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REVIEW

Conservation translocations: a review of common difficulties and promising directions

O. Berger-Tal[1], D. T. Blumstein[2] & R. R. Swaisgood[3]

1 Mitrani Department of Desert Ecology, Jacob Blaustein Institutes for Desert Research, Ben-Gurion University of the Negev, Midreshet Ben-Gurion, Israel

2 Department of Ecology and Evolutionary Biology, University of California Los Angeles, Los Angeles, CA, USA

3 Recovery Ecology, Institute for Conservation Research, San Diego Zoo Global, Escondido, CA, USA

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Correspondence
Oded Berger-Tal, Mitrani Department of Desert Ecology, The Jacob Blaustein Institutes for Desert Research, Ben-Gurion University of the Negev, Midreshet Ben-Gurion, 8499000, Israel.
Email: bergerod@bgu.ac.il

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Abstract

Translocations are a common conservation and management strategy, but despite their popularity, translocations are a high-cost endeavor with a history of failures. It is therefore imperative to maximize their success by learning from our collective experience. The Global Re-introduction Perspectives Series is a collection of conservation translocation case studies, generated by the IUCN's Conservation Translocation Specialist Group, and presented in a structured format with an emphasis on practical information. All 293 animal translocation case studies to date include a section in which the authors list the difficulties they have faced during the translocation project, with over 1200 difficulties described so far. We reviewed all difficulties reported in the series to get insights into the common perceived difficulties faced by wildlife managers during animal translocations. The most reported-upon problems had to do with animal behavior, followed by monitoring difficulties, lack of funding, quality of release habitat, lack of baseline knowledge and lack of public support. We scrutinized each of these difficulties to highlight future research directions that are most likely to improve translocation success, and put a special emphasis on difficulties stemming from animal behavior, and on solutions that may alleviate these problems and improve conservation translocation success world-wide.

Introduction

Translocations of animals to recover populations and reduce extinction risk are now a common practice that has made a significant difference in the conservation status of many species (Seddon *et al.*, 2014; Hoffmann *et al.*, 2015). Conservation translocations are the deliberate movement of organisms from one site to another where the primary objective is a conservation benefit (IUCN/SSC, 2013). The most common types of conservation translocations (hereafter, translocations) are reintroductions, where organisms are released into areas where the species previously existed but has been extirpated, and reinforcements, where organisms are released into areas with existing populations of conspecifics to enhance the viability of the extant population (IUCN/SSC, 2013). All types of translocations are inherently complex. To maximize the probability of success, wildlife managers must possess extensive knowledge of the released species' ecology and behavior, gain the support of local communities, secure continuous funding, coordinate activities among numerous stakeholders and monitor outcomes in an adaptive management framework. All of these factors add a high degree of complexity to the translocation process, which may be the reason for the low success of many past translocation efforts, especially those not supported by good planning and sound science (Germano *et al.*, 2014; Taylor *et al.*, 2017).

The high cost of conservation translocation projects coupled with their complexity makes it imperative for wildlife managers to maximize the chances of translocation projects to succeed. Learning from past translocation successes and failures may therefore be a vital step, beginning at the planning stages of a translocation project. However, translocation projects that are reported upon in the peer-reviewed literature may be biased toward prolific and successful translocation projects, since some authors may be reluctant to report failed translocations (Scargle, 2000; Schooler, 2011). In addition, the papers reporting successful translocation programs often do not report all challenges faced by the managers along the way. While this may serve to promote translocations as an important conservation tool, it makes it extremely hard for wildlife managers to learn from the difficulties encountered by other managers and to be able to use this knowledge to improve future translocations.

The International Union for Conservation of Nature (IUCN) Conservation Translocation Specialist Group (who until recently was known as the Reintroduction Specialist Group) is a network of global voluntary professionals that aims to provide reintroduction and translocation practitioners with useful management tools. The group publishes the Global Re-introduction Perspective Series (Soorae, 2008, 2010, 2011, 2013, 2016, 2018), which is specifically designed to record and share practical information from both successful and unsuccessful translocations without many of the barriers associated with the primary literature (Batson *et al.*, 2015). Importantly, this underutilized series contains translocation case studies that are presented in a highly structured format with an emphasis on practical information. The success criterion for each case study is self-evaluated and highly subjective, making it difficult to use this criterion in any objective analysis. However, all case studies include a section in which the authors list the difficulties they have faced during the various stages of the translocation project – planning, implementation and post-release monitoring. Thus, the Global Re-introduction Perspectives Series provides rare and invaluable insights into the translocation difficulties that wildlife managers face across geographical regions and biological taxa (Ewen, Soorae & Canessa, 2014; Batson *et al.*, 2015).

