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Guidelines for evaluating the conservation value of African lion (*Panthera leo*) translocations

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As the top predator in African ecosystems, lions have lost more than 90% of their historical range, and few countries possess strong evidence for stable populations. Translocations (broadly defined here as the capture and movement of lions for various management purposes) have become an increasingly popular action for this species, but the wide array of lion translocation rationales and subsequent conservation challenges stemming from poorly conceived or unsuitable translocations warrants additional standardized evaluation and guidance. At their best, translocations fill a key role in comprehensive strategies aimed at addressing the threats facing lions and fostering the recovery of wild populations in their historic range. At their worst, translocations can distract from addressing the major threats to wild populations and habitats, divert scarce funding from more valuable conservation actions, exacerbate conflict with humans in recipient sites, disrupt local lion demography, and undermine the genetic integrity of wild lion populations in both source and recipient sites. In the interest of developing best practice guidelines for deciding when and how to conduct lion translocations, we discuss factors to consider when determining whether a translocation is of conservation value, introduce a value assessment for translocations, and provide a decision matrix to assist practitioners in improving the positive and reducing the negative outcomes of lion translocation.

KEYWORDS

lion translocation, carnivores, human-wildlife conflict, livestock-depredation, management, policy, predator

1. Introduction

Being the top carnivore in African ecosystems, lions (*Panthera leo*) provide important ecological, economic, and cultural value (Wolf and Ripple, 2018). Despite this, lions have lost more than 90% of their historical range, and in most countries, show evidence of continued population decline (Riggio et al., 2013; Bauer et al., 2015; Riggio et al., 2016). An array of anthropogenic factors has driven these dynamics (Bauer et al., 2020); thus, integrated, and comprehensive conservation actions are needed to address these declines. Common causes of decline include the loss of habitat, prey depletion due to bushmeat poaching, inappropriate hunting quota setting, mortalities of lions due to persecution associated with human-lion conflict, snaring by-catch and increasingly, targeted poaching of lions for their body parts (Henschel et al., 2014; Bauer et al., 2015; Williams et al., 2015; Williams et al., 2017; Lindsey et al., 2017; Everatt et al., 2019; Jacobsen et al., 2020; Williams et al., 2021). However, when lions, as well as their habitat and prey are well-protected, the species recovers rapidly (Riggio et al., 2013; Miller and Funston, 2014; Lindsey et al., 2017; Mweetwa et al., 2018). Recovery or re-establishment of lion populations can be supported through translocations by

introducing individuals into an existing population, or into an area where they have been locally extirpated (Briers-Louw et al., 2019). Although the opportunities to utilize translocations for this goal are still very limited (Hunter et al., 2007), there are increasing instances in Africa where conservation challenges that caused lions to be locally extirpated are being addressed (Hodgetts et al., 2018), creating potentially suitable habitat for reintroducing them. South Africa was pioneering in this regard and has an established metapopulation of lions in small, fenced reserves that rely on translocations to mimic natural systems within a metapopulation, including dispersal and gene flow (Funston, 2008; Slotow and Hunter, 2009; Miller et al., 2013; Miller et al., 2015). Translocations since the early 1990s have re-established wild lions in >50 sites in South Africa (Miller et al., 2013; Miller and Funston, 2014). Recent high-profile examples have also resulted in the translocation of lions into countries where the species had been completely extirpated, including reintroduction of lions into Majete Game Reserve and Liwonde National Park in Malawi, and Akagera National Park in Rwanda (Briers-Louw et al., 2019), and a reintroduction is also planned for Bateke National Park in Gabon for 2022.

Indeed, lion translocations sometimes occur across multiple countries or regions and are becoming increasingly common

throughout Africa (Wolf and Ripple, 2018; Bertola et al., 2022). There are a variety of motivations for translocations, including restoration of locally extirpated populations or augmentation of existing populations, human-lion conflict mitigation, re-establishing populations for tourism purposes, and for a range of other commercial, personal, ethical, and financially motivated reasons (Table 1; Stander, 1990; Funston et al., 2001; Hunter et al., 2007; Trinkel et al., 2008; Miller and Funston, 2014; Morapedi et al., 2021). Substantial guidance exists to ensure translocations benefit the conservation of species and habitats (IUCN/SSC, 1998; Pérez et al., 2012; IUCN/SSC, 2013; IUCN/SSC, 2018; Soorae, 2018; Berger-Tal et al., 2019). For example, the International Union for the Conservation of Nature (IUCN) has produced comprehensive protocols for conservation translocations, which they define as “the deliberate movement of organisms from one site for release in another. It must be intended to yield a measurable conservation benefit at the level of a population, species or ecosystem, and not only provide benefit to translocated individuals” (IUCN/SSC, 2013). However, many lion translocations have not considered or followed the IUCN best practice guidelines for conserving species and habitats (Bauer et al., 2018; Bertola et al., 2022). Reasons for this are variable; often decision-making is required urgently, leading to suboptimal decisions; international collaboration is usually insufficient; suboptimal source animals are readily available

versus suitable wild individuals; and translocations are often driven by a need to remove lions from a source population (e.g. problem animals, metapopulation surpluses) rather than the needs of the recipient area and population. This is a concern because it undermines the potential conservation value of such endeavors, by devaluing translocation benefits, producing adverse welfare outcomes for lions and people at release sites, and posing a risk of introducing animals of inappropriate genetic composition (Slotow and Hunter, 2009; Bertola et al., 2022).

A recent study evaluating CITES permit data for lions translocated between countries from 1988-2019 found that 848 out of 1056 individuals (80%) were listed as ‘captive-sourced’ on the permit, referring mostly to intensively managed lion populations, not to be confused with captive-bred lions for body parts or canned hunting purposes (Williams and ‘t Sas-Rolfes, 2019), for which the origin could be traced for only 76 individuals (7%). Since the genetic background of the remaining individuals was unknown, these translocations (73%) were categorized as ‘unsuitable’, where preserving genetic integrity within naturally occurring clades of wild lions was the primary criterion (Bertola et al., 2022). Given that genetic diversity is directly related to persistence and resilience of populations, and that the local adaptations of lion populations evolved over millennia and are not fully understood, genetic considerations are important. Translocations disregarding genetic

TABLE 1 Primary reasons for lion translocations. There is a wide array of rationales for translocating lions, encompassing a wide range of ecological, management, financial and personal objectives.

