Ecology of the white lion: conservation management of the white lion (Panthera leo melanochaita Hamilton Smith 1842) in the Greater Kruger Park Region, South Africa

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Conservation Management of the white lion
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1 General Introduction

1.1 Background

Protected areas and conservation strategies are typically designed to protect populations, species, and community diversity. However, preserving genetic and phenotypic diversity is increasingly considered. Coat colour variation, resulting from gene mutations, is present in several mammalian taxa and has been detected in mammals as far back as 14,000 years ago (Searle 1968). Natural intraspecific coat colour variation has been observed in a number of mammalian species, including deer mice (*Peromyscus spp.),* black bear (*Ursus americanus*), cheetah (*Acinonyx jubatus*), leopard (*Panthera pardus*), Bengal tiger (*Panthera tigris tigris*), common seal *(Phoca vitulina*) and African lion (*Panthera leo*) (Searle 1968; Cruickshank & Robinson 1997; Marshall & Ritland 2002; Kaelin, Xu, Hong, David, McGowan et al. 2013; Xu et al. 2013). Natural selection determines which coat colour will persist, based on whether the colour is a benefit or not to the survival of that species (Darwin 1904-1914; Hoekstra 2010). Common colour mutations in big cats are albinism (pure white), chinchilla (white with pale markings), leucism (partial albinism/cream) and melanism (black) (Searle 1968; Schneider, Henegar, Day, Absher, Napolitano et al. 2015). Rare and unique variants may have distinctive morphology, life history traits, or habitat use, which often signal local adaptation to ecological conditions, or else they may represent cultural significance to specific peoples (Crandall, Bininda-Emonds, Mace, & Wayne 2000;

Garibaldi & Turner 2004). The black jaguar for example, is a rare dark-coated morph of the more common spotted-coated jaguar (Panthera onca), and it plays an integral role in the culture and mythology of indigenous communities in the Americas (Saunders 1998). More broadly, the need to safeguard organisms of cultural significance, in relation to indigenous people's rights, has been reaffirmed at international conservation governance forums (United Nations General Assembly 2007). Important to both cultures and ecosystems, conservation is often more effective when targeted towards culturally valuable species or forms (DeRoy, Darimont, & Service 2019; Gavin et al. 2015). The white lion is a rare colour variant of the African lion (*Panthera leo*, Linneaus 1758), that has cultural significance for the indigenous communities (Tsonga and Sepedi) in the Greater Kruger Park Region of South Africa (Tucker 2003).

The African lion (*Panthera leo*) is a highly enigmatic and charismatic species that plays an integral role in ecosystem functioning (Jackson 1972). Being the apex predator in African ecosystems, lions generate important ecological, economic, and cultural value (Wolf & Ripple 2018). The lion can also be classified as a flagship species due to its unquestionable symbolic and ritual role in traditional and modern cultures (Simberloff 1998; Tucker 2003; Coals et al. 2022). Even though they are a flagship species, lions have lost more than 90% of their historical range, and especially in West, Central and East Africa, they show continued population decline (Bauer & Van Der Merwe 2004; Hazzah et al. 2009; Kat 2012; Riggio et al. 2013; Bauer et al. 2015; Riggio et al., 2016). Only in southern Africa lion populations show a stable trend (Riggio et al., 2016; Bauer et al. 2015). According to a study by Riggio et al. (2013), the current extent of the area where free-ranging lion populations live is 3.4 million km^2, or about 25% of the total savannah area. More than half of this area is a hunting zone (Lindsey et al. 2006). Riggio et al. (2013) identified 67 lion areas (Lion Conservation Units), ten of which have been qualified as strongholds (four in East-Africa and six in southern Africa). A lion stronghold contains at least 500 individuals, is located within a protected area or a designated hunting zone, and has a stable or increasing number of lions (Riggio et al. 2013). A variety of anthropogenic activities have caused the ongoing population decline (Bauer et al. 2020). The most significant causes of decline include habitat loss, prey depletion due to bushmeat poaching, poor enforcement of regulations on hunting leading to excessive quotas, mortality due to human-lion conflict, indiscriminate snaring, and 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). A multidisciplinary and adaptive approach to conservation action is needed to address these declines.

Based on recent genetic research, *Panthera leo* is further split into two subspecies (Kitchener et al. 2016). *Panthera leo leo* (Linnaeus, 1758) inhabits West and Central Africa and India, and is currently undergoing local extinctions even in nominally protected areas (Riggio et al. 2013; Bauer et al. 2016; Kitchener et al. 2016). The other subspecies, *Panthera leo melanochaita* (Hamilton Smith, 1842), populates East and southern Africa (Bauer et al. 2016; Kitchener et al. 2016). This reclassification is necessary to regionally ascertain the threat level of the respective subspecies of lions. Currently, the IUCN has listed *Panthera leo* as Globally Vulnerable on the global IUCN Red List (category A2abcd ver 3.1, 2017), but states that it actually meets the criteria for 'Regionally Endangered' in East and Central Africa, with lions in West and Central Africa being 'Regionally Critically Endangered' (Henschel et al. 2014; Bauer et al. 2015). Bauer et al. (2016) have estimated the global number of adult lions to be between 23,000 and 39,000 individuals.

Lions were extirpated from most of their range in South Africa by the 1900s (Nowell & Jackson 2011; Miller et al. 2015) due to habitat loss, human-lion conflict, poaching and trophy hunting (Miller et al. 2016), with historic populations remaining only in Kruger National Park and Kgalagadi Transfrontier Park. Today just over ~3500 wild-ranging lions are protected in South Africa within these and other large national parks and game reserves, with all populations either stable or increasing (Bauer et al. 2015; Miller et al. 2015; Miller et al. 2016). This is confirmed by the 2016 Red List of Mammals of South Africa, Lesotho and Swaziland, which states that the lion populations in these regions are stable or increasing in major reserves, and also increasing through the addition of small reserves or through the formation of private conservancies (IUCN 2016). Over the last three decades lions have also been reintroduced into over 49 smaller, mostly fenced, reserves in South Africa with a total population of managed wild lions of about 800 individuals (Miller et al. 2015). In addition to these wild and 'managed wild' lion populations, South Africa also has substantial numbers of captive-bred lions (Coals et al. 2019). Since the lion population in South Africa is regarded as stable, the conservation status of lions has been downlisted from Regionally Vulnerable to Regionally Least Concern (Miller et al. 2016; IUCN 2016). However, the recent legalisation of the trade in lion bones from captive lions in South Africa in 2016 has led to concerns that this could prompt an increase in poaching and most likely illegal trade (Williams et al. 2017; EWT 2017). According to the same authors, this illegal trade could become a serious threat to wild-ranging lion populations in South Africa. This subject is discussed in detail in Chapter 5 of this doctoral study.

The Kruger National Park has the largest lion population in South Africa and, as part of the Greater Limpopo Transfrontier Park, is one of only ten lion strongholds in the world (Riggio et al. 2013). The white lion is a rare natural occurrence and colour variant. They are only found as wild-ranging lions within the lion population in the central Kruger National Park and neighbouring Associated Private Nature Reserves (Greater Timbavati Region). At the time of this study there was a perception that the white lions' colouration prevents them from displaying the natural hunting, social, or territorial behaviour of wild lions, and that therefore they cannot survive in the wild (McBride 1977; McBride 1981; Smuts 1982). So far, no research has specifically covered the ecology and behaviour of white lions compared to tawny lions. I hypothesise that white lions do not differ from tawny lions in their social structure and interaction, their hunting and other territorial behaviour, their movement and home ranges. To broaden the focus of this study, I will go on to discuss the reintroduction and conservation management of white lions in the Greater Kruger Park Region, and its relevance to the metapopulation management of lions in South Africa.

1.1.1 History of the White Lion

The white lion has only ever been observed in the wild in the Timbavati, Klaserie and Umbabat Private Nature Reserves, and the Central Kruger National Park – the Greater Kruger Park Region (McBride 1981; Robinson & De Vos 1981; Cruickshank & Robinson 1997; Tucker 2003; Cesare 2011). The white lion is a rare phenotype or colour variant of the African lion (*Panthera leo*, Linneaus, 1758) that has a white coat colour with either yellow, blue or green eyes. The white coat colour is not due to albinism (Robinson & De Vos 1982), but rather leucism resulting from a double recessive allele (Cruickshank & Robinson 1997).

The first recorded sighting of a white lion in the wild was by Joyce Little in 1938, in the area now known as the Timbavati Private Nature Reserve (Tucker 2003). The presence of white lions was documented for the first time in the Central Kruger National Park in 1959 (Smuts 1982) and in the Timbavati Private Nature Reserve (TPNR) in 1975 (McBride 1977). There were probably no sightings of white lions in these area prior to 1938 and 1959, respectively, since the Timbavati Private Nature Reserve and Kruger National Park were large remote wilderness areas seldom visited by tourists or officials. The frequency of occurrence of white lions in their natural endemic habitat increased until they were removed (Robinson & De Vos 1982; Cruickshank & Robinson 1997; Tucker 2003). From the 1970s onwards, prized for their rarity, the white lions, and many normal coloured (tawny) lions carrying the white lion allele, were removed from the wild and put into captive breeding and trophy hunting programmes or sent to zoos and circuses around the globe (McBride 1981; 2003). Combined with lion culling in Central Kruger National Park (Smuts 1982) and trophy hunting of pride male lions in Timbavati Private Nature Reserve (Cadman 2006) it is our assertion that these actions removed the white lions and decreased the occurrence of the white lion allele, such that white lions were absent from the wild between 1994 and 2006 (Smuts 1982; Cadman 2006). One could add to this the natural lion cub mortality in the wild of up to 50%, and the fact that white lions are particularly sought after for both legal and illegal trade in their body parts and derivatives, due to their rarity and the cultural beliefs around white lions that are held by Tsonga and Sepedi communities within the Greater Kruger Park Region (Tucker 2003; Cesare 2011; Gomersall 2022).

1.1.2 White Lion Reintroduction to Managed Free-Roaming Conditions

Wildlife reintroduction has become necessary as a conservation tool for many species, due to the unprecedented rate of decline and extinction of species populations. This is mostly due to anthropogenic activities, resulting in loss of habitat, population decline due to over-harvesting, and persecution through human-wildlife conflict (IPBES 2019). Reintroduction of species has been used as a conservation tool for the recovery of many endangered species including African wild dogs in South Africa (*Lycaon pinctus*) (Gusset et al. 2010), tigers in India (Reddy 2016), and the Eurasian lynx (*Lynx lynx*) in Europe (Linnell et al. 2009). Ex situ reintroduction is defined as the release of individuals from captive origin into the wild within the historical range of the species (New 2006). This method can be used to supplement, establish, or re-establish wild populations. Captive bred animals are reintroduced into the wild by means of a process called rewilding. Due to high failure rates and high costs, rewilding is generally discouraged (Miller, Ralls, Reading, Scott & Estes 1999; Jule, Leaver & Lea 2008; Griffith, Scott, Carpenter & Reed 1989; Snyder et al. 1996). However, the use of captive-born individuals becomes necessary when no wild representatives remain, or when the surviving wild population is no longer viable (Stuart 1991). Ex situ reintroduction of carnivores has been successfully conducted for species worldwide, including the red wolf (Roth et al. 2008; U.S. Fish & Wildlife Service 2014), the Mexican wolf (*Canis lupus baileyi*) (Hedrick & Fredrickson 2008; 2010), and the Eurasian lynx (Linnell et al. 2009). Ex situ reintroduction of lions (white and tawny) has been successfully done at the Sanbona Wildlife Reserve (58 000 ha) in the Western Cape (Gomersall 2022) and the Pumba Game Reserve (6500 ha) in the Eastern Cape of South Africa (Howarth 2022). Both these wildlife reserves have successfully introduced free-roaming prides that were comprised of the wild-born offspring of rewilded white lions integrated with wild non-white lions. The only published results for ex situ reintroduction of lions, at the time of this study, are the publications by Abell et al. (2013) and Dunston (2016). Whilst there is a frequently accepted perception that certain captive felids, particularly lions, cannot hunt successfully or survive in the wild (Jule et al. 2008), the findings of Dunston (2016) cast some doubt on this assertion. Dunston (2016) concluded in her study that there was no difference in the sociality and the territorial and hunting behaviour of captive-origin lions near Antelope Park (Zimbabwe) and wild-origin lions in the Greater Makalali Private Game Reserve (South Africa). These findings support the postulation by Abell et al. (2013), who advocate that the offspring of a captive-origin lion pride, which are able to hunt self-sufficiently and are not human-imprinted, can be successfully reintroduced to a suitable wildlife area.

Since no adult white lion had been seen in their natural habitat since 1994 due to illegal removal (translocation), infanticide caused by trophy hunting of pride male lions, and a natural mortality rate of 50% of cubs not surviving the first year in the wild, the white lion was absent in the wild until 2006 (Turner et al. 2015). The reintroduction of white lions within their natural habitat was therefore initiated by the Global White Lion Protection Trust[1] in 2006, based on the successful lion reintroduction technique described by Van Dyk (1997), as used at Phinda Resource Reserve (Hunter 1998), and at Welgevonden Game Reserve (Kilian 2003), and subsequently in reintroductions at the Greater Makalali Private Game Reserve (Druce et al. 2004), Karongwe Conservancy (Lehmann et al. 2008), and the Karoo National Park (Miller, Bloomer, Harper, Hofmeyr & Funston 2015). These lion reintroductions all involved a soft rather than a hard release (Brock, Gustafson & Major 1990). Soft release is generally more successful than hard release (Price 1991). The first condition for success is that it involves a period of captivity (boma or other enclosure) of three weeks to three months at the release site, during which the animal can adjust to its surroundings (Moore & Smith 1990; Linnell, Aanes, Swenson, Odden & Smith 1997). A second condition is that a lion is kept together with other conspecifics that may be released with it as a group or pride (Brock et al. 2015; Van Dyk 1997). Hard release does not include this period of acclimation and group release.

The initial reintroduction involved a pride of white lions of captive origin that was reintroduced to the Tsau Wildlife Area – a 1700 ha fenced wildlife area bordering the Timbavati Private Nature Reserve in the Kruger and Canyons Biosphere Reserve (Turner et al. 2015). This white lion pride was successfully rewilded and became self-sufficient (ibid.). The white lion offspring of this pride of white lions were subsequently integrated with other free-roaming tawny lions to form a constructed pride. More details about this reintroduction and the conservation principles applied are given in Chapter 5.

1.1.3 (Re) Birth of White Lions in the Wild

In 2006, the same year that the Global White Lion Protection Trust reintroduced the above-mentioned pride of white lions to the Tsau Wildlife Area, the first white lion cubs were born naturally again in the Timbavati Private Nature Reserve (Cadman 2006). At the time of writing, a total of 17 births of white lions had been recorded over the past 16 years, in seven different prides in the Timbavati Private Nature Reserve, neighbouring Umbabat Private Nature Reserve, Klaserie Private Nature Reserve, and Central Kruger National Park, confirming that white lions are a natural occurrence and that the recessive gene is still present in the wild population (Dicks 2022). However, no scientific study had been done so far to determine the distribution of the white lions, their frequency of occurrence in the wild, or their ecology: their social structure, home range, movement patterns, or hunting ability.