One major source of complexity in animal translocations may be predicting and accounting for the behavior of the translocated individuals. Surviving the translocation process depends to a large extent on the translocated individual's behavior and decision-making during the time following the release (Bell, 2016). However, translocated animals may face a unique situation of encountering a completely novel environment. In such a situation, their initial behavioral responses should rely on the species evolutionary history and on each individual's past experiences (e.g. captive or wild origin), which will govern decisions about dispersing from the release site and control the rate of learning and adapting to differences between the source and release environments (Stamps & Swaisgood, 2007; Le Gouar *et al.*, 2012). However, it is highly likely that these initial behavioral responses will not be optimal in the new environment, and should therefore change as the animal gains experience in its new habitat, becoming more adaptive with time (Berger-Tal *et al.*, 2014). This change can be termed 'post release behavioral modification', and knowledge of this behavioral change can assist wildlife managers in evaluating the state of the translocated animals (Berger-Tal & Saltz, 2014).

We reviewed all the difficulties reported in the Global Re-introduction Perspectives Series to identify the common difficulties encountered by wildlife managers when releasing individuals into the wild. Our goal was to gain deeper insights into the nature of common translocation difficulties and to highlight possible solutions and future research directions that are most likely to improve translocation success worldwide. Conservation translocations are a truly multi-disciplinary endeavor, and in order to succeed, wildlife managers must incorporate knowledge from many different fields of research (e.g. genetics, veterinary science, sociology, economics, etc.). In this review, we chose to put a special emphasis on recording the prevalence of occurrences in which the behavior of the translocated animals hindered the translocation process in some way. Our choice mostly reflects the fact that the growing field of conservation behavior (i.e. applying animal behavior knowledge to improve conservation programs) offers an increasing number of possible solutions to behavioral problems, which in turn, can increase the success of a large number of conservation translocation projects. However, it is important to note that any approach to conservation translocations other than a multi-disciplinary one is bound to result in failure, and any behavioral solution chosen must be integrated within a truly multi-disciplinary plan in order to make a difference.

Materials and methods

The six volumes of the Global Re-introduction Perspective Series contain 349 case studies of translocations, out of which 293 describe translocations of animals and 56 of plants. We chose to concentrate only on the animal translocation case studies because of the inherent and large differences between animal and plant translocations. The animal translocation case studies are divided among the taxa as follows: 28 invertebrate translocations, 35 fish, 20 amphibians, 37 reptiles, 66 birds and 106 mammal translocations. Overall, the case studies cover the translocations of 270 species in 76 countries world-wide. Approximately 90% of the species were only reported upon in a single case study, reducing the chances for pseudo-replication. Similarly, when considering the main authors of the case studies (i.e. the first and last authors of each case study), over 93% of the authors contributed only a single case study to the series.

All case studies are structured in the same way and contain the following sections: introduction, goals, success indicators, project summary (usually divided to evaluate feasibility, implementation and post-release monitoring), major difficulties faced, major lessons learned and a self-evaluated ranking of the success of the project with reasons for success/failure. We thoroughly read all sections of each case study in order to get the appropriate context, but for analysis purposes have concentrated on the 'major difficulties faced' section. In this section, the difficulties reported by the authors are always presented as a list, with each entry describing one difficulty. We first assigned each difficulty into one of five groups: Administrative and logistic difficulties (e.g. lack of funding or lack of skilled personnel); intrinsic difficulties (i.e. difficulties having to do with the species released into the wild – such as lack of genetic diversity, or small propagule size); difficulties concerning the physical environment (e.g. the quality of the release habitat); difficulties concerning the socio-political environment (e.g. lack of public support, or conflict among stakeholders); and difficulties concerning the biotic environment (e.g. predation, or invasive species).

Within each group, we assigned each difficulty to a specific category, initially using a set of predetermined categories. We created new categories as needed to adequately describe the difficulty (see Table 1 for a full list of difficulties' categories). Each difficulty in the list of difficulties was assigned to one category only. We similarly assigned 'reasons for success/failure' to specific categories. If the 'reasons for success/failure' section contained any reason for failure that was not already included in the 'difficulties' sections, we added it to our list. Whenever the difficulty referred to any type of animal behavior (such as movement, foraging, or social interactions), we noted the type of behavior mentioned and ascribed this difficulty to the 'animal behavior' category, regardless of whether the word 'behavior' was actually used in describing this difficulty.

Results

The 293 animal translocation case studies contained 1204 different entries under the 'major difficulties faced' or 'reasons for failure' sections that we categorized into 39 different categories (Table 1). Each case study reported 0–12 difficulties with a median of 4. It is important to note that our results represent the most prevalent difficulties encountered by the many authors of the Global Re-introduction Perspective Series, but do not give any information on the severity of these difficulties. One difficulty may be common but merely inconvenient while another may be rare, but bring translocation projects to a halt. In addition, it should be noted that the difficulties identified are often perceived as difficulties by the managers, rather than having been robustly identified as actual difficulties. The subjective nature of the success criterion of the series made it impossible for us to link the different difficulties with their consequences and we therefore concentrated on their prevalence, mapping the most common difficulties encountered during conservation translocations programs.

