into the wild did not differ from those of wild animals of the same age, which shows they retained similar antipredator behaviors (Alberts et al. 2004). Although the source of release individuals may be less of an issue for herpetofauna than for mammals and birds, more releases are still composed of wild individuals than captive ones.

Although we found no significant difference in the outcomes of wild and captive translocations, the release of individuals held or bred in captivity added a number of issues that must be considered. It is crucial that disease risks associated with captive-breeding and release programs be considered. The risks that the released animals will transmit diseases and new parasites to wild populations and that inbreeding depression and acclimation may result in the inability of released animals to deal with such challenges in the wild (Jacobson 1993; Cunningham 1996). Recent tests of the fitness of captive-bred and wild toads show that important fitness attributes and high levels of heterozygosity can be maintained for several generations in captivity (Kraaijeveld-Smit et al. 2006). Nevertheless, other work shows that captivity can change the phenotype of animals, which may have implications for their ability to cope in a natural environment (Connolly & Cree 2008). If captive animals are to be released into the wild, these issues must be taken into account.

Another important factor to consider for translocation programs is the developmental stage of released animals. Although we found no difference in success rates, the results of several studies do suggest that certain age groups are more appropriate for translocation than others (Bloxam & Tonge 1995; Cooke & Oldham 1995; Trenham & Marsh 2002; Tocher & Brown 2004; Tocher et al. 2006). When dealing with species that show strong homing tendencies, it may be beneficial to release eggs or younger individuals rather than older adults that have had sufficient time to develop strong associations with a home site (Gill 1979; Bloxam & Tonge 1995; Semlitsch 2002; Tocher & Brown 2004). In addition, for aquatic-breeding amphibians, it may be preferable to move eggs or animals in early larval stages due to the large numbers available, which aids in ease of collection and maximizes genetic diversity. In addition, in aquatic amphibians, eggs are often available for collection from the wild for longer periods than adults, which may appear only at breeding locations for short periods (Semlitsch 2002). For many species, however, the greatest threats to individual survival come at younger life stages, when animals are more vulnerable to predators and the normal dangers of life in the wild and in these projects, so it may be better to release adults or large juveniles (Haskell et al. 1996; Nelson et al. 2002; Alberts 2007). This is particularly useful in the case of herpetofaunal species restricted to islands, where the main cause of juvenile mortality is caused by introduced mammals (Nelson et al. 2002; Alberts 2007). Outside the species-specific and logistical choices of whether to release eggs, juveniles, or adults, there is little-if anyexperimental work that tests the suitability of different herpetofaunal age classes for translocation programs and the effect of developmental stage on outcomes.

A number of amphibian and reptile translocations have failed because of the release of insufficient numbers of animals (Cook 2008). When release numbers are too small, Allee effects may come into play, and the new population may fail owing to problems associated with social behavior, finding mates, and group living (Courchamp et al. 1999; Stephens & Sutherland 1999). For amphibians, translocation projects that released over 1000 individuals were the most successful, although we found no correlation between release number and outcome of reptile translocations.

For aquatic amphibians Semlitsch (2002) suggests the release of 10,000-50,000 eggs over several years to reach an adult population of 100 individuals. Nevertheless, for most herpetofaunal species, there is no easy number to use as a guideline. Several amphibian translocation programs used population modeling as a tool to make recommendations on the optimal number of animals to be captured and released (Geraud & Keinath 2004; Tocher et al. 2006). These models are most useful for species for which adequate population and life-history data are known. Although adequate release numbers are essential in birds and mammals, the relationship between number of animals released and the probability of success is thought to be asymptotic in nature, so releasing an overabundance of animals does not necessarily increase success (Griffith et al. 1989).

Quality of the release habitat and the location of this habitat within the historic range of the species (Griffith et al. 1989; Dodd & Seigel 1991) are also important factors for translocation success. If the release habitat is not of high quality, then the chances of a positive outcome are low even when all other factors are taken into consideration. Although we could not evaluate habitat quality in the publications we reviewed, poor or unsuitable habitat was one of the most often reported reasons for translocation failure.

The causes of decline must be addressed prior to the translocation of amphibians and reptiles (Dodd & Seigel 1991). For many amphibian species, this means taking action against Batrachochytrium dendrobatidis (the amphibian chytrid fungus) because it can cause the often fatal chytridiomycosis disease. All necessary precautions should be taken to avoid further spread of the disease through human-mediated movement of animals, and release areas for amphibians susceptible to the fungus should be amphibian-chytrid free. Any amphibian release area should also be sufficiently distant from infected areas because the amphibian-chytrid fungus spreads at a rate of up to 120-160 km/year in Australia and 28-42 km/year in Central America (Lips 1998; Alexander & Eischeid 2001; Lips et al. 2006). Recently, a few failed translocations have been traced back to chytridiomycosis, and the amphibianchytrid fungus has been found in released toads (Fellers et al. 2007; Fisher & Garner 2007).

Future Research and Recommendations for Amphibian and Reptile Translocations

Stress affects translocated animals (Moore et al. 1991; Coddington & Cree 1995; Mathies et al. 2001; Lance et al. 2004; Alberts 2007; Teixeira et al. 2007), and even short holding periods can cause significant acute stress responses, which may exist for up to a month after release (Alberts 2007) in herpetofauna (Moore et al. 1991; Tyrrell & Cree 1998; Lance et al. 2004). A number of researchers have examined the effects of stress from capture, but few have looked at the effects of stress in herpetofauna after release into a new environment. It must be considered that individuals undergoing translocation face several stressors, including capture, captivity, and transportation, that may cause a larger "distress" effect in individuals (Platenberg & Griffiths 1999; Teixeira et al. 2007).

Released animals may be more likely to settle near release sites when they are provided with natal cues that are linked to positive experiences at an earlier life stage (Stamps & Swaisgood 2007). With this in mind, future researchers should investigate soft releases (which allow the animals a period to acclimate to their new environment [Griffith et al. 1989]), resource provisioning, and other such supportive measures to determine whether they increase the success rates of translocations. Little work has been done with natal-habitat preference or soft releases as they apply to herpetofaunal translocations, but there are a few cases that show they can increase site fidelity and translocation success for reptiles (Tuberville et al. 2005; Alberts 2007).

Although there are far fewer studies on the outcomes and effects of amphibian and reptile restocking or augmentation, such techniques may be useful for restoring genetic diversity in inbred populations or improving population recovery (Madsen et al. 1999; Muñoz & Thorbjarnarson 2000; Wilson et al. 2004).

Although the success rate of amphibian and reptile translocations has increased, further improvements are needed. More research is necessary on techniques such as soft release, on how to improve site fidelity, and on short-distance translocation and fencing off problem animals. Translocation projects should never be undertaken without thorough consideration of the ecological implications they may have on the source population, the individuals being released, and the ecosystem into which they are reintroduced. In addition, it is critical that a commitment be made to monitor the reintroduced populations over the short and long term and that these results be made available to the general public regardless of outcome through a centralized database. Without the publication of both successful and unsuccessful projects and the details involved, it is impossible for wildlife managers and scientists to make informed decisions for the future translocations of species.

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