

RESEARCH ARTICLE

The impacts of management interventions on the sociality of African lions (*Panthera leo*): Implications for lion conservation

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Abstract

1. African lion (*Panthera leo*) populations normally consist of several neighbouring prides and multiple adult males or groups of males that interact competitively. In large, open systems, cub defence from infanticidal males and territory defence drive group living in lions. However, in smaller (<1000 km²), fenced wildlife reserves, opportunities for natural immigration and emigration are limited which means that the evolutionary drivers of lion sociality may collapse.
2. Here, we use lion behavioural data collected from 16 wildlife reserves across South Africa to test how management-induced ecological conditions alter lion social dynamics.
3. The number of lionesses observed together was best predicted by pride size, prey biomass and biome. Lionesses were less likely to group together as pride size increased, but more likely to group together as prey biomass and habitat productivity increased. In addition, adult males were observed more frequently with prides that had young (<12 months) cubs in reserves that had unfamiliar adult males present compared to reserves without any unfamiliar adult males.
4. Our results demonstrate how intraspecific competition between lions drives their sociality, and this may break down in small, fenced wildlife reserves where lions are actively managed. Although small, fenced reserves in South Africa have made a significant contribution to increasing lion numbers on the continent, our work highlights several important ecological implications of active lion management. For wildlife managers, mimicking the outcomes of different levels of intraspecific competition is likely a critical management tool for the persistence of lions in small reserves.

KEYWORDS

carnivore, cub defence, grouping behaviour, infanticide, meta-population management, South Africa, territory defence

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1 | INTRODUCTION

African lions (*Panthera leo*) are unique as they are the only truly social cats (Packer et al., 1990). However, when the ultimate drivers of their sociality are disrupted, the necessity to group may be less pronounced. Foraging efficiency and/or food protection from spotted hyaenas (*Crocuta crocuta*) is believed to have driven the fusion–fission social system of lions (Caraco & Wolf, 1975; Cooper, 1991). Lions also cooperate with each other when hunting large, and potentially dangerous, prey (Scheel & Packer, 1991). However, a cost–benefit analysis in the Serengeti National Park (NP) highlighted that lions do not typically forage in groups just to optimize their energy intake (Schaller, 1972). Smaller prides often foraged in maximal group sizes, but foraging group size was not correlated with prey abundance (Packer et al., 1990). Significantly, in open, typically unmanaged systems, lion populations consist of several neighbouring prides and multiple adult male groups that interact competitively (Packer et al., 1990). Thus, the leading hypotheses behind sociality in lions are cub defence from infanticidal males and territory defence (Mosser & Packer, 2009; Packer et al., 1990).

Infanticide by unfamiliar male lions can decrease cub survival considerably (Packer & Pusey, 1983, 1987). The oestrus cycles of pride females are naturally synchronous (Packer & Pusey, 1983), often leading to ‘crèche’ formation (Packer et al., 1990; Rudnai, 1973). There are no nutritional advantages evident from lion crèches, but synchronous litters have higher survival rates than asynchronous litters (Bertram, 1975; Packer et al., 1990). In addition, lionesses in groups are better able to defend themselves from unknown males than solitary lionesses (Packer & Pusey, 1987; Packer et al., 1990). The formation of crèches also promotes increased protection from interspecific competitors like hyaenas (Packer et al., 1990). In the Serengeti NP, however, most small prides consistently formed maximal group sizes regardless of the presence of cubs, and nearly all prides included lionesses without young cubs (Mosser & Packer, 2009; Packer et al., 1990), indicating that there may be alternative drivers of lion sociality.

Lions in the Serengeti NP encounter rival lions once every 5 days, with larger groups ousting smaller ones in ~50% of all encounters (Packer et al., 1990). Lions can also assess the number of individuals in a rival group based on their vocalizations and gauge their response accordingly (McComb et al., 1994). In the Serengeti NP, larger prides (≥ 4 lionesses) maintained higher quality territories, showed higher reproductive success and had lower lioness mortality than smaller prides (Mosser & Packer, 2009). In addition, lioness reproductive success declined, and injury level increased, with an increasing number of adult female neighbours (Mosser & Packer, 2009). Furthermore, lionesses from smaller prides that were surrounded by more female neighbours were less often alone than those in smaller prides with fewer neighbours (Packer et al., 1990). Thus, individual lionesses in prides had a lower risk of encountering an individual from a rival pride on their own.