Roughly a third of the difficulties encountered by wildlife managers were administrative or logistical (357 difficulties). Another third was due to some aspect of the translocated species biology or ecology (328 difficulties). The rest of the difficulties were due to extrinsic factors which were divided more or less evenly among three types – the physical environment (140 difficulties), the socio-political environment (164 difficulties) and the biotic environment (135 difficulties) (Fig. 1). Eighty difficulties were extremely specific and could not be categorized into any general category. We annotated them as 'other' and did not assign them to any specific type of difficulty.

We found that the difficulty that was most commonly reported was animal behavior issues (reported 106 times, Table 1). However, this is partly the result of several case studies that separately listed more than one animal behavior as a difficulty. In terms of percentage of case studies reporting difficulties, animal behavior came third, following monitoring difficulties (reported 96 times) and lack of funding (reported 95 times). Other common difficulties were quality of the release habitat (reported 77 times), lack of baseline knowledge (64 times) and gaining public support (61 times).

Dispersal and movement were, by far, the types of behavior that caused the most difficulties in translocation programs (45.3% of all types of behavior reported; Fig. 2), followed by learning (16.0%), foraging (10.4%), competitive behavior such as territoriality (8.5%) and social behavior (8.5%).

Discussion

The contributors to the Global Re-introduction Perspective Series described over 1200 difficulties that they have encountered during the process of translocating animals to the wild. Since many of these case studies have never been reported in peer reviewed journals, the list of difficulties provides an invaluable and rarely considered glimpse into the common perceived obstacles of this popular management tool. The reported difficulties were highly diverse, but they divided more or less evenly among intrinsic difficulties related to the biology of the reintroduced species, external difficulties stemming from the biotic, physical or socio-political environmental conditions and logistic difficulties, which were mostly administrative.

In one of every three cases, wildlife managers had difficulty with the post-release monitoring of released individuals. Monitoring is a fundamental part of the translocation process (IUCN/SSC, 2013). It enables researchers to evaluate the translocation progress within an adaptive management framework (Seddon *et al.*, 2007; Saltz *et al.*, 2011; Berger-Tal *et al.*, 2012) and test a priori hypotheses and questions regarding the reintroduced populations (Bar-David *et al.*, 2005; Armstrong & Seddon, 2008; Gusset *et al.*, 2008). Monitoring difficulties may therefore risk the success of the entire translocation endeavor. Twenty-two percent of the monitoring difficulties were caused by the cryptic nature of the released animals, which may stem from cryptic morphology, cryptic behavior, or both. Crypsis is of course an important contributor to translocation success because it is a critically important component of anti-predator behavior, and can be used less effectively by naïve animals in novel environments (Nafus *et al.*, 2015). Thus, managers need to improve monitoring techniques rather than select environments that afford fewer opportunities for crypsis. The reasons for monitoring difficulties in the rest of the cases varied and included the topography and remoteness of the release site, the availability of skilled personnel, and the existence of suitable tracking equipment.

Not surprisingly, lack of funding was another very prevalent difficulty, reported for almost a third of all cases. This was also the only difficulty that made it to the 'top problems' lists of all taxa. In this respect, translocations mirror the financial pressures that are the harsh reality of many conservation programs and initiatives, especially long-term ones (Swaisgood *et al.*, 2010).

A recurring difficulty across taxa was the quality of the release habitat. It is a well-researched fact that the release habitat quality is one of the main predictors of translocation

Table 1. A list of all difficulties reported in the IUCN/SSC Global Re-introduction Perspective Series