[1] From 2004 to 2020, the author was an ecologist with the Global White Lion Protection Trust, and part of the research team. At the time of writing the author is an independent environmental consultant.

The conservation authorities in the Kruger to Canyons Biosphere Reserve perceived the white lion to be an albino that cannot hunt due to a lack of camouflage (McBride 1981). Genetic studies have now proved that the white coat is not caused by albinism but rather by leucism (Robinson & De Vos 1981; Cruickshank & Robinson 1992; Cho et al. 2013). However, the perception that white lions cannot hunt successfully due to a lack of camouflage had never been tested scientifically prior to this study and was not based on any quantifiable data.

1.1.4 Cultural Meaning of White Lions

White lions have a long history of being regarded as culturally and spiritually significant by several population groups in South Africa and other parts of Africa (Tucker 2003). In accordance with ancient African tradition, in which clans had specific totem animals that were revered and protected, the white lion was regarded as sacred and protected as a totem animal by specific Tsonga, Sepedi, Swazi, and Khoi San (Bushmen) local communities, dating back centuries. The knowledge passed down through their oral tradition indicates that the white lions appeared over 400 years ago during the reign of Queen Numbi, in the area known today as Timbavati Private Nature Reserve (Tucker 2003). A similar cultural importance has been recorded for the Kermode bear (*Ursus americanus kermodei*) in British Columbia, Canada, by the First Nations Kitasoo people (Marshall & Ritland 2002). Several studies have also described cultural and spiritual beliefs, or taboos, held by indigenous communities regarding large carnivores, that led these communities to show much restraint and tolerance of large carnivores in spite of the threats they pose to human interests, and allowing coexistence (Jones, Andria & Hockley 2008; Chapron et al. 2014; Goodale, Parsons & Cherren 2015; Vucetich, Bruskotter & Nelson 2015; Kolipaka, Persoon, De Iongh & Srivastava 2015).

1.1.5 Reintroduction and social cohesion of white lions

Since the 1990s a number of free-ranging lion populations have been introduced to over 49 smaller (<1000 km^2) fenced reserves in South Africa, currently totalling ~800 lions (Funston & Levendal 2015). Bauer et al. (2015c) and Packer et al. (2013) have recently suggested that lions may increasingly depend on populations in small, fenced, intensively managed reserves for their continued survival. The reintroduction of white lions to managed free-roaming conditions created the opportunity for the first comprehensive scientific comparison between white lions with non-white (tawny) lions under managed free-ranging conditions (Turner et al. 2015; 2022a; 2022b).

Lions live in social fission-fusion groups called prides. The core of a pride is composed of a group of related females and their offspring (Bertram 1973; Schaller 1972). Males are considered part of a pride, but are transient within that pride. Although the pride is a cohesive social unit, its members may be scattered in several groups throughout the pride's range at any one time (Van Orsdol et al. 1985), and it is rare to find all pride members together (Packer 1986). It was expected that the social cohesion and behaviour of the white lion pride would be similar to that of the non-white (tawny) lion pride. A key factor that influences the success of lion reintroduction is the social cohesiveness of the prides being released. A lack of social cohesion has been observed to increase mortality and dispersal postrelease (Hunter 1998). Postrelease failure of carnivores can be due to reduced reproductive success and increased dispersal from the release site, both of which have been linked to a lack of group cohesion (Somers & Gusset 2009). The social cohesion was therefore important to the successful establishment of the white lion pride at the Tsau Wildlife Area, and their integration with wild non-white (tawny) lions under free-ranging conditions. For the purpose of this study, the integration of white and non-white lions was important since white lions are born naturally into non-white lion prides, as occurred in the Greater Timbavati Region and Central Kruger National Park (Mcbride 1981; Tucker 2003). The social cohesion of the constructed pride is then compared with that of captive and wild non-white lion prides, as discussed in Chapter 2. I hypothesise that there will be no difference between the social cohesion of white lions and tawny lions, based on earlier observations of white lions showing natural social behaviour as part of wild prides in the Timbavati Private Nature Reserve (McBride 1981; Cruickshank & Robinson 1997; Tucker 2003; Cesare 2011).

1.1.6 Home Range and Movement Patterns

The metapopulation management approach to lions in South Africa requires translocation between smaller fenced reserves, to promote genetic diversity and regulate population size (Miller et al. 2015; 2016). Home range establishment is an indication of translocation and reintroduction success. The motivation for this part of the study was to evaluate whether white lions are able to establish a home range in a similar way to non-white lions, thereby displaying the natural behaviour of wild lions. The movement patterns and habitat selection of white lions were also compared to those of wild tawny lions. The home range behaviour of white lions was important to determine whether the reintroduction of the managed-wild white lion pride at the Tsau Wildlife Area was a success, and a preliminary indication that the long-term objective of reintroducing a pride of white and tawny lions to fully free-roaming conditions is likely to be successful. I hypothesize that there will be no difference between home ranges of white lions and tawny lions, because white lions in the wild historically occurred as part of tawny lion prides, that displayed natural home ranging behaviour (Cruickshank & Robinson 1997; Cesare 2011; Turner et al. 2015).

1.1.7 Hunting Success

Lions have a cascading influence on ecological communities and ecosystems (Ripple et al. 2014), and are the apex predator in African savannah ecosystems, including the Kruger National Park. As apex predators, lions are highly adaptable in terms of their prey selection, hunting strategy, killing technique, activity pattern, and use of different habitat types. Many studies have been done to date on the hunting success of lions and the influence of lion predation on prey populations (e.g. Hirst 1969; Pienaar 1969; Schaller 1972; Smuts 1982; Van Orsdol 1985; Mills & Shenk 1992; Hanby et al. 1995; Viljoen 1997; Funston 1999; Druce et al. 2004; Lehmann et al. 2008). The hunting ability of white lions has, however, never been compared to that of non-white lions. A common perception is that white lions cannot hunt as successfully as tawny lions due to a lack of camouflage (Mcbride 1981). The hunting ability of the reintroduced white lions was compared to that of the non-white lions at the Tsau Wildlife Area, and at a number of other small game reserves in South Africa, using kill rate and consumption rate as indices of hunting success. Hunting success and therefore self-sufficiency are important criteria for assessing the success of lion reintroduction (IUCN / SSC 2013). I hypothesize that there will be no difference between the hunting success of white lions and tawny lions due to a lack of camouflage, since historically white lions were observed to survive naturally as part of wild tawny lion prides.

1.1.8 White Lion Reintroduction, Anthropogenic Impact, and Conservation Management

The conservation management and ecology of white lions in the Greater Kruger Park Region have never been investigated, nor have the anthropogenic activities that are suggested to have led to the absence of white lions in the wild. Although the lion population in South Africa is regarded as being stable, and anthropogenic activities are therefore regarded as not having a significant impact, since there are only 13 wild-managed white lions and three wild lions in the Greater Kruger Park Region, white lions may be more vulnerable to anthropogenic impact (Riggio et al. 2013; Turner et al. 2015; 2022a; 2022b). The reintroduction and conservation management of white lions by the Global White Lion Protection Trust (GWLPT) is therefore described in this chapter. Since lion conservation policy in South Africa was under review at the time of this study, reference is made to the draft policies (Government Gazette 45160; Government Gazette 46687) and biodiversity framework (Government Gazette 39468), and particularly the potential anthropogenic threats to lions (white and tawny) in the Greater Kruger Park Region. A possible conservation role is also discussed for the reintroduction and management of white lions to the Greater Kruger Park Region, in relation to the metapopulation approach to lions in South Africa.

1.2 Study Aim and Research Importance

This is the first study to compare the ecology and conservation management of white lions to that of non-white (tawny) lions, and to evaluate the potential role of white lions in the Greater Kruger Park Region, a critical part of the metapopulation management of lions in South Africa. Being the first study on this particular topic, the findings, although preliminary, are expected to advance existing knowledge of the ecology of white lions, to establish if the ecology of white lions is similar to that of non-white lions, and to determine if white lions display behaviour that is similar to that of wild tawny lions.

The aim of this study was to compare the ecology of lion prides dominated by white lions with prides dominated by non-white lions. I hypothesise that the social cohesion, home ranging behaviour, movement patterns, habitat selection, and hunting success are comparable between both lion groups, and have defined the following hypotheses:

Hypothesis a.
There is no difference in social cohesion between prides dominated by white lions and prides dominated by non-white (tawny) lions, because the social behaviour of white lions is similar to that of wild tawny lions

Hypothesis b.
There is no difference between the home ranges of white lions and tawny lions, because white lions display natural home ranging behaviour similar to that of wild tawny lions.

Hypothesis c.
There is no difference between the hunting success of white lions and tawny lions due to a lack of camouflage, because white lions show natural hunting behaviour similar to that of wild tawny lions.

The sub-aims of my study are to: (i) outline the reintroduction of white lions to a managed free-roaming area, and describe the implications for social cohesion of prides dominated by white lions compared to those dominated by non-white (tawny) lions, (ii) investigate the home ranges, movement patterns, and habitat selection of white lions compared to non-white (tawny) lions, (iii) evaluate the hunting success of white lions compared to that of non-white (tawny) lions under managed free-roaming conditions; and (iv) to describe the reintroduction and conservation management of white lions by the GWLPT in the Kruger to Canyons Biosphere Reserve, and the anthropogenic activities that may have led to their absence in the wild, in the context of the draft conservation policies for metapopulation management of lions in South Africa (Government Gazette 45160; Government Gazette 46687; Government Gazette 39468; Miller et al. 2015).

The intention of this study is that its findings will contribute to improving the conservation management and protection of white lions in the investigated region, and in other wildlife reserves that have wild white lions, in accordance with the metapopulation management of lions in South Africa.

1.3 Research Theme and Questions

Overall, this study aims to investigate the reintroduction of white lions to free-roaming conditions, and to compare the ecology, and conservation management, of white lions to that of non-white lions. The specific research objectives, associated with the hypotheses to be tested, are:

1. What is the social cohesion of prides dominated by white lions compared to prides dominated by non-white (tawny) lions?
2. Can a pride comprised of white lions and tawny lions form a socially cohesive unit, and do they show natural pride social behaviour?
3. What are the home ranges, movement patterns and habitat selection of white lions, and are these comparable to those of non-white lions, and natural wild lion behaviour?
4. What is the prey selection and hunting success of white lions compared to that of non-white lions?
5. Does the white lion reintroduction and conservation management by the Global White Lion Protection Trust provide insight into the anthropogenic activities that may have led to the absence of white lions in the wild from 1994 to 2006, and the low survival rate of white lions in the wild from 2006 to 2022, and can it contribute to the metapopulation management approach to lions in South Africa?

1.4 Study Area

The objectives of the study will be achieved by utilising the Global White Lion Protection Trust's Tsau Wildlife Area within the Kruger to Canyons Biosphere Reserve, in the Limpopo Province of South Africa (Figure 1).

The following sub-categories will be outlined for the study area:

I. Location
II. Climate
III. Vegetation, Soils and Geomorphology
IV. Fauna and Flora

I. Location

The Tsau Wildlife Area is a 1700 ha wildlife area established by the Global White Lion Protection Trust (GWLPT), in the Kruger to Canyons Biosphere Reserve, Limpopo Province, South Africa (Figure 1 and 2). The Kruger to Canyons (K2C) Biosphere Reserve is the third largest biosphere reserve[2] in the world, as declared by UNESCO in 2001

[2] Biosphere reserves are sites established by countries and recognized under UNESCO's Man and the Biosphere (MAB) Program to promote sustainable development by combining core protected areas with zones where sustainable development is fostered (Reyers 2013).

(Pool-Stanvliet 2013). The Kruger to Canyons Biosphere Reserve is the largest of six biosphere reserves that occur in South Africa, encompassing savannahs, grasslands and forests that roughly cover over 4.8 million hectares of land in South Africa and Mozambique. It is situated in the northeastern section of South Africa and includes two of South Africa's key environmental and ecotourism sites – the Kruger National Park and the Blyde River Canyon, as well as one of the leading international floral hotspots, the Wolkberg Region. The current boundaries of the registered Biosphere Reserve extend from the Letaba River in the north to the Sabie River in the south and from the Blyde Escarpment in the west to the Mozambique border in the east (Pool-Stanvliet 2013).

The Kruger to Canyons Biosphere Reserve consists of 2,474,700 ha, of which the core zone takes up 898,300 ha, the buffer zone 476,400 ha and the transition zone 1,100,000 ha. The core zone is a wilderness area with no human impact; in the buffer zone conservation management takes place with limited human infrastructure or activities, and the transition zone is an area that allows a higher level of human habitation and development of infrastructure, whilst still having an overall objective of conservation. Within this region, there are approximately 1,155 permanent residents in the core zones, 10,475 in the buffer zone and 1,488,684 in the transition zones – with the latter living on communal land.

The Tsau Wildlife Area is situated at the centre of the Kruger to Canyons Biosphere Reserve, and specifically within the Greater Kruger National Park Region, the only area where white lions have occurred naturally in the wild (Figure 1). This wildlife area is part of an important buffer area - the Greater Kruger Environmental Protection Zone (GKEPZ) - between the Kruger National Park, local communities, and the semi-urban town of Hoedspruit.

The Tsau Wildlife Area is comprised of three separately fenced wildlife areas (see Figure 2): (i) the 700 ha Tula Tsau Wildlife Area; (ii) the 300 ha Shidolo Wildlife Area; and (iii) the 715 ha Mbube Wildlife Area. The three properties are separately fenced and not contiguous. The three properties are separately fenced and not contiguous. The Shidolo and Tula Tsau Wildlife Areas are in close proximity, being separated by a public servitude road (Guernsey Road). The Mbube Wildlife Area is 21 km south of the Tula Tsau and Shidolo Wildlife Areas Area. There are several other separately fenced wildlife areas between the northern and southern wildlife areas of the GWLPT. The historical land use of the area was cattle and crop farming (tobacco, mangos, and tomatoes), and later game farming and hunting.

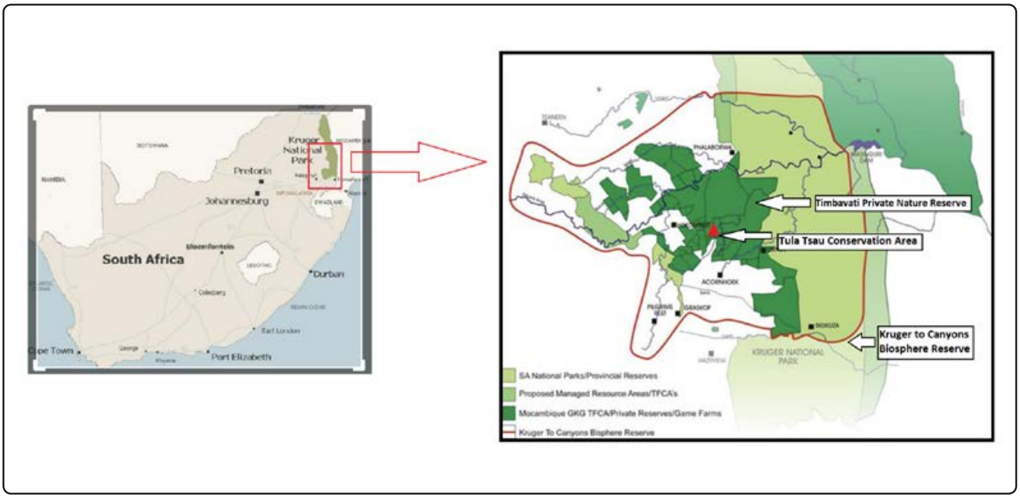

Figure 1 Map showing the Tula Tsau Conservation Area, Kruger National Park, and Timbavati Private Nature Reserve, within the Kruger to Canyons Biosphere Reserve, South Africa.

