Received: 4 May 2023 | Accepted: 30 April 2024

DOI: 10.1002/2688-8319.12341

Ecological Solutions and Evidence | BRITISH ECOLOGICAL SOCIETY

RESEARCH ARTICLE

Wild lions in small, fenced reserves in South Africa conform to a meta-population

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Handling Editor: Kilian Murphy

Abstract

1. Lions (*Panthera leo*) are declining across their range, mainly due to human-induced habitat fragmentation and prey depletion. However, the South African lion population continues to grow. Unlike other range states, South Africa actively manages wild lions across a continuum of landscapes and ecological constraints. Many of these lions are in small, fenced reserves where managers seek to mimic ecological processes in small landscapes. However, the effectiveness of this management approach has not been evaluated against meta-population criteria.
2. Given that meta-population dynamics allows species living in fragmented habitats to persist, we evaluated how South Africa's lion population complies with meta-population criteria using national audit data between 2010 and 2019 from 49 fenced, wild lion reserves.
3. The small, fenced reserves holding wild lions fulfil the criteria for meta-population functionality. However, this functionality was achieved through haphazard and uncoordinated management actions and not through a coordinated approach.
4. Our main recommendation is to consider implementing a more coordinated meta-population management approach. At the very least, meta-population management guidelines should be reviewed and updated on a regular basis, regular audits should be conducted and periodic genetic evaluation of the meta-population (every 10 years) should be instituted. We recommend incentivising lion managers to enhance the conservation of lions in South Africa within a meta-population framework. We also recommend a focus on improving decision making and policy procedures that facilitates compliance with relevant legislation aimed at achieving high levels of lion conservation-governance efficiency.

5. South Africa's meta-population approach to wild lion management in small, fenced reserves is effective at conserving lions and contributing to lion conservation more broadly. In an increasingly fragmented landscape, the need for human management actions to ensure persistence of large carnivores is likely to increase. A managed meta-population approach of fenced (or unfenced, but geographically isolated) populations is a useful tool for conservationists to consider worldwide.

KEYWORDS
carnivores, conservation, fenced reserves, fragmented landscapes, *Panthera leo*, translocation, wildlife management

1 | INTRODUCTION

Africa supports some of the most diverse terrestrial carnivore communities in the world. These carnivores evolved within large, heterogeneous ecosystems where they roamed freely (Wolf & Ripple, 2017). Thus, they occupy extensive home ranges and require large prey populations for their survival, and so only vast, relatively intact ecosystems can support viable populations without substantial human interventions (Sillero-Zubiri & Laurenson, 2001). Consequently, when human populations expand and alter environments, large carnivores are some of the first to decline (Ripple et al., 2014; Sillero-Zubiri & Laurenson, 2001).

Lions (*Panthera leo*), Africa's largest carnivore, are no exception and are declining across their range mainly due to human-induced habitat fragmentation and prey depletion (Bauer et al., 2015; Loveridge et al., 2022; Riggio et al., 2013). South Africa was one of the first countries to lose the majority of their carnivores; lions (and many other large carnivores) were extirpated from most of their range by the early 20th century, with only a few populations surviving at the edges of the country (Carruthers, 2008; Hayward et al., 2007).

The right of ownership of wildlife, combined with a growing understanding in the private sector of the ecological resilience linked to sustainability of wildlife ranching, financial benefits from commercial wildlife ranching and significantly reduced subsidies for conventional agriculture, led to the establishment of a formal wildlife sector in South Africa (Carruthers, 2008). The subsequent expansion of game reserves, especially since the early 1990s, resulted in an increased range for lion with many small, fenced properties (including national parks, provincial protected areas, conservancies and private reserves of <1000 km^2 in area) reintroducing wild lions such that they now occur in all provinces of South Africa, except for the Free State (Miller et al., 2013; Miller & Funston, 2014; Figures S1 and S2). These lions, along with the larger populations in Kruger National Park and Kgalagadi Transfrontier Park, have resulted in a growing population of lions (McEvoy et al., 2021; Miller & Funston, 2014) that were classified as Least Concern in a recent regional Red List assessment (Miller et al., 2016). As of December 2021, lions on smaller, fenced reserves had increased to 871 on 50 small reserves (Table S1), representing approximately 27% of the total South African lion population.

The smaller, fenced populations of lions come with challenges (see Box 1). Unlike in open systems where male lions disperse as sub-adults looking for territories where they can eventually mate and breed and lionesses also disperse, albeit at much lower frequencies (Funston, 2011; Pusey & Packer, 1987), these natural processes are cut off by predator-proof fences, isolating these areas from each other (Miller et al., 2015; Slotow & Hunter, 2009). Thus, the lions on individual reserves require intensive management to mimic the natural systems that have broken down due to habitat fragmentation (Ferreira & Hofmeyr, 2014; Miller et al., 2013, 2015). This intensive management led to a classification of 'Managed Wild' in the Biodiversity Management Plan (BMP) for lions in South Africa (Funston & Levendal, 2015; see the Supporting Information S1 for more details on existing legislation and meta-population management of wild lions). For the purposes of our research, we include 'Managed Wild' when we refer to wild lions (Table 1). In isolation these lion populations are not large enough to be ecologically functional and their conservation value has been questioned (Hunter et al., 2007; Slotow & Hunter, 2009).

The challenge for conservationists is thus to find a way to improve the conservation value of these fragmented lion populations. Meta-populations naturally exist in the wild, allowing some species to exist across patchy landscapes, like the fragmentation caused by fencing small areas. While lions, and most large mammals may not historically have existed primarily as meta-populations (but see Olivier et al., 2009), the principles of a meta-population could be used to establish a 'managed meta-population' for any artificially fragmented species including lions, cheetah (*Acinonyx jubatus*) (Buk et al., 2018) and wild dogs (*Lycaon pictus*) (Davies-Mostert et al., 2009) in South Africa.

