INCREASING CONSERVATION TRANSLOCATION SUCCESS BY BUILDING SOCIAL FUNCTIONALITY IN RELEASED POPULATIONS

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ABSTRACT

The importance of animal behavior to successful wildlife translocations has been acknowledged in recent decades, and it has been increasingly considered and more frequently incorporated into translocation management and research. However, explicit consideration of social behavior is often overlooked in this context. Social relationships take a variety of forms (e.g., cooperative partners, members of a dominance hierarchy, territorial neighbors) and play important roles in survival, reproduction, and resource exploitation. We review the ways in which concepts from studies of social behavior in wild populations may be leveraged to increase translocation success. Social structure and cohesion, social roles, social learning, and social competency may all be important to consider in building populations that are resilient and likely to persist. We argue that relevant data collected at all stages of translocation, including candidate selection, and during pre-release, release, and post-release monitoring, may inform the

establishment of functional social structure post-release in species dependent on social processes. Integrating knowledge of social behavior into management decisions may be particularly useful when comparing the success of alternative release protocols or release candidate behavioral traits. Complementary datasets on a range of fitness-related metrics post-release will further leverage our understanding of social establishment in translocated populations. We illustrate the potential of these ideas using Asian and African elephants as a model. Both species are particularly challenging to manage but are translocated frequently; thus, evidence-based protocols for conservation translocations of elephants are urgently needed.

INTRODUCTION

Wildlife translocations, defined as "the deliberate movement of organisms from one site for release in another" may occur in several contexts, including *reintroduction* in which organisms are released into native range where populations no longer occur and *reinforcement* in which organisms are released to enhance existing populations in their native range (International Union for Conservation of Nature, 2013). Translocations are an indispensable conservation tool with the potential to bolster the viability of populations of endangered species, restore locally extinct species, and repair ecosystem integrity (Hayward and Slotow, 2016; International Union for Conservation of Nature, 2013). Despite this potential, many release efforts have failed as a result of poor planning, inadequate resources, and small founder populations, among other reasons (Fischer and Lindenmayer, 2000; Seddon et al., 2007). As efforts have been made to improve success rates, particularly through hypothesis-driven studies that test the relative success of alternative approaches (Seddon et al., 2007; Taylor et al., 2017), there has been a growing recognition that animal behavior can play a large part in determining whether a relocated animal will succeed in its new environment (Greggor et al., 2016; Reading et al., 2013). For example, temperament (Bremner-Harrison et al., 2004), loss of predator response in captivity (McPhee, 2004), and movement (Berger-Tal and Saltz, 2014) may all affect survival or reproduction following release. The inclusion of behavioral ecological theory into wildlife releases has enriched the field and improved standards (e.g., testing alternative pre-release training approaches in black-footed ferrets (*Mustela nigripes*) resulted in a new standard for release that improved post-release survival) (Dobson and Lyles, 2000; Moore et al., 2008; Reading et al., 2013).

Despite the growing embrace of behavior within wildlife release programs, social behavior remains underused in this field and in applications of conservation management generally (Berger-Tal et al., 2016; Brakes et al., 2019; Somers and Gusset, 2009). Social behavior is a fundamental aspect of living that facilitates exploitation of resources (Mueller et al., 2013), survival (Carter and Wilkinson, 2015), and reproduction (McDonald, 2007). In wild populations, the social networks that animals maintain serve to provide alternative sources of ecological information (Kerth et al., 2006), mating opportunities (Mulder et al., 1994), clearly defined dominance/territorial relationships (Rowell, 1974), predator avoidance (Hasenjager and Dugatkin, 2017), and learning opportunities (Custance et al., 2002). The importance of social behavior is reflected in the varied literature on sociality in behavioral ecology (Silk, 2007a) and within other fields (e.g., the influence of social factors on gene expression (Runcie et al., 2013), the impact of partner loss on physiology and neurochemistry (Sun et al., 2014), and the importance of natural social behavior to animal welfare in captive settings (Koene and Ipema, 2014)). The more social behavior is integrated across disciplines, the more it is found to influence fundamental biological processes. Indeed, social relationships (e.g., group membership, mating partners, parent-offspring) or social structures (e.g., territories, network properties, fission-fusion processes, dominance hierarchies) may be closely tied to individual and population persistence (Royle et al., 2012; Silk, 2007b).