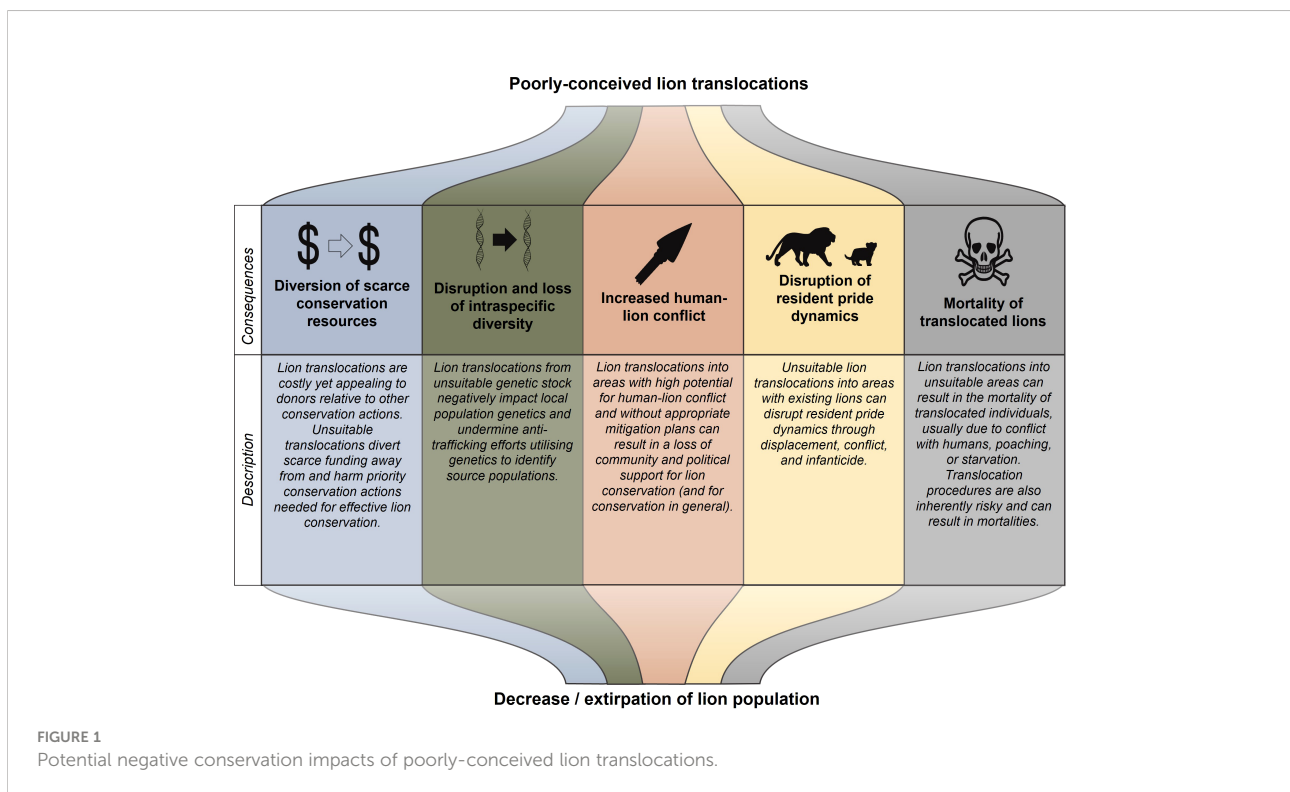
Rationale for Translocation	Description	Examples
Reintroduction	Translocating lions into areas they historically occurred but have been extirpated	(Hayward et al., 2007; Hunter et al., 2007; Tambling et al., 2015; Wolf and Ripple, 2018; Briers-Louw et al., 2019)
Apex predator restoration	Translocating lions to restore the functional ecological role of natural apex predators	Tambling et al., 2013
Metapopulation management	Translocating lions into/out of populations to mimic the natural metapopulation processes of immigration, emigration, births and deaths	(Funston, 2008; Slotow and Hunter, 2009; Hayward and Kerley, 2009; Trinkel et al., 2010; Miller et al., 2013; Ferreira and Hofmeyr, 2014; Miller et al., 2015)
Genetic Rescue/Augmentation	Translocating lions to mitigate negative fitness effects resulting from inbreeding by addition of new individuals, hereby increasing genetic diversity	(Druce et al., 2004; Trinkel et al., 2008; Trinkel et al., 2010; Miller et al., 2020)
Overpopulation management	Translocating individual lions from populations at or over carrying capacity	Kettles and Slotow, 2009; Slotow and Hunter, 2009; Miller et al., 2013; Miller and Funston, 2014
Protecting prey populations	Translocating lions from populations to mitigate predation impacts on herbivore populations	(Kettles and Slotow, 2009)
Personal/financial gain	Translocating individuals into areas for political, personal or financial gain	(Slotow and Hunter, 2009)
Private reserves	Translocation of wild or captive-raised lions to private reserves to introduce or augment populations for eco-tourism	(Slotow and Hunter, 2009; Mossaz et al., 2015)
Hunting	Translocating lions into hunting concessions for purposes of trophy hunting	(Williams and ‘t Sas-Rolfes, 2019)
Tourism	Translocating lions into safari tourism areas intending to increase tourism as a result	(Mossaz et al., 2015)
Problem Animals	Translocation of problem lions (usually livestock depredation) away from areas of conflict	(Standar, 1990; Linnell et al., 1997; Morapedi et al., 2021)

differentiation between populations, risk leading to homogenization, outbreeding depression, and overall loss of diversity. However, it could be argued that genetic suitability should be a consideration only after the rationale for a translocation is clearly established. The wide array of lion translocation rationales (Table 1) and subsequent outcomes stemming from poorly conceived or unsuitable translocations warrants additional standardized evaluation and guidance beyond genetic considerations (Bertola et al., 2022).

While lions are translocated for several reasons, perhaps of greater consideration is that the decision to translocate is often taken within financial and political constraints, with limited time and resources available and regularly in a reactive (e.g., reserve-to-reserve level management), rather than proactive context (e.g., coordinated, long-term and range-wide management strategies). For instance, the drive to translocate often stems from management issues in a source population, such as through the removal of damage-causing animals or surplus pressure in the metapopulation, rather than from the needs of the recipient area or population (Slotow and Hunter, 2009). Lions are deeply charismatic, making for good publicity and tourism value, but their size, breeding success and rate of consumption also places significant pressure on reserve capacity and stocking costs – a difficult balance to manage in smaller, less well-resourced reserves (Miller et al., 2013; Miller and Funston, 2014). In addition, range-

wide strategies are currently restricted by a general lack of collaboration (e.g., countries refusing to provide suitable stock to neighboring countries) and compromised policy (e.g., it is easier to acquire captive-bred lions from elsewhere (Williams and 't Sas-Rolfes, 2019). The interplay of such factors has often and will continue to lead to suboptimal translocation decisions without range-wide consideration, standardized protocols, and a unified strategy for the species (Hodgetts et al., 2018; Bauer et al., 2018; Bauer et al., 2020).

Ideally, translocations should serve a pivotal role in a holistic and comprehensive strategy targeted toward mitigating the threats facing lions and encouraging the recovery of wild populations. At their worst, translocations can distract from addressing the real threats to wild populations and habitats, divert scarce funding from more useful conservation actions, exacerbate conflict with humans and livestock, and undermine the genetic integrity of wild lion populations, among other impacts (Figure 1). Toward developing systematic protocols and decision-making tools for deciding when and how to conduct lion translocations, we summarize the essential factors to consider when determining whether a translocation is of conservation value, introduce a value assessment for future translocations, and provide a decision matrix for managers to consider for improving lion management and conservation outcomes (Figure 2).



2. Factors determining the value of lion translocation as a conservation action

Multiple, inter-related factors affect the likelihood of translocation success, and even more so, whether such intervention is of conservation value to the species. The following section summarizes important factors to consider in determining whether a lion translocation is advisable, and provides zero, moderate and high value scenarios for each (Table 2).

2.1. Translocation (recipient) site factors

2.1.1. Prospects for natural or assisted recovery and recolonization

As remaining lion habitat continues to diminish, there is an increasing focus on retaining existing diversity and ensuring viable lion populations through connectivity, natural recovery, and local recolonization wherever possible (Soorae, 2018; Berger-Tal et al., 2019). From an ecological perspective, natural recovery, or recolonization without translocations from

other populations is ideal and should always remain a top priority, as this ensures that site and population-specific diversity is retained and has benefits far beyond single species (Lindsey et al., 2017; Bauer et al., 2020). Importantly, the pervasive influence of humans on virtually all remaining lion populations means that natural recovery or recolonization of lions is only possible where significant management interventions (e.g., robust law enforcement, protection, community engagement, land-use planning, and human-lion conflict mitigation) are already in place or can be put in place. We make a distinction here between that scenario (i.e., what we term assisted recovery: natural recovery assisted by management interventions creating suitable conditions) versus resorting to translocations. Nevertheless, even where a strong management presence is in place, the time needed to restore connectivity or allow for natural recovery may be several decades and prohibitive, populations may be too small or not genetically viable, and in some cases this will be impossible. Translocations should therefore clearly evaluate the need against the potential for natural recovery and recolonization, providing clear justification why a translocation is needed in this specific context. The value of translocation is therefore potentially greatest where the prospect for recovery and recolonization can be shown to be very low or non-existent.