Indeed, progress in managing the fragmented lion populations collectively has been made: the Lion Management Forum (LiMF), formed in 2010, provides a platform for these properties to facilitate translocations in an ad hoc manner. Furthermore, implementation of the meta-population principles adopted by South Africa's Scientific Authority (Selier & Ferreira, 2017) is encouraged on these properties and often discussed at LiMF meetings. A logical step

BOX 1 Summary of management challenges associated with wild lions on fenced reserves and available management interventions currently used to overcome these challenges by mimicking the natural systems that have broken down due to small population size

Management challenges in fenced reserves (Miller et al., 2013):

Prolonged pride tenure—with smaller populations there is less natural competition to stimulate pride takeovers. Pride takeovers can be simulated by introducing new males with or without first removing existing pride males.

Fast growth rates—smaller, fenced reserves experience higher than average growth rates due to younger ages of first reproduction, shorter interbirth intervals and increased cub survival. Various approaches are used to reduced growth rates—see below.

Lack of immigration/emigration of sub-adults—fencing and smaller property sizes can prevent sub-adult lions from leaving their natal territory.

Management actions:

Translocation—physically transporting a lion(s) from one property to another to simulate, dispersal, pride take-overs and sub-adult immigration/emigration (Miller et al., 2013).

Chemical contraception—deslorelin implant into sub-adult or adult lionesses to delay the age of the first litter or increase inter-birth intervals to mimic dynamics found in open system lionesses (Miller et al., 2013; Miller & Funston, 2014; McEvoy et al., 2019).

Litter size reduction—experimental unilateral hysterectomies to reduce litter size; preliminary results suggest the first methods used had limited success (Miller et al., 2013, Miller & Funston, 2014, McEvoy et al. 2019); research is ongoing.

Euthanasia—selective removal of individuals to mimic natural processes when translocation is not an option (Miller et al., 2013).

Hunting—selective removal of individuals to mimic natural processes (e.g. removal of older males that would not be expected to live as long in an open system; Miller et al., 2013).

would be to assess these lions in small, fenced reserves to determine if they are functioning as a meta-population, based on criteria established for wild meta-populations of other species. If they are, this would validate this conservation approach and it could then be applied to other fragmented lion populations across the continent (e.g. West Africa), and potentially other species of large carnivore around the world, that are suffering declines due to fragmented landscapes.

To assess wild lions in small, fenced reserves functioning as a meta-population, we needed to define relevant criteria. The term meta-population was first used to describe populations in which interacting local groups exist in discrete habitat patches (Levins, 1969). Suitability of habitat that varies across these patches results in asynchronous birth and death rates between patches, colonisation and extinction of species within a patch, and dispersal between local populations (Hanski, 1999). For large mammals, the time- and spatial-scale over which population dynamics play out can be explained with only two meta-population criteria: breeding populations should be discrete; and populations should have dissimilar growth rates (Table 2) (Elmhagen & Angerbjörn, 2001; Olivier et al., 2009). The framework predicts that without management interventions, such as the translocation of lions, the South African lion population in small, fenced reserves would not be functioning as a *bone fide* meta-population. We hypothesised that management interventions, specifically translocations, have resulted in lions in small, fenced reserves in South Africa functioning as a meta-population. We then assess the importance of conservation management actions to overcome ecological constraints of evolved species-specific responses to fragmented landscapes as a model for guiding large carnivore conservation more broadly within an increasingly complex and evolving African and global conservation context.

2 | MATERIALS AND METHODS

2.1 | Data collection

The South African National Biodiversity Institute (SANBI) sent questionnaires to 59 fenced reserves (<1000 km^2) with lions present for any number of years between 2010 and 2019. Although the process was voluntary, it supported reserve managers compliance with national and provincial regulations as part of government seeking to certify reserves as belonging to the meta-population. The survey thus did not require ethics approval. Questionnaires collected information on introductions, translocations, and other interventions between 2000 and 2019. Single-blinded identification numbers ensured that reserve ownership remained confidential. These data and additional data held by the LiMF were used for all analyses.

2.2 | South African lion population stakeholders

Wild lions in South Africa are all owned by the people or organisation on who's land they occur (Republic of South Africa: The Presidency, 1991). Both national and provincial government regulations apply to ownership and management of wild lions as outlined in the BMP (Funston & Levendal, 2015). Briefly, owners of wild lions include: South African National Parks (SANParks)—publicly funded, national parks; various provincial authorities with

Type of wild lion population	Explanation	Examples
Wild—open systems	No active management, lions exist in areas large enough for natural systems to function without intervention	Kruger NP Kgalagadi TF
Wild—managed meta-population	Active management of lions within fenced areas <1000 km^2. Managers actively manipulate some vital rates and demographics to mimic natural systems that have broken down due to the constraints of the fences. This is mostly to reduce population growth rates which are higher than in open systems. The smaller the property, the more management is required	Pilanesberg NP Addo Elephant Park Welgevonden PGR Phinda PGR Tembe Elephant Park

TABLE 1 Wild lion populations in South Africa.

TABLE 2 Meta-population criteria and standards defined for measuring compliance of individual populations for each criterion. Classic (Hanski, 1999) and lenient (Elmhagen & Angerbjörn, 2001) criteria.