A primary goal of wildlife translocations is for released animals to survive and reproduce at release sites (Kleiman, 1989). Leveraging the social relationships that influence post-release establishment is an essential part of reaching this goal, particularly as animals face multiple challenges in adjusting to new environments (Goossens et al., 2005). This is true for solitary species as much as it is for interactive species (Shier and Swaisgood, 2012). The decisions managers make may facilitate appropriate social environments for relocated populations, yet the elements emphasized in translocation projects commonly exclude functional social structure. In this perspective, we build on previous research to identify aspects of sociality that may influence metrics relevant to wildlife translocations, and we call on translocation researchers to leverage available information from studies of sociality in wild populations. We develop these ideas under the assumption that the greatest understanding of how managers can facilitate the social structure needed for successful releases will come from hypothesis-driven approaches, set in adaptive frameworks, that direct evidence-based management actions (Armstrong and Seddon, 2008; Taylor et al., 2017). Thus, we outline steps researchers can take to facilitate this process (Figure 1). Finally, we discuss a particularly challenging taxon that is frequently the subject of translocations—elephants (Asian elephants, *Elephas maximus*, and African savannah elephants, *Loxodonta africana*)—to highlight the ways in which these ideas may be applied to improve outcomes (Table 1).

SOCIAL FUNCTIONALITY IN TRANSLOCATED POPULATIONS

Kleiman (Kleiman, 1989) suggested that studies of social behavior could be used to inform translocations, referencing social group composition and social training. Since then, others have elaborated on this idea, with an emphasis on the importance of release cohort composition as a determinant of success (Somers and Gusset, 2009; Swaisgood, 2010). Currently, the consideration of sociality remains secondary to the more common factors that structure release approaches. Many releases grouped animals on criteria that were not socially based, rather by demographic (Sarrazin and Legendre, 2000) or genetic (Haig et al., 1990) considerations. At times, these cohorts have been housed together at release sites prior to release to increase familiarity (Hayward et al., 2007), though such approaches are not necessarily expected *a priori* to result in functional relationships (Franks et al., 2018; Kilian and Bothma, 2003; Somers and Gusset, 2009).

Social Structure and Cohesion

Familiarity within cohorts has been the primary focus of the few studies that have tested the role of social behavior, with apparent success: territorial Stephens' kangaroo rats (*Dipodomys stephensi*) that were translocated with pre-release neighbors settled, survived, and reproduced better than those moved without neighbors (Shier and Swaisgood, 2012); colonial black-tailed prairie dogs (*Cynomys ludovicianus*) released with family groups survived better than those released without family groups (Shier, 2006); and black-eared miner (*Manorina melanotis*) colonies that were captured and translocated as intact units remained anchored to release sites together (Clarke et al., 2003). The investment involved in establishing new relationships may be costly, particularly at a time when released animals are acclimating to a new environment (Linklater and Swaisgood, 2008; Shier and Swaisgood, 2012; Wallace, 1994). This suggests that new social partners may add rather than mitigate stresses related to translocation.

There is a growing literature that suggests that selecting animals with established social relationships to be released together improves translocation success, and thus should be more widely adopted (Somers and Gusset, 2009). However, recent insights from the field of social networks within behavioral ecology (Krause et al., 2007) suggest that it may be important to consider familiarity in cohort construction not only related to an individual's closest interaction partners (e.g., direct neighbors, breeding partners, group mates), but to the larger social network or into an existing social network where individuals reinforce existing populations. Increasingly, social networks are revealing the importance of indirect relationships and larger population topology to the survival and reproduction of individuals, and these factors may indeed be important to post-release survival and recruitment (Snijders et al., 2017). Examples of the importance of extended networks from the literature on wild populations are diverse: vampire bats (*Desmodus rotundus*) with a larger network of weak relationships suffer less during food shortages than those with fewer weak relationships (Carter et al., 2017), elephants strengthen ties within their extended networks when their closest associates die (Goldenberg et al., 2016), and yellow-bellied marmots (*Marmota flaviventris*) are less likely to disperse if they are more embedded in their social networks (Blumstein et al., 2009). There have been other examples from the literature that support this idea in the specific context of translocation: releasing several pairs of red-cockaded woodpeckers (*Picoides borealis*) within dispersal distance of each other, combined with existing wild birds at the release site, provided released birds with options for mating that resulted in an increase in the number of breeding pairs at the site (Carrie et al., 1999). More recently, loss of pre-translocation associates tended to be correlated with higher mortality in translocated hihi (*Notiomystis cincta*) in New Zealand (Franks et al., 2018).