Limited by space, many small (<1000 km²), fenced wildlife reserves in South Africa have lion populations consisting of one pride and one adult male/coalition (McEvoy et al., 2021). Therefore, all lions can be

familiar with each other. With restricted opportunities for immigration and emigration to expose resident lions to new and unfamiliar lions, competition between lions is likely negligible, affecting the intrinsic drivers of lion sociality (Ferreira & Hofmeyr, 2014). In addition, solitary lions are known to be effective hunters (Caraco & Wolf, 1975). Thus, reduced cohesion within prides can increase predation pressure and degrade natural predator–prey dynamics in fenced reserves because there are more individuals potentially hunting more prey (Ferreira & Hofmeyr, 2014). Furthermore, prey abundances generally remain high year-round in fenced reserves in South Africa (Lehmann et al., 2008; Miller & Funston, 2014), reducing the need for lions to roam outside of their core territories and reducing the risk of encountering conspecific rivals (*sensu* Heinsohn, 1997). However, intraspecific competition for the highest value territories in densely populated areas is expected to be intense when rival groups are present (Mosser & Packer, 2009).

Without the motivation to protect territories from neighbouring prides (Mosser & Packer, 2009) or to protect cubs from infanticidal males (Packer et al., 1990), pride integrity in small, fenced reserves could be reduced. Significantly, social network analyses have identified that keystone individuals are important for maintaining pride integrity in lions (Abell et al., 2013; Dunston et al., 2017). Therefore, although the active management of lion populations in small, fenced wildlife reserves in South Africa has been successful in terms of increasing lion numbers (McEvoy et al., 2021), it is unclear how lion sociality is affected. Thus, our research aimed to understand how management interventions in small, fenced wildlife reserves influence grouping behaviour in lions. Specifically, we predicted that lion population structure (i.e. number of prides and number of male/coalitions present) and the disruption of natural reproductive cycles through contraception would degrade pride dynamics. Such knowledge can inform lion conservation management protocols in terms of mimicking the outcomes of natural social dynamics in small, fenced reserves, ultimately promoting lion conservation.

2 | MATERIALS AND METHODS

We obtained ethical clearance for our work through the Rhodes University Ethical Standards Committee (RU-HSD-15-02-0002). We collected lion behavioural data between October 2015 and March 2017 across 16 reserves in South Africa (see McEvoy et al., 2021 for details). The lion populations were either managed wild lions (Funston & Leven-dal, 2015) within small, fenced reserves or wild lions within the Associated Private Nature Reserves (APNR), adjoining the Kruger NP. The latter constituted an unmanaged, control population with numerous prides and multiple roaming adult males because the APNR reserves are all unfenced and are open to the Kruger NP. Following McEvoy et al. (2021), study populations were categorized according to the resident lion population structure as follows:

- A. One pride and a single adult male lion/coalition present;
- B. More than one pride, but with only one adult male/coalition present;

- C. More than one pride and more than one adult male/coalition present;
- D. Control lion population (multiple prides and roaming males).

We established a standardized lion monitoring system whereby information was recorded every time lions were observed by trained research volunteers on each reserve. Most of the reserves included in our study are ecotourism reserves where field guides take visitors on safari drives twice a day, once in the early morning (5:00–10:00 AM) and once in the late afternoon/evening (4:30–7:30 PM). Almost all our volunteers were the field guides who took guests on safari drives. When on these drives, the volunteers recorded which lions were observed together (≤ 100 m). Although these observations were opportunistic in nature, they were conducted in a semi-systematic matter that included the known crepuscular peaks in lion activity (Hayward & Slotow, 2009). In addition, historical ‘in-house’ data from reliable databases held by some reserves were also collected when available and combined for components of the analyses (see below). The latter data set included a total of 1424 additional observations of lions across 10 reserves between 2010 and 2017.