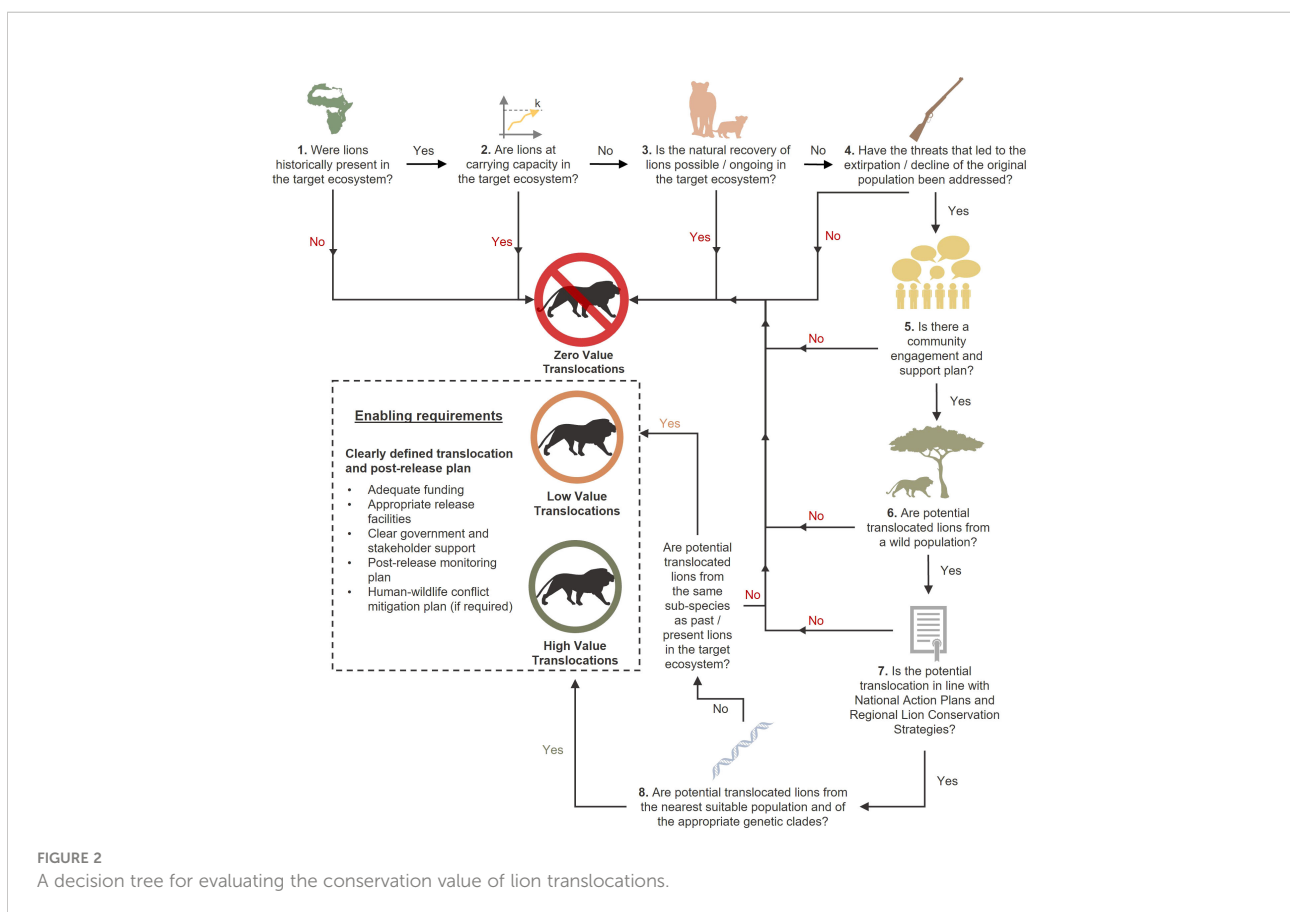


TABLE 2 Factors to consider for assessing the conservation value of translocations.

	Conservation Value of Translocation Consideration		
	Zero Conservation Value	Low Conservation Value	High Conservation Value
RECIPIENT SITE CONSIDERATIONS			
<i>Natural recolonization or assisted recovery</i>	High chance	Medium chance	No chance
<i>Lion population</i>	At or close to capacity*	Under capacity/naturally increasing	Extirpated/greatly reduced
<i>Prey availability</i>	Low-very low	Reduced/slowly recovering	Surplus
<i>Level of threat</i>	High	Low to Medium	Controlled
<i>Human & livestock presence</i>	High	Medium	Low/absent
ORIGIN OF TRANSLOCATED LIONS			
<i>Wild vs captive</i>	Captive-origin	Captive-origin when suitable wild founders are unavailable	Wild
<i>Genetic alignment with naturally occurring clades</i>	Distant wild populations, Unknown origin, Hybrids between clades.	Regionally adjacent wild clade	Wild population from within same clade.
<i>Problem animals</i>	Known killers of people. Long-term habitual livestock killers	First-case/non-habitual livestock killers	Dispersing animals prior to evidence of conflict
GOVERNANCE CONSIDERATIONS			
<i>Consistent with National Strategic plan/ equivalent</i>	No	Partially	Yes
<i>Long-term management capacity/resources in place</i>	No	Partially	Yes
<i>Community Engagement and Support Plan</i>	No	Partially	Yes

*Capacity, as dictated by current factors; see the text for explanation.

The ideal translocation scenario in maximizing the potential conservation value is one in which the status of every factor is high value. Such a situation is elusive in the real world, where translocation is likely to be undertaken under a mixed high and low value scenario. Zero value scenarios, particularly in site considerations and the use of problem animals as founders have elevated risks of failure of translocation and are best avoided (see the text for exceptions on problem animals).

2.1.2. Have the factors that extirpated or reduced lions been adequately addressed?

Range-wide analyses have identified bushmeat poaching and retaliatory killing of lions due to human-lion conflict as the two most serious threats to African lion populations (Lindsey et al., 2017; Bauer et al., 2020). Because of their high-profile public appeal (i.e., charisma) and immediate impact, translocations are generally popular and relatively easy to generate financial and public support for compared to other actions such as human-lion conflict mitigation, law enforcement, land-use planning, and other comprehensive and long-term strategies fundamental to securing lion populations and their habitat. However, translocations are strongly discouraged if the underlying threats that led to lion extirpation or decline in the first place have not been addressed.

A comprehensive evaluation and understanding of the factors leading to lion disappearance or decline in an ecosystem should be undertaken, and programs should be implemented to address and control these threats, with clear evidence of success before a translocation is considered. Serious consideration must also be given as to whether translocation is the best tool available to address population or ecosystem recovery. While conservation translocations can play an important role in lion conservation, it is worth noting that the

most urgent threat assessments and management or action plans do not identify an urgent need for reintroductions or augmentations of lions; instead, these plans emphasize the need to address the underlying causes of decline or extirpation (Bauer et al., 2020).

Fragmentation of habitat (e.g., through fencing, land transformation, change in land use, human encroachment, and human population increases) may result in conservation areas that are too small for long-term lion population viability (Björklund, 2003). These areas can still be considered for translocations if a long-term connectivity plan, such as a managed metapopulation or corridor creation through functional zonation and ecological restoration, is in place to link isolated populations to each other or to larger populations. The first approach has been applied to wild dogs, cheetahs, and lions in southern Africa, mainly South Africa (Supplementary Material, Davies-Mostert et al., 2015; Miller et al., 2015; Buk et al., 2018). There is a growing body of literature dedicated to the management of fragmented populations and negative fitness trends because of low genetic heterozygosity that can be reversed by genetic rescue (Frankham et al., 2017; Ralls et al., 2018; Frankham et al., 2019; Ralls et al., 2020). Genetic rescue of the isolated lion population in Hluhluwe-iMfolozi Park, for instance, has shown that heterozygosity, and thus resilience,

can be increased through introduction of genetically diverse individuals (Trinkel et al., 2008; Miller et al., 2020). As fragmentation of lion habitat increases, mimicking natural movements through translocations to ensure genetic integrity and long-term survival of isolated populations will likely be increasingly necessary. This should not detract from efforts to increase and secure lion habitat and improve connectivity between isolated populations, but it can be a useful tool to supplement these efforts, even as a short-term measure.

2.1.3. Presence and ecological carrying capacity of lions at the translocation (recipient) site

Knowing the status of lions at a proposed translocation site is essential for assessing the conservation value of translocation. Translocation has considerably greater conservation value where lions are absent or limited due to the presence of dispersing males, which can travel hundreds of kilometers from resident populations (Dolrenry et al., 2014). Where lions are already resident, there are many more factors to consider ensuring high conservation value, foremost the ability of a lion population to absorb translocated individuals. The current and potential ecological carrying capacity for lions at the translocation (recipient) site is an important factor here. If lions are at or near carrying capacity at the site (defined as both suitable and sufficient space, habitat, and prey available), a translocation will be of minimal value. This scenario is likely to create problems for both resident and translocated animals, as there are simply insufficient resources (e.g., space, prey, and mates) for additional lions. Within the population, incoming individuals, particularly males, can kill cubs and disrupt pride dynamics (Borrego et al., 2018). In the broader ecological context, they can create problems for surrounding communities and livestock should lions become displaced or disperse in search of available space, prey or breeding opportunities (see below). Critically, this situation often applies in depleted lion populations; that is, even a population well below its natural carrying capacity may have reached the limits imposed by current prey or habitat availability, and thus cannot accommodate translocated individuals until those conditions change in a direction that fosters population growth. In this case, investing additional resources to significantly reduce any remaining threats at the destination site and to restore prey populations for several years prior to release (depending on the degree of depletion). Closely related to ecological carrying capacity is the size of the recipient area in which the translocations will occur. The area must be large enough to hold a viable population, and the potential for anthropogenic edge effects from conflict and poaching must be mitigated. If areas are small and surrounded by human-dominated landscapes they are likely to require fencing, and intensive metapopulation management to ensure viability (Appendix A, Slotow and Hunter, 2009, see below).