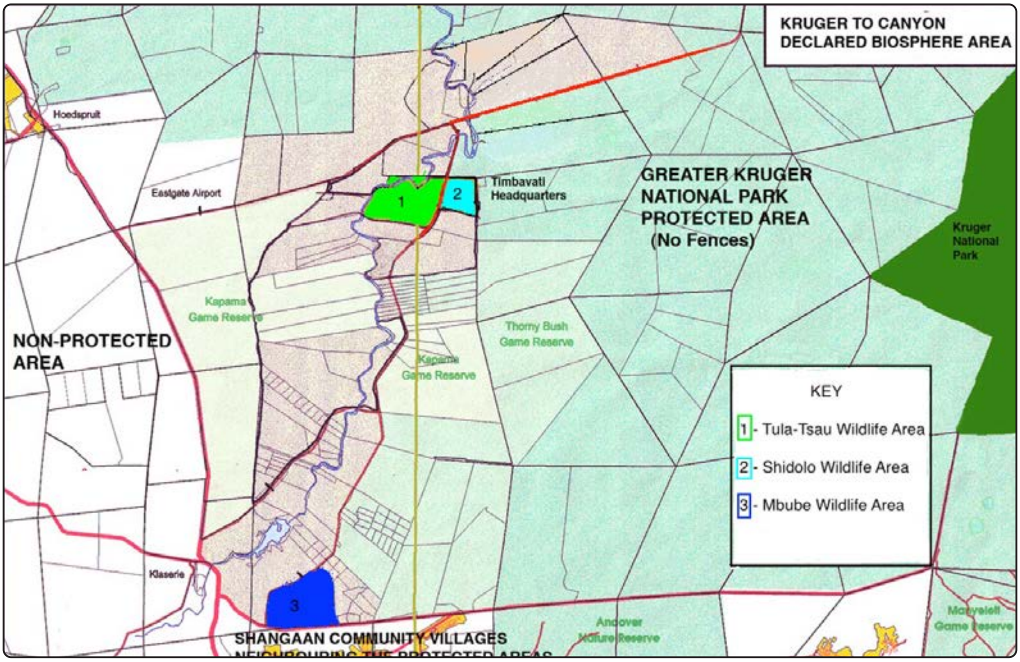

Figure 2 Map showing the wildlife areas that comprise the Tsau Wildlife Area – (1) Tula Tsau, (2) Shidolo and (3) Mbube Wildlife Areas - within the Kruger to Canyons Biosphere Reserve, South Africa.

II. Climate

The mean annual rainfall in the region ranges from 513 mm to 671 mm, with a mean of 613 mm/annum. The rainy season is predominantly in summer from October to March when more than 90% of the total annual rainfall is measured. The annual rainfall in dry and wet years may range from 445 mm to 847 mm respectively.

The mean annual temperature of the region is 21°C. The mean maximum monthly temperatures are 29.2°C and 23.7°C for January and June, respectively. The mean minimum monthly temperatures for January and June are 18.7°C and 9.5°C respectively. The extreme maximum and minimum temperatures measured for the region are 41.4°C and 1.5°C.

Vegetation, Soils and Geomorphology

The Tsau Wildlife Area is a managed wildlife area that consists of a mixed vegetation type that is classified as Arid Lowveld (Acocks 1988; Mucina & Rutherford 2006). It is an undulating landscape consisting of plains, woodlands of various densities and riverine vegetation. From north to south in the Granite Lowveld, the Swazian Goudplaats gneiss, Makhutswi gneiss and Nelspruit Suite (granite gneiss and migmatite) form the major basement geology of the area. The Tsau Wildlife Area is underlain by grey to pale-brown, medium to coarse-grained quartz-feldspar-biotite gneiss with subordinatemafic to ultramafic xenoliths. Archaean granite and gneiss weather into sandy soils in the uplands and clayey soils with high sodium content in the lowlands.
There are three permanent water points as well as numerous seasonal water points and streams.

III. Fauna and Flora

The area is populated by indigenous flora and fauna and contains the following mammalian prey species: blue wildebeest (*Connochaetes taurinus*), common warthog (*Phacochoerus africanus*), Cape porcupine (*Hystrix africaeaustralis*), impala (*Aepyceros melampus*), steenbok (*Raphicerus campestris*), aardvark (*Orycteropus afer*), bushbuck (*Tragelaphus scriptus*) and grey duiker (*Sylvicapra grimmia*). Conspecifics and large prey animals such as African buffalo (*Syncerus caffer*) and giraffe (*Giraffa camelopardalis*), which are dangerous for inexperienced lions to hunt, have been excluded from the Tsau Wildlife Area. Black-backed jackals (*Canis mesomelas*), and caracal (*Caracal caracal*) occur in the primary reintroduction area, and both leopard (*Panthera pardus*), and spotted hyaena (*Crocuta crocuta*), while seen intermittently, are not established in the reserve. Wild lions occur on neighbouring wildlife areas that border three of the four boundary fences of the Tsau Wildlife Area.
There are three lion groups at the Tsau Wildlife Area; one group of lions at each of the three wildlife areas that comprise the Tsau Wildlife Area (Figure 2). The lion groups at the Tula Tsau Wildlife Area and Shidolo Wildlife Areas are free-roaming.

The Tsau Wildlife Area is surrounded by a 22-strand electrified (9000 V) predator-proof fence that is 2.4 m high, has a triple bracket at the bottom with two double brackets above and a trip wire that is 600mm from the fence. A solar-powered Gallagher MBX2500 energiser with a lead-acid battery backup electrifies the fence. A second electrified fence, 1.5 m high with ten closely spaced strands, was placed ten meters inside the perimeter fence to minimise the risk of conflict with the lions from the two neighbouring private nature reserves. The double fence also minimised the risk of the lions escaping the area if a prey animal ran into the fenceline whilst being hunted by the lions. The neighbouring wildlife areas are fenced in a similar fashion, but with a single electrified fence only, and their predominant land use practices are photographic and hunting safaris.

1.5 Study Outline

This PhD dissertation is based on articles and it is divided into six chapters. The individual chapters have been published in several scientific journals. The articles are formatted to suit the layout style of this book but the content remains unchanged. Whilst the articles that comprise Chapter 2 and 3 were published recently (2022), the article comprising Chapter 4 was published in 2015 and some relevant text (dates and numbers of white lions born in the wild) has been updated. While I am the main author in all the articles, they are all written in cooperation with several other co-authors. So the reader may find the use of words like "we" in chapters 2 to 4. The contributions of different co-authors are listed at the end of each chapter.

Chapter 1 gives general introduction and review, with particular focus on the background of the white lion, their origin, genetics, area of occurrence, cultural and spiritual value. The motivation for the study is outlined, including the perceptions about white lions that had not yet been investigated. The relevance of the white lion reintroduction, and study, to lion conservation in the Kruger to Canyons Biosphere Reserve is discussed, in the context of the anthropogenic threats to lions in the region, and the metapopulation approach to lions in South Africa. Reference is also made to the current lion conservation policy in South Africa. After this review, the research questions to be addressed and the hypotheses to be tested are presented. The study area and region of occurrence are then described.

Chapter 2 describes the reintroduction of white lions to managed free-roaming conditions at the Tsau Wildlife Area. The social structure of a reintroduced lion pride, consisting of white lions integrated with non-white (tawny) lions, is compared to that of non-white (tawny) lion prides from wild and captive origin. Since white lions were absent from the wild for nearly 15 years, and there were no adult white lions at the time of this study, the successful introduction of a captive-origin pride of white lions and a constructed pride of rewilded white and wild tawny lions to managed free-roaming conditions, was critical for studying the ecology and conservation management of the white lions.

Chapter 3 compares the home range and movement patterns of the reintroduced white lions to those of non-white (tawny) lions. This study provides the first assessment of home range and movement behaviour of white lions as an index of reintroduction success. It assesses the home range and movement of a pride of reintroduced white lions and a constructed pride consisting of reintroduced white lions and translocated wild tawny lionesses in small, fenced reserves.

Chapter 4 investigates the hunting success of the white lion, with a particular focus on the effect of colouration on hunting ability, which had never been tested scientifically until this study. Specifically, the prey selection and hunting success of the reintroduced white lions is compared to that of wild non-white (tawny) lions in the same study area, and then to lion prides in other South African wildlife reserves.

Chapter 5 describes the reintroduction and conservation management of white lions in the Greater Kruger Park Region, as well as the conservation principles applied by the Global White Lion Protection Trust. From 1994 to 2006, white lions were absent from the wild, most likely due to anthropogenic impact. Between 2006 and 2022, white lion cubs were born in the Greater Kruger Park Region, confirming that the recessive gene is still present in the wild lion population. However, at the time of writing (2023), only three adult white lions had survived in the wild, and the GWLPT proposed that this was due to anthropogenic activities. In 2006, there were no adult white lions in the wild, which is why the Global White Lion Protection Trust (GWLPT) reintroduced a pride of white and tawny lions to free-roaming conditions, to study their ecology and the anthropogenic activities that could have an impact on white lions, historically and at the time of this study. The anthropogenic threats to lions (white and tawny) in South Africa are listed, as described by the draft lion conservation policy being developed by the South African government. In conclusion, the conservation management of white lions in the Greater Kruger Park Region is discussed in the context of the metapopulation approach to lions in South Africa.

Chapter 6 gives a synthesis of the thesis. It is expected that the findings of this study regarding the reintroduction, social structure, home range, movement patterns, and hunting success of the white lion will advance existing knowledge about white lions, their conservation management, and the anthropogenic threats to white lions in South Africa. The limitations of this study will be outlined with recommendations for future research on white lions. The findings of the study will be interpreted and discussed in relation to their implications for the conservation of lions (white and tawny) in the Greater Kruger Park Region, a key part of the metapopulation of lions in South Africa. Particular focus will be on the anthropogenic threats to lions (white and tawny) in the Greater Kruger Park Region, with reference to the lion conservation policy in South Africa which was under review at the time of this study. Finally, recommendations will be made for wildlife managers to better manage white lions as part of wild tawny lion prides, in accordance with the metapopulation management approach to wild lion populations in South Africa.

Photo 2.1 Social bonding between adult white lion males at Tula Tsau Wildlife Area, South Africa.
© Global White Lion Protection Trust

2 Social Behaviour of White Lions

Assessing the Social Cohesion of a Translocated Pride of White Lions Integrated with Wild Tawny Lions in South Africa, Using Social Network Analysis.

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Simple Summary: Lions in South Africa are protected in national parks and smaller fenced private wildlife reserves. Population sizes and genetics within fenced reserves are managed through moving lions between reserves. One component of successful lion movements is their ability to form prides post-release, which is influenced by the strength of social bonds and interactions between individual lions. White lions are a natural colour variant of the African lion, occurring within certain tawny lion prides in the Greater Kruger National Park, South Africa. Human impact, including trophy hunting, led to the removal of white lions from the wild until their reintroduction in 2006. The social behaviour of a pride consisting of captive-origin white and wild tawny lions was compared to captive-origin and wild tawny lion prides, with similarities and differences in the social behaviour of prides found. The study concluded that the pride of white and tawny lions was more strongly bonded than either the captive-origin or wild tawny prides. This suggests that a constructed pride of captive-origin white and wild tawny lions can successfully form a socially functional lion pride, and indicates that white lions are capable of surviving in the wild in the absence of negative human impact.

Abstract: In South Africa, lions are protected in national parks and smaller fenced reserves. Translocating lions between fenced reserves, whilst necessary to maintain gene tic diversity, is disruptive and can impact survivorship and pride cohesion. Critical to translocation success is pride cohesion. White lions are a natural colour variant occurring in the Greater Kruger Park Region, where anthropogenic threats eliminated this population until reintroduction in 2006. Through social network analysis (SNA), the sociality of a released pride of captive-origin white and wild tawny lions was compared to two captive-origin and wild prides of tawny lions. Social interactions and pride dynamics were recorded for each pride. For all prides, cubs and subadults were central to the play network, while adults received the most social interactions. White and wild tawny adult males initiated more social interactions than captive-origin tawny males, whilst a keystone adult female was identified in each pride. For the constructed pride, social interactions were more evenly distributed, suggesting a high level of connectedness and cohesion. This is the first study to demonstrate that captive-origin white and wild tawny lions can form a socially functional pride, suggesting that white lions would survive in the wild in the absence of anthropogenic threats.

Keywords: African lion; *Panthera leo melanochaita*; white lion; conservation; translocation; behaviour; social interactions

2.1 Introduction

The conservation status of the African lion (*Panthera leo*) in Southern Africa is listed as 'Vulnerable' (Bauer & Van der Merwe 2004). Significant population declines are due to prey depletion, loss of habitat, human-wildlife conflict, climate change, inbreeding depression, and disease (Bauer & Van der Merwe 2004; Hazzah et al. 2009; Kat 2012; Riggio et al. 2013; Bauer et al. 2015; Bauer et al. 2016). In South Africa, lions went extinct throughout much of their former range during the early 20th century (Nowell & Jackson 1996), with approximately 1875 lions located in three populations (Castley et al. 2002; Ferreira & Funston 2010; Funston 2011). According to Bauer et al. (2015) and Packer et al. (2013) this species' survival in southern Africa may increasingly depend on populations in fenced, intensively managed reserves.

The translocation of lions between fenced reserves in South Africa is required regularly to maintain genetic diversity and population management (Miller et al. 2015). Such translocations between small, fenced reserves (<1000 km^2) have occurred from 1990 to 2013, involving approximately 800 lions (Funston & Levendal 2015), with this population now managed as a metapopulation (Miller et al. 2014; 2015). The use of wild individuals in translocations is preferred due to the higher failure rate reported for captive-origin animals (Beck et al. 1994; Fischer & Lindenmayer 2000; Jule et al. 2008), and, according to Hunter et al. (2013), this also applies specifically to lion translocations. However, captive-born lions may become necessary when no suitable wild individuals remain, or when the surviving wild population is no longer viable (Stuart 1991; Abell et al. 2013a; 2013b). Known as ex situ reintroduction (New 2006), the release of captive-origin individuals has been performed successfully for many species, including the golden lion tamarin (Witzenberger & Hochkirch 2011), the red wolf (Oakleaf et al. 2004), the California condor (Toone & Wallace 1994), the Arabian oryx (Stanley Price 1991), and the black-footed ferret (Jachowski & Lockhart 2009), proving to be an important tool that has prevented the wild extinction of some of these species.