Meta-population criteria		Grouped criteria	Standards	
Classic criteria	Lenient criteria		No active interventions	Active interventions
1. Dispersal occurs between local populations		Dispersal	Natural arrival and leaving of individuals	Introduction and removal of individuals
2. Colonisation and extinction take place		Colonisation	Natural arrival of individuals where there were none before. Natural disappearance of all individuals from an area	Introduction where there were no individuals before. Removal of all individuals from a discrete area
3. The dynamics of local populations are asynchronous	Local populations have dissimilar growth rates	Dynamics	Variance of population growth together with that of the five closest reserves—ratio of manage *r* to potential *r* in the absence of management is larger than 1	
4. Habitat patches support local breeding populations with colonisable vacant habitat	Breeding local populations should be discrete rather than inhabiting discrete habitat patches	Discrete	Closest other reserve to a specific reserve is more than five home range diameters away with no physical barriers in between[a]	Disregarding distance of the closest reserve to a specific reserve, there is a physical barrier between a reserve and the closest other reserve

[a]We defined dispersal as a permanent movement shifting five home ranges away (see Funston et al., 2003).

publicly funded properties; private landowners; and local community owned reserves (often in conjunction with government and/or private owners). Policies are developed by government, in consultation with stakeholders, including the South African National Biodiversity Institute (SANBI) at a national level by the Department of Forestry, Fisheries and the Environment as well as at a provincial level by the provincial conservation agencies and all policies are implemented by provincial conservation agencies through a concurrent mandate. Eight out of nine provinces in South Africa have wild lions and thus eight provincial legislative bodies are involved in permitting and compliance at the provincial level. Privately owned reserves have various approaches to management but must abide by national and provincial regulations (see Supporting Information S1 for details). Most wild lion reserves are represented at LiMF (over 80%), academic institutions, veterinarians and national and provincial governments are also well represented. LiMF is a registered NGO with a vision and mission (limf.co.za), however it does not have a legal mandate within South Africa. Thus, LiMF acts as an unofficial channel for communication and policy development. LiMF principles encourage a conservation-based approach which has been developed from the bottom-up by LiMF members (Miller et al., 2013). LiMF also has international members who are involved in the management of small lion populations across Africa. LiMF does not actively engage with stakeholders other than government, this is the remit of individual reserve representatives and LiMF provides a platform for members to discuss any challenges associated with other stakeholders. The collective knowledge of LiMF is often used by members to justify management actions to various stakeholders.

2.3 | Evaluation of meta-population functionality

We assessed meta-population functionality as suggested by Olivier et al. (2009) by evaluating compliance with the classical (Hanski, 1999), and more lenient (Elmhagen & Angerbjörn, 2001) criteria for a meta-population (Table 2 and below). For this, we objectively assessed whether an individual lion population complied with a criterion because of management actions (Table 2 and below). Overall compliance with the four criteria collectively by all reserves was used to determine how well the reserves were functioning as a meta-population (see details below for each criterion). We anticipated that high frequencies of reserve-specific compliance with the criteria will reflect a functioning meta-population.

2.3.1 | Criterion 1: Dispersal

To visualise compliance with criteria based on dispersal between discrete patches, we mapped populations and linked them based on translocations that took place between 2000 and 2019 (Table 2). This was a binary result: 0, no translocations occurred in or out; 1, at least one translocation either in or out occurred. In large populations, males disperse from natal ranges by 4 years of age (Funston et al., 2003), but dispersal rates in fragmented landscapes are likely to be substantially lower and even rare (Kerr et al., 2018), thus only one translocation in 10 years was required for compliance.

2.3.2 | Criterion 2: Colonisation

To determine if reserves had a past colonisation or extinction event we investigated the history of the property, disregarding the time frame of our study between 2010 and 2019. For a colonisation event, we determined if lions were previously extirpated or if lions were already present when the reserve was established. For extinction, we checked whether reserves had permanently removed lions. We used these results to categorise a reserve as having experienced a colonisation or an extinction event, indicated when this occurred and whether it was due to a management action. This was a binary result: 0, neither occurred; 1, one or both occurred. Translocation of lions is an example of a management action that could result in colonisation (translocation onto a property) or extinction (translocation of all lions out of a property). More details on management actions and their function are summarised in Box 1 and explained more fully in the Supporting Information S1.

2.3.3 | Criterion 3: Dynamics

The annual number of lions on each reserve included the outcomes of management actions applied to mimic natural lion dynamics in that calendar year along with natural births and deaths (McEvoy et al., 2021). Management actions included translocation of lions (both onto or out of a reserve), euthanasia, hunting, and contraception; details of when these actions are utilised and why are summarised in Box 1 and explained more fully in the Supporting Information S1. If these management actions improved compliance with meta-population criteria, we predicted increased variation in population growth rates compared to the expected growth of lion populations without any management actions. Thus, we compared calculated growth rates from populations with management interventions against estimated expected growth rates of lion populations without interventions by fitting two models:

The first model was $N_{t+x} = N_t e^{rx}$, where r is exponential growth and N_t is population size at the end of year t, and x is the years between surveys. This equation reflects growth influenced by interventions. The second model required estimating the underlying population growth in the absence of removals, introductions, and contraception. We adapted our model to $N_{t+x} = N_t e^{\left(r - \frac{N_{a,t}}{N_t} b_t l_t s_t^x\right)x} - N_{\underset{Re}{t \to t+x}} + N_{\underset{In}{t \to t+x}}$, where $N_{\underset{Re}{t \to t+x}}$ is the number of lions removed from time t to time $t+x$, $N_{\underset{In}{t \to t+x}}$ is the number of lions introduced from time t to time $t+x$, $N_{a,t}$ is number of adult females on contraception, b_t is birth rate (inverse of birth intervals), l_t is litter size and s_t is annual cub survival rate. We used average estimates of birth rates, litter size and cub survival in small reserves extracted from previous studies (McEvoy et al., 2021; Miller & Funston, 2014). A maximum likelihood approach (Johnson & Omland, 2004) allowed the estimation of r. We focussed only on the point estimate to evaluate our criterion. We compared the distribution of growth rates without interventions against the observed growth rates inclusive of interventions. We compared the variance of the two distributions (Hartley, 1950) and expected variance of growth rates inclusive of interventions to exceed that without interventions.