Prides were defined as groups of lionesses (≥ 3 years) that were maternally related ($n = 26$ prides), unrelated lionesses that had been artificially bonded ($n = 1$ pride) (Killian & Bothma, 2003) or solitary females (with offspring) that maintained a territory ($n = 8$ lionesses). Prides were defined as separate prides after ≥ 5 years had passed since pride fissure or dispersal (van der Waal et al., 2009). Through the Lion Management Forum (LiMF), lions in fenced reserves in South Africa are managed as a meta-population where the mimicking of natural ecological processes with respect to lion management is a key goal (Miller et al., 2018). The LiMF provides an important platform for reserve managers and scientists to share evidence-based information for best practice management (Miller et al., 2018). As part of this information sharing, the LiMF maintains a database of all South African lion genetics, translocations and population management interventions (e.g. McEvoy et al., 2019, 2021; Miller et al., 2015). These data are routinely shared among LiMF members, especially when lions are translocated. Moreover, because most fenced reserves in South Africa have fewer than three prides present (McEvoy et al., 2021), it was comparatively easier for our research volunteers to identify individual lions during field observations, based on natural marks and overall pride make up.

All statistical tests were carried out in RStudio using R3.4.4 (R Core Team, 2018). Observations of the same individual lions/prides were separated by 5-day intervals to ensure statistical independence (Packer et al., 1990). Thus, while our observational data were continuous between 2010 and 2017, multiple observations of the same individual/pride were excluded when they were made within 5 days of each other. For each pride, we calculated the total number of adult (≥ 3 years) neighbours as a count of extra-pride individuals—in terms of (i) females, (ii) males and (iii) total. Adult males were not classified as neighbours to prides in which they had sired offspring or were known to associate with. Lion density (lions/100 km²) was accurately known for all managed wild prides (categories A–C). For the control lion population (category D), lion density was estimated based on data from the adjacent

Kruger NP (Ferreira & Funston, 2010). Prey biomass was derived from the most recent aerial census data for each reserve and reduced to (kg/km²) for modelling purposes.

We modelled the percentage of pride adult females observed together based on a series of predictor variables using Generalized Linear Mixed Modelling (see Supporting Information; Table SA1). Pride identity was a repeated, random variable (pseudo-replication). We used Generalized Linear Modelling, with a binomial distribution, to analyse the presence/absence of adult males with prides across our predictor variables (Table SA2). Non-significant terms were removed through backwards stepwise model simplification (Kuznetsova et al., 2017).

3 | RESULTS

3.1 | Study populations

Lion population structure and pride size varied across reserves (see Tables SA3 and SA4). Managed wild lion populations consisted of between 1 and 3 prides and 1 and 3 adult males/coalitions, comprising $33.26\% \pm 16.69\%$ adult females, $16.86\% \pm 12.04\%$ adult males, $24.15\% \pm 17.42\%$ sub-adults and $25.72\% \pm 19.32\%$ cubs (Table SA4).

A total of 6642 lion observations was collected across 16 reserves (2010–2017; Table SA3). The reserves were dominated by Savanna ($n = 10$), Thicket ($n = 5$) and Succulent-Karoo ($n = 1$) vegetation and included data from a total of 94 adult lionesses across 32 prides and 43 adult males. Pride size fluctuated during the study and was influenced by natal sub-adult recruitment ($n = 18$ lionesses) and the death ($n = 10$) and translocation ($n = 4$) of adult lionesses. There was one case of sub-adult immigration from a non-natal pride. Eighty-five per cent of each managed wild ($n = 22$) and control prides ($n = 6$) had dependent offspring (< 3 years) present during our study. Lioness age (in population categories A–C) varied between 3.17 and 18.35 years (7.95 ± 4.02 ; mode = 5.00). Adult male lions varied in age from 4.00 to 11.01 years (6.99 ± 1.87 ; mode = 5.58). Forty-four lionesses, across 19 prides, had either been sterilized ($n = 6$) or treated with the contraceptive deslorelin ($n = 29$), or had undergone a unilateral hysterectomy ($n = 9$), including one lioness that underwent both latter two treatments. When observations were separated by 5-day intervals, there was a total of 1749 lion observations available for analysis (Table SA5).