A consistent theme in reviews of reintroductions is the higher success rates that arise when more, relative to fewer, animals are released together (Fischer and Lindenmayer, 2000). Further studies have refined this idea to stress that the number of groups may be more important than the number of individuals involved in a release (Hayward and Slotow, 2016). As discussed above, it is possible that larger releases or releases involving more distinct social units have provided richer—and subsequently more beneficial—social context for released wildlife, which in turn boosts survival (Taweepoke Angkawanish, personal communication). These insights may be valuable in a number of translocation contexts, including those in which small starting populations may preclude the ability to facilitate optimal social environments. In such cases, it may be effective to manipulate the *perceived* social environments of released animals, for example using sensory cues to mimic social density and conspecific spacing (Linklater and Swaisgood, 2007; Parker et al., 2007; Robbins and Kim McCreery, 2003). Considerations related to the networks that translocated animals have access to may differ depending on whether reintroductions or reinforcements are being implemented. For example, familiarity within release cohorts may be an important feature of reintroductions, whereas familiarity with established individuals at release sites (or with their cues) may be more relevant in the context of reinforcements.

Social Roles

In addition to consideration of immediate and extended interaction environments, the social roles represented within networks—within release cohorts and among wild animals at release sites—may be particularly important, especially in regards to social learning and mentoring. The growing literature on social networks in nonhuman animals has highlighted the disproportionate role that some individuals play in biological processes within a population. For example, whooping cranes (*Grus americana*) migrate more efficiently if they travel in flocks with older, more experienced birds (Mueller et al., 2013), and adult banded mongoose (*Mungos mungo*) foraging escorts shape the forage niches of accompanying pups for the rest of their lives (Sheppard et al., 2018). In the conservation translocation literature, a study that measured the survival of released hand-reared and parent-reared sandhill cranes (*Grus canadensis*) found that flocks containing birds from both backgrounds had the highest survival, which the authors attributed to distinct behavioral skill sets within the group that birds could learn (Ellis et al., 2000). Young male African elephants released following culling operations engaged in aberrant behavior that was only corrected once older bulls were introduced to the population (Slotow et al., 2000).

Release group composition or social exposure to wild animals can also be designed to leverage individuals with a disproportionate anchoring or mentoring effect. In elephants (Thitaram et al., 2015) and cooperatively breeding birds (Clarke et al., 2003), the presence of dependent young tied released animals to the social group and may have prevented long-distance dispersal. In a rehabilitated group of western lowland gorilla (*Gorilla g. gorilla*) orphans comprised of both captive and wild-born animals, group cohesion declined after the death of one wild-born orphan (Le Flohic et al., 2015), suggesting that the presence of that orphan had a cohesive effect on the larger group. Identification of individual traits associated with such group-level influence may increase the ability to promote group cohesion even when there are perturbations to the social network like deaths. The identities of social anchors or mentors will depend on the biology and social structure of the species of interest, but careful consideration of anchors or mentors may improve cohesion and social learning opportunities for group members following translocation.

Social Competency and Learning

Long-term studies of translocated animals indicate social learning can hasten information acquisition about beneficial behavior (Jesmer et al., 2018; Whitehead, 2010), and should be encouraged in cohort construction and exposure to wild animals at release sites to improve release outcomes (Brakes et al., 2019; Watters and Meehan, 2007). The negative aspects of social learning also should be considered in translocations, and may be especially relevant when there is the potential for human-wildlife conflict. Undesirable behaviors among wildlife can be socially learned, as with bottlenose dolphins (*Tursiops aduncus*) begging for food from boats (Donaldson et al., 2012), elephants crop-raiding (Chiyo et al., 2012), or California sea lions (*Zalophus californianus*) predating on federally protected salmonids (Schakner et al., 2016). These studies have found particular individuals within networks to disproportionately affect the spread of negative interactions with humans. As reintroduced wildlife often become habituated in captivity, the incidence and spread of negative interactions with humans can be particularly concerning. Screening animals for differences in characteristics like fearfulness around humans or prior histories of problematic behaviors may inform cohort choice composition, and social networks can be used to model the spread of behaviors of interest (Allen et al., 2013; Schakner et al., 2016). Negative interactions with humans often lead to fatal consequences for wildlife (Fisher, 2016), and analysis of social groups based on the potential for conflict may indicate some animals or cohorts that are unsuitable for reintroduction. Conversely, caution should be taken when releasing animals naïve to undesirable behaviors into a population in which incidence of these behaviors is common.