To evaluate the stringent criterion of 'dynamics of local populations are in asynchrony' (Hanski, 1999) and the more lenient criterion of 'local populations should have dissimilar growth rates' (Elmhagen & Angerbjörn, 2001), we compared the growth rates for each population to the five geographically closest populations. We ranked the growth of a population of interest in the context of the series of growth rates noted together with the five closest populations. We then extracted the frequency of populations that had the lowest or highest growth rate recorded in the focal cluster of closest populations. We anticipated that some populations would be the lowest and some the highest complying with Criterion 3. In addition, we checked whether the ratio of the variance of observed growth rates to potential growth rates was larger than 1 within the cluster of closest reserves. If it was, we concluded that entire set of populations in the cluster of closest reserves had more asynchrony in dynamics and dissimilar growth rates because of management actions.

2.3.4 | Criterion 4: Discrete

Population or habitat patches are discrete. Fully fenced reserves comply with this criterion as all lion populations included in this study were 'breeding populations' (although some were using contraception to reduce breeding rates) and the fence creates a physical barrier resulting in discrete 'patches'. There were no partially fenced reserves included as part of this study and thus there was no need to calculate anything to determine if populations or habitat patches were discrete.

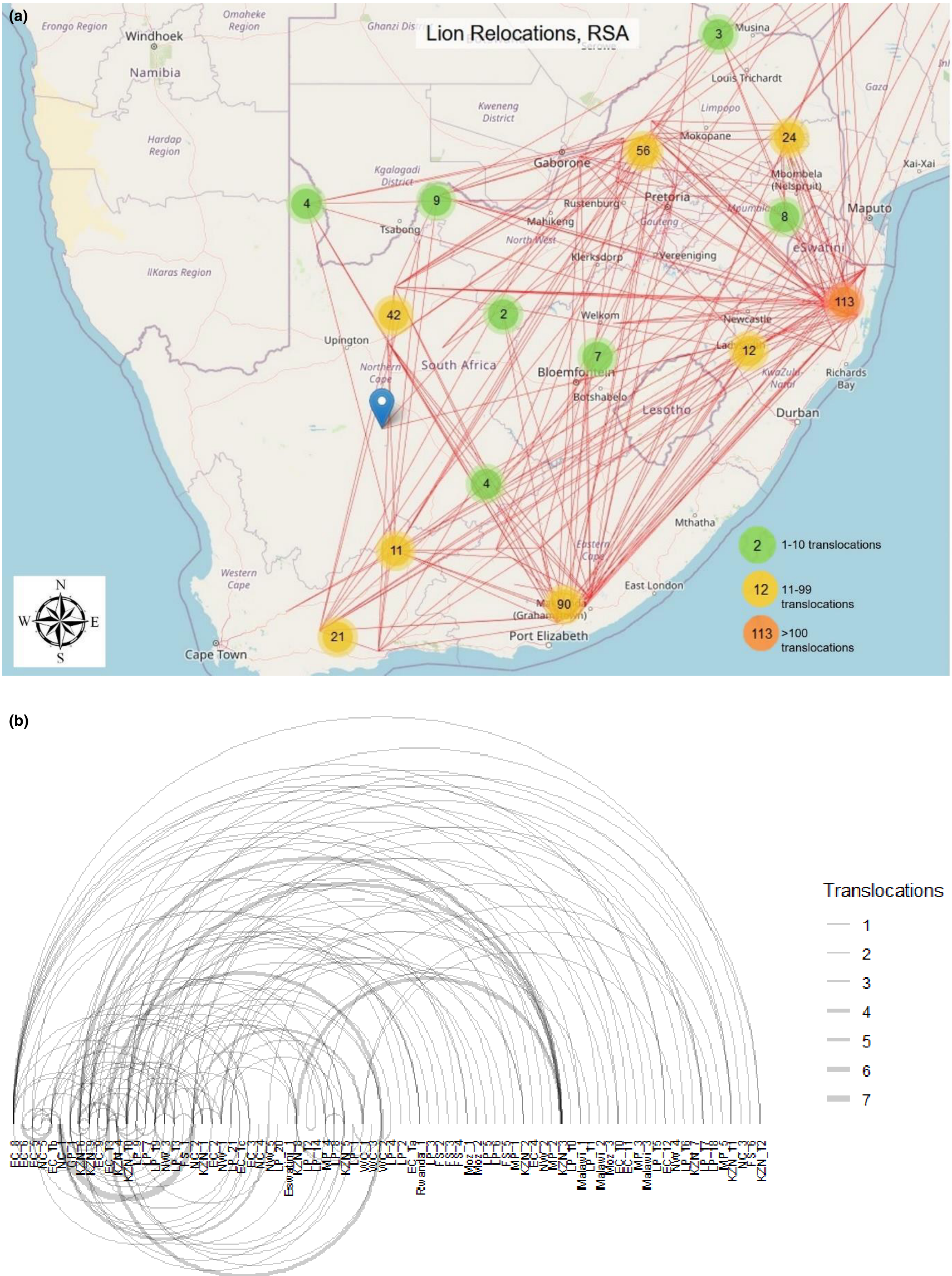
(a)
Lion Relocations, RSA
Erongo Region
Omaheke Region
Ghanzi District
Windhoek
Namibia
Musina
Louis Trichardt
Limpopo
Gaza
Kweneng District
Hardap Region
Mokopane
Gaborone
Xai-Xai
Kgalagadi District
Mbombela (Nelspruit)
Rustenburg
Pretoria
Maputo
Tsabong
Mahikeng
Gauteng
Mpumalanga
North West
eSwatini
IIKaras Region
Klerksdorp
Vereeniging
Welkom
Newcastle
Upington
Northern Cape
South Africa
Bloemfontein
KwaZulu-Natal
Richards Bay
Botshabelo
Lesotho
Durban
Mthatha
Eastern Cape
Western Cape
East London
Port Elizabeth
Cape Town
1-10 translocations
11-99 translocations
>100 translocations
(b)
Translocations
1
2
3
4
5
6
7

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FIGURE 1 (a and b) A summary of the translocation of lions between reserves from 2000 to 2019. These interventions represent assisted emigration and immigration dispersal between reserves. (a) Geographical representation of translocation events within Southern Africa, indicating the number of individuals translocated. Green <10, Yellow 11–99, Orange >100. (b) Arc diagram representing the link between reserves. The thickness of lines represents the number of translocations between each property (higher resolution available online through Figshare at https://doi.org/10.25375/uct.20367273). (c) The network analysis of each property depicting which reserves have more influence within the meta-population framework.