Difficulty	Number of times reported	% of cases reported	Taxa breakdown	Category
Animal behavior issues	106	27.6	I(10.71%),F(11.43%),A(15.00%),R(40.54%),B(46.97%),M(47.17%)	Intrinsic
Monitoring difficulties	96	32.8	I(25.00%),F(11.43%),A(35.00%),R(51.35%),B(39.39%),M(31.13%)	Administrative/logistic (76) and intrinsic (20)
Lack of funding	95	32.4	I(32.14%),F(34.29%),A(50.00%),R(35.14%),B(24.24%),M(33.02%)	Administrative/logistic
Other	80	27.3	I(25.00%),F(25.71%),A(35.00%),R(24.32%),B(28.79%),M(27.36%)	Other
Quality of release habitat	77	26.3	I(39.29%),F(40.00%),A(45.00%),R(16.22%),B(19.70%),M(22.64%)	Physical environment
Lack of baseline knowledge	64	21.8	I(28.57%),F(20.00%),A(45.00%),R(18.92%),B(16.67%),M(20.75%)	Intrinsic
Gaining public support	61	20.8	I(7.14%),F(25.70%),A(5.00%),R(18.92%),B(16.67%),M(29.25%)	Socio-political environment
Lack of institutional support	46	18.4	I(7.14%),F(20.00%),A(10.00%),R(18.92%),B(18.18%),M(22.64%)	Administrative/logistic
Predation	44	17.7	I(7.14),F(14.29%),A(20.00%),R(16.22%),B(28.79%),M(15.09%)	Biotic environment
Conflict among stakeholders	47	16.0	I(10.71%),F(25.71%),A(5.00%),R(10.81%),B(22.73%),M(14.15%)	Socio-political environment
Environmental conditions	43	14.7	I(32.14%),F(11.43%),A(20.00%),R(10.81%),B(13.64%),M(12.26%)	Physical environment
Disease and parasites	42	14.3	I(7.14%),F(8.57%),A(25.00%),R(18.92%),B(9.09%),M(17.92%)	Intrinsic
Shortage of skilled personnel	42	14.3	I(14.29%),F(5.71%),A(10.00%),R(13.51%),B(16.67%),M(16.98%)	Administrative/logistic
Captive breeding challenges	34	11.6	I(14.29%),F(14.29%),A(15.00%),R(10.81%),B(12.12%),M(9.43%)	Intrinsic
Poaching	33	11.3	I(3.57%),F(14.29%),A(5.00%),R(10.81%),B(6.06%),M(16.98%)	Socio-political environment
Obtaining stock for breeding or translocation	31	10.6	I(3.57%),F(14.29%),A(10.00%),R(2.70%),B(12.12%),M(13.21%)	Biotic environment
Lack of genetic diversity	27	9.2	I(14.29%),F(11.43%),A(0%),R(8.11%),B(10.61%),M(8.49%)	Intrinsic
Invasive species	27	9.2	I(0%),F(34.29%),A(20.00%),R(13.51%),B(4.55%),M(2.83%)	Biotic environment
Missing infrastructure	23	7.8	I(3.57%),F(2.86%),A(5.00%),R(13.51%),B(6.06%),M(10.38%)	Administrative/logistic
Small population size	20	6.8	I(7.14%),F(2.86%),A(20.00%),R(0%),B(7.58%),M(7.55%)	Intrinsic
Lack of management plan	17	5.8	I(0%),F(0%),A(5.00%),R(10.81%),B(4.55%),M(8.49%)	Administrative/logistic
Remoteness of release sites	16	5.5	I(0%),F(5.71%),A(5.00%),R(8.11%),B(6.06%),M(5.66%)	Administrative/logistic
Inter-specific competition	14	4.8	I(3.57%),F2.86%),A(0%),R(0%),B(9.09%),M(5.66%)	Biotic environment
Human-wildlife conflict	13	4.4	I(0%),F(0%),A(0%),R(2.70%),B(1.52%),M(10.38%)	Socio-political environment
Habitat destruction	12	4.1	I(3.57%),F(2.86%),A(5.00%),R(2.70%),B(3.03%),M(5.66%)	Physical environment
Stress	11	3.8	I(0%),F(2.86%),A(0%),R(0%),B(4.55%),M(6.60%)	Intrinsic
Collisions with vehicles	11	3.8	I(0%),F(0%),A(5.00%),R(5.41%),B(7.58%),M(2.83%)	Physical environment
Failure of radio-collars	10	3.4	I(0%),F(0%),A(0%),R(5.41%),B(1.52%),M(6.60%)	Administrative/logistic
Low reproduction	10	3.4	I(0%),F(0%),A(15.00%),R(2.70%),B(6.06%),M(1.89%)	Intrinsic
Pollution and poisoning	8	2.7	I(0%),F(8.57%),A(0%),R(0%),B(7.58%),M(0%)	Physical environment
Long life history	6	2.0	I(0%),F(0%),A(0%),R(8.11%),B(3.03%),M(0.94%)	Intrinsic
Low juvenile survival	4	1.4	I(3.57%),F(0%),A(0%),R(0%),B(3.03%),M(0.94%)	Intrinsic
Civil unrest	4	1.4	I(0%),F(0%),A(0%),R(0%),B(0%),M(3.77%)	Socio-political environment
Identification of species	4	1.4	I(10.71%),F(0%),A(0%),R(0%),B(0%),M(0.94%)	Intrinsic
Escape from release enclosures	4	1.4	I(0%),F(0%),A(0%),R(5.41%),B(0%),M(1.89%)	Administrative/logistic
Hybridization	4	1.4	I(0%),F(2.86%),A(0%),R(0%),B(1.52%),M(1.89%)	Biotic environment
Electrocution	1	0.3	I(0%),F(0%),A(0%),R(0%),B(1.52%),M(0%)	Physical environment
Unregulated tourism	1	0.3	I(0%),F(0%),A(0%),R(0%),B(0%),M(0.94%)	Socio-political environment

The table reports the number of times each difficulty was reported, the percentage of case studies reporting this difficulty, the percentage of cases reporting this difficulties within each taxon [invertebrates (I), fish (F), amphibians (A), reptiles (R), birds (B), and mammals (M)], and the category the difficulty belongs to. Animal behavior issues were the most reported upon difficulty, but since the same case study could report more than one animal behavior difficulty, the percentage of cases reporting it is lower.