3.2 | Effects of demography and management interventions on lion sociality

Across all prides that had two or more lionesses (1382 observations), the percentage of adult lionesses sighted together was negatively correlated with increasing pride size ($r_s = -0.40$, $df = 1,38$, $p < 0.01$). Pride size, prey biomass and biome were significant predictors of the number of adult lionesses observed together (Table SA6). The model had an overall explanatory power of 53% ($R^2 = 0.16$; random = pride ID and deslorelin implant). The mean percentage of pride lionesses

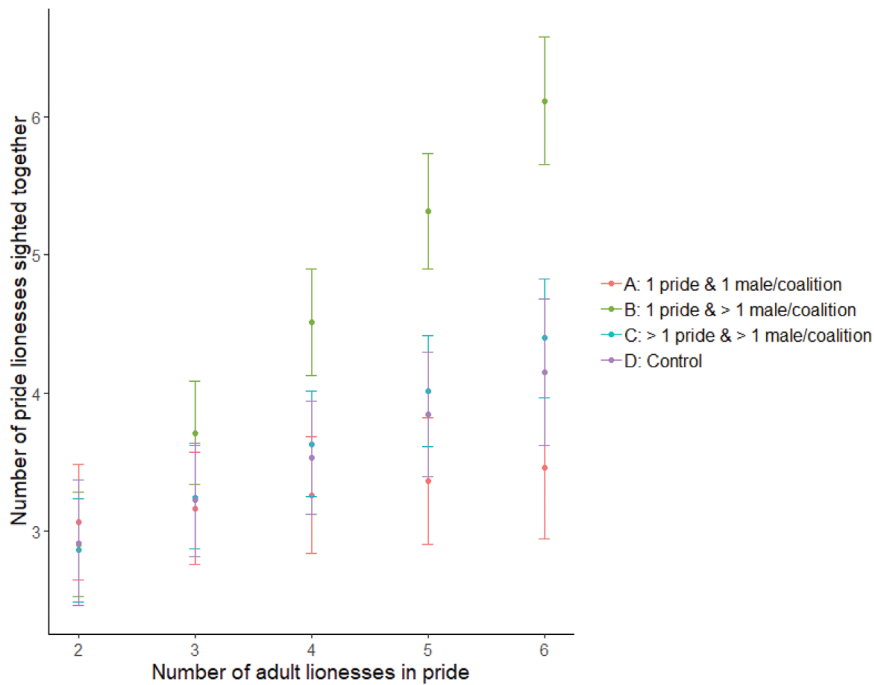


FIGURE 1 The interaction between pride size and lion population structure (A–D) and its effect on the number of pride lionesses observed together across 16 wildlife reserves with lions in South Africa

TABLE 1 The mean and mode of adult female group sizes across 16 wildlife reserves in South Africa in relation to pride size determined by the number of adult females present

Pride composition	Mode	Mean	SD (\pm)	Sightings (<i>n</i>)
2 adult females	2	1.69	0.46	476
3 adult females	3	2.04	0.80	568
4+ adult females	1	2.26	1.16	338

observed together was highest in reserves with largely unconstrained pride dynamics (category D: mean = $79\% \pm 27.6\%$). However, this was not significantly different from other prides (Table SA6). The probability of observing a separate pride increased with increasing pride size, except for managed wild prides in reserves with more than one pride (category B) (Figure 1). Prides in reserves with a single pride and adult male (category A) were generally observed in smaller groups (mean = $67\% \pm 28.9\%$; Figure 2) and had a greater chance of being separate as pride size increased (Table SA6). There was less variation in the percentage of lionesses observed together in small prides (2–3 lionesses) compared with larger prides (≥ 4 lionesses) (Figure 1). However, the percentage of adult females grouped together in a single pride within the Succulent-Karoo increased with increasing prey biomass. However, it declined in prides in both Savanna- and Thicket-dominated reserves (Table SA6).