2.1.4. Prey availability

One of the key determinants of lion carrying capacity is the availability of wild prey (Schaller, 1972). Prey depletion, particularly of preferred larger species such as buffalo, has been shown to not only reduce the density of lions and reduce cub recruitment and pride sizes (Vinks et al., 2021), but can also increase prey base homogenization and niche compression, with a multitude of effects on lion energetics, interspecific competition, and snaring by-catch susceptibility (Creel et al., 2018). It is important that there is a sufficient and suitable prey base to sustain a lion population and minimize the probability of translocated animals roaming and preying upon livestock in nearby human-dominated landscapes (Trinkel and Angelici, 2016; Kettles and Slotow, 2009). Problematically, many areas with a suitable prey base already support a corresponding density of lions (Lindsey et al., 2017), so the mere presence of abundant prey does not necessarily increase the value of a potential translocation given the constraints of ecological carrying capacity.

2.1.5. Human-livestock dimensions

Considerations of the human community dynamics within or surrounding the translocation site are critical to assessing its conservation value (Treves and Karanth, 2003; Kettles and Slotow, 2009; Bavin et al., 2020). Some degree of conflict between people and reintroduced lions is likely, even if it only occurs many years post-release, and a proactive mitigation plan must be in place before lions are released (Jacobsen et al., 2020). This applies whether people and livestock are living within the release site, or outside it. If the release site is small and surrounded by high densities of people, fencing may be required to prevent potential conflict with people and livestock, and corresponding high rates of anthropogenic mortality of lions (Bauer et al., 2020). In most instances, especially where people live in or near the protected area (PA), consulting local leadership and communities and obtaining support for the reintroduction is advisable at minimum and often necessary to ensure optimal outcomes (see below, Treves and Karanth, 2003). In addition, long-term engagement, and if appropriate, support, for communities potentially impacted by the translocation should be obligatory (Bavin et al., 2020). This is particularly important in areas where lion have been extirpated long ago, and local knowledge on coexistence has been lost and requires work with community elders to reimplement traditional coexistence measures.

2.2. Origins of translocated lions

2.2.1. Wild versus captive origins

The use of captive-bred or captive-raised lions (including orphaned cubs) for reintroduction in southern Africa has been

extensively analyzed and rejected (Hunter et al., 2013). There are considerable risks associated with such reintroductions, including potential inbreeding deficits (Boakes et al., 2007; Leberg and Firman, 2007), a lack of clarity regarding the genetic origin of captive animals (Williams et al., 2021), elevated risks that they are habituated to humans and thus create hazards for local people (Shepherd et al., 2014), and evidence that they are poorly equipped to life in nature compared to their wild-born counterparts (Jule et al., 2008). As summarized by Hunter et al. (2013), “for every objective criterion by which reintroductions are planned and evaluated, wild lions are better candidates for increasing the likelihood of success”. In general, there is no shortage of sites from which wild-born lions can be sourced without impacts on the source population, and thus very little need to rely on captive-bred animals for reintroductions. An important exception may apply in rare cases where suitable wild founders are not available, for example, in ensuring a close genetic match of a restored population (e.g., in West Africa, see genetic considerations). In this case, well-managed *ex-situ* populations could represent a viable source, although apart from the Indian population, the northern subspecies of lion (*P. leo leo*) is barely represented in accredited zoos (Bertola et al. *in prep.*) and source animals are undesirable from commercial lion breeding operations (e.g., for body parts and ‘canned’ trophy hunting). Even so, resorting to the use of captive-born or raised lions will significantly raise both risks of failure and the costs of implementation, and should be regarded as low value.

2.2.2. Genetic considerations

Genetic considerations are outlined extensively in Bertola et al. (2022), and we do not add to this except to emphasize that translocations should adhere to the decision matrix for suitable genetic clades. We should avoid the risk of homogenization, which may occur when ignoring known patterns of genetic diversity (Olden et al., 2004; Gippoliti et al., 2018). As ongoing developments in genetic technology will likely continue to make differences between populations more apparent and may also provide insight into the importance of local adaptation, a useful ‘rule of thumb’ is to be cautious and to source populations as close to the target area as is possible, while adhering to identified boundaries delineating different genetic clades (Bertola et al., 2022). We acknowledge difficulties in sourcing nearest populations (e.g., translocations in Rwanda and Malawi), particularly between countries, and recommend one future component of lion action plans be greater cooperation between neighboring countries in assisting with suitable sourcing of animals for reintroduction. Lastly, given the rise in illegal trafficking of lion skins and other body parts (Everatt et al., 2019), wildlife forensics and anti-trafficking depend in part on the ability to trace seizures back to their source populations, for which

genetics can be a useful tool. Failure to consider genetics in translocations can compromise these tracing efforts by mixing populations and weakening global anti-trafficking operations.

2.2.3. Translocation of problem lions

Wildlife authorities in Africa are often faced with unenviable choices when lions move into human-dominated landscapes lacking sufficient wild prey and begin preying upon livestock. In such instances, the choices are limited to 1) waiting it out and hoping the lions move on; 2) attempting to drive the lions from the area; 3) lethal control of some or all lions; or 4) translocation. A wildlife management authority adopting any of these options is likely to be heavily criticized by different stakeholders. Thus, translocation in such instances, while unlikely to meet the criteria outlined for a satisfactory outcome, may be seen as the least poor option. There are steps that can be taken to minimize the likelihood of such scenarios unfolding, including fencing of PAs bordering on conflict-prone communities, managing to prevent overabundance of lion population in PAs, establishing buffer zones around PAs and – most importantly – working with communities to minimize conflict and promote successful coexistence (see Lindsey et al., 2021 for examples). However, the reality is that due to increasingly fragmented lion distribution, increasingly incompatible land use practices surrounding PAs in many countries, and long-distance dispersal capabilities of lions, it is inevitable that lions will occasionally end up in areas unsuitable for their survival, and that in many such instances they will turn to livestock depredation for survival.

Translocation of problem or Damage-Causing Animals (DCAs) presents a particularly challenging scenario and requires careful consideration (Linnell et al., 1997). Relocation of problem lions is often used to address human-lion conflict but there is very limited evidence showing useful conservation outcomes (Weilenmann et al., 2010; Boast et al., 2016). While it might address the immediate and local conflict problem, the effect is typically temporary unless resources are invested in improving livestock husbandry and in other measures that reduce the opportunities for lions to become a problem in the first place (Morapedi et al., 2021). Translocating problem animals can also simply displace conflict to the recipient site, particularly where there are already resident lions, producing poor outcomes for both lions and human communities near the translocation site (Morapedi et al., 2021). This can often be the case on a small scale within an ecosystem, where problem lions are translocated back into national parks and into other areas, only to either return or cause problems elsewhere. In addition, aging lions can present additional problems regardless of wild prey abundance, as they can be prone to preying on livestock. Further research is needed on the efficacy of translocation for conflict mitigation but very careful scrutiny of both the individuals (especially in terms of their history of conflict-

causing behavior) and the recipient site is essential (Linnell et al., 1997), as well as understanding the drivers of human-lion conflict in the source area. This should be combined with strong human-lion conflict mitigation plans and strategies as part of a mandatory post-release monitoring framework to avoid simply displacing the problem to a different area. In general, translocations of problem animals, particularly into PAs with established lion populations, should be discouraged. While politically sensitive and often favored by politicians and wildlife authorities, lethal control should also still be considered in circumstances where other options have been exhausted, in cases of man-eating, and where translocation is a costly diversion of scarce conservation resources and likely to simply transfer the problem to the recipient site.

Problem lions may be candidates for translocations in exceptional circumstances, where recipient sites currently lack lions or have a minimal presence, and where livestock is largely absent. These circumstances exist in parts of Mozambique for example, where translocation of problem lions has been successful, both at the source site, where they were causing significant harm to livelihoods and would have likely been killed; and at the recipient site where they have mostly survived, having helped to re-establish new populations, and are unlikely to cause problems for local people (J. Almeida *pers. comm.*, 2021). Similarly, sub-adult dispersers with a high potential for conflict-causing behavior along the edge of PAs were often prioritized for translocation efforts into fenced reserves in South Africa, resulting in population establishment and minimal conflict at the release sites (Hunter et al., 2007; Slotow and Hunter, 2009; Hunter et al., 2013).