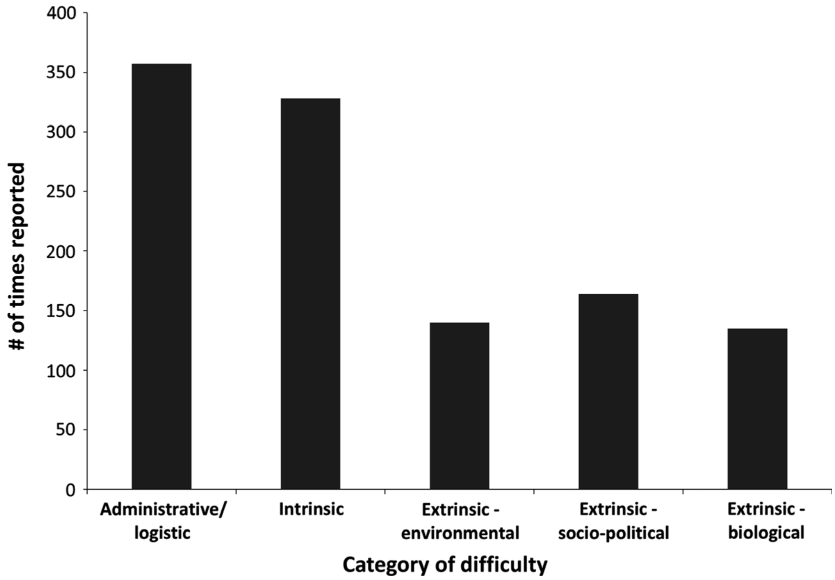

Figure 1 The difficulties reported in translocations' case studies broken into five categories: Administrative and logistic, intrinsic characteristics of the released species, the physical environment, the socio-political environment and the biotic environment.

success (Griffith *et al.*, 1989; Wolf *et al.*, 1996). Still, the case studies show many examples where animals were released into a low-quality habitat either because it was erroneously deemed of higher quality prior to the release, deteriorated in quality after the release, or was chosen despite its low quality since no better habitat was available. The errors in estimating the true quality of the release environment ties in with the fact that more than a fifth of the case studies reported that the managers of the translocation project lacked important ecological and behavioral information on the species or the release environment, which hindered the success of the project.

While some difficulties, such as lack of funding, habitat quality, or lack of baseline information were common across all or most taxa, others were more taxon-specific. Animal behavior issues, for example, were very prevalent in reptiles, birds and mammals, but much less so in invertebrates, amphibians and fishes (Fig. 3). Releasing invertebrates into the wild seems to present managers with a unique set of challenges that are less common in other taxa. These translocations were hindered by environmental conditions such as harsh weather or natural catastrophes, shortage of skilled personnel, lack of genetic diversity and complications in the captive breeding facilities. Invasive species were a major problem in fish and amphibian translocations, and lack of public support was a common difficulty for fishes and mammals. For fish, these seemingly unrelated difficulties were sometimes connected in cases where invasive fish species that were eradicated from streams or lakes prior to the translocation were used by locals for recreational fishing, and consequently, the translocation efforts were in several cases undermined by locals re-releasing these invasive fish species to the habitat. Lastly, amphibian releases were frequently hampered by the small size of the released populations. Small population size is a well-known problem for

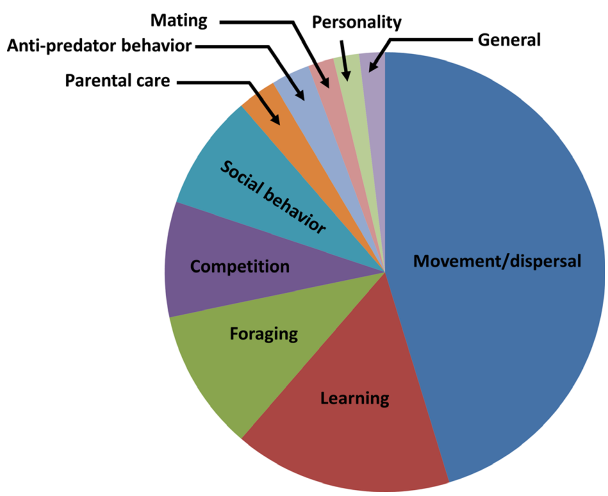

Figure 2 A break-down of the 'animal behavior issues' category into the specific types of behavior reported as causing the difficulty. [Colour figure can be viewed at zslpublications.onlinelibrary.wiley.com.onlinelibrary.wiley.com.]

introduced populations (Le Gouar *et al.*, 2012) that need to establish themselves in a new environment, but our results suggest that this problem is especially challenging in releases of amphibians, or that practitioners in amphibian releases are more sensitive to this problem. Germano & Bishop (2009) evaluated the published literature on amphibian translocations between 1991 and 2006 and concluded that the outcomes of these translocations were primarily related to the number of animals released; releasing fewer than 1000 individuals greatly increased the chances of failure. The case studies we surveyed support this notion and all cases reporting difficulties stemming from low population size in amphibians had