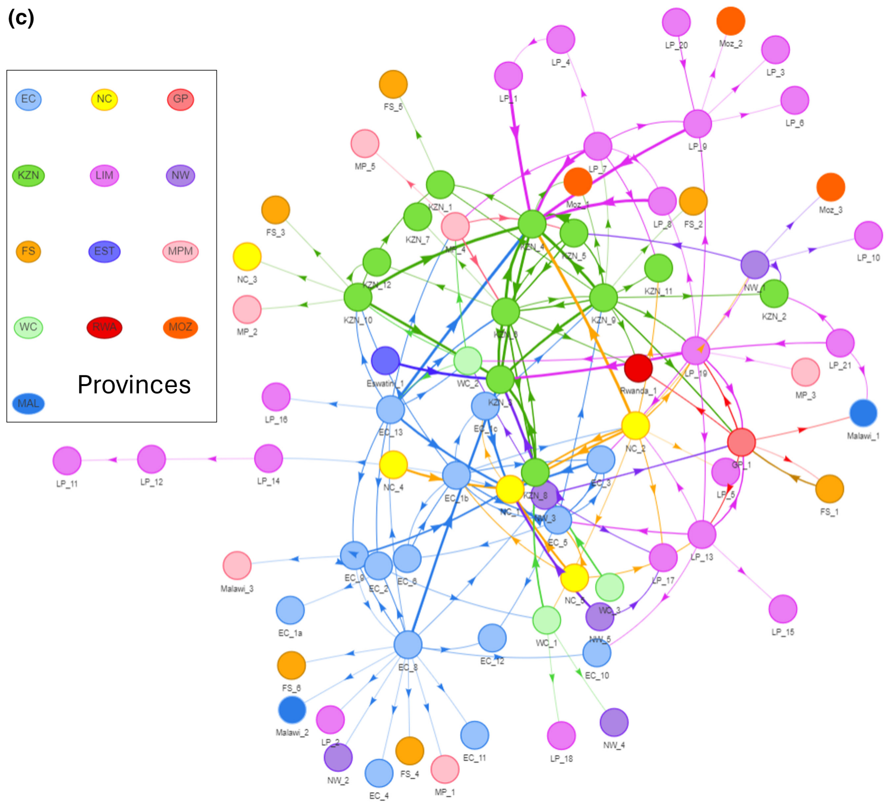

FIGURE 1 (Continued)

2.4 | The persistence of lions in fragmented landscapes

Finally, we assessed the overall size of the South African meta-population of lions in fenced reserves. Several time series had some years with no specific counts. We used our model results for a specific reserve to interpolate these missing data. For each year, we added all the individual reserve count estimates together and fitted both an exponential and a Ricker model (Caughley, 1977). The level of fit was used to choose the best model (Johnson & Omland, 2004).

3 | RESULTS

Data are available online through Figshare at https://doi.org/10.25375/uct.20367273 (Selier et al., 2024).

Forty-nine of the 59 reserves (83%) with lions completed the questionnaire. In 2019, 771 lions were present on these reserves. Two hundred and nine translocation events to 73 reserves, involving 492 individuals, were initiated by 41 reserves over the period 2000 to 2019 (Figure 1a). A total of 80 reserves were involved in lion translocations. All reserves within South Africa were fenced as were a few beyond the borders of South Africa (two out of five). KwaZulu-Natal, Eastern Cape, and Limpopo were the top three provinces providing and receiving animals. These three provinces contained the majority (80%) of the 49 respondents (KwaZulu-Natal—11; Eastern Cape—14, Limpopo—14).

Despite the spatial isolation of reserves, most reserves (93%) were linked with at least one other property through either a translocation or an introduction (Figure 1b), thereby complying with criterion 1. Seven reserves only donated lions, while 39 reserves only received lions. Network analysis (Figure 1c) highlighted five reserves that were key contributors to the translocation of lions, two of which were located within KwaZulu-Natal. One property in KwaZulu-Natal received lions from 10 separate translocation events, while another property in KwaZulu-Natal shared nine links with other reserves.

One property in the Eastern Cape provided lions to other reserves during 15 separate translocation events. Overall, 27 reserves acted as sources (lions removed from a property > lions introduced to a property), 49 as sinks (lions removed from a property < lions introduced to a property), and 4 as neutral (lions removed from a property = lions introduced to a property).

Within our focal period of evaluation (2010–2019), 16 out of 49 reserves introduced lions into vacant areas, and only one property permanently removed their lions. One of the reserves was established through enclosing lions naturally dispersing from a nearby population. The remainder of the reserves were established, without lions due to extirpation of lions from much of South Africa in the early 20th century, and all these reserves had established populations through re-introduction at some point (Miller et al., 2015; Slotow & Hunter, 2009). Thus, all but one reserve demonstrated assisted colonisation, with one reserve demonstrating natural colonisation, or extinction, thereby complying with criterion 2.