2.3. Governance and management factors

2.3.1. Compatibility with conservation plans for lions

Given the array of anthropogenic threats facing lion populations, substantial amounts of time, expertise and resources have been invested in developing regional conservation strategies and national action plans (or their equivalent) for African lions. These strategies provide clear evaluations of the most important challenges and threats to lion conservation in any given area, the objectives and actions needed to address them, and are developed from comprehensive expert assessments and reviews of the status and threats to lions—at an international level through regional assessments and at a national and local level through national action and management plans (IUCN/SSC 2006a; IUCN/SSC 2006b; IUCN/SSC, 2018). Regional strategies exist for lions, and most range states have a national action plan or similar guiding documents (e.g., Packer et al., 2009; ZAWA, 2009;

MDNPW, 2010; Funston and Levendal, 2015; ANAC, 2016; NMET, 2016; ZPWMA, 2019). Translocations should therefore be considered in the context of whether they are in accordance with the objectives and actions highlighted by a given national action plan and regional strategy. It is worth noting that conservation translocations as a key action for lion conservation are not identified in regional strategies and most national action plans (but see Malawi (MDNPW, 2010), Mozambique (ANAC, 2016), and South Africa (Funston and Levendal, 2015)). This is not surprising when one considers that the opportunities to restore wild lion populations are profoundly limited by the same anthropogenic pressures that have led to the species' decline. Recognizing this, range state governments and practitioners have generally not regarded reintroduction as a high-value priority. Unfortunately, this may not prevent poorly conceived projects operating outside national priorities. For example, a commercial lion 'reintroduction' programme in Zambia and Zimbabwe benefited financially from portraying the countries' lion populations as being in dire need of new, translocated individuals, yet the National Action Plans for lions in both countries make no mention of translocations as a key need for wild populations and habitats versus better resource protection and conflict mitigation (ZPWMA, 2019; ZAWA, 2009, ZDNPW, 2021). While ecotourism benefits of wild lion populations are usually legitimate (Mossaz et al., 2015), financially driven operations such as cub-petting and cub-walking often tout these activities as supporting conservation through eventual translocation of lions into the wild; however, these programs provide no conservation benefit and can be detrimental for conservation of wild populations (Hunter et al., 2013). Similarly, lion translocations into trophy-hunting areas must be carefully assessed to ensure there is no conflict of interest between donors and management to ensure the aim of the action is conservation versus financial, as donors may be unaware that the population is intended to be harvested. Nevertheless, given the high-profile and appealing nature of translocations, they are often much easier to promote and fund than the less glamorous actions identified for lion conservation in regional and national plans. This disparity in favor of translocations can undermine legitimate conservation strategies, and often produces minimal to no long-term conservation value (Hunter et al., 2013).

2.3.2. Translocations should be well-planned and resourced with a long-term post-release management plan

Translocations can frequently be reactionary in their development and implementation, particularly in the case of conflict lions (see above). A translocation should clearly provide justification for why such action is necessary, how it complements national and regional strategies (see above) for addressing threats in the target system, and why translocation is

the best conservation action for the given population or ecosystem. Goals, objectives, justification, management actions, and timelines should all be included, as well as long-term post-release monitoring to evaluate success and progress toward goals and objectives (Berger-Tal et al., 2019). Evidence of sufficient resources and expertise to conduct all work, as well as a clear plan for and long-term commitment, should be provided prior to any action. Translocations should ideally utilize ‘soft-release’ methods (Hunter et al., 2007) and have adequate facilities and experienced, qualified personnel available for this well in advance and throughout the procedure, including post-release monitoring (van Dyk, 1997; Miller et al., 2013). The latter should not be short-term in nature (i.e., several weeks) but rather a commitment to intensive, long-term monitoring to confirm the success or failure of the translocation and avert any problems encountered. In addition, for areas that are severely depleted and unlikely to be supplemented by natural recolonization, or in highly fragmented landscapes where managed metapopulations are necessary (Supplementary Material, Miller et al., 2015), a long-term translocation strategy should be implemented given that population viability will typically depend on the continued introduction of individuals over time (e.g., Miller et al., 2015). Similarly, it is essential to clearly articulate management options for rapid lion population growth that maximize conservation outcomes and reduce potential impacts on prey species and other biodiversity (Slotow and Hunter, 2009; Miller and Funston, 2014). Given the high profile and political considerations around translocations, proactive and consistent management will be necessary and may entail lethal intervention.

2.3.3. Community engagement and support plan

Lion translocations should always entail close collaboration with local wildlife authorities, and deep and long-term involvement of human communities near the release site. Even with extensive planning and consultation, anthropogenic mortality of reintroduced lions is likely in most settings (e.g. Hunter et al., 2007), and the human dimensions of lion restoration can easily jeopardize project success even where biological and technical considerations are met. Involving all potentially impacted communities well in advance of releases (e.g., three years, see Hunter et al., 2007) is the first step. Beyond that, a long-term commitment to communities with approaches that foster tolerance for reintroduced lions will contribute substantially to project success. Most importantly, the provision of training and resources for reducing sources of conflict with lions (e.g., by building night corrals/bomas for livestock and related husbandry measures that mitigate depredation) as well as a focus on providing skills training and employment associated with the project, e.g., in tourism, monitoring or research, should be regarded as essential.

3. Actionable recommendations & discussion

The conservation utility of translocations can be summarized thus:

Scenario 1: High-value translocations (HVT)

Suitable translocations are in line with the national action plan and regional strategy objectives for lion conservation. The translocations are into areas where the threats that led to lion declines or extirpation have been evaluated and have been or are being actively addressed and the potential for natural recolonization has been assessed and is not possible, or efforts at connectivity are concurrent but not likely to result in natural recolonization. There has been active involvement with government, partners and stakeholders and community attitudes toward translocations have been addressed with constant engagement and conflict mitigation measures. Translocated lions are from the nearest suitable wild population, matching genetic clades and source population stability. There is a clear translocation plan complete with rationale and post-release monitoring plans. The recipient site has adequate and suitable prey, and if problem lions are being translocated it is not into an area with lions already at or near carrying capacity, and livestock conflict potential is likely to be minimal. Translocations to assist connectivity between isolated populations within a managed metapopulation network (see Supplementary Material for more guidance), or as a less regular occurrence to fulfill genetic augmentation to avoid the need for genetic rescue efforts, are also suitable, provided they are part of a national action plan and regional strategy. If well managed, this can lead to additional strongholds for lions.

Scenario 2: Low-value translocations (LVT)

Passable lion translocations are into areas where such actions may not be necessary, but source animals are from suitable populations and genetic stock and the release site has suitable numbers of prey and the threats leading to population decline or extirpation have been evaluated and addressed. There is a clear reintroduction plan, a soft-release, and post-release monitoring. There is no relevant conservation plan to refer to, but the translocation would not contravene the factors outlined above. Another example might be the translocation of problem lions into suitable sites with no or low numbers of lions, far from communities and livestock populations, and where the causes

for the initial extirpation or reduction of lion numbers have been addressed.

Scenario 3: Zero-value translocations (ZVT)

Unsuitable translocations would include any of the following factors: the source lions for translocations are captive bred, of distant (e.g., different subspecies) or unknown or unsuitable hybrid genetic stock, the threats that lead to lion declines or extirpation at the recipient site have not been evaluated and are not being addressed, or lions are being translocated and released within the same landscape as a reaction to conflict. Natural recovery and recolonization are probable or occurring without translocation of additional lions, and translocations are not in accordance with or undermine national action plans and regional conservation strategies for lions. Translocated lions having a history of conflict with livestock being released into areas with communities and livestock. The recipient site has a population at or near carrying capacity or high potential for conflict with surrounding communities and no human-wildlife conflict mitigation program has been implemented. Consultation with government wildlife agencies, partners, and stakeholders, and address of community attitudes and active human-wildlife conflict mitigation has been minimal or absent.