Mean group size of adult lionesses was close to 2 across all prides, and the modal number was lowest in larger prides (Table 1). Individuals of prides in which females had previously received deslorelin contraception were sighted together less frequently (group mean = $69\% \pm 26.7\%$, $n = 777$ observations) than those that had never received treatment (group mean = $75\% \pm 29.1\%$, $n = 605$ observa-

tions) (Figure 2). Adult males were observed significantly less often with prides in reserves that had multiple managed wild prides and a single resident male (category B), and in control prides (category D), than any other category (Table SA7). In addition, adult males were observed significantly more often with prides that had cubs in the control population (category D) compared to the managed wild populations (categories A–C; Table SA7). However, the likelihood of adult males being observed with female prides decreased significantly as lion density increased (Table SA7).

4 | DISCUSSION

Our study demonstrates that the key factors affecting lioness sociality were overall lion population structure (categories A–D), lion density, pride size and the presence/absence of dependent cubs. Prides in which at least one member was treated with the contraceptive deslorelin were also less likely to group together presumably due to the absence of dependent cubs. Mean group size (1.69–2.26) was slightly lower in our study compared to prides in the Kgalagadi Transfrontier Park (2.4) (Funston, 2011), and was similar as pride size increased. The pattern of solitary behaviour ($\sim 30\%$ of observations) in our study was also similar for small prides (≤ 3 lionesses). However, lionesses were observed more often in larger groups on reserves that contained more complex population structures (categories B and C) than on those with only one pride and one adult male/coalition present (category A). In addition, lions in our control population (category D) were observed in the largest groups, supporting our prediction that the drivers of lion sociality are degraded in managed wild prides. It is important, however, to recognize that our analysis utilized proportional changes in the number of females sighted together, potentially resulting in more discreet and

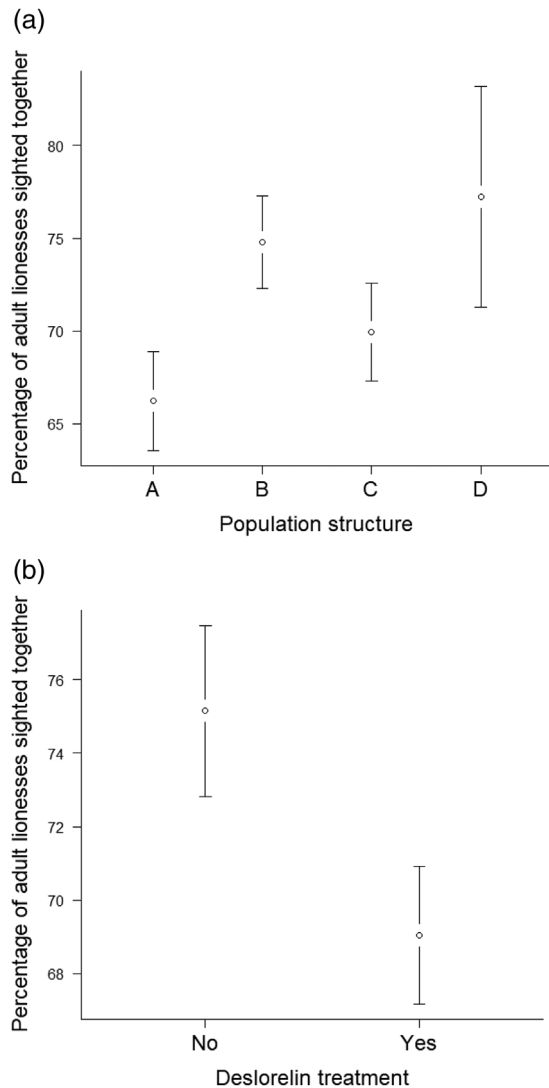


FIGURE 2 The mean percentage of pride lionesses observed together across reserves with different lion population structures (a) and prides that varied in the application deslorelin as a contraceptive measure (b)

variable changes when pride sizes were smaller. Thus, caution should be used when interpreting these findings.