The white lion is a natural colour variant, or leucistic form, of the southern subspecies of the African lion (*Panthera leo melanochaita*) that had been prevalent in the Greater Timbavati Region (McBride 1977; McBride 1981; Cesare 2011) and Central Kruger Park Region (Robinson & De Vos 1982; Smuts 1982; Cruickshank & Robinson 1997) of South Africa since 1938 (Tucker 2003). Being extremely rare in the wild, white lions and many tawny lions that had the recessive gene were removed from the wild for captive breeding and hunting programmes, zoos and circuses worldwide (McBride 1981; Tucker 2003; Cesare 2011). The combination of lion culling in Central Kruger National Park (Smuts 1982), in addition to trophy hunting and illegal removal from the Greater Timbavati Region into captive breeding centres (McBride 1981; Tucker 2003; Cesare 2011; Turner et al. 2015), resulted in white lions being absent from their natural region up until 2006. Even though white lion cubs were born into the Greater Timbavati Region from 2006 to 2009, in 2011, 2014, 2015, 2018, and 2019, and in Central Kruger National Park in 2015 and 2016, only three of the seventeen cubs had survived at the time of the present study, due to anthropogenic impact. The specific impacts were illegal removal to breeding centres, the continued lion trophy hunting of pride males, which caused infanticide, and high-impact ecotourism leading to undue stress on lionesses with young cubs during regular viewing by tourist or lodge vehicles (Whitman & Packer 1997; Whitman et al. 2004; Dicks 2022). In addition to the anthropogenic impact, the natural high mortality rate of 50% of lion cubs within the first year (Funston et al. 2003) would also have contributed to the low survival rate of white lion cubs between 2006 and 2019. Adult white lions were therefore reintroduced to a managed free-roaming wildlife area in 2006 by the Global White Lion Protection Trust, and became self-sufficient and successfully raised offspring. Turner et al. (2015) showed that there was no difference in the hunting success of the two reintroduced white lion groups compared to wild tawny lions in the same study area, Madjuma Lion Reserve (MLR), Karongwe Game Reserve (KGR), Welgevonden Game Reserve (WGR), Makalali Game Reserve (MGR) and the Associated Private Nature Reserves (APNR) in South Africa. The home range behaviour of white lions was also shown to be similar to that of wild tawny lions by Turner et al. (2022).

Although the overall success of lion reintroduction is the raising of offspring and population increase post-release, a key factor in determining the short-term success of either lion translocation or reintroduction is group cohesion (Hunter 1998; Somers & Gusset 2009; Marneweck et al. 2019). Lack of social cohesion can increase mortality and dispersal post-release (Hunter 1998), and reduce reproductive success, ultimately resulting in post-release failure (Somers & Gusset 2009). A lion pride is a cohesive social unit composed of a core of related females, their cubs and one or more males (Schaller 1972). Naturally, lion prides are composed of between two and nine adult females (range of 1-21), their dependent cubs and subadults, and between two and six adult males (range of 2-9) (Mosser & Packer 2009), with the average pride consisting of 15 individuals but ranging from 4 to 37 (Schaller 1972). Prides exist as a fission-fusion society, with pride members regularly splitting into smaller groups and then reforming, seldom all being grouped together (Schaller 1976). Social cohesion and cooperation are fundamental to the success of the pride, with benefits including territory defence to increased reproductive success (Mosser & Packer 2009), coordinated hunting (Packer et al. 2001) and communal nurturing of young (Matoba et al. 2013). Social greetings and allogrooming are regarded as critical in the maintenance of social bonds between lions in captive (Matoba et al. 2013) and wild prides, whereas play behaviour is mainly carried out by cubs as part of their development (Schaller 1972). Social Network Analysis (SNA) has previously been found useful in assessing and quantifying animal social structures, at both a group and individual level (Krause et al. 2007; Sih et al. 2009). Abell et al.

(2013a) provided the first SNA on lions, focusing on a captive-origin lion pride with wild-born cubs, identifying that the roles of individuals, sexes and age groups varied and that the pride was socially cohesive. Dunston et al. (2017) conducted the first SNA to compare the sociality of two captive-origin lion prides with that of a wild lion pride, finding that the captive-origin prides were socially cohesive, displaying behaviour and interactions similar to that of the wild pride. SNA has also been used more recently by Mzileni et al. (2019) to study horizontal disease transmission in wild lions in Kruger National Park, by looking at the behavioural interfaces of lions. However, SNA has never been used to determine whether reintroduced captive-origin (white) lions integrated into a pride can form a socially cohesive pride.

Our study used SNA to determine whether a pride consisting of two white lion males from captive origin had formed a socially cohesive pride with two translocated wild tawny lionesses and their offspring. This was achieved by comparing our pride to previously studied captive-origin and wild prides. Notably, the two tawny lionesses were unrelated, originating from two different wildlife reserves in South Africa, further complicating the development of a cohesive pride. Establishing the sociality of reintroduced lion prides is an important aspect of determining post-release success and will inform future translocation and reintroduction programmes, which may prove critical to the metapopulation management approach. This is particularly pertinent due to the increasing impact of anthropogenic threats to lions, including poaching, trophy hunting, and human-lion conflict.

2.2 Materials and Methods

2.2.1 Study Site

This study was conducted at the Tula Tsau Conservation Area (17,2 km^2), a fenced wildlife area in the Kruger to Canyons Biosphere, Limpopo Province, South Africa. The Tula Tsau Conservation Area is part of an important buffer area (Greater Kruger Environmental Protection Zone (GKEPZ)) between the Kruger National Park, rural communities, and the semi-urban town of Hoedspruit (Figure 1).

The Tula Tsau Conservation Area is a managed wildlife area that consists of a mixed vegetation type that is classified as Arid Lowveld (Mucina & Rutherford 2006), with an undulating landscape consisting of plains, woodlands, thickets, and riverine vegetation. A wide variety of large mammalian prey species occur, including the blue wildebeest (*Connochaetes taurinus*), Burchell's zebra (*Equus quagga*), the greater kudu (*Tragelaphus strepsiceros*), the common warthog (*Phacochoerus africanus*), and the impala (*Aepyceros melampus*). Black-backed jackals (*Canis mesomelas*) and caracals (*Caracal caracal*) are commonly seen in the area, and both leopards (*Panthera pardus*) and spotted hyaenas

(*Crocuta crocuta*), while seen intermittently, are not established in the reserve. Prides of wild lions occur in the two neighbouring private nature reserves.

Since there were no adult white lions in the wild in 2004, a founder group of white lions of captive origin was translocated to the Tula Tsau Conservation Area - a 17.2 km^2 fenced wildlife area bordering the Timbavati Private Nature Reserve in the Kruger to Canyons Biosphere. In 2006, the founder pride of white lions was successfully translocated to the Tula Tsau Conservation Area and became self-sufficient, hunting sufficient natural prey to satisfy the needs of the pride without requiring any human intervention (Turner et al. 2015). In 2013, the two male offspring of the founder pride were subsequently integrated with translocated wild tawny lions at the Tula Tsau Conservation Area to form the Tsau pride.

The Tsau pride comprised two eight-year-old sibling adult white lion males that were integrated with two unrelated wild tawny lionesses, translocated from other reserves in 2013 and 2015, respectively. The first lioness (six years old) originated from the 111, 000 ha Tswalu Kalahari Reserve (TKR), and the second lioness (12 years old) came from the 12, 000 ha Kapama Private Nature Reserve in the Limpopo Province of South Africa. In December 2018, a single litter of three tawny lion cubs was born.

The lions were fitted with VHF radio tracking collars and monitored from a research vehicle twice daily, at dawn and dusk, from 7 April to 10 May 2019 for between 1-5 hours per session. At each monitoring session, pride location, group composition and social interactions were recorded. Group composition was recorded at the start and end of each monitoring session, or when a change in the composition took place due to a pride

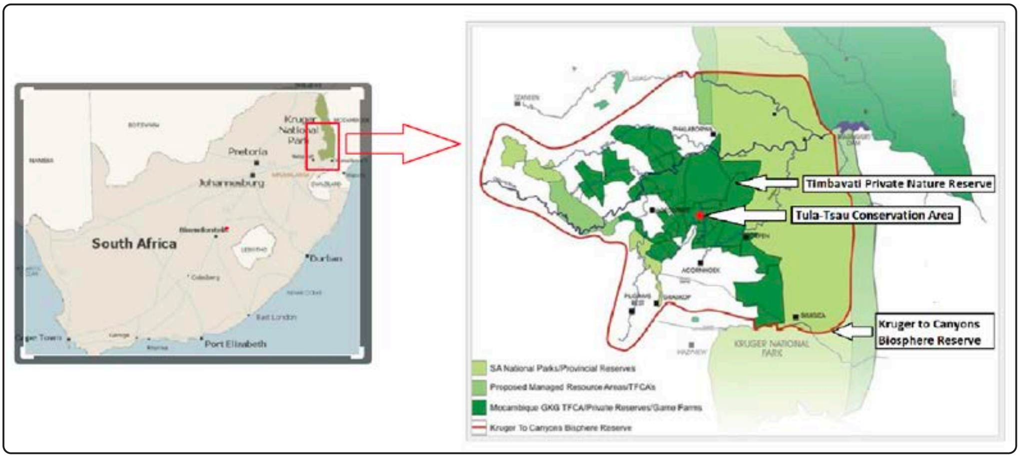

Figure 1 **Location of the Tula Tsau Conservation Area, Kruger to Canyons Biosphere Reserve, South Africa**

Table 1: Density values for each network, per pride, with a value of 0 indicating an unconnected pride and 1 indicating a highly connected pride.

Pride	Greet	Groom	Play	Aggression	All social	Pride Composition
Tsau	0.643	0.476	0.643	0.595	0.929	1
Ngamo	0.891	0.664	0.145	0.136	0.964	1
Dambwa	0.78	0.303	0.515	0.515	0.939	1
Makhutswi 1	0.394	0.091	0.114	0.114	0.492	1
Makhutswi 2	0.106	0.015	0.091	0.038	0.22	1

member leaving or joining, with each lion being recorded as present or absent. Social interactions were recorded via all-occurrence sampling, recording the interaction type (greet, groom, play and aggression, as previously described by Schaller (1972)), the individual who initiated and received the interaction, and whether it was accepted, ignored, or rejected. A social interaction event was deemed to have ended after one minute without interaction. In the case of multiple interactions being observed, only the initial interaction type was recorded, avoiding pseudo-replication.

The focal lion group for this study was the Tsau pride. The social behaviour and cohesion of this pride was compared to previously studied captive-origin tawny and wild prides, detailed in Dunston et al. (2017). The two captive-origin prides were situated in Livingstone, Zambia (Dambwa pride) and Gweru, Zimbabwe (Ngamo pride). The wild pride was located at the Greater Makalali Private Game Reserve (GMPGR) (Makhutswi pride) and was studied twice, in 2014 and 2015, respectively, because the pride composition changed, and is therefore referred to as the Makhutswi 1 and Makhutswi 2 prides. All prides occurred in fenced reserves within different countries in southern Africa. The pride composition for the five prides is detailed in Table 1.

2.2.2 Statistical Analysis

Statistical analysis of the social interaction data was based on the approach used by Abell et al. (2013a) and Dunston et al. (2017). All of the social interaction data were standardized for each pride on a pairwise and hourly basis. The prides were observed on 66, 46, 20, 26 and 30 separate occasions for the Tsau, Ngamo, Dambwa, and Makhutswi 1 and 2 prides, respectively. The total observation time (hours) and number of social interactions recorded for each pride was as follows: the Tsau pride (93 h; 622 interactions), the Ngamo pride (98 h; 667 interactions), the Dambwa pride (67 h; 841 interactions), the Makhutswi 1 pride (62 h; 162 interactions), and the Makhutswi 2 pride (30 h; 43 interactions). Asymmetrical (directional), weighted matrices were calculated for greeting, social grooming, play, aggression, and all social interaction types, and standardized by dividing the number of interactions collected per pair of lions by the total number of hours each pair was observed together per pride. A symmetrical matrix was compiled from pride composition data, and a modified ratio index (Abell et al. 2013a) was used to show individual association value within the pride.

Social interactions and pride compositions were analysed at an individual (degree and betweenness centrality) and pride level (density and clique) for each of the five prides. The density, degree (indegree and outdegree), betweenness centrality, and clique groups for each network per pride were calculated using the SNA statistical programme UCINET, version 6.543 (Borgatti et al. 2002). Symmetrical matrices were generated prior to calculating betweenness centrality and cliques for each network per pride. Normalized indegree and outdegree values were generated using UCINET, and a Spearman's correlation was conducted to test for dependence within and between networks for each pride. Kendall's tau correlation was used to examine any relationships for betweenness (centrality) and degree (indegree and outdegree). For a detailed explanation of density, degree, betweenness centrality and cliques, please refer to Abell et al. (2013a), Sih et al. (2009), Dunston et al. (2017), and Wey et al. (2008). The sociograms and clique figures for each network were generated using NETDRAW, version 2.1476 (Borgatti et al. 2002; Dunston et al. 2017). The association between social interaction matrices and age, gender, kinship, pride composition, and a random network was assessed by means of a Mantel test using SOCPROG version 2.4 (Whitehead 2009). The random network was generated in UCINET for each pride.

Photo 2.2 **Social behaviour of subadult white lioness and white lion males at play.** © *Global White Lion Protection Trust*

Table 2. Pride composition, GPS coordinates, reserve size and observational period of each pride

	Adult (> 4 years)		Sub Adult (2 - 4 years)		Cub (< 2 years)		Total	GPS Coordinates	Reserve Size	Observation Period
	Male	Female	Male	Female	Male	Female				
Tsau	2*	2	0	0	2	1	7	24°23'S 31°08'E	700 ha	7th April - 10 May 2019
Dambwa	1*	6*	0	0	3	3	13	17°50'S 25°45''E	286 ha	21st Sept - 6th Dec 2014
Ngamo	1*	5*	1	4	0	0	11	19°30'S 29°44'E	163 ha	14th May - 21st June 2014
Makhutswi 1	2	3	4	1	1	1	12	29°09'S 30°32'E	25 000 ha	1st July - 12th Sept 2014
Makhutswi 2	2	2	0	1	2	3	10	29°09'S 30°32'E	25 000 ha	17th Aug. - 20th Oct 2015

** Indicates an individual who is of captive-bred origin.*

2.3 Results

Analyses showed that social interactions at the group and individual level within each pride differed between networks, indicated by density, degree, and betweenness centrality. There was no significant association between any of the interaction networks with a random network, indicating that interactions were non-randomly distributed within each pride. Tsau pride density values for all social and greet matrices were similar to both captive-origin prides (Ngamo and Dambwa), which were all higher than the wild Makhutswi prides, indicating that these prides were highly connected (Table 2).