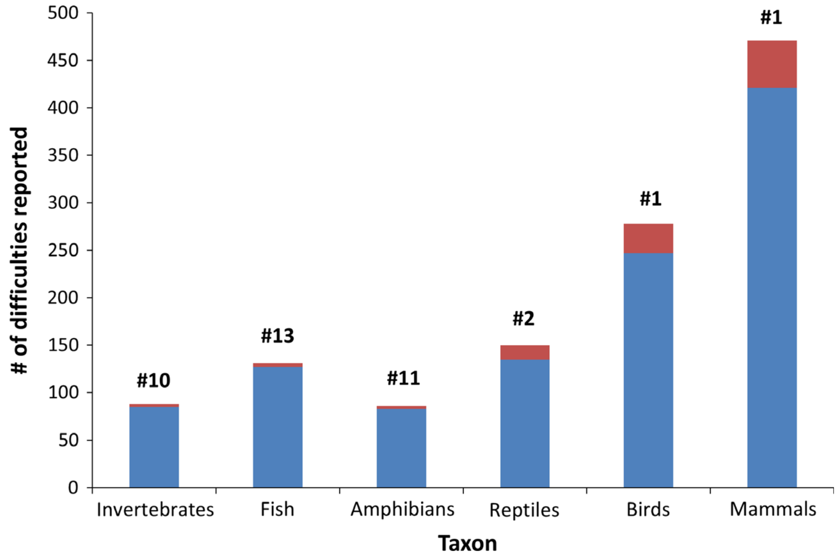

Figure 3 The difficulties reported for each taxon. The red part of each column is the portion of difficulties (out of all reported difficulties) categorized as 'animal behavior issues'. The number at the top of each column is the rank of 'animal behavior issues' among all difficulties (e.g. for mammals, behavioral difficulties were the most prevalent difficulty reported). [Colour figure can be viewed at zslpublications.onlinelibrary.wiley.com.onlinelibrary.wiley.com.]

considerably fewer than 1000 individuals released into the wild.

Animal behavior difficulties

As noted above, we chose to put a special emphasis on animal behavior difficulties and on possible behavioral solutions. However, any such solution must be integrated within a truly multi-disciplinary plan in order to truly improve translocation success. Difficulties stemming from the behavior of the reintroduced species were the most reported-upon problems, although in terms of the percentage of cases reporting it, animal behavior came third because in some cases managers had various challenges stemming from different types of behavior in the same program (Table 1).

Dispersal and movement were the types of behavior that were most commonly reported as difficulties in the translocations of animals (Fig. 2). Notably, dispersal issues would usually be among the behavioral problems easiest to detect, and therefore the true prevalence of other behavioral problems may be higher. The most common dispersal problem reported was long-distance dispersal away from the release site, reducing probability of survival (although distinguishing dispersal from other forms of mortality is often extremely difficult to do, especially in small animals). Long-distance dispersal is already known to be an important factor limiting translocation success (Harrington *et al.*, 2013; Swaisgood & Ruiz-Miranda, 2018). Accordingly, understanding and reducing post-release dispersal has been nominated as one of the 10 most important questions in translocation biology (Armstrong & Seddon, 2008) and as one of the top 50 questions in conservation behavior (Greggor *et al.*, 2016). Examples in the case studies include the dispersal of hihi, *Notiomystis cincta*, individuals outside the protected areas to which they were released (Ewen *et al.*, 2013), and long-distance dispersal of swift foxes, *Vulpes velox*, that reduced the productivity of the reintroduced population (Sasmal & Phillips, 2016). In some cases, long distance dispersal was reported as a leading cause for translocation failure, such as when the majority of translocated Hamilton's frogs, *Leiopelma hamiltoni*, homed back to the point of their capture (Bell *et al.*, 2010). Homing behavior was also a major limiting factor for the success of the Agassiz's desert tortoise, *Gopherus agassizii* (Hinderle *et al.*, 2015). Rapid dispersal from the release site can be motivated by a number of behavioral factors, including lack of conspecifics at the release site, stress associated with the response to a novel environment, or Natal Habitat Preference Induction, where animals disperse in search of habitats that contain the same cues as their natal habitats, even when these habitats are of lesser quality (Stamps & Swaisgood, 2007; Le Gouar *et al.*, 2012). Such dispersal is sometimes non-intuitive because animals may reject perfectly suitable habitats if the cues they use to determine suitability are absent (also termed perceptual traps, Patten & Kelly, 2010). There are various methods that can reduce long-term dispersal away from the release site such as providing the animals with cues from the release site already in captivity (in the case of a captive-bred population) to familiarize them with the new environment (Stamps & Swaisgood, 2007), providing food in the vicinity of the release site (e.g. Armstrong *et al.*, 2007), using playbacks of conspecific calls around the release site (e.g. Bell *et al.*, 2005), or selecting sites with specific resources that will help anchor animals at the release site (Nafus *et al.*, 2016). In some cases, the dispersal difficulty managers faced was of the opposite nature – the reintroduction of the white-winged guan, *Penelope albipennis*, in Peru failed to achieve some of its main goals of connecting isolated populations, because individuals failed to disperse from the release site (Pratolongo, 2011). The same methods outlined above to prevent dispersal could potentially also be used to promote it by attempting to attract the animals to areas away from the release site.