In addition to translocation actions which contributed to the dispersal and colonisation criteria of Hanski (1999), regional variance in the growth with active management generally exceeded regional variance in the expected growth in the absence of management actions (Figure 2) (Slope = 1.49, $t_{43} = 9.77$, $p < 0.01$). Overall, the median annual growth outcome following management actions was 0.046 (95% CI: −0.11 to 0.96; variance = 0.075; CV = 194%) compared with 0.221 (95% CI: 0.00 to 0.91; variance = 0.053; CV = 90%) expected without management actions. The percentage confidence intervals ([upper 95% confidence interval—lower 95% confidence interval]/average growth rate; Barnes, 2002) with management actions was significantly larger than without management actions (F_{max}-test, $F_{1,44} = 5.64$, $p < 0.01$). At the reserve level, 11 focal reserves (25.6%) had the lowest growth rate in the sample of five populations that were closest geographically clustered to the focal populations ($n = 43$ reserves assessed). Five reserves (11.6%) had the highest growth rate in the closest cluster. Sixteen reserves (37.2%) thus had

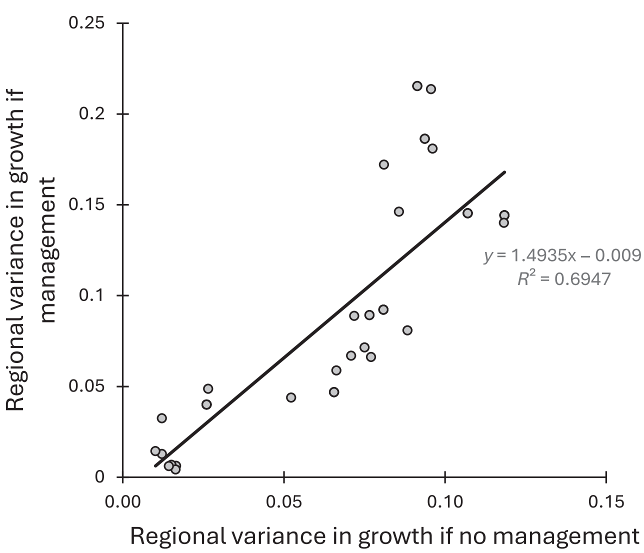

FIGURE 2 Variance in growth rates of lions with management to the potential without management.

the strongest dissimilarity with growth recorded on other, neighbouring reserves, thereby complying with criterion 3.

All reserves were fully fenced, creating an effective barrier between reserves irrespective of distances between them and thus demonstrating compliance with criterion 4.

With or without management actions, most meta-population criteria had high compliance across most reserves (Figure 3a). Criterion 3 (asynchrony in dynamics and/or differential growth rates) had the lowest number of compliant reserves (37.2%), but most reserves (98%) complied with three or more of the meta-population criteria (Figure 3b). These high levels of compliance indicated that wild lions in small, fenced reserves in South Africa were functioning as a meta-population at the time of our assessment. The meta-population increased with the population trends best described by the Ricker model (Figure 4; $N_{t+1} = N_t e^{0.48\left(1-\frac{N_t}{789}\right)}$; $R^2 = 0.76$).

4 | DISCUSSION

Overall, wild lions in South Africa's small reserves complied with both the classical (Hanski, 1999) and more lenient (Elmhagen & Angerbjörn, 2001) meta-population criteria. Crucially, translocation interventions substantially contributed to the dispersal and colonisation criteria of Hanski (1999). Reserves also had dissimilar growth rates and discrete local breeding populations, rather than inhabiting discrete habitat patches, which complies with Elmhagen and Angerbjörn's (2001) criteria. However, median growth rates were predicted to be higher in reserves that remained unmanaged, but this is likely due to 37% of all reserves not being compliant in criterion 3 (asynchrony in dynamics and/or differential growth rates) (Elmhagen & Angerbjörn, 2001).

Applying the classical or more lenient meta-population theory to long-lived mammals that normally range widely across stochastic environments where they can conceivably resist extinction can be problematic (Olivier et al., 2009). For example, longevity and slow population turnover typical of medium- and large-sized mammals are difficult to record given the short period of most studies (Olivier et al., 2009). In addition, for rare animals such as large carnivores, both external (e.g. environmental stochasticity) and internal (e.g. population demographics) factors can affect their extinction risk (Bull et al., 2007). In general, increased environmental stochasticity reduces the persistence of rare species within the landscape and may result in non-compliance with meta-population criteria (Bull et al., 2007). For example, increased fragmentation may completely constrain dispersal opportunities between remaining fragments. However, we have demonstrated that with targeted management action, lions, as a relatively long-lived and rare large mammal, can persist and contribute to population stability regionally, linked to meta-population theory. Significantly, while the concept of meta-population management has been alluded to as a potential conservation vehicle for African elephants (*Loxodonta africana*) (Olivier et al., 2009), grey wolves (*Canis lupus pallipes*) in India