In addition to the role of learning, conditions in captivity may have precluded release candidates from developing the social behavioral skills necessary to succeed in the wild (Guy et al., 2013). For example, captive maned wolves (*Chrysocyon brachyurus*) with richer histories of interaction with conspecifics responded appropriately to intraspecific cues by marking territory, whereas a wolf without such history exhibited a fearful response to such cues (Coelho et al., 2012). Such circumstances may necessitate some degree of social training prior to releasing animals into wild settings. Pre-release training has been used successfully in several systems (e.g., predator training in burrowing bettongs (*Bettongia lesueur*) (West et al., 2018), hunting skill development in cheetah (*Acinonyx jubatus*) and leopard (*Panthera pardus*) (Houser et al., 2011)). Pre-release training may aim to build social competency (e.g., through exposure to conspecific scents and vocalizations or interactions with conspecifics) or skills that are facilitated through social mechanisms (e.g., by exposing experienced and naïve individuals to one another to facilitate social learning). Regardless of the particular species or research question, hypothesis-driven approaches to translocations would do well to consider building social resiliency or social access opportunities for released animals. As we detail below, there are many opportunities for data to inform translocation success concerning social processes.

STEPS FOR SOCIAL BEHAVIORAL INTEGRATION IN TRANSLOCATION RESEARCH

Within the conservation translocation literature that has considered social behavior, quantification of sociality has primarily been focused on monitoring following release. However, to inform the establishment of functional social structure in released populations, socially-focused monitoring should occur at all stages of the translocation process (i.e., pre-release, release, and post-release), including pre-release candidate selection (Fig. 1). The first step should be determining the role and degree of influence that social processes (e.g., coordinated predator defense (Templeton et al., 2005), resource access (Firth et al., 2015), pair bonding (Teitelbaum et al., 2017), territorial behavior (Rioux et al., 2017)) play in the fitness of a taxon of interest, if any. Where research is sparse or unavailable on sociality in a given species, comparison to taxa with similar social systems (e.g., anti-predator grouping, social roles in reproduction) or ecological niches (e.g., social foraging/hunting) may be informative as a starting point. In these cases limited by a lack of data, monitoring social behavior and the establishment of social relationships throughout the stages of translocation may be especially valuable in order to build a baseline understanding of the social needs of the species that may inform future efforts (Sah et al., 2016). Basic research on sociality in remaining populations of the species or comparable species may be important for the same reason.

Following identification of the social factors that may be important to release success, there are multiple points across the stages of release when research can inform the process. Data from candidate animals prior to release, when paired with information collected during later stages (International Union for Conservation of Nature, 2013), may provide a powerful way to illuminate the social factors of importance to release success. This may be possible in multi-release translocations for which each translocation is informed by outcomes from the previous translocation(s) or in single translocations that may provide lessons for translocation of the species elsewhere. Such data can take many forms, the choice of which will depend on aims and resources. Behavioral observations (Somers and Gusset, 2009), multi-individual GPS tracking (Berger-Tal and Saltz, 2014), and keeper surveys (Freeman et al., 2010) may all be effective methods for quantification of existing social characteristics prior to selection. In cases where releases serve to reinforce existing populations, data collection and analysis on wild populations at proposed release sites prior to release—where possible—may be a critical part of constructing functional social systems and understanding how released animals affect existing structures, which in turn may help guide management decisions related to social behavior.

The protocols used to release wildlife into new areas may influence response to new surroundings, and social interactions during this period may mediate observed responses. Many studies have housed captive animals together at release sites in restricted areas to facilitate familiarity, with mixed results following release (Franks et al., 2018; Gusset et al., 2006; Kilian and Bothma, 2003). The effects of these practices may be better understood if comparable social data are collected following release (Franks et al., 2018). Social cues may also be used to simulate or amplify social exposure and thus familiarize or anchor animals to release sites when social housing during soft release is not possible. When rooted in an understanding of social interaction within a species, such cues can be used to achieve management aims. Social cues in the form of audio playbacks have been used to attract African wild dogs (*Lycaon pictus*) to particular areas (Robbins and Kim McCreery, 2003); decoys, conspecific calls, and mirrors have been used to attract colonial seabirds to breeding habitat (Parker et al., 2007); and conspecific urine and feces distributed around release sites has been used to anchor released black rhinoceros (*Diceros bicornis*) to a target area (Linklater and Swaisgood, 2007). Social cues may be particularly useful where release sites do not contain the conspecific density preferred by individuals, or where managers seek to familiarize released animals with established animals at release sites. Quantifying the response to such interventions given an understanding of social context will improve efficacy of release protocols.