The second most common behavioral difficulty had to do with the failure of animals to learn. These difficulties usually occurred with animals that were transferred to an environment unlike their natal one (whether they were born in captivity or in the wild) and had trouble learning to behave in an adaptable manner, such as Arabian oryx, *Oryx leucoryx*, that had difficulty adapting to their release site in Jordan, because it was very different from their source habitat with regard to climate, vegetation and topography (Zaidaneen & Hasaseen, 2008), or reintroduced captive Columbia Basin pygmy rabbits, *Brachylagus idahoensis*, which suffered from high mortality because of their naïve behavior (Becker & DeMay, 2016). Another common problem was habituation of animals to humans after their release. For example, translocated Hawaiian monk seals, *Monachus schauinslandi*, had become habituated to humans and had to be taken back to captivity to address public and seal safety concerns (Baker *et al.*, 2013). For captive-bred populations, problems concerning learning how to properly behave in the new environment can be addressed by training the animals prior to their release, a tactic that can be made more successful through social learning from wild-caught demonstrators (Shier, 2016), or other in situ techniques (Moseby *et al.*, 2015; Blumstein *et al.*, 2019). For species that have a tendency to habituate, it is also crucial to reduce any human contact during their upbringing in captivity (e.g. through puppet-rearing of chicks, Valutis & Marzluff, 1999).

Foraging difficulties varied, but mainly concerned unnatural foraging behavior that usually reduced the animals' fitness and the probability of the program's success (e.g. reintroduced bush stone-curlew, *Burhinus grallarius*, that were not sufficiently prepared to forage in the wild, starved to death in the weeks following the release, leading to the failure of the project; Kemp & Roshier, 2016), and cases where the foraging habits of the released individuals made it difficult to monitor them (e.g. Hawaii Akepa, *Loxops coccineus coccineus*, and Hawaii creeper, *Oreomystis mana*; Kohley & Lockyer, 2008). Foraging deficiencies are probably underrepresented in the translocation literature because they are difficult to detect without careful study. However, starvation has been implicated as a significant source of mortality in reintroduced captive carnivores (Jule *et al.*, 2008) and training with natural diets in captive-bred pheasants *Phasianus colchicus* resulted in higher post-release survival (Whiteside *et al.*, 2015). Careful experimentation is often required to reveal differences in feeding efficiency between captive-bred and wild individuals (Mathews *et al.*, 2005).

Examples for competitive behavior that have caused difficulties include territorial aggression by established vinaceous Amazon parrots, *Amazona vinacea*, towards newly released birds that required the temporary recapture of previously released birds (Saidenberg *et al.*, 2013), and aggressive behavior of Lichtenstein's hartebeest, *Alcelaphus buselaphus*, where fighting in adults bulls led to many deaths of subadults in the release enclosure (Clegg *et al.*, 2013). Social behavior reported include retarded social development and behavior of reintroduced Barbary macaque, *Macaca sylvanus*, that have been confiscated from illegal pet traders (Waters *et al.*, 2016), or insufficient social bonding in a pride of reintroduced African lions, *Panthera leo*, that caused social instability and deaths in the group (Youldon *et al.*, 2016). Territorial aggression has also been implicated in negative translocation outcomes for kangaroo rats (Shier & Swaisgood, 2012), black rhinoceros (Linklater & Swaisgood, 2008) and Indian leopards, *Panthera pardus fusca* (Athreya *et al.*, 2011).

Surprisingly, anti-predator behavior (or lack of such behavior) was only reported as a difficulty in two case studies, despite the fact that it is a well-known fact that many captive-bred animals have demonstrably deficient anti-predatory behavior which leads to high predation levels and lower survival of captive-bred individuals in comparison to those who were born in nature (Shier, 2016; Swaisgood & Ruiz-Miranda, 2018). Indeed, predation was one of the most common difficulties reported in the case studies (Table 1). Increased predation may also be prominent in wild-sourced prey species, not because of inherent behavioral deficiencies arising in a captive environment, but because animals have not learned how to use the available habitat to avoid predation or find refuge, or engage in behavior that increases vulnerability. It may also be that because the problem of deficient anti-predator behavior in captive-bred individuals is already so well-established in the translocation literature and pre-release anti-predator training is common practice in many translocation programs that anti-predator behavior no longer pose a difficulty for most translocations (and indeed, pre-release training protocols were discussed for at least 12 of the case studies). Alternatively, managers may be unaware or unprepared to train animals and have resorted to lethal predator control. The efficacy of pre-release training varies greatly among studies, and active research seeks to develop and evaluate new methods of preparing naïve prey to coexist with their predators (e.g. Moseby *et al.*, 2015).