Translocations of lions are undertaken for a variety of reasons (Wolf and Ripple, 2018) and the tool can play an important role in re-establishing or augmenting depleted populations. However, unless translocations are properly planned, they can create an array of challenges for the lions to be translocated, and for local people and lions at the recipient site and in the worst case undermine conservation of lions and their habitat. Consequently, it is important to critically assess translocations in line with a set of key criteria to determine whether they are advisable. It should be acknowledged that conservation, as only one of a variety of motivations for the translocation of wildlife (i.e., lions), may ultimately be trumped by some other competing needs. This piece presents guidelines and arguments from the perspective of lion conservation and thus is to be used as a tool to bring clarity in the overall adjudication of the conservation value of lion translocations. Thus, we hope that in the future similarly detailed treatment is given to other aspects of lion translocations such as socio-economic and political considerations.

References

ANAC (2016). *National action plan (NAP) for the conservation of the African lion (Panthera leo leo) in Mozambique* (ANAC, Maputo, Mozambique: Administracao Nacional de Areas de Conservacao (ANAC). Available at: <https://www.cms.int/sites/default/files/document/Lion%20Action%20Plan%20-%20Logical%20Framework%2012%2005%202016.pdf>.

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Conflict of interest

The authors declare that the research was conducted in the absence of any commercial or financial relationships that could be construed as a potential conflict of interest.

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Supplementary material

The Supplementary Material for this article can be found online at: <https://www.frontiersin.org/articles/10.3389/fcosc.2022.963961/full#supplementary-material>

Bauer, H., Chapron, G., Nowell, K., Henschel, P., Funston, P., Hunter, L. T. B., et al. (2015). Lion (*Panthera leo*) populations are declining rapidly across Africa, except in intensively managed areas. *PNAS* 112 (48), 14894–14899. doi: 10.1073/pnas.1500664112

Bauer, H., Dickman, A., Chapron, G., Oriol-Cotterill, A., Nicholson, S. K., Sillero-Zubiri, C., et al. (2020). Threat analysis for more

effective lion conservation. *Oryx* 56(1) 108–115. doi: 10.1017/S0030605320000253

Bauer, H., Nowell, K., Sillero-Zubiri, C., and Macdonald, D. W. (2018). Lions in the modern arena of CITES. *Conserv. Lett.* 11 (5), e12444. doi: 10.1111/conl.12444

Bavin, D., MacPherson, J., Denman, H., Crowley, S. L., and McDonald, R. A. (2020). Using q-methodology to understand stakeholder perspectives on a carnivore translocation. *People Nat.* 2 (4), 1117–1130. doi: 10.1002/pan3.10139

Berger-Tal, O., Blumstein, D. T., and Swaisgood, R. R. (2019). Conservation translocations: A review of common difficulties and promising directions. *Anim. Conserv.* 23 (2), 121–1131. doi: 10.1111/acv.12534

Bertola, L. D., Williams, V. L., Miller, S. M., Naude, V. N., Coals, P., Dures, S. G., et al. (2022). Genetic guidelines for translocations: maintaining intra-specific diversity in the lion (*Panthera leo*). *Evol. Appl.* 15, 22–39. doi: 10.1111/eva.13318. x(x)

Björklund, M. (2003). The risk of inbreeding due to habitat loss in the lion (*Panthera leo*). *Conserv. Genet.* 4 (1), 515–523. doi: 10.1023/A:1024737317695

Boakes, E. H., Wang, J., and Amos, W. (2007). An investigation of inbreeding depression and purging in captive pedigreed populations. *Heredity* 98 (1), 172–182. doi: 10.1038/sj.hdy.6800923

Boast, L., Good, K., and Klein, R. (2016). Translocation of problem predators: Is it an effective way to mitigate conflict between farmers and cheetahs *Acinonyx jubatus* in Botswana? *Oryx* 50 (3), 537–544. doi: 10.1017/S0030605315000241

Borrego, N., Ozgul, A., Slotow, R., and Packer, C. (2018). Lion population dynamics: do nomadic males matter? *Behav. Ecol.* 29 (3), 660–666. doi: 10.1093/beheco/ary018

Briers-Louw, W. D., Verschuuren, S., and Leslie, A. J. (2019). Big cats return to majete wildlife reserve, Malawi: evaluating reintroduction success. *Afr. J. Wildl. Res.* 49 (1), 34–50. doi: 10.3957/056.049.0034

Buk, K. G., van der Merwe, V. C., Marnewick, K., and Funston, P. J. (2018). Conservation of severely fragmented populations: Lessons from the transformation of uncoordinated reintroductions of cheetahs (*Acinonyx jubatus*) into a managed metapopulation with self-sustained growth. *Biodivers. Conserv.* 27 (1), 3393–3423. doi: 10.1007/s10531-018-1606-y

Creel, S., Matandiko, W., Schuette, P., Rosenblatt, E., Sanguinetti, C., Banda, K., et al. (2018). Changes in large carnivore diets over the past half-century reveal depletion of large prey. *J. Appl. Ecol.* 55, 2908–2916. doi: 10.1111/1365-2664.13227

Davies-Mostert, H. T., Mills, M. G. L., and Macdonald, D. W. (2015). The demography and dynamics of an expanding managed African wild dog metapopulation. *Afr. J. Wildl. Res.* 45 (2), 258–273. doi: 10.3957/056.045.0258

Dolrenry, S., Stenglein, J., Hazzah, L., Lutz, R. S., and Frank, L. (2014). A metapopulation approach to African lion (*Panthera leo*) conservation. *PLoS One* 9 (2), e88081. doi: 10.1371/journal.pone.0088081

Druce, D. J., Druce, H. C., Braak, J., Greatwood, S., Delsink, A. K., Kettles, R., et al. (2004). Population demography and spatial ecology of a reintroduced lion population in the greater makalali conservancy, south Africa. *Koedoe* 47 (1), 103–118. doi: 10.4102/koedoe.v47i1.64

Everatt, K. T., Kokes, R., and Lopez Pereira, C. (2019). Evidence of a further emerging threat to lion conservation; targeted poaching for body parts. *Biodivers. Conserv.* 28 (1), 4099–4114. doi: 10.1007/s10531-019-01866-w

Ferreira, S. M., and Hofmeyr, M. (2014). Managing charismatic carnivores in spatially restricted areas: Large felids in south Africa. *S. Afr. J. Wildl.* 44 (1), 32–42. doi: 10.3957/056.044.0102

Frankham, R., Ballou, J., Ralls, K., Eldridge, M., Dudash, M., Fenster, C., et al. (2017). *Genetic management of fragmented animal and plant populations* (UK: Oxford University Press). Available at: <https://doi.org/10.1093/oso/9780198783398.001.0001>.

Frankham, R., Ballou, J., Ralls, K., Eldridge, M., Dudash, M., Fenster, C., et al. (2019). *A practical guide for genetic management of fragmented animal and plant populations* (UK: Oxford University Press). Available at: <https://doi.org/10.1093/oso/9780198783411.001.0001>.

Funston, P. J. (2008). “Conservation and management of lions in southern Africa: status, threats, utilization, and the restoration option,” in *Management and conservation of large carnivores in West and central Africa*. Eds. B. Croes, H. H. de Longh and H. Bauer (Leiden: Institute of Environmental Sciences), 109–131. Available at: https://leofoundation.org/wp-content/uploads/2017/01/W-C-Africa_large-carnivores_seminar-2006.pdf.

Funston, P. J., and Leventhal, M. (2015). *Biodiversity management plan for African lion (Panthera leo)* (Pretoria, South Africa: Department of Environmental Affairs (DEA)). Available at: <https://cer.org.za/wp-content/uploads/2010/05/African-lion.pdf>.