Post-release monitoring has been the stage of translocation in which social behavior is most often studied, despite the historically overall low incidence of any monitoring following release across translocation projects (Seddon et al., 2007). While post-release monitoring is vital to assessing the degree of success (International Union for Conservation of Nature, 2013), the absence of cohort information or release metrics regarding behaviors of interest to which post-release data can be compared limits the ability to inform future releases (Shier and Swaisgood, 2012). Analysis of post-release monitoring may be particularly insightful when trait variability among released individuals is known in advance of release that can be paired with observations following release (Guy et al., 2013). Measurable post-release outcomes can include commonly collected data on survival and reproduction (King et al., 2012), but may also include temporal processes tied to social environments like movement phases leading to settlement (Berger-Tal and Saltz, 2014), the time it takes for target social relationships to emerge (Gusset et al., 2006), or the return of glucocorticoid stress hormones to baseline levels (Teixeira et al., 2007; Viljoen et al., 2008). Multiple complementary datasets on released individuals throughout the stages of release (e.g., behavioral and physiological data) would provide an even richer picture of the process of release and the role of social behavior in it.

THE CASE OF ELEPHANTS

As ecosystem engineers and iconic members of the megaherbivores that are threatened and endangered, elephants are exceptional candidate species for release efforts (Louys et al., 2014). They play unique roles in their ecosystems through herbivory and seed dispersal (Campos-Arceiz and Blake, 2011; Dublin et al., 1990), such that released elephants may benefit a number of other species and facilitate habitat restoration. Additionally, elephants are singular in their cultural significance and enjoy tremendous public support (Bowen-Jones and Entwistle, 2002), which can be a critical component of release success (Kleiman, 1989). Yet despite the support and broader benefits inherent to elephant release projects, elephants are challenging animals to translocate. In addition to the widely acknowledged hurdles facing wildlife managers planning releases, (e.g., genetic diversity and habitat suitability (International Union for Conservation of Nature, 2013)), the highly mobile and potentially destructive nature of elephants and their generalist foraging strategies (Owen-Smith, 1988) must also be considered. Human-elephant conflict is a significant problem in both Africa and Asia, and conflict is often high near protected areas (Gubbi, 2012; Pinter-Wollman, 2012; Wilson et al., 2015) where conservation translocations are often focused. If elephants to be released have been in captivity for any period of time, habituation to humans may present additional challenges (McKnight, 1995) with considerable consequences for both elephants and humans.

Many elephant translocations have been carried out in Asia and Africa, with mixed results that all too often include human-elephant conflict or homing behavior (Fernando et al., 2012; Pinter-Wollman, 2009). Such outcomes create new problems for managers and squander limited resources. Considering the resources needed and the stakes involved in elephant translocations, the need for sound science to inform release efforts (Seddon et al., 2007) will go a long way in the management of these species. A greater integration of the distinct sub-fields that shed light on social disruption in elephants (e.g., wild elephants experiencing poaching (Gobush et al., 2009; Goldenberg and Wittemyer, 2017), captive elephants moved among facilities (Prado-Oviedo et al., 2016)) will advance understanding of elephant behavior within translocation contexts and related management.

Elephants are highly social animals that exhibit frequent fission and fusion in their aggregation patterns in the wild, albeit with distinctly different patterns emergent from their social associations across species (de Silva and Wittemyer, 2012). They have clear social preferences among their multi-generational associates, which are usually close relatives (Archie et al., 2006; Chakraborty et al., 2014). However, research in wild populations (Vidya et al., 2007; Wittemyer et al., 2009) and in captive settings (Freeman et al., 2010) indicates that elephants can establish strong bonds with nonrelatives in the absence of family, though this process may take place over years (Goldenberg et al., 2016; Goldenberg and Wittemyer, 2017). In addition to a subset of strong bonds, elephants associate with many other individuals with which they have weaker relationships (de Silva et al., 2011; Wittemyer et al., 2005), and it is thought that these might provide distinct benefits within their social system (e.g., information exchange, mating opportunities, dominance resolution). These broader social relationships can be influential to key spatial behaviors (Wittemyer et al., 2007) and appropriate responses to stressors (McComb et al., 2000). Given the species' extreme reliance on sociality, elephant releases must consider the ways in which the emergence of natural social behavior can be facilitated.