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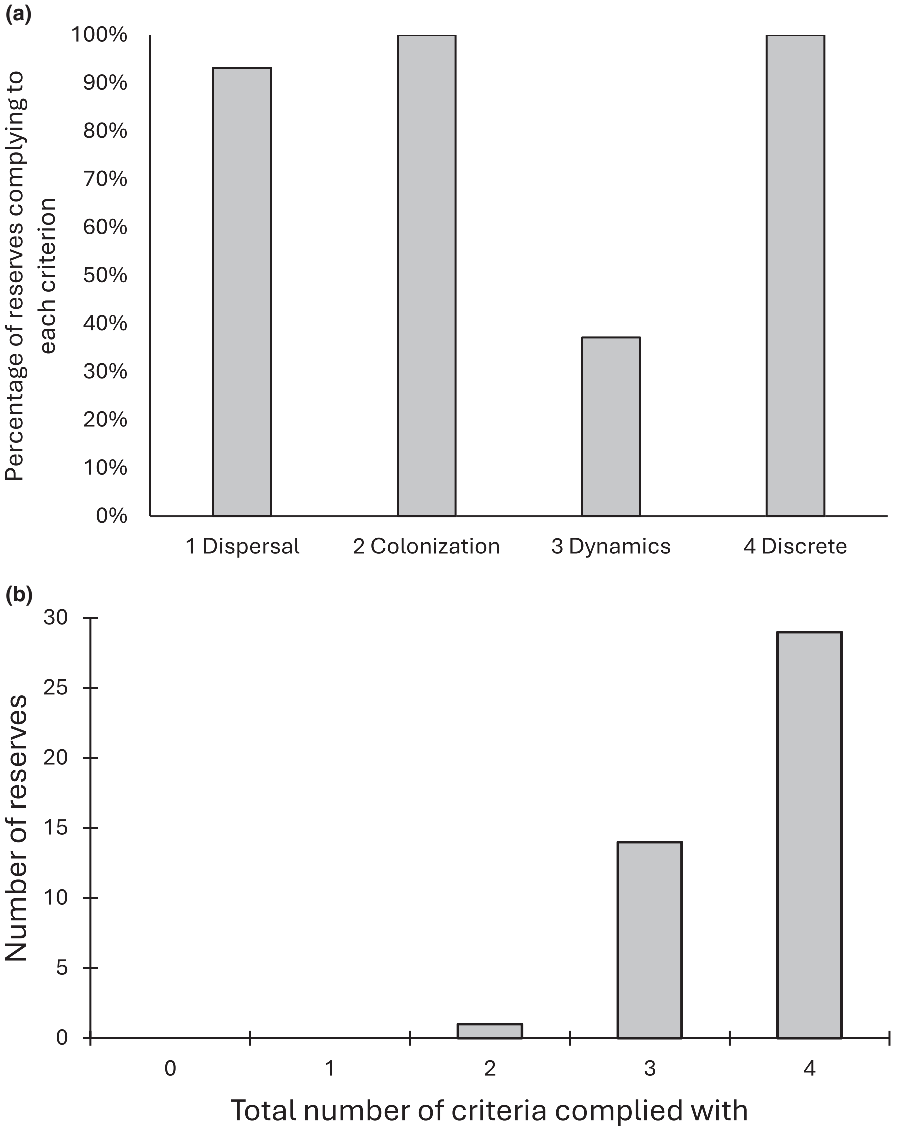

FIGURE 3 Comparative compliance of reserves to meta-population criteria. (a) Percentage of the assessed reserves that complied with a specific criterion. (b) Frequency of reserves categorised by the total number of criteria that reserves complied to.

(Singh & Kumara, 2006), and mountain lions (*Puma concolor*) in the USA (Sweanor et al., 2000), our study represents the first formal assessment of the implementation of meta-population theory for the conservation management of a large carnivore and may provide a theoretical blueprint for carnivore conservation more broadly. In fact, a structured meta-population management approach has guided the management of both cheetahs and wild dogs in South Africa (Buk et al., 2018; Davies-Mostert et al., 2009) providing further support for the targeted management approach we describe above for lions. The success of the cheetah and wild dog meta-populations have been evaluated in terms of population growth rates and their contributions to the overall population (Buk et al., 2018; Nicholson et al., 2020) and genetics (Magliolo et al., 2022; Tensen et al., 2019) and are both considered successes. It would be useful to apply the analysis we have followed here to both of these metapopulations (and other species being 'managed as a metapopulation') to see if they also conform to metapopulation principles. Validating this approach on a variety of species would strengthen the possible application of managed metapopulation principles throughout the global conservation management community when similar challenges are encountered.

Although lion populations in South Africa appear to be compliant with meta-population criteria, this compliance also carries several ecological consequences. The primary implications of such compliance are increased lion population growth rates (McEvoy et al., 2021; Miller et al., 2013) which, in turn, can result in rapid prey depletion, especially in fenced areas, and large numbers of 'excess' lions (McEvoy et al., 2021). In addition, because intraspecific competition drives lion sociality, active, but uncoordinated, lion management has the potential to erode pride functionality (McEvoy et al., 2022). Moreover, Becker et al. (2022) highlight that ill-conceived lion translocations can distract from addressing the causal threats to lion populations, inflame human-lion conflict, and potentially undermine the genetic integrity of wild lions. However, we suggest that with a carefully considered, and slightly more coordinated approach, meta-population dynamics can be maintained, ultimately promoting the conservation of lions and

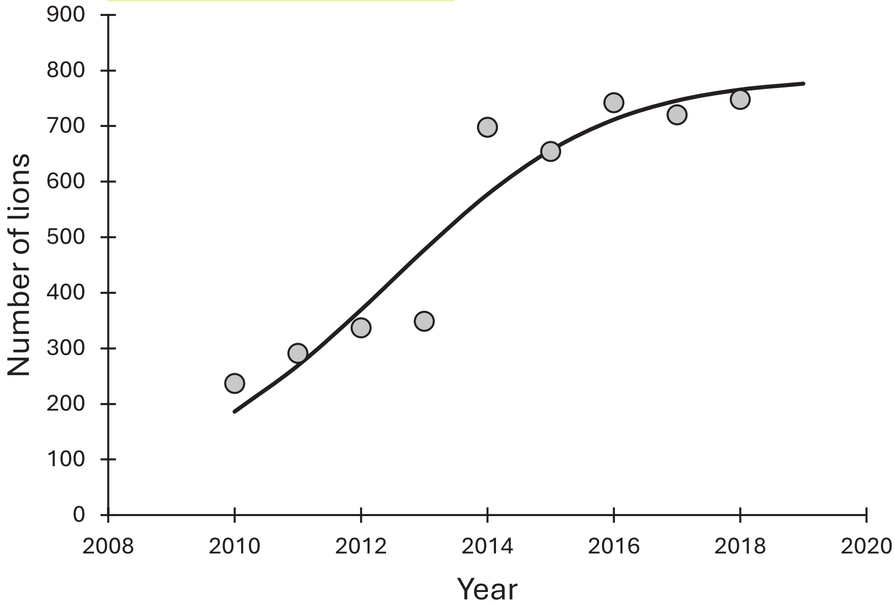

FIGURE 4 Overall trend in the South African lion meta-population achieved through management interventions that mimic lion dynamics. The line represents the best model describing the trend over a decade.

the aspirations of South Africa as envisioned within the lion BMP (Funston & Levendal, 2015).