A correlation was found between all social and greeting matrices for all prides, with the majority of pride members being connected for each of these networks (Figure 2 and 3). For the Tsau pride, all social and greeting interactions between some individuals were lower. This is reflected in the clique matrices for both networks, where adult female C is associated with one clique and adult male M with the second clique (Figures 2 and 3). Interactions between individual lions were also absent within the Ngamo and both Makhutswi prides, resulting in 2 and 4, 5 and 5, and 8 and 1 cliques found for all social and greeting matrices for these prides, respectively. The Dambwa pride had only one clique for these matrices and had all lions involved in the clique. For four prides, a cub (Tsau = Cu1, Dambwa = LE1) or subadult (Ngamo = AS5, Makhutswi 1 = SA) was most likely to initiate social interactions (Figure 4), while an adult lion was observed to be the recipient of interactions (Tsau = T, Ngamo = AS, Dambwa = ZU, and Makhutswi = LB), and least likely to initiate interactions (Ngamo = MI, Dambwa = ZU,

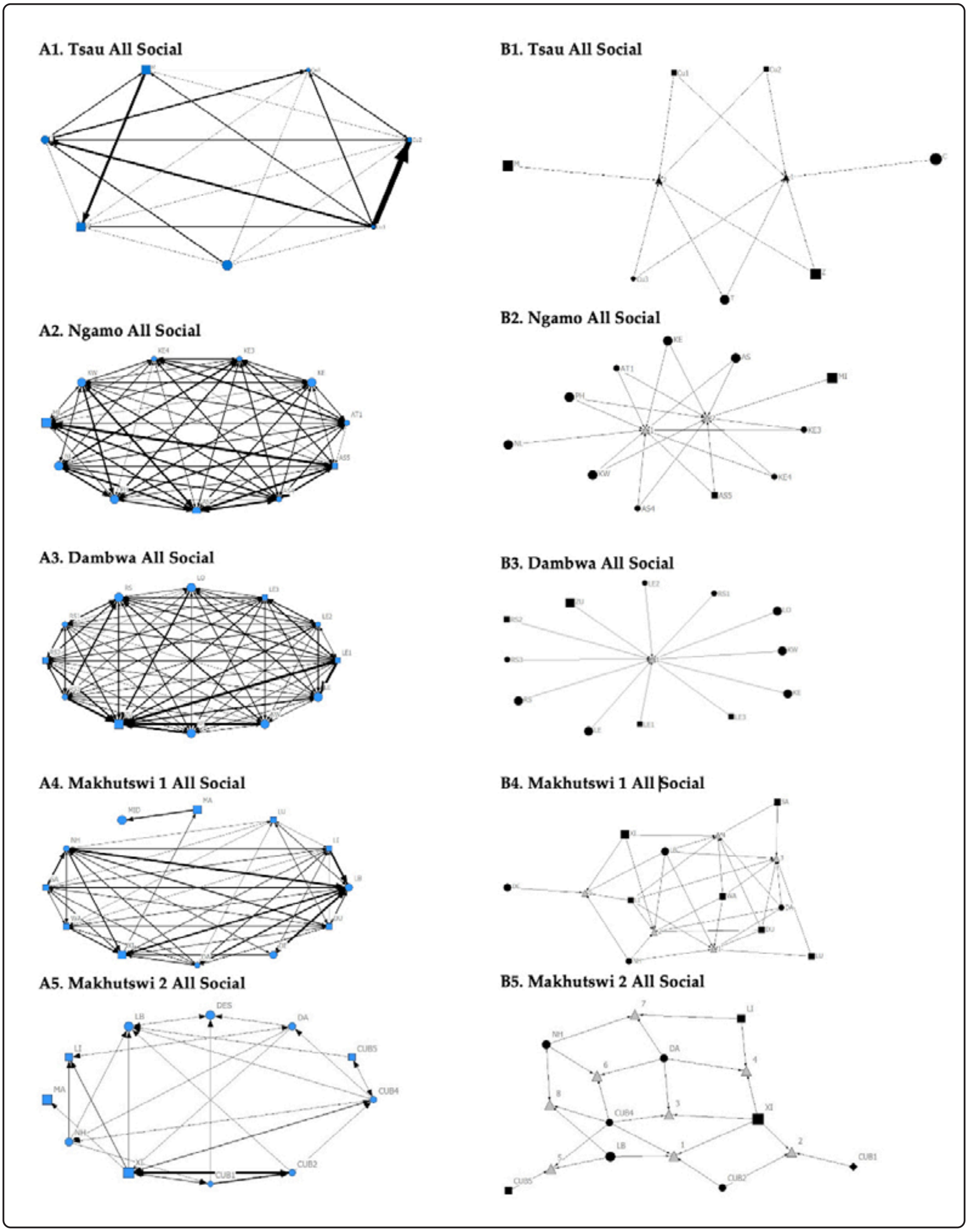

Figure 2 Sociogram (A1 - A5) and clique (B1 - B5) matrices of all social interactions, per pride. For both matrix types, squares (male), circles (female) and diamond (unknown sex) are nodes, representing individual lions, with node size indicating lion age (the larger the symbol, the older the lion). For the sociograms, line thickness between dyads represents the strength of the association between lions. For the cliques, triangles signify a clique.

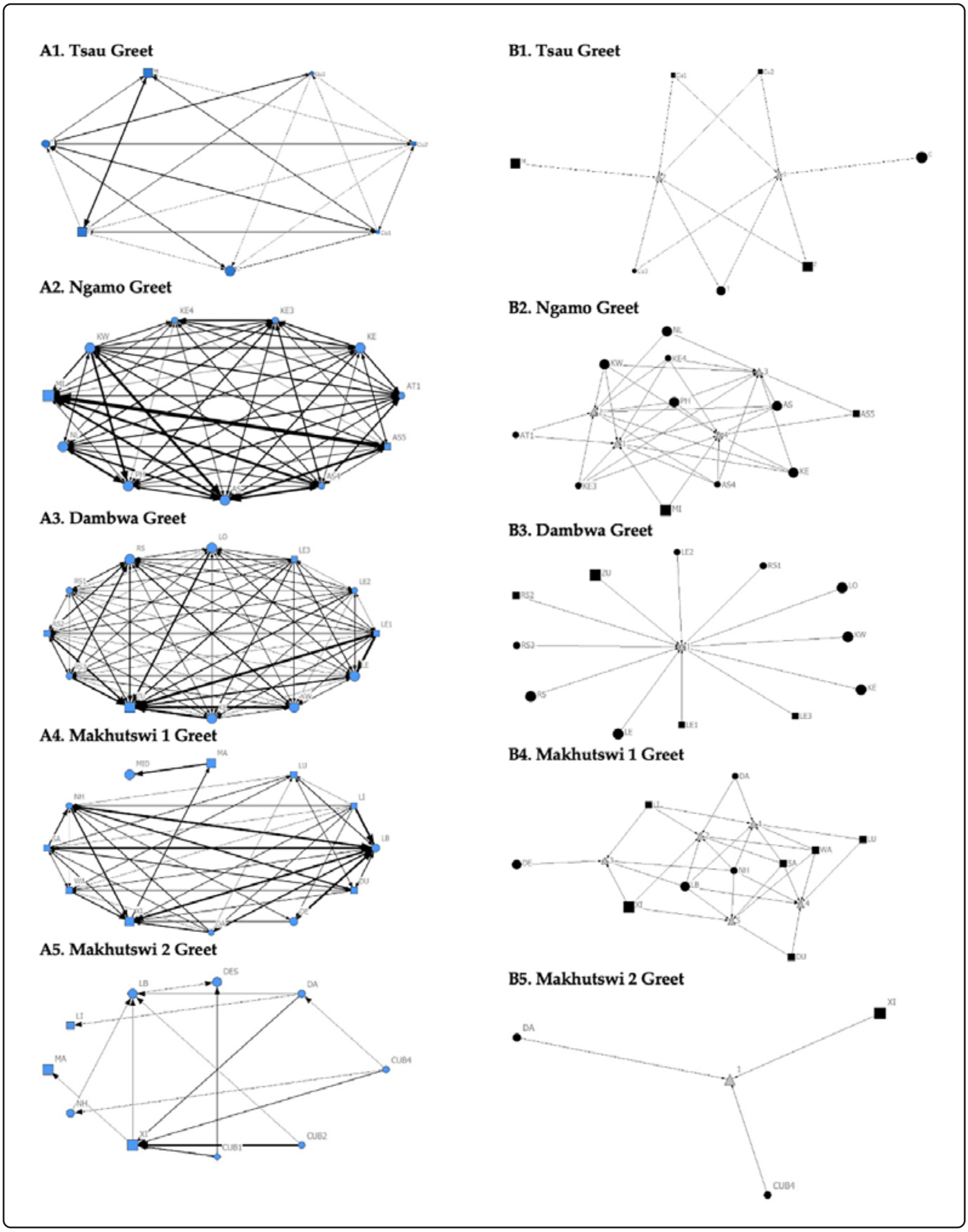

Figure 3 Sociogram (A1 - A5) and clique (B1 - B5) matrices of greet interactions, per pride. For both matrix types, squares (male), circles (female) and diamond (unknown sex) are nodes, representing individual lions, with node size indicating lion age (the larger the symbol, the older the lion). For the sociograms, line thickness between dyads represents the strength of the association between lions. For the cliques, triangles signify a clique.

and Makhutswi 1 = MID). In contrast, for the Tsau pride, a male cub (Cu1) was observed to receive a low number of interactions, whilst another male cub (Cu2) received the most social interactions and initiated a low number of interactions (Figure 4 and 5). Similarly, the Makhutswi 2 pride had a cub (Cub2) that initiated and received the second highest number of social interactions, but the highest number of social interactions was initiated and received by an adult male (XI) (Figure 4 and 5).

The Tsau pride greet matrix showed that interactions between adult males M and Z, between male Cub1 and Z, and between the three cubs and adult female T were strongest. Strong connections between adult and subadult pride males were also observed for the Ngamo, Dambwa and Makhutswi 2 prides, while connections between pride females and their cubs were found for all prides (Figure 3). A positive association between the greeting and all social interactions for all five prides was found: Tsau ($_{r}M = 0.5949$, $p = 0.0003$), Ngamo ($_{r}M = 0.8828$, $p = 1.000e^{-13}$), Dambwa ($_{r}M = 0.9276$, $p = 1.000e^{-13}$), Makhutswi 1 ($_{r}M = 0.9201$, $p = 1.000e^{-13}$), and Makhutswi 2 prides ($_{r}M = 0.7077$, $p = 2.0006e^{-13}$). Spearman's correlation found no association between greet indegree and greet outdegree for the Tsau (п = -0.018, $p = 0.869$), Makhutswi 1 (п = 0.536, $p =$

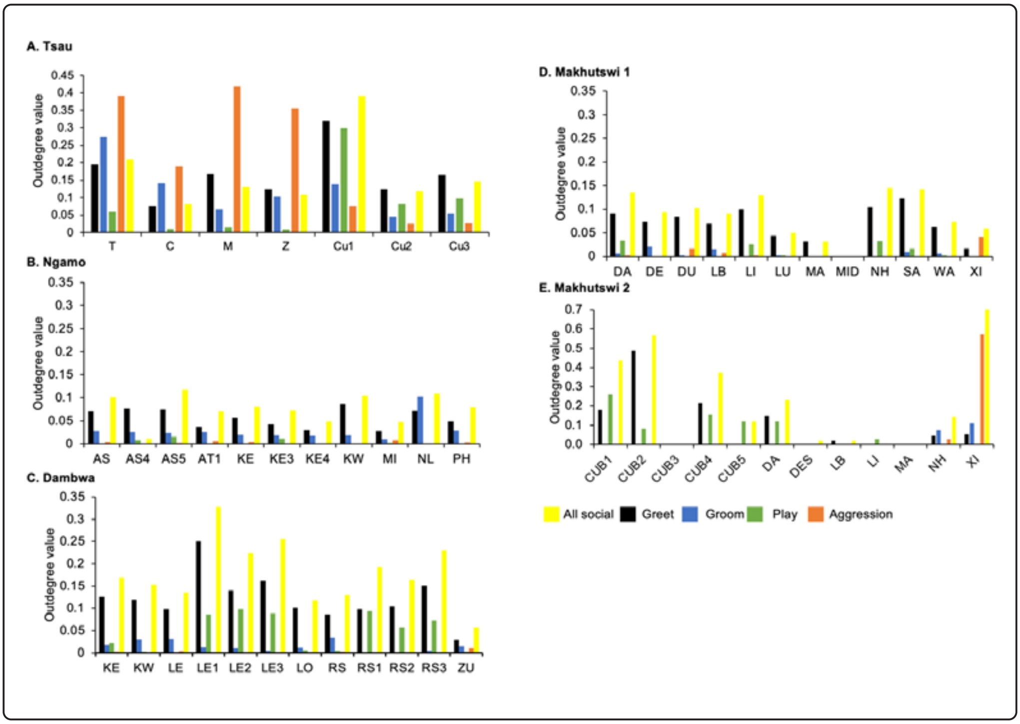

Figure 4 Normalised outdegree per social network (all social, greet, groom, play and aggression), per lion, per pride.

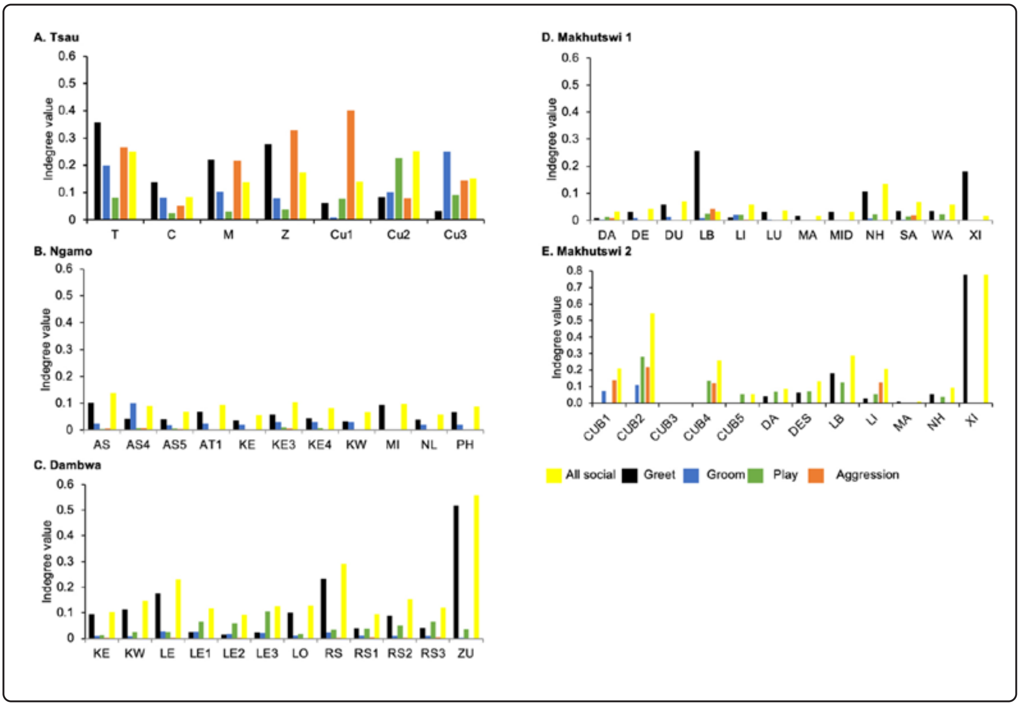

Figure 5 **Normalised indegree per social network (all social, greet, groom, play and aggression), per lion, per pride.**

0.329) and Makhutswi 2 prides (п = 0.719, p = 0.432), but was negatively associated for the Ngamo (п = 0.627, p = 0.039) and Dambwa (п = 0.785, p = 0.003) prides. Kendall's Tau analysis found no association between greet centrality and any of the other indegree or outdegree social interactions for the Tsau pride (p > 0.05) (Appendix A: Table A2).