Funston, P. J., Mills, M. G. L., and Biggs, H. C. (2001). Factors affecting the hunting success of male and female lions in the Kruger national park. *J. Zool.* 235 (4), 419–431. doi: 10.1017/S0952836901000395

Gippoliti, S., Cotterill, F. P. D., Groves, C. P., and Zinner, D. (2018). Poor taxonomy and genetic rescue are possible co-agents of silent extinction and biogeographic homogenization among ungulate mammals. *Biogeographia* 33 (1), 41–54. doi: 10.21426/B633039045

Hayward, M. W., and Kerley, G. I. H. (2009). Fencing for conservation: Restriction of evolutionary potential or a riposte to threatening processes? *Biol. Conserv.* 142 (1), 1–13. doi: 10.1016/j.biocon.2008.09.022

Hayward, M. W., Kerley, G. I. H., Adendorff, J., Moolman, L. C., O'Brien, J., Sholto-Douglas, A., et al. (2007). The reintroduction of large carnivores to the Eastern cape, south Africa: An assessment. *Oryx* 41 (2), 205–214. doi: 10.1017/S0030605307001767

Henschel, P., Coad, L., Burton, C., Chataigner, B., Dunn, A., McDonald, D., et al. (2014). The lion in West Africa is critically endangered. *PLoS One* 9 (1), e83500. doi: 10.1371/journal.pone.0083500

Hodgetts, T., Lewis, M., Bauer, H., Burnham, D., Dickman, A., Macdonald, E., et al. (2018). Improving the role of global conservation treaties in addressing contemporary threats to lions. *Biodivers. Conserv.* 27 (1), 2747–2765. doi: 10.1007/s10531-018-1567-1

Hunter, L. T. B., Pretorius, K., Carlisle, L. C., Ricketon, M., Walker, C., Slotow, R., et al. (2007). Restoring lions *Panthera leo* to northern KwaZulu-natal, south Africa: short-term biological and technical success but equivocal long-term conservation. *Oryx* 41 (2), 196–204. doi: 10.1017/S003060530700172X

Hunter, L. T. B., White, P., Henschel, P., Frank, L., Burton, C., Loveridge, A., et al. (2013). Walking with lions: Why there is no role for captive-origin lions *Panthera leo* in species restoration. *Oryx* 47 (1), 19–24. doi: 10.1017/S0030605312000695

IUCN/SSC (1998). *Guidelines for re-introductions* (IUCN Gland, Switzerland and Cambridge, UK: International Union for the Conservation of Nature (IUCN)/ Species Survival Commission (SSC) Re-introduction Specialist Group). Available at: <https://portals.iucn.org/library/sites/library/files/documents/PP-005.pdf>.

IUCN/SSC (2006a). *Conservation strategy for the lion in East and southern Africa* (IUCN Johannesburg, South Africa: International Union for the Conservation of Nature (IUCN)/ Species Survival Commission (SSC) Cat Specialist Group). Available at: https://www.environment.gov.za/sites/default/files/docs/pantheraleo_conservationstrategy_regionalafrica.pdf.

IUCN/SSC (2006b). *Conservation strategy for the lion in West and central Africa* (IUCN Yaoundé, Cameroon: International Union for the Conservation of Nature (IUCN)/ Species Survival Commission (SSC) Cat Specialist Group). Available at: https://www.environment.gov.za/sites/default/files/docs/pantheraleo_conservationstrategy_regionalafrica.pdf.

IUCN/SSC (2013). *Guidelines for reintroductions and other conservation translocations* (IUCN Gland, Switzerland: International Union for the Conservation of Nature (IUCN)/ Species Survival Commission (SSC) Re-introduction Specialist Group). Available at: <https://portals.iucn.org/library/sites/library/files/documents/2013-009.pdf>.

IUCN/SSC (2018). *Guidelines for the conservation of lions in Africa* (IUCN Muri/Bern, Switzerland: Prepared by the International Union for the Conservation of Nature (IUCN)/ Species Survival Commission (SSC) Cat Specialist Group). Available at: https://www.cms.int/sites/default/files/publication/GCLA%20%20181220%20%28E%29_0.pdf.

Jacobsen, K. S., Dickman, A. J., Macdonald, D. W., Mourato, S., Johnson, P., Sibanda, L., et al. (2020). The importance of tangible and intangible factors in human-carnivore coexistence. *Conserv. Biol.* 35 (4), 1233–1244. doi: 10.1111/cobi.13678

Jule, K. R., Leaver, L. A., and Lea, S. E. G. (2008). The effects of captive experience on reintroduction survival in carnivores: A review and analysis. *Biol. Conserv.* 141 (2), 355–363. doi: 10.1016/j.biocon.2007.11.007

Kettles, R., and Slotow, R. (2009). Management of free-ranging lions on an enclosed game reserve. *S. Afr. J. Wildl.* 39 (1), 23–33. doi: 10.3957/056.039.0103

Leberg, P. L., and Firman, B. D. (2007). Role of inbreeding depression and purging in captive breeding and restoration programmes. *Mol. Ecol.* 17 (1), 334–343. doi: 10.1111/j.1365-294X.2007.03433.x

Lindsey, P., Baghai, M., Bigurube, G., Cunliffe, S., Dickman, A., Fitzgerald, K., et al. (2021). Attracting investment for africa's protected areas by creating enabling environments for collaborative management partnerships. *Biol. Conserv.* 255 (1), e108979. doi: 10.1016/j.biocon.2021.108979

Lindsey, P. A., Petrucci, L. S., Funston, P. J., Bauer, H., Dickman, A., Everatt, K., et al. (2017). The performance of African protected areas for lions and their prey. *Biol. Conserv.* 209 (1), 137–149. doi: 10.1016/j.biocon.2017.01.011

Linnell, J. D. C., Aanes, R., Swenson, J. E., Odden, J., and Smith, M. E. (1997). Translocation of carnivores as a method for managing problem animals: A review. *Biodivers. Conserv.* 6 (1), 1245–1257. doi: 10.1023/B:BIOC.0000034011.05412.cd

MDNPW (2010). *Conservation status of the lion (Panthera leo Linnaeus 1758) in Malawi* (MDNPW, Lilongwe, Malawi: Malawi Department of National Parks and Wildlife (MDNPW)). Available at: <http://www.catsg.org/fileadmin/filessharing/3>.

[Conservation_Center/3.2._Status_Reports/African_lion/Mesochina_et_al_2010_Conservation_status_of_the_lion_in_Malawi.pdf](#).