While LiMF is an active platform for sharing of information and assisting with translocations (Miller et al., 2013), this is currently done on an ad hoc basis (McEvoy et al., 2021). While this appears to be working presently, there is no guarantee that it will continue to be successful in the future—as the number of reserves increases and managers turnover, there is a risk that the current ad hoc system will not result in the best outcome for these populations. A potential solution could be for managers to be incentivised through for example a Green certification system, to meet criteria set out by national government to belong to the meta-population and comply with guidelines, including those established by the IUCN/SSC to inform translocations and reintroductions (IUCN/SSC, 2013) without micro-managing lion movements. In addition, willingness to participate would likely be high when policies and best practice guidelines are co-developed with managers. The goal would be to create a more resilient landscape for lions in South Africa and would be developed in consultation with existing role players.

A key consideration with active lion management, however, is the maintenance of the genetic integrity of the population (Becker et al., 2022). Genetic signals of lion social and population dynamics develop over multiple generations, if the processes that managers have mimicked or provided opportunities for, to play out as expected, genetic integrity should be maintained. For example, regular turnover of pride males through translocations should prevent inbreeding with related females as happens in wild unmanaged populations (Packer & Pusey, 1993). Genetic monitoring at regular intervals, reflecting the generation length of lions, could thus assist in evaluating the success of meta-population implementation on a national and regional scale. A genetic assessment of many of the lions in small reserves was done in the early 2010s along with a discussion of how the genetics could be managed within a managed meta-population setup (Miller et al., 2015). Although the lion BMP recommends genetic evaluation every 5 years (Funston & Levendal, 2015), functionality of meta-populations suggests a more reasonable interval of 10 years, equivalent to one to two lion generations (Bauer et al., 2015).

We have demonstrated that the managed meta-population approach for lions clearly has conservation merit and may be useful in other parts of Africa, especially in landscapes where human-wildlife conflict appears to be causing major declines in lion populations (Bauer et al., 2015). While completely fencing individual lion populations may not be the best approach everywhere (Bauer et al., 2015; Pekor et al., 2019), lion range and overall numbers continue to decline precipitously (Loveridge et al., 2022), suggesting that some level of fencing (Di Minin et al., 2021), combined with human-mediated movement, may be useful in the short-term. Such an approach would allow for lion population growth with adequate gene flow while other conservation interventions seek to link populations and improve gene flow, thus reducing the need for human-mediated movements in the future. Translocations should follow the general and genetics guidelines outlined in two recent publications (Becker et al., 2022; Bertola et al., 2022). In cases such as West Africa where lion populations are already small and geographically isolated, the meta-population approach may be viable, even without fencing, although it would have the added complication of involving several countries. Having a structured approach that member states could sign onto could help alleviate these challenges.

4.1 | Management recommendations

Improved and coordinated management of the South African lion meta-population is likely needed to enhance their continued contribution to the global lion population. Thus, our main recommendation is to consider implementing a more coordinated meta-population management approach by implementing one or more of the following:

1. Incentivise meta-population guideline compliance amongst wild lion reserves.
2. Establish nodes for meta-population management within South Africa.
3. Appoint a meta-population coordinator to collate management needs and coordinate meetings.
4. Establish an online platform for data collection and coordination.

Regardless of the implementation of any of the above, we recommend:

1. Review and update meta-population management guidelines on a regular basis.
2. Conduct regular audits, ideally against management plans.
3. Conduct a genetic evaluation of the meta-population every 10 years.

Developing a meta-population strategy for lions is a complex and ongoing process. Our work represents the first phase of developing a realistic, comprehensive decentralised approach to manage South Africa's lion meta-population, which may be beneficial for lion populations elsewhere.

AUTHOR CONTRIBUTIONS

Brent Coverdale, Dan M. Parker, Johan Kruger, Jeanetta Selier and Sam Ferreira conceived the ideas and designed the methodology; Brent Coverdale, Johan Kruger, Jeanetta Selier and Sam Ferreira collected and analysed the data; Susan M. Miller, Dan M. Parker and Sam Ferreira led the writing of the manuscript. All authors contributed critically to the drafts and gave final approval for publication.

ACKNOWLEDGEMENTS

We thank all provincial conservation agencies, reserve managers/landowners and LiMF for their assistance with data collection. We thank Gareth Tate for assistance with the statistical analyses.

FUNDING INFORMATION

This research received no specific grant funding.

CONFLICT OF INTEREST STATEMENT

The authors declare no conflict of interest.

PEER REVIEW

The peer review history for this article is available at https://www.webofscience.com/api/gateway/wos/peer-review/10.1002/2688-8319.12341.

DATA AVAILABILITY STATEMENT

Data used in the analyses are available from the University of Cape Town's open-access institutional data repository, ZivaHub at https://doi.org/10.25375/uct.20367273 (Selier et al., 2024).

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SUPPORTING INFORMATION

Additional supporting information can be found online in the Supporting Information section at the end of this article.

Figure S1: The current distribution of lions in South Africa including both open systems and reintroduced populations.

Figure S2: Regional nodes for management of lion reserves as a meta-population as proposed in Miller et al. (2013). Figure originally published as part of Miller et al. (2013).

Table S1: The number of small properties (<1000 km^2) and lions present on State and private land in South Africa by 2022.

How to cite this article: Selier, J., Miller, S. M., Coverdale, B., Ferreira, S., Kruger, J., & Parker, D. M. (2024). Wild lions in small, fenced reserves in South Africa conform to a meta-population. *Ecological Solutions and Evidence*, *5*, e12341. https://doi.org/10.1002/2688-8319.12341