4.1 | The role of male lions

Prides with cubs were regularly observed without resident males present. This finding confirms that the drivers behind grouping behaviour are likely both to protect cubs and maintain a higher value territory when dependent cubs are present, with larger group sizes providing the competitive advantage (Bygott et al., 1979; Funston et al., 2003; Packer et al., 1990). This result also reflects the important role that resident males play in the direct protection of territories from other adult males which, in turn, likely protects cubs (Bygott et al., 1979). The evolutionary pressure for male lions to group together is also significant. In the Serengeti and Kruger NPs, males in larger coalitions

had higher reproductive success than smaller coalitions/solitary males (Bygott et al., 1979; Funston et al., 2003). The key benefits of coalition formation appear to be linked with the acquisition of gregarious, sexually mature lionesses.

Interestingly, most reserves in our study had only one or two resident adult males/coalitions, and only one reserve had a higher male coalition to pride ratio. Nearly 20% of lion populations in open, unmanaged systems consist of nomadic males (Funston et al., 2003). Therefore, the level of competition between unfamiliar males was probably limited in our managed wild prides (categories A–C). Minimal intrasexual competition between adult males likely also affected lioness grouping behaviour, similar to the findings of Mosser and Packer (2009) who demonstrated that lioness group size increased with the density of adult male neighbours in the Serengeti NP. Prides with young cubs in the APNR reflected previous observations from the Kruger NP (Funston et al., 2003), in that they were observed more often with adult males than prides without cubs. Adult males would search for other mating opportunities and leave the pride after their sired cubs had reached the less vulnerable age of 6–12 months (Funston et al., 2003). However, the absence of competition from unfamiliar males in some reserves (category B) may have driven resident males to search for other available mating opportunities, reducing interactions between prides with cubs and adult males. With the ratio of male groups to prides low in most of the small reserves we assessed (including category C), the motivation for resident males to protect cubs from roaming males was likely reduced. The absence of male protection in reserves with reduced competition between males emphasizes their important role in tenure retention in systems with high, natural levels of opposition from unfamiliar males (Bygott et al., 1979).

4.2 | The effect of female contraception

Lionesses are less likely to introduce their cubs to prides that already have potentially dangerous, older aged dependent offspring (Packer et al., 1990; Rudnai, 1973). The use of deslorelin contraception likely reduced the natural levels of reproductive synchronicity among prides. Even if deslorelin implants are applied synchronously, the variability in response between lionesses would likely reduce synchronicity (McEvoy et al., 2019). Prides in which at least one member was treated with deslorelin formed smaller groups than untreated prides. This grouping behaviour supports the notion of disruption to oestrus synchrony as a possible driver for reduced cohesion, rather than a direct response to the treatment itself. Lionesses with cubs did not exhibit the same fissuring behaviour in reserves with more than one adult male/coalition (category C) or in our control prides (category D), indicating that the motivation to group to protect cubs from infanticidal males had been eroded (Packer & Pusey, 1987). The relatedness of individuals likely also played an important role. The closer paternal/maternal relationships among some prides may have reduced the infanticidal threat, and the subsequent need to group when young cubs were present. However, we could not test this contention, making it a logical avenue for future research.

4.3 | Prey availability, competition and dispersal

Most reserves within the population category B were dominated by the Thicket Biome, whereas the majority within population category C were dominated by Savanna. Lions preferentially occupy habitats with higher prey availability, which are often linked with the proximity to water and habitats that can sustain sufficient numbers of suitable prey (Spong, 2002). In small, fenced reserves in the Thicket Biome, lions preferentially select more open habitats (O'Brien, 2012), especially as lion density increases (Bissett, 2008). Since the Thicket Biome is characterized by a dense layer of lower-to-medium storey vegetation, competition for access to more suitable, open hunting areas may have been more intense in these reserves. Similarly, the relative positioning of a lion within its territory affects grouping, with lions less often fragmented on the outskirts of a territory (Mosser & Packer, 2009). However, given our relatively small sample sizes for reserves from separate biomes, these results should be interpreted with caution.