- Miller, S. M., Bissett, C., Parker, D. M., Burger, A., Courtenay, B., Dickerson, T., et al. (2013). Management of reintroduced lions in small, fenced reserves in south Africa: an assessment and guidelines. *S. Afr. J. Wildl.* 43 (2), 138–154. doi: 10.3957/056.043.020
- Miller, S. M., Druce, D. J., Dalton, D. L., Harper, C. K., Kotzé, A., Packer, C., et al. (2020). Genetic rescue of an isolated African lion population. *Conserv. Genet.* 21 (1), 41–53. doi: 10.1007/s10592-019-01231-y
- Miller, S. M., and Funston, P. J. (2014). Rapid growth rates of lion (*Panthera leo*) populations in small, fenced reserves in south Africa: A management dilemma. *S. Afr. J. Wildl.* 44 (1), 43–55. doi: 10.3957/056.044.0107
- Miller, S. M., Harper, C. K., Bloomer, P., Hofmeyr, J., and Funston, P. J. (2015). Fenced and fragmented: Conservation value of managed metapopulations. *PLoS One* 10 (12), e0144605. doi: 10.1371/journal.pone.0144605
- Morapedi, M., Reuben, M., Gadimang, P., Bradley, J., Given, W., Reading, R. P., et al. (2021). Outcomes of lion, *Panthera leo*, translocations to reduce conflict with farmers in Botswana. *S. Afr. J. Wildl.* 51 (1), 6–12. doi: 10.3957/056.051.0006
- Mossaz, A., Buckley, R. C., and Castley, J. G. (2015). Ecotourism contributions to conservation of African big cats. *Nat. Conserv.* 28 (1), 112–1118. doi: 10.1016/j.jnc.2015.09.009
- Mweetwa, T., Christianson, D., Becker, M., Creel, S., Rosenblatt, E., Merkle, J., et al. (2018). Quantifying lion (*Panthera leo*) demographic response following a three-year moratorium on trophy hunting. *PLoS One* 13 (5), e0197030. doi: 10.1371/journal.pone.0197030
- Namibia Ministry of Environment and Tourism. (2016). *Human-lion conflict management plan for Northwest Namibia*. Windhoek, Namibia: Ministry of Tourism and the Environment.
- Olden, J. D., LeRoy Poff, N., Douglas, M. R., Douglas, M. E., and Fausch, K. D. (2004). Ecological and evolutionary consequences of biotic homogenization. *Trends Ecol. Evol.* 19 (1), 18–24. doi: 10.1016/j.tree.2003.09.010
- Packer, C., Lichtenfeld, L., Trout, C., Kiondo, M. R., Magoma, N., Konzo, E., et al. (2009). “The Tanzania lion and leopard conservation action plan,” in *Tanzania Carnivore conservation action plan*. Eds. S. M. Durant, K. Whitman, L. Lichtenfeld, A. Lobora and I. Lejora (Tanzania: Tanzania Wildlife Research Institute), 65–111. Available at: http://www.catsg.org/fileadmin/filesharing/3.Conservation_Center/3.4._Strategies:_Action_Plans/African_lion/TAWIRI_2009_Tanzania_Lion_and_Leopard_Conservation_Action_Plan.pdf.
- Pérez, I., Andon, J. D., Díaz, M., Nicola, G. G., Tella, J. L., and Giménez, A. (2012). What is wrong with current translocations? a review and a decision-making proposal. *Front. Ecol. Evol.* 10 (9), 494–501. doi: 10.1890/110175
- Ralls, K., Ballou, J. D., Dudash, M. R., Eldridge, M. D. B., Fenster, C. B., Lacy, R. C., et al. (2018). Call for a paradigm shift in the genetic management of fragmented populations. *Conserv. Lett.* 11 (2), e12412. doi: 10.1111/conl.12412
- Ralls, K., Sunnucks, P., Lacy, R. C., and Frankham, R. (2020). Genetic rescue: A critique of the evidence supports maximizing genetic diversity rather than minimizing the introduction of putatively harmful genetic variation. *Biol. Conserv.* 251 (1), e108784. doi: 10.1016/j.biocon.2020.108784
- Riggio, J., Caro, T., Dollar, L., Durant, S. M., Jacobson, A. P., Kiffner, C., et al. (2016). Lion populations may be declining in Africa but not as Bauer et al. suggest. *PNAS* 113 (2), 107–108. doi: 10.1073/pnas.1521506113
- Riggio, J., Jacobson, A., Dollar, L., Bauer, H., Becker, M., Dickman, A., et al. (2013). The size of savannah Africa: A lion's (*Panthera leo*) view. *Biodivers. Conserv.* 22 (1), 17–35. doi: 10.1007/s10531-012-0381-4
- Schaller, G. B. (1972). *The Serengeti lion: A study of predator-prey relations* (Chicago: University of Chicago Press), 127–163.
- Shepherd, S. M., Mills, A., and Shoff, W. H. (2014). Human attacks by large felid carnivores in captivity and in the wild. *Wilderness Environ. Med.* 25 (2), 220–230. doi: 10.1016/j.wem.2014.01.005
- Slotow, R., and Hunter, L. T. B. (2009). “Reintroduction decisions taken at the incorrect social scale devalue their conservation contribution: the African lion in south Africa,” in *Reintroduction of top-order predators*. Eds. M. W. Hayward and M. J. Somers (Oxford: Blackwell Publishing Ltd), 41–73. doi: 10.1002/9781444312034.ch3
- Soorae, P. S. (2018). *Global reintroduction perspectives: Case studies from around the globe* (Abu Dhabi: International Union for the Conservation of Nature (IUCN)/Species Survival Commission (SSC) Re-introduction Specialist Group. IUCN Gland, Switzerland and Environment Agency).
- Stander, P. E. (1990). A suggested management strategy for stock-raiding lions in Namibia. *S. Afr. J. Wildl.* 20 (2), 37–43. https://hdl.handle.net/10520/AJA03794369_3323.
- Tambling, C. J., Ferreira, S. M., Adendorff, J., and Kerley, G. I. H. (2013). Lessons from management interventions: Consequences for lion-buffalo interactions. *S. Afr. J. Wildl.* 43 (1), 1–11. doi: 10.3957/056.043.0116
- Tambling, C. J., Minnie, L., Meyer, J., Freeman, E. W., Santymire, R. M., Adendorff, J., et al. (2015). Temporal shifts in activity of prey following large predator reintroductions. *Behav. Ecol. Sociobiol.* 69 (1), 1153–1161. doi: 10.1007/s00265-015-1929-6
- Traves, A., and Karanth, K. U. (2003). Human-carnivore conflict and perspectives on carnivore management worldwide. *Conserv. Biol.* 17 (6), 1491–1499. doi: 10.1111/j.1523-1739.2003.00059.x
- Trinkel, M., and Angelici, F. M. (2016). “The decline in the lion population in Africa and possible mitigation measures,” in *Problematic wildlife*. Ed. F. Angelici (Cham, Switzerland: Springer). doi: 10.1007/978-3-319-22246-2_3
- Trinkel, M., Ferguson, N., Reid, A., Reid, C., Somers, M., Turelli, L., et al. (2008). Translocating lions into an inbred lion population in the hlhluwe-impfolozi park, south Africa. *Anim. Conserv.* 11 (2), 138–143. doi: 10.1111/j.1469-1795.2008.00163.x
- Trinkel, M., Funston, P., Hofmeyer, D., Dell, S., Packer, C., and Slotow, R. (2010). Inbreeding and density-dependent population growth in a small, isolated lion population. *Anim. Conserv.* 13 (4), 374–382. doi: 10.1111/j.1469-1795.2009.00344.x
- van Dyk, G. (1997). “Reintroduction techniques for lion (*Panthera leo*),” in *Proceedings of a symposium on lions and leopards as game ranch animals*. Ed. J. van Heerden (Onderstepoort, South Africa: Wildlife Group of the South African Veterinary Association), 82–91.
- Vinks, M. A., Creel, S., Schuette, P., Becker, M. S., Rosenblatt, E., Sanguinetti, C., et al. (2021). Response of lion demography and dynamics to the loss of preferred larger prey. *Ecol. Appl.* 31 (4), e02298. doi: 10.1002/eap.2298
- Weilenmann, M., Gusset, M., Mills, D. R., Gabanapelo, T., and Schiess-Meier, M. (2010). Is translocation of stock-raiding leopards into a protected area with resident conspecifics an effective management tool? *Wildl. Res.* 37 (8), 702–707. doi: 10.1071/WR10013
- Williams, V. L., and ‘t Sas-Rolfes, M. J. (2019). Born captive: A survey of the lion breeding, keeping, and hunting industries in south Africa. *PLoS One* 14 (1), e0217409. doi: 10.1371/journal.pone.0217409
- Williams, V. L., Coals, P. G., de Bruyn, M., Naude, V. N., Dalton, D. L., and Kotzé, A. (2021). Monitoring compliance of CITES lion bone exports from south Africa. *PLoS One* 16 (4), e0249306. doi: 10.1371/journal.pone.0249306
- Williams, V. L., Loveridge, A. J., Newton, D. J., and Macdonald, D. W. (2017). A roaring trade? the legal trade in *Panthera leo* bones from Africa to East-southeast Asia. *PLoS One* 12 (10), e0185996. doi: 10.1371/journal.pone.0185996
- Williams, V. L., Newton, D. J., Loveridge, A. J., and Macdonald, D. W. (2015). *Bones of contention: An assessment of the south African trade in African lion panthera leo bones and other body parts* (Oxford, UK: TRAFFIC, Cambridge, and WildCRU). Available at: https://www.traffic.org/site/assets/files/2474/bones_of_contention_report.pdf.
- Wolf, C., and Ripple, W. J. (2018). Rewilding the world's large carnivores. *R. Soc. Open Sci.* 5 (3), e172235. doi: 10.1098/rsos.172235
- Zambia Department of National Parks and Wildlife (2021). *Conservation action plan for the lion in Zambia*. (Chilanga, Zambia: Zambia Department of National Parks and Wildlife).
- ZAWA (2009). *Conservation action plan for the lion in Zambia* (ZAWA Chilanga, Zambia: Zambia Wildlife Authority (ZAWA). Available at: http://www.catsg.org/fileadmin/filesharing/3.Conservation_Center/3.4._Strategies:_Action_Plans/African_lion/Zambia_Wildlife_Authority_2009_Conservation_strategy_and_action_plan_for_the_lion_in_Zambia.pdf.
- ZDNPW (2021) *Zambia Lion Conservation Strategy and Action Plan* (Research Unit, Chilanga, Zambia: Zambia Department of National Parks and Wildlife (ZDNPW)).
- ZPWMA (2006). *Conservation strategy and action plan for the lion (Panthera leo) in Zimbabwe* (ZPWMA, Harare, Zimbabwe: Zimbabwe Parks and Wildlife Management Authority (ZPWMA). Available at: http://www.catsg.org/fileadmin/filesharing/3.Conservation_Center/3.4._Strategies:_Action_Plans/African_lion/PWMA_2006_Conservation_Strategy_and_Action_Plan_Lion_Zimbabwe.pdf.
- ZPWMA (2019). *Zimbabwe National Lion Conservation Strategy and Action Plan 2020-2025*. (Zimbabwe Parks and Wildlife Management Authority (ZPWMA), Harare, Zimbabwe: Zimbabwe Parks and Management Authority (ZPWMA)).

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