To date, elephant translocations have targeted several objectives, including reducing problematic behaviors (Fernando et al., 2012; Pinter-Wollman et al., 2009), captive release to augment wild populations and reduce captive populations (Evans et al., 2013; Thitaram et al., 2015), and orphan rehabilitation (McKnight, 1995; Miththapala, 2009). Most elephant releases, spanning source populations from captivity and the wild, have not quantified social behavior prior to release. Rather, social aspects of elephant releases have primarily been measured following release typically to report on social integration (Pinter-Wollman et al., 2009; Thitaram et al., 2015). In circumstances in which groups from the wild are selected for translocation, selection of cohorts or individuals based on minimal field observations may not adequately capture social structure owing to the fission-fusion nature of elephant sociality. Such circumstances may have precipitated homing behavior of female elephants in a large-scale translocation of African elephants in Kenya (Pinter-Wollman, 2009) and have resulted in extreme duress when families have been separated (Wittemyer pers. obs.). The high homing and dispersal rate of male elephants following translocations may also be attributable to a failure to account for their social nature (Fernando et al., 2012). Where sourcing of elephants to be translocated is more constrained, as in captive populations, captivity histories and keeper knowledge may be used to identify logical cohorts for release, and research into existing social structure at release sites may be leveraged to facilitate integration of formerly captive cohorts (Letty et al., 2007). Cohorts may be constructed to reflect emergence of social structure hypothesized to be important, and their associated success evaluated. Where data collection prior to release is impossible or impractical, observational and experimental data may be collected immediately following release and for an extended period thereafter, though such circumstances preclude management decisions from acting on social behavior at the outset. At a minimum, care should be taken to maintain the structure of a group targeted for translocation. Observations of social interactions may improve understanding of existing social structure.

There are a variety of research directions that will address the gaps in our understanding of successful elephant releases if carried out systematically, some examples of which are described in Table 1. While it is acknowledged that resource and logistical constraints may limit data collection or analysis, a better understanding of the social context of elephant releases—to any extent that it is possible to be obtained—is likely to yield insight for management that improves outcomes. The growing consensus within reintroduction biology that testable approaches are the most effective way forward (Seddon et al., 2007; Swaisgood, 2010) indicates that releases without systematic data collection may no longer be justified. In elephants, multi-year monitoring following release that is modeled on long-term research projects (e.g., physiology (Jachowski et al., 2013), demography (Turkalo et al., 2016), movement (Goldenberg et al., 2018)), may be necessary because of the long period over which social and demographic processes play out in these species.

Figure 1. Roadmap for integration of social behavioral concepts in conservation translocations. Rectangles represent considerations at the hypothesis formation stage and ovals represent measurable parameters hypothesized to be important to post-release success. For example, for a social carnivore, a primary benefit to being social may be cooperative hunting, which relies on social cohesion and social roles within a group. Researchers may quantify bonds and social roles like hunting position among animals being considered for release. Parameters collected in the post-release stage like group cohesion or hunting success rate may be related to parameters collected at earlier stages, like the bond and role composition of release cohorts. Parameters are not exhaustive.