In the absence of competition from unfamiliar adult males, lions formed significantly larger groups in reserves that contained unfamiliar prides. Therefore, the driver to protect a territory from an unfamiliar pride was sufficient to drive significant changes in lion grouping behaviour in small, fenced reserves (categories A–C). The relative importance of competition from adult males on lioness grouping behaviour appeared to be directly linked with the presence of dependent cubs and may, therefore, be a secondary driver of lioness grouping behaviour in small, fenced wildlife reserves. The lack of competition from unfamiliar adult males was likely a significant factor affecting the grouping behaviour of prides that had young cubs. The lack of competition from unfamiliar males also likely reduced the drivers for resident males to group with prides that had young cubs.

An important factor not analysed in our study was female dispersal. There were at least two cases where dispersing sub-adult lionesses did not return to their pride after the removal of their littermates for management purposes. Further research should therefore be directed toward assessing patterns of female dispersal and pride formation, focussed on sites with limited sub-adult removal and newly introduced prides.

4.4 | Implications for managing lions in fragmented landscapes

Many species persist in fragmented habitats because of meta-population dynamics (Hanski, 1998). Landscapes are typically heterogeneous, with patches of suitable habitat and varying resource gradients driving how a species may use a particular landscape (Jetz et al., 2004), and how their vital rates respond (Gaillard et al., 1998). Species persist if they can overcome the risks imposed by fragmentation of suitable habitat at the landscape scale. In the African context, lions are no different, with broad-scale habitat fragmentation being a key feature across their range (Riggio et al., 2013). Within South Africa, fences accentuate the isolation of such fragments (Miller et al., 2013).

Mimicking meta-population dynamics by facilitating lion social processes such as dispersal and male tenure turnover (Ferreira & Hofmeyr, 2014) is embedded within a suite of best practice guidelines adopted by managers of fenced reserves (Miller et al., 2013). Adoption of such interventions which likely induce meta-population dynamics, however, is a recent phenomenon and managers must routinely address the consequences of past, haphazard management interventions (Miller et al., 2015). Nevertheless, meta-population theory (Levins, 1969) dictates that highly stochastic local population dynamics can lead to local extinction, but with the possibility of recolonization through dispersal from other sub-populations. For large mammals such as lions, the time and spatial scales over which population dynamics play out result in expectations that local breeding will be discrete, and that these populations should have dissimilar growth rates—that is some local populations may increase while, at the same time, others will decrease (Olivier et al., 2009).

Our study shows that variable, proximate ecological scenarios influence the primary drivers of lion sociality—cub and territory defence (Mosser & Packer, 2009; Packer et al., 1990)—and appear to play key roles in achieving variable population demography across the landscape, a known feature of the fenced reserves of South Africa (McEvoy et al., 2021). Our work further suggests that different mechanisms of intraspecific competition, which are often case specific, are at play. Thus, for wildlife managers, mimicking the outcomes of different levels of intraspecific competition may be a critical management intervention for enhancing the conservation of lions living in fragmented landscapes. For example, increasing the number of nomadic or unknown males to small reserves may increase male–male competition which would likely drive greater pride cohesion and mimic more regular pride takeovers.

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CONFLICT OF INTEREST

The authors declare no conflict of interest.

AUTHOR CONTRIBUTIONS

OKM, SFM and DMP designed the research collectively. OKM collected and analysed the data. OKM, SFM and DMP participated in the interpretation of the data and the writing of the manuscript.

PEER REVIEW

The peer review history for this article is available at <https://publons.com/publon/10.1002/2688-8319.12135>.

DATA AVAILABILITY STATEMENT

Data available on Zenodo Digital Repository: <https://doi.org/10.5281/zenodo.5930578> (Parker, 2022)

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