Across all prides, subadults were most likely to receive grooming interactions (Tsau = Cu3, Ngamo = AS4, Dambwa = LE1, Makhutswi 1 = DA, Makhutswi 2 = Cub2) (Figure 5 and 6). For each pride, an adult female and pride subadults had the highest betweenness centrality for the grooming network (Figure 7), with cubs/sub-adults most likely to receive and adult females or adult males (when involved) to initiate interactions (Figure 4 and 5). Pride males, in all prides except the Tsau pride, were the least likely to receive grooming interactions, and for the Ngamo and Makhutswi 1 prides, initiated the least number of this interaction type. In contrast, for the Makhutswi 2 pride, the pride male (XI) initiated the most grooming interactions. For the Tsau pride, adult female C and cubs Cu1 and Cu2 received a lower number of grooming interactions compared to the pride males. A positive association between grooming and all social interactions for four of the prides was found: Tsau ($_{r}M$ = 0.4672, p = 0.0393), Ngamo ($_{r}M$ = 0.2896, p = 0.0114), Makhutswi 1 ($_{r}M$ = 0.1944, p = 0.0372), and Makhutswi 2 ($_{r}M$ = 0.6750, p

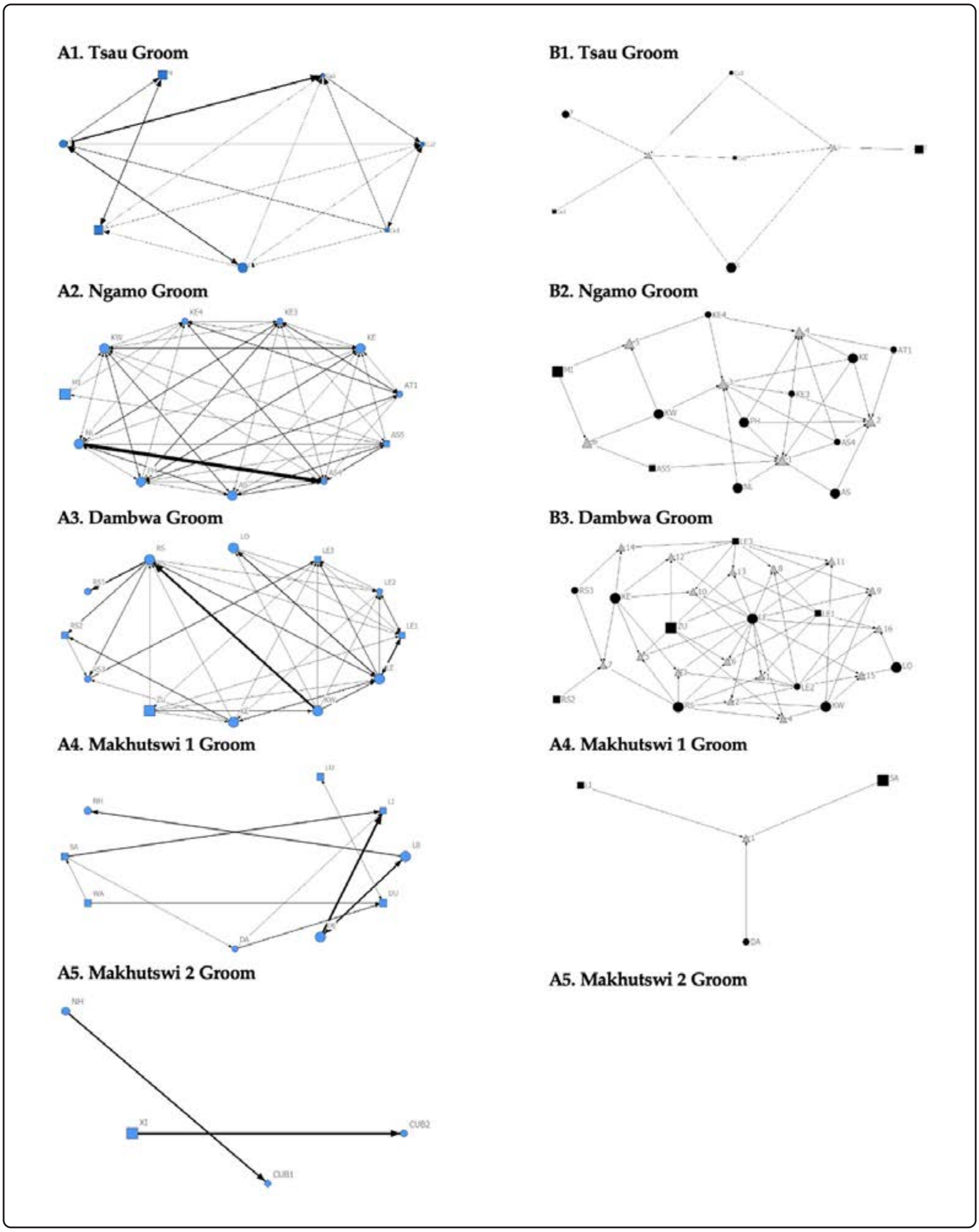

Figure 6 Sociogram (A1 - A5) and clique (B1 - B5) matrices of groom interactions, per pride. For both matrix types, squares (male), circles (female) and diamond (unknown sex) are nodes, representing individual lions, with node size indicating lion age (the larger the symbol, the older the lion). For the sociograms, the line thickness between dyads represents the strength of the association between lions. For the cliques, triangles signify a clique.

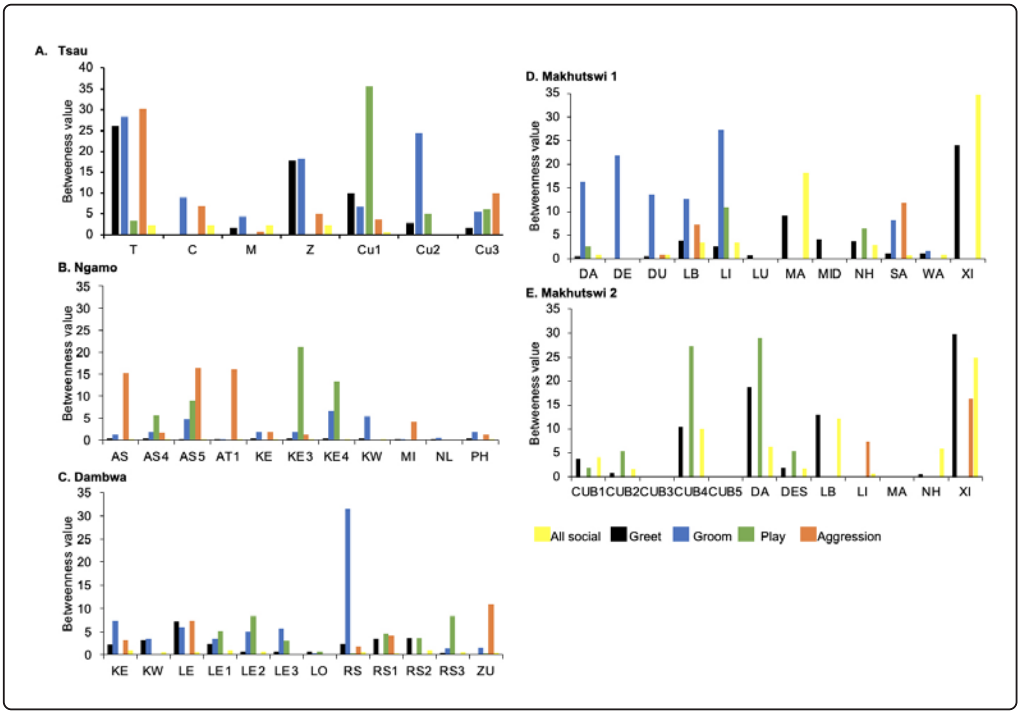

Figure 7 **Normalised betweenness centrality per social network (all social, greet, groom, play and aggression), per lion, per pride.**

= 0.0030). No association between grooming indegree and grooming outdegree, nor between grooming centrality and any of the other indegree or outdegree social interactions, was observed (*p* > 005) (Appendix A: Tables A1 and A2).

Across all play matrices, cubs/sub-adults were both central to and most likely to initiate and receive play interactions (Figure 6), with some to most adults of the pride involved to a lesser extent (Figure 4 and 5). Prides that consisted of cubs (Tsau, Dambwa and Makhutswi 2 pride in particular) had more pride members involved in this network (Figure 5). For all prides, cubs and subadults initiated and received the greatest number of play interactions (Figures 8 and 9), which was reflected in these lions having high betweenness centrality values for this network. For the Tsau pride, the cubs who initiated and received the most play interactions also initiated and received the most cumulative social interactions, respectively ($_r$M = 0.821, p = 0.034, $_r$M = 0.786, p = 0.048). For the Dambwa pride, individuals who received the most play interactions also initiated the most social ($_r$M = 0.741, p = 0.006), greeting (п = 0.581, p = 0.047), and grooming interactions (п = 0.680, p = 0.038). The Tsau pride cubs that received the most play interactions also received the greatest number of all social interactions (п = 0.821, p = 0.034). Positive correlations between play indegree and

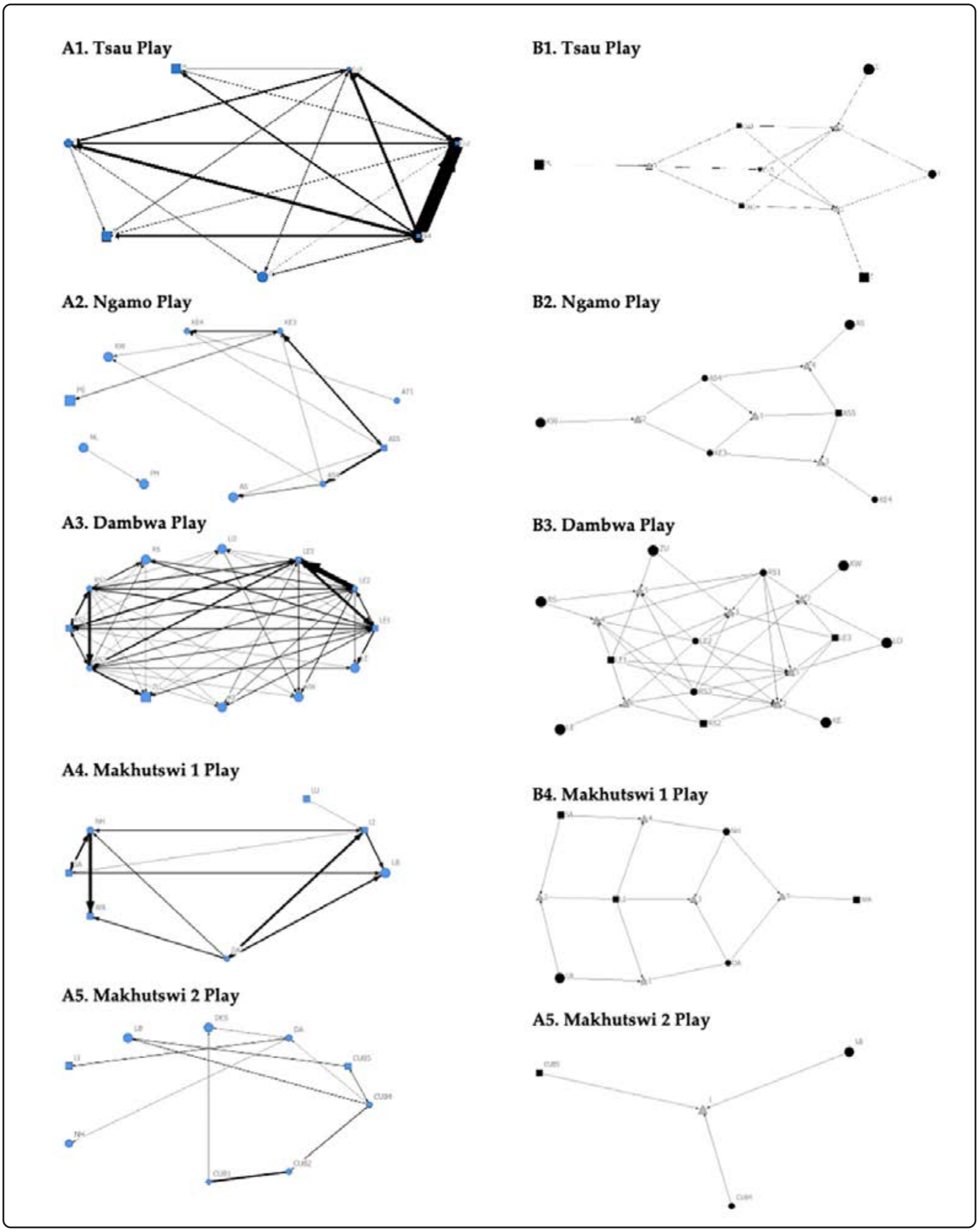

Figure 8 Sociogram (A1 - A5) and clique (B1 - B5) matrices of play interactions, per pride. For both matrix types, square (male), circles (female) and diamond (unknown sex) are nodes, representing individual lions, with node size indicating lion age (the larger the symbol, the older the lion). For the sociograms, line thickness between dyads represents the strength of the association between lions. For the cliques, triangles signify a clique.