Disease is another top difficulty for translocations (just out of the top ten with 42 case studies reporting it to be a difficulty) where understanding animal behavior can play a critical role in mitigating its effects. Behavioral traits can be used to identify individuals that are most susceptible to disease, as well as 'super-spreaders' individuals that have a key role in spreading diseases (Snijders *et al.*, 2017). Indeed, in a recent list depicting the behavioral questions that have the greatest potential to resolve critical conservation problems, disease played a prominent role with questions such as 'which interspecific and intraspecific behavioral interactions increase cross-species disease transmission?' (Greggor *et al.*, 2016). A greater understanding of behavioral variability and interactions among translocated individuals has the potential to reduce the impact of disease and parasites on translocations success.

The Global Re-introduction Perspective Series is written by the conservation practitioners' community and it reflects what they consider to be the important aspects of their translocation projects. Our review shows that one of the most common difficulties that practitioners encounter when translocating animals is animal behavior. However, this fact does not necessarily mean that behavioral interventions are being used to mitigate these difficulties (Berger-Tal *et al.*, 2016). This point can be exemplified by Ewen *et al.* (2014), who reviewed all herpetofauna translocation case studies in the first four books of the series in order to identify the objectives set by reintroduction practitioners, the indicators of success they chose and the types of difficulties they encountered. As expected, the major difficulties listed by Ewen *et al.* (2014) reflect the difficulties reported here – lack of funding, difficulties in monitoring, conflicts among stakeholders, quality of the release sites, and so forth. But a notable exception is that Ewen *et al.* (2014) do not mention animal behavior issues at all. Rather, their results accurately reflect the way many practitioners treat and report behavioral problems – they either talk of a specific behavior (dispersal, foraging, learning), or of behavioral processes (habituation, aggression). While the difference may seem only semantic in nature, it may serve to hide the fact that so many difficulties practitioners are facing are behavioral in nature, and may be one of the main reasons that behavioral interventions in translocations have not been called for as often as they should have. Understanding mechanisms is vitally important for devising mitigation strategies specifically addressing them, so that obstacles to success can be overcome. To cite one example of the importance of understanding the mechanistic underpinnings for a translocation failure – a number of attempts to translocate the endangered Stephens's kangaroo rats, *Dipodomys stephensi*, have failed, yet behavior was never implicated in these failures. Only after consulting a group of behavioral ecologists was it revealed that the social environment was largely responsible for these failures. Taking the social behavior of the species into consideration has yielded a 24-fold increase in the number of pups produced after 1 year, and have made this failing translocation project successful (Shier & Swaisgood, 2012).

Conclusions

Conservation translocations are in many cases still a high risk–high cost endeavor, and we therefore implore wildlife managers to consult the case studies depicted in the series before attempting a translocation project of their own. Case studies of similar species should be especially relevant. Wildlife managers must understand that translocations require an extremely long-term commitment and it is imperative that funding for the entire length of the project be secured in advance. More often than not, funding is only secured up to the release stage, leaving no money for post-release monitoring, and in some cases, this may doom the project to failure. We suggest that the feasibility plan for the project should include a section on monitoring feasibility. Many programs were hindered by their inability to perform adequate post-release monitoring, and in many cases, preparing for this task from the planning stages – by securing funds, acquiring the suitable equipment and providing proper training for the relevant personnel, would have solved the problem. Research on innovative monitoring methods is a promising venue that is bound to increase translocations' success. In addition, the feasibility analysis must ensure that the release habitat is of sufficient quality to sustain the released population. While this seems obvious, the fact that in one out of four cases the quality of the release habitat was listed as a difficulty that may have hindered translocation success might imply that we need to be more rigorous in our evaluation of release habitats.

Our results also emphasize the importance of the broad field of behavioral ecology to conservation and the need for more innovative behavioral ecology solutions in wildlife management (Blumstein & Fernandez-Juricic, 2010; Berger-Tal *et al.*, 2011; Berger-Tal & Saltz, 2016), and especially in animal translocations (Somer & Gusset, 2009; Le Gouar *et al.*, 2012; Berger-Tal & Saltz, 2014; Ebrahimi *et al.*, 2015). We strongly suggest that behavioral ecologists (preferably ones that are working with the species released or with similar species) be consulted with during the planning stages of the project. This will help ensure that the full diversity of tactics is considered when developing translocation processes (Batson *et al.*, 2015).

Every translocation project, whether successful or not, increases our knowledge of translocation practices. It is our responsibility to make use of this accumulated knowledge, so that every new translocation project will have a better chance of succeeding than the ones preceding it.

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Authors' contributions

OBT, DTB and RRS conceived the study; OBT collected and analyzed the data; OBT led the writing of the manuscript. All authors contributed to the drafts and gave final approval for publication.

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