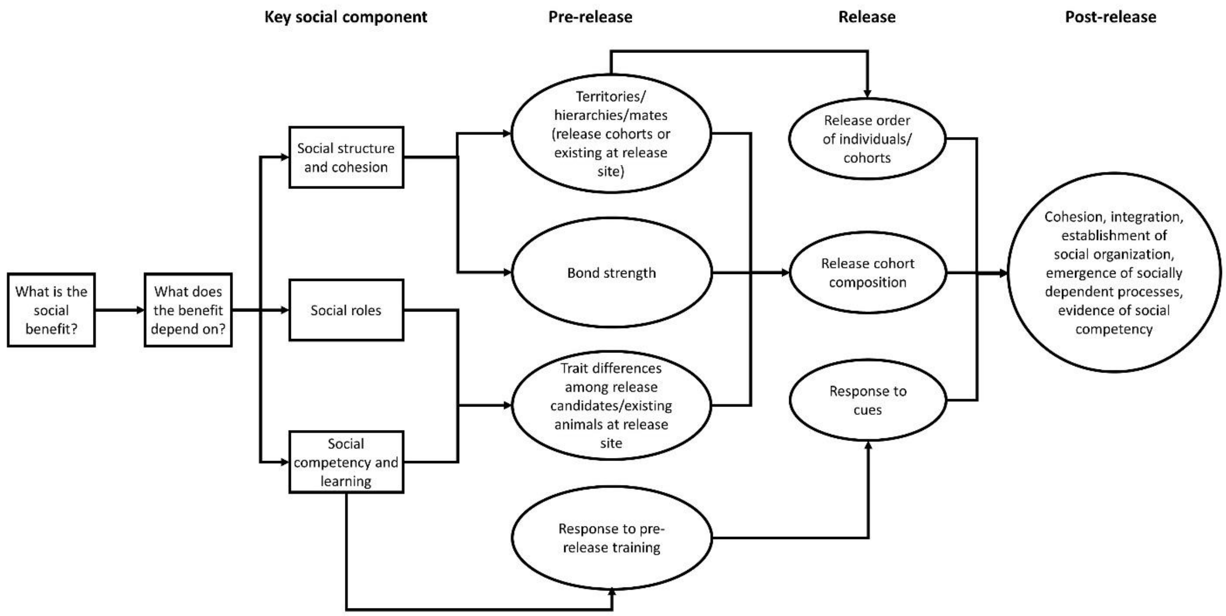

Table 1. Primary considerations to build social functionality in conservation translocations, with a focus on elephants. See text for discussion.

Considerations	Application in conservation translocations	Example elephant research hypotheses	Key references
Social structure and cohesion	Determining release cohort composition Selecting release sites with existing social structure that will be enhanced through release or accommodate release cohort	Bondedness within release cohorts affects dispersal distance from release sites Familiarity among released individuals lowers stress responses Bondedness is positively correlated with reproductive success in a post-release context	Shier 2006 Shier & Swaisgood 2012 Viljoen et al. 2008
Social roles	Determining release cohort composition Selecting release sites with key individuals present	Young calves facilitate integration between released and existing populations Socially exploratory elephants facilitate integration between released and existing populations	Le Flohic et al. 2015 Slotow et al. 2000 Thitaram et al. 2015
Social learning	Determining release cohort composition	Home range establishment within cohorts is related to	Chiyo et al. 2012

	Selecting release sites with key individuals present Managing human-wildlife conflict	the presence of older elephants or elephants familiar with the release site Bondedness with elephants that exhibit problematic behaviors (e.g., crop-raiding, habituation) leads to higher incidence of problematic behaviors post-release Home range establishment is positively correlated with the number of distinct social units or behavioral types present at a release site	Donaldson et al. 2012 Ellis et al. 2000 Mueller et al. 2013
Social competency	Conditioning pre-release Manipulating release site	Exposure to a broader suite of conspecific cues (e.g., dung, urine, audio playbacks of vocalizations) and partners pre-release facilitates integration with unfamiliar elephants post-release Distribution of conspecific cues around a release site leads to post-release settlement	Coelho et al. 2012 Linklater & Swaisgood 2007 Robbins et al. 2003

CONCLUSION

For species in which social processes play important roles in the fitness of individuals, quantification of social factors should be incorporated in release programs early, often and in testable frameworks. It has long been recognized that hypothesis-driven approaches are essential to increase conservation translocation success (Armstrong and Seddon, 2008; Fischer and Lindenmayer, 2000; Seddon et al., 2007), a concept which should be no different when applied to social behavior. Though the collection of extensive data prior to, during, and following release is resource intensive, not identifying important factors in release success may be squandering limited resources and compromising animal welfare. Understanding of the complexity of social behavior in both wild and captive populations has greatly expanded over recent years, in part attributable to methodological creativity and advancements available to study social behavior (Farine and Whitehead, 2015; Pinter-Wollman et al., 2013). There is no reason that such approaches should not be employed in release programs that involve species for which social processes are important. Indeed, given the failure rates known to be pervasive in this field (Fischer and Lindenmayer, 2000; Griffith et al., 1989), it may be unjustified not to quantitatively consider social aspects of management decisions. We have provided a framework for doing so, identifying the multiple stages at which data may inform this process and highlighting a frequently translocated taxon that would benefit tremendously from more rigorous social analysis. We anticipate that wide adoption of hypothesis-driven management decisions related to social behavior will hone protocols and make more efficient use of conservation resources.

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