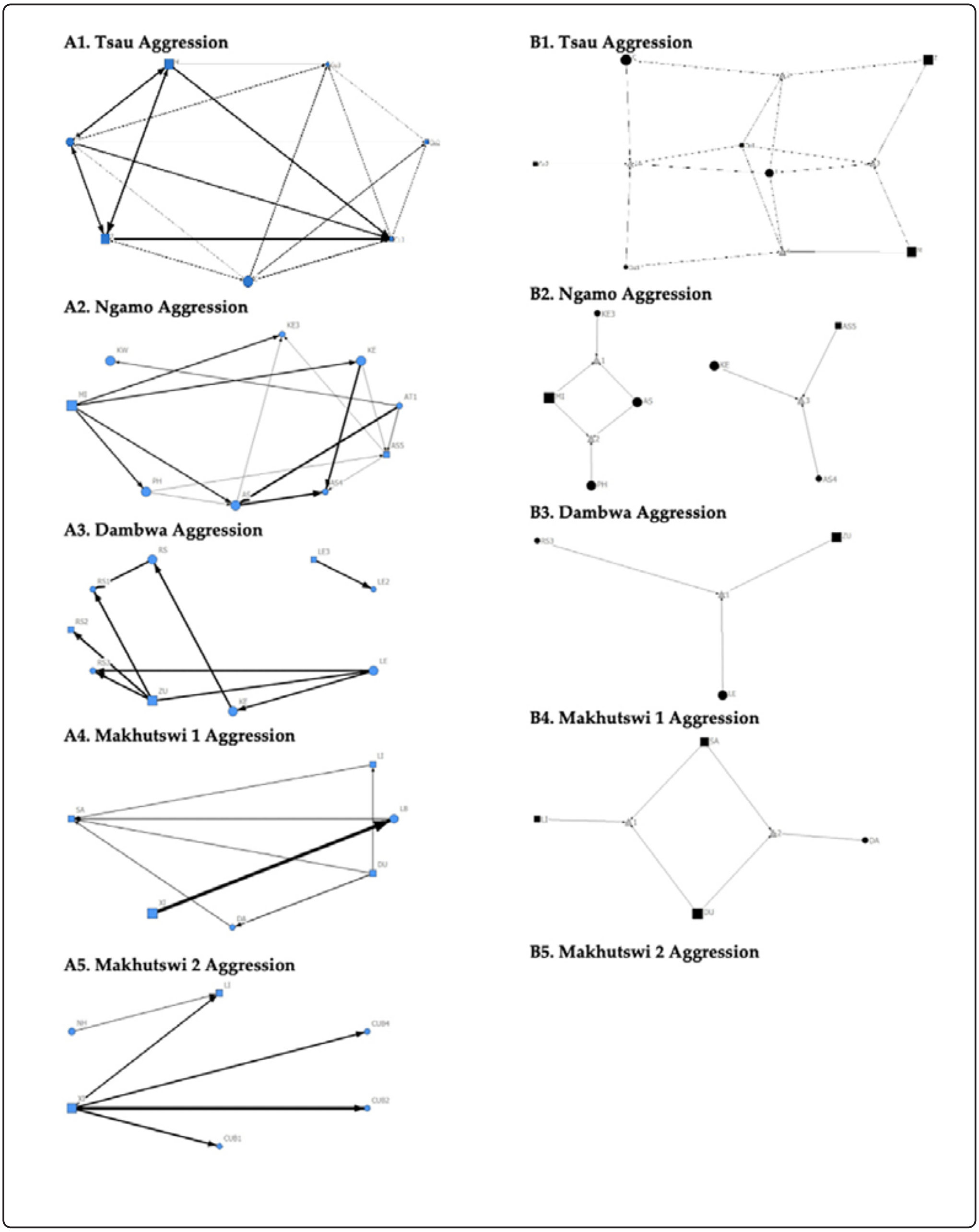

Figure 9 Sociogram (A1 - A5) and clique (B1 - B5) matrices of aggression interactions, per pride. For both matrix types, square (male), circles (female) and diamond (unknown sex) are nodes, representing individual lions, with node size indicating lion age (the larger the symbol, the older the lion). For the sociograms, line thickness between dyads represents the strength of the association between lions. For the cliques, triangles signify a clique.

outdegree were found for the Dambwa (п = 0.680, p = 0.015) and Makhutswi 1 pride (п = 0.764, p = 0.004), while four of the five prides had a positive association between play centrality and play outdegree (Tsau: п = 0.926, p = 0.005; Ngamo: п = 0.607, p = 0.024; Dambwa: п = 0.667, p = 0.003; Makhutswi 1: п = 0.620, p = 0.019). The Tsau pride also had a positive association between play indegree and all social centrality (п = 0.700, p = 0.042) and a positive association between play and all social interactions ($_{r}M$ = 0.8255, p = 0.001).

For the aggression matrix, the Tsau pride was the only pride to have all pride members involved and mostly connected in this social network, but still had four cliques, indicating that interactions were not distributed evenly (Figure 6). Most aggression interactions were acts of discipline directed towards the male Cub1 from both adult males and adult female T, with aggression also observed as a territorial or defensive display between the adult males and between the adult males and adult female T. Aggression interactions from adults, particularly parents, towards pride cubs/sub-adults were observed for all prides, while some interactions between adult pride members were also observed. A positive association was found between aggression and the cumulative social interactions for the Makhutswi 1 (rM = 0.2353, p = 0.0341) and Makhutswi 2 prides (rM = 0.8035, p = 2.0006e–13). No association between aggression indegree and aggression outdegree was found for the Tsau pride (п = 0.536, p = 0.498), nor any association between aggression centrality and any indegree or outdegree networks (p > 0.05) (Appendix A: Table A2), indicating that the lion that was central to this network (adult lioness T) did not receive or initiate the most social interactions for those networks.

Social interaction networks for all prides were not significantly associated with the random network, indicating that the interactions were non-randomly distributed within each of the prides (Appendix A: Tables A3-A7). The degree to which individuals initiated and received interactions within each pride indicated their role within an interaction (Figures 8 and 9). There was no significant correlation between initiated and received social interactions for the Tsau pride for any network (p > 0.05) (Appendix A: Table A1), indicating that social interactions were more evenly split between pride members and suggesting a high level of connectedness. In contrast, for the Dambwa and Makhutswi prides, all social indegrees and outdegrees were negatively correlated (п = -0.727, p = 0.007; п = 0.729, p = 0.002), and for the Makhutswi 2 pride, all social indegrees and outdegrees were positively correlated (п = 0.712, p = 0.009), indicating that social interactions for these networks were less evenly split between pride members. For the Tsau, Dambwa and Makhutswi 2 prides, pride members who initiated the most cumulative social interactions were also found to initiate the most greetings (п = 0.955, p < 0.001, п = 0.767, p = 0.000, and п = 0.855, p < 0.001). The test of association for the Tsau pride found no correlation between the centrality for greeting, grooming or aggression and any outdegree or indegree social interactions (p > 0.05) (Appendix A: Table A2), indicating that the lions who were central to these networks did not receive or initiate the most social interactions for those networks. A positive association was found for the Tsau pride between the grooming and greeting social interactions ($_{r}M = 0.4297$, $p = 0.0384$) and between grooming and all social interactions (п = 0.46715, $p = 0.0393$).

The Mantel test results per pride indicated whether there was an association between the social interaction networks and full siblings, age, sex, and pride composition. Full siblings and age were not associated with cumulative social interactions for the Tsau, Ngamo, or Makhutswi 2 prides (Appendix A: Tables A3-A5). A positive association was found between social interactions and full siblings ($_{r}M = 0.1329$, $p = 0.039$, and $_{r}M = 0.2096$, $p = 0.0189$) and age ($_{r}M = 0.1445$, $p = 0.0218$, and $_{r}M = 0.2096$, $p = 0.0188$) for the Dambwa and the Makhutswi 1 prides. For the Tsau, Dambwa and Makhutswi 2 prides, no significant association was found between any of the social networks with sex (Appendix A: Tables A3-A5) or for age for the Tsau, Ngamo, and Makhutswi 2 prides (Appendix A: Tables A3, A4 and A6).

The Tsau and Makhutswi 1 prides had a positive association between pride composition and grooming ($_{r}M = 0.4658$, $p = 0.0245$, and $_{r}M = 0.2188$, $p = 0.0230$), play ($_{r}M = 0.3721$, $p = 0.0191$, and $_{r}M = 0.2817$, $p = 0.0338$), and all social ($_{r}M = 0.4965$, $p = 0.0027$, and $_{r}M = 0.2797$, $p = 0.0385$) interactions. For the Ngamo pride, no significant association was found between pride composition and any social networks, full siblings, sex, or age (Appendix A: Table A4). For the Dambwa and Makhutswi 1 prides, a positive association was found for pride composition and full siblings ($_{r}M = 0.7031$, $p = 1.0003e^{-13}$, and $_{r}M = 0.4468$, $p = 1.000e^{-13}$) and for pride composition and age ($_{r}M = 0.5571$, $p = 0.0021$, and $_{r}M = 0.4468$, $p = 1.000e^{-13}$). A positive association was found between pride composition and full siblings for the Makhutswi 2 pride ($_{r}M = 0.5369$, $p = 0.0008$).

2.4 Discussion

Critical to determining short-term successful reintroduction of a gregarious species is group cohesion. This study provided the first assessment of sociality of a constructed pride of African lions consisting of captive-origin white lions and wild tawny lionesses. By comparing the sociality of this pride (Tsau pride) to two previously studied captive-origin and two wild prides, we identified similarities and differences in social behaviour at an individual and pride level. Networks across all prides were found to be non-random, indicating that individuals chose to interact socially with other pride members. Social interactions were more evenly split between pride members in the Tsau pride compared to both the captive-origin and wild prides, suggesting a high level of connectedness and pride cohesion. The Tsau pride was identified to exhibit natural and expected social behaviours, leading to the identification of a keystone lioness and subadults/cubs to be central to the play network. Interestingly, Tsau pride males had a lesser role in the grooming network, while all pride members were involved in the aggression network (as a territorial defensive, or disciplinary display), compared to all other prides.

The Tsau pride was found to display natural social behaviours, with similarities to both the captive-origin and wild prides. All social and greeting interactions for all prides indicated that most of the pride members were connected and showed social cohesion for those networks. The Tsau pride was found to be highly connected due to most pride members being involved in all social networks. This was indicated by the high density values for all social networks for the pride, which were between the values found for the captive-origin prides and the wild prides. For all prides, there was a strong connection between adult and subadult pride males and between pride females and their cubs. This is typical of wild lion prides and is fundamental to the role that males and females play in prides and overall pride cohesion (Schaller 1972). Similar to the captive-origin and wild prides, the cubs and subadults of the Tsau pride were central to, and most likely to initiate and receive, play interactions. Play behaviour is typical of cubs, as they hone the skills necessary to hunt prey successfully and defend themselves from attack by conspecifics or other carnivores (Schaller 1972), indicating that the cubs from the Tsau Pride were behaving naturally as wild cubs do. The social behaviour observed for both captive-origin white males and their offspring show no indications of being impaired by a captive origin or human impact. For each pride, an adult female and pride subadults had the highest betweenness centrality for the groom network. This was not unexpected given that it is regarded as a behaviour that strengthens bonds between mothers and their offspring and between adult females, with pride males largely absent from allogrooming (Schaller 1972; Dunston et al. 2017). Each of the five prides had a keystone adult female, with three of the four females having offspring within their prides and all being of a similar age (six to nine years old). Keystone females were involved in the majority of the social networks and played a critical role in connecting peripheral members to the rest of the pride. The role of a keystone female is critical to pride structure and stability within wild prides, but in their study, Dunston et al. (2017) concluded that a captive history does not prevent this role from being fulfilled. Our study on the Tsau pride has shown that the integration of captive-origin white lion males with wild translocated tawny females did not inhibit the ability of one of the lionesses to establish themself as a keystone female. Importantly, the fact that the two adult lionesses in the Tsau pride were unrelated and translocated from different reserves, yet were highly connected to each other and formed a socially cohesive pride, indicates that such human management and intervention can be successful.

The Tsau pride expressed some social behaviours that differed from those previously observed for the captive-origin and wild prides. Tsau pride males received more grooming interactions than all other pride males. The most probable reason is that the Tsau pride males were brothers and therefore very closely bonded, whereas the captive-origin prides only had one pride male and the wild pride males were related (uncle/nephew) but were not siblings. For the Tsau and Makhutswi 2 prides, a pride male initiated a high number of the grooming interactions, which is probably due to the presence of cubs in both these prides, which often results in more frequent social interaction. Interestingly, despite the social cohesion of the Tsau pride, a greater number of aggressive interactions were observed compared to the other four prides. This mostly involved defensive or territorial behaviour rather than damage-causing behaviour between the four adult members of the Tsau pride and took place either when the adult lionesses were in oestrus, leading to more male to male and female to male aggression, or when the pride were feeding on a kill. These incidences of aggression are consistent with natural pride dynamics, especially during feeding and where a male coalition is present (Schaller 1972), indicating that the social behaviour of the Tsau pride was not negatively influenced by a captive origin or human impact.

The roles that individuals, sexes and age groups have on social interactions and pride social cohesion varied between prides. The Tsau pride was the only pride that had no correlation between full siblings for any of the social networks. However, this was unsurprising considering that the only full siblings in this pride were the adult males, and other than the groom network, the number of interactions between them was not sufficient to show a significant correlation. Adult males in wild prides are known to have a low level of overall social interaction (Schaller 1972; Funston et al. 1998). The Tsau pride lionesses were unrelated and therefore not full siblings. Social interactions within the Tsau pride were also not significantly associated with the sex of the lions; however, a sex bias was observed, with lionesses directing these interactions to other lionesses, and a high number of greeting interactions taking place between the adult males. The adult males being siblings with a long period of association (eight years), and the natural tendency of lionesses to interact socially with each other (Schaller 1972), is the likely explanation for this sex bias for the Tsau pride. The captive origin of the Tsau males is probably another reason. A similar sex preference is common in captive lions that are kept in zoos (Matoba et al. 2013). Although a sex bias was also observed for the Ngamo pride, it was only for the lionesses. These findings support our other observations that there is a high level of connectedness and pride cohesion within the Tsau pride, despite a captive origin and a history of human impact through translocation.

Pride composition was influenced by various factors (social interactions, full siblings, sex and age) that differed between prides, suggesting that the origin of the pride (wild or captive origin) is an unlikely influence. The pride composition for the Tsau pride was, however, more similar to that of the wild Makhutswi 1 pride, being positively associated with groom, play, and all social interactions, suggesting that the social interactions and bonds between the white lion males and the rest of the pride was similar to that of a wild pride. This also implies that the integration of white lion males with tawny lionesses has been successful in forming a socially cohesive pride that behaves as a wild pride.

Overall, the Tsau pride was more highly connected socially than either the captive-origin or wild prides. The captive-origin Ngamo and Dambwa prides were in small reserves that had no other lions in the area and they did not have to spend time being separated for hunting and territory maintenance behaviours, allowing more time to conduct social behaviour. In contrast, the Tsau pride did have to hunt for themselves and respond to territorial threats on the reserve boundaries, a natural behaviour for wild prides, and was therefore more similar to the Makhutswi prides. The wild prides had fewer social interactions compared to the Tsau pride due to a greater level of pride dispersal and a larger territory size. Adult pride members were often absent from the wild Makhutswi prides, compared to the integrated Tsau pride and the captive-origin Ngamo and Dambwa prides. Dispersal of pride members is not uncommon, with lion prides living in a fission-fusion society (Schaller 1972; Packer et al. 2001; Mosser & Packer 2009), and adult males regularly being away from their prides is a natural occurrence (Schaller 1972; Krause et al. 2007; Turner et al. 2022). The wild male lions were often absent when spending time with another pride within their territory and when away patrolling the territory. The higher level of social interaction and presence of male lions observed within the Tsau, Dambwa and Ngamo prides could be accounted for by the difference in vegetation type and smaller reserve size. In dense vegetation, visibility is inhibited, requiring the pride, and particularly males, to be more mobile and active. In Kruger Park, pride males occur more regularly with their pride in open habitat compared to woodland habitat (Loveridge et al. 2009). The territory of the Makhutswi prides was covered with both open and closed woodland, and vegetation is therefore a possible factor affecting the presence and absence of the Makhutswi males with the two prides. By the same token, the territory of the Tsau pride included many open plain and open woodland areas, a likely factor leading to the males spending more time with the pride. Additionally, the smaller territory size of the Tsau, Ngamo and Dambwa prides led to less fission-fusion changes within these prides, resulting in a greater number of pride members being present more frequently. The Tsau pride was located in a reserve four times the size of that of the Ngamo pride, and double the size of that of the Dambwa pride, but a fraction of the size of the reserves of the Makhutswi prides (Table 1). Lion territory sizes vary significantly depending on prey availability and pride size, and the fenced reserves of the Tsau, Ngamo and Dambwa prides are significantly smaller than the average territory sizes of wild prides; with a range of 50 to 7400 km^2 (Funston 2008; Slotow & Hunter 2009; Tumenta et al. 2010; Tuqa et al. 2014), and a mean of 56 km^2 (range of 15 to 219 km^2) (Mosser & Packer 2009), nearly 20% of the wild lion population in South Africa is protected within 49 smaller fenced reserves, with several of them being significantly smaller than the reserve of the Makhutswi pride: Mabula Game Reserve (16.5 km^2), Thanda Private Game Reserve (70 km^2), Karongwe

Game Reserve (79 km^2), Thornybush Nature Reserve (116 km^2), and Shamwari Game Reserve (139 km^2) (Miller et al. 2015). Lion prides within these smaller fenced reserves are now being managed as a metapopulation (Slotow & Hunter 2009; Hayward & Kerley 2009; Trinkel et al. 2010), based on natural metapopulation structures (Miller et al. 2014), which require lion translocation to maintain genetic diversity and to prevent overpopulation (Miller et al. 2015). The success of lion reintroduction and translocation has been linked to group cohesion, with post-release failure often being due to lower fecundity and a greater incidence of dispersal from the release site (Somers & Gusset 2009). Lion prides located in smaller reserves with more open habitats therefore seem to have a higher level of social interaction and cohesion and may account for translocation success in South Africa. The Tsau pride showed social cohesion and pride stability, despite the varying origins of its members. This cautiously suggests that captive-origin and wild lions can be successfully integrated and reintroduced to smaller reserves, if such management is required under metapopulation management.

The present study had several important findings, but also limitations and factors that need to be considered. As stated by Dunston et al. (2017), the captive origin of pride members needs to be considered as having a possible impact on the social interactions of these prides. For the Tsau pride the captive origin of the white lion males may have led them to be more strongly bonded than wild males, increasing the level of interaction between them and with other pride members. The small territory size may also have caused the white lion males to spend more time with the pride, leading to more social interaction and cohesion than in the case of the wild males. The fact that one of the two adult lionesses was not genetically related to the other adult lioness, as would be typical within a wild pride, must also be considered. Further study is required to determine whether a white lioness would be established as a keystone female if integrated with wild tawny lionesses, and ultimately form a socially cohesive unit. Turner et al. (2015) studied a pride of all white lions and observed that the pride formed a cohesive unit, hunting self-sufficiently and displaying similar behavioural interactions to wild lion prides, but unfortunately SNA was not used in that study. Historically, white lions have been observed as fully functional, socially connected members of wild tawny prides in the Timbavati Private Nature Reserve (McBride 1977; Tucker 2003; Cesare 2011), and Kruger National Park (Robinson & De Vos 1982; Smuts 1982; Cruckshank & Robinson 1997), but this is the first time that SNA has been applied to better understand the social dynamics of white lions and to assess whether their social interactions are any different to those of wild tawny lions. Future studies should consider the limitations of this study by increasing the sample size, the territory size, and the number of male and female white lions in the pride to approximate that of wild lion prides. An increased sample size and territory size would mean a more natural ecosystem with more than one pride, so that the effects of territoriality and intraspectific competition on social behaviour can be more fully studied.

2.5 Conclusions

Social network analysis (SNA) showed that integrating white lion males of captive-origin with wild translocated tawny lionesses can lead to the formation of a socially cohesive and highly connected pride. Importantly, the white lion males displayed many of the expected social behaviours that have been observed in wild tawny lions. That a socially cohesive pride was observed is important, as this pride included individuals of differing backgrounds and was constructed by human intervention. This provides valuable knowledge on the social interactions of translocated lions, which may be relevant to the metapopulation management approach occurring in South Africa. Such information will become more pertinent if wild populations continue to decline and become more fragmented due to increasing anthropic pressure, resulting in the species being conserved within smaller fenced reserves.

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Institutional Review Board Statement: Ethical approval was not required since the study was conducted non-invasively on free-roaming lions from a vehicle.

Informed Consent Statement: This was not required, since J.A.T. was an authorized agent for the Global White Lion Protection Trust.

Data Availability Statement: This research and its data forms part of a PhD thesis registered with Leiden University, Leiden, The Netherlands.

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Conflicts of Interest: The authors declare no conflicts of interest.

Appendix A

Table A1. Spearman's correlation for dependence within and between social networks (greet, groom, play, aggression and all social) using degree (In = Indegree; Out = outdegree), and centrality (Cntrl = betweenness centrality) for Tsau pride, Tula Tsau Conservation Area, South Africa.

		GREET_Out	GROOM_Out	PLAY_Out	AGGRESSION_Out	ALL SOCIAL_Out	GREET_In	GROOM_In
GREET_Out	Spearman's rho	—						
	p-value	—						
GROOM_Out	Spearman's rho	0.234	—					
	p-value	0.613	—					
PLAY_Out	Spearman's rho	0.613	–0.25	—				
	p-value	0.144	0.595	—				
AGGRESSION_Out	Spearman's rho	0.252	0.536	–0.571	—			
	p-value	0.585	0.236	0.200	—			
ALL SOCIAL_Out	Spearman's rho	0.955	0.143	0.786	0.000	—		
	p-value	< .001***	0.783	0.048*	1.000	—		
GREET_In	Spearman's rho	–0.018	0.536	–0.714	0.786	–0.214	—	
	p-value	0.969	0.236	0.088	0.048*	0.662	—	
GROOM_In	Spearman's rho	0.072	–0.214	0.143	0.071	0.179	0.000	—
	p-value	0.878	0.662	0.783	0.906	0.713	1.000	—
PLAY_In	Spearman's rho	0.216	-0.500	0.643	-0.643	0.429	–0.357	0.393
	p-value	0.641	0.267	0.139	0.139	0.354	0.444	0.396
AGGRESSION_In	Spearman's rho	0.721	0.286	0.179	0.321	0.607	0.214	–0.393
	p-value	0.068	0.556	0.713	0.498	0.167	0.662	0.396
ALL SOCIAL_In	Spearman's rho	0.072	–0.286	0.179	–0.321	0.179	0.179	0.214
	p-value	0.878	0.556	0.713	0.498	0.713	0.713	0.662
AGGRESSION_Cntrl	Spearman's rho	0.090	0.607	-0.071	0.214	0.179	0.214	0.429
	p-value	0.848	0.167	0.906	0.662	0.713	0.662	0.354
ALL SOCIAL_Cntrl	Spearman's rho	–0.060	0.697	–0.777	0.896	–0.299	0.837	–0.179
	p-value	0.898	0.082	0.04*	0.006**	0.515	0.019*	0.701
GREET_Cntrl	Spearman's rho	0.491	0.306	0.054	0.198	0.450	0.505	–0.144
	p-value	0.263	0.504	0.908	0.670	0.310	0.248	0.758
GROOM_Cntrl	Spearman's rho	–0.162	0.321	-0.179	–0.107	–0.107	0.500	–0.071
	p-value	0.728	0.498	0.713	0.840	0.840	0.267	0.906
PLAY_Cntrl	Spearman's rho	0.542	–0.222	0.964	–0.667	0.741	–0.704	0.037
	p-value	0.209	0.632	< .001***	0.102	0.057	0.077	0.937

* p < .05, ** p < .01, *** p < .001

PLAY_In	AGGRESSION_In	ALL SOCIAL_In	AGGRESSION_Cntrl	ALL SOCIAL_Cntrl	GREET_Cntrl	GROOM_Cntrl	PLAY_Cntrl
— —							
0.000 1.000	— —						
0.821 0.034*	0.143 0.783	— —					
−0.036 0.963	0.036 0.963	−0.036 0.963	— —				
−0.797 0.032*	0.179 0.701	−0.378 0.402	0.259 0.575	— —			
0.360 0.427	0.739 0.058	0.685 0.090	0.180 0.699	0.141 0.763	— —		
0.357 0.444	0.000 1.000	0.714 0.088	0.214 0.662	0.100 0.832	0.631 0.129	— —	
0.704 0.077	0.259 0.574	0.296 0.518	0.000 1.000	-0.806 0.029*	0.187 0.688	−0.037 0.937	— —

Table A2. Kendall's Tau correlation for betweenness (Cntrl = betweenness centrality) and degree (In = Indegree; Out = Outdegree) within and between social networks (greet, groom, play, aggression and all social) for Tsau pride, Tula Tsau Conservation Area, South Africa.

		GREET_Out	GROOM_Out	PLAY_Out	AGGRESSION_Out	ALL SOCIAL_Out	GREET_In	GROOM_In
GREET_Out	Kendall's tau B	—						
	p-value	—						
GROOM_Out	Kendall's tau B	0.195	—					
	p-value	0.543	—					
PLAY_Out	Kendall's tau B	0.488	−0.143	—				
	p-value	0.129	0.773	—				
AGGRESSION_Out	Kendall's tau B	0.195	0.429	−0.333	—			
	p-value	0.543	0.239	0.381	—			
ALL SOCIAL_Out	Kendall's tau B	0.878	0.048	0.619	0.048	—		
	p-value	0.006**	1.000	0.069	1.000	—		
GREET_In	Kendall's tau B	0.000	0.429	−0.524	0.619	0.143	—	
	p-value	1.000	0.239	0.136	0.069	0.773	—	
GROOM_In	Kendall's tau B	0.098	−0.143	0.238	0.048	0.238	0.048	—
	p-value	0.761	0.773	0.562	1.000	0.562	1.000	—
PLAY_In	Kendall's tau B	0.098	−0.333	0.429	−0.524	0.238	-0.143	0.238
	p-value	0.761	0.381	0.239	0.136	0.562	0.773	0.562
AGGRESSION_In	Kendall's tau B	0.683	0.333	0.143	0.143	0.524	0.143	−0.238
	p-value	0.033*	0.381	0.773	0.773	0.136	0.773	0.562
ALL SOCIAL_In	Kendall's tau B	0.000	−0.238	0.143	−0.238	0.143	0.143	0.143
	p-value	1.000	0.562	0.773	0.562	0.773	0.773	0.773
AGGRESSION_Cntrl	Kendall's tau B	0.098	0.524	−0.048	0.143	0.143	0.143	0.333
	p-value	0.761	0.136	1.000	0.773	0.773	0.773	0.381
ALL SOCIAL_Cntrl	Kendall's tau B	−0.060	0.583	−0.583	0.816	0.233	0.700	-0.117
	p-value	0.864	0.089	0.089	0.017*	0.497	0.042*	0.734
GREET_Cntrl	Kendall's tau B	0.350	0.195	0.098	0.195	0.293	0.390	−0.098
	p-value	0.282	0.543	0.761	0.543	0.362	0.224	0.761
GROOM_Cntrl	Kendall's tau B	−0.098	0.238	−0.143	0.048	0.048	0.429	0.048
	p-value	0.761	0.562	0.773	1.000	1.000	0.239	1.000
PLAY_Cntrl	Kendall's tau B	0.474	−0.103	0.926	−0.411	0.617	-0.514	0.103
	p-value	0.154	0.754	0.005	0.210	0.060	0.117	0.754

* p < .05, ** p < .01, *** p < .001

PLAY_In	AGGRESSION_In	ALL SOCIAL_In	AGGRESSION_Cntrl	ALL SOCIAL_Cntrl	GREET_Cntrl	GROOM_Cntrl	PLAY_Cntrl
—							
—							
–							
0.048	—						
1.000	—						
0.714	0.048	—					
0.03*	1.000	—					
–							
0.048	0.048	0.048	—				
1.000	1.000	1.000	—				
—							
0.700	0.117	–0.350	0.233	—			
0.042*	0.734	0.308	0.497	—			
0.293	0.488	0.586	0.195	0.179	—		
0.362	0.129	0.068	0.543	0.607	—		
0.238	–0.048	0.524	0.143	0.117	0.488	—	
0.562	1.000	0.136	0.773	0.734	0.129	—	
0.514	0.206	0.206	0.000	–0.630	0.158	0.000	—
0.117	0.530	0.530	1.000	0.077	0.634	1.000	—

Table A3. Mantel test for association between networks and attributes for the Tsau pride.												
	Greet		Groom		Play		Aggression		All Social		Pride Composition	
	P-value	Matrix coefficient	P-value	Matrix coefficient	P-value	Matrix coefficient	P-value	Matrix coefficient	P-value	Matrix coefficient	P-value	Matrix coefficient
All Social	/	/	/	/	/	/	/	/	/	/	0.0027	0.49652
Greet	/	/	/	/	/	/	/	/	0.0003	0.5949	0.0661	0.3692
Groom	0.0384	0.4297	/	/	/	/	/	/	0.0393	0.46715	0.0245	0.4658
Play	0.4089	0.1239	0.332	0.1164	/	/	/	/	0.001	0.8255	0.0191	0.3721
Aggression	0.1862	0.2159	0.5515	0.0896	0.5334	-0.13567	/	/	0.2789	0.1964	0.7763	-0.1087
Full Brother	0.6270	0.0975	0.5402	0.0937	0.3812	-0.1965	0.7973	0.0970	0.6699	-0.0782	0.9518	0.0483
Sex	0.2805	-0.2872	0.1236	-0.3202	0.3644	-0.1440	0.4732	-0.0206	0.0961	-0.2875	0.6114	-0.0365
Age	0.7255	-0.0300	0.3803	-0.1544	0.4253	-0.1413	0.2472	-0.2303	0.2836	-0.1985	0.3258	-0.1663
Random	0.1434	0.2232	0.0109	0.34615	0.443	0.12646	0.3787	-0.13419	0.1182	0.22378	0.084	0.2980

Table A4. Mantel test for association between networks and attributes for the Ngamo pride.												
	Greet		Groom		Play		Aggression		All Social		Pride Composition	
	P-value	Matrix coefficient	P-value	Matrix coefficient	P-value	Matrix coefficient	P-value	Matrix coefficient	P-value	Matrix coefficient	P-value	Matrix coefficient
All Social	/	/	/	/	/	/	/	/	/	/	0.2844	0.066299
Greet	/	/	/	/	/	/	/	/	1.0003e-13	0.88284	0.7305	-0.046657
Groom	0.127	0.099793	/	/	/	/	/	/	0.0114	0.28955	0.3831	0.043903
Play	0.3253	0.033417	0.266	0.012247	/	/	/	/	0.0151	0.27068	0.0528	0.17593
Aggression	0.9299	-0.14212	0.9069	-0.072184	0.0994	0.13604	/	/	0.6015	-0.028754	0.7493	-0.059935
Full sister	0.5521	-0.029675	0.1879	0.0287	0.0034	0.44491	0.6335	-0.014731	0.1771	0.11408		0.17739
Half sister	0.5514	-0.017404	0.2935	0.04425	0.0177	0.30013	0.8211	-0.079541	0.1088	0.14595	0.0035	0.34139
Gender	0.0651	0.19738	0.0009	0.16971	0.9659	-0.22276	0.9475	-0.17462	0.0521	0.22426	0.0577	0.49731
Age	0.633	-0.033072	0.485	-0.012649	0.062	0.18982	0.6699	-0.024224	0.2133	0.079506	0.2207	0.054996
Random	0.3746	0.027174	0.8766	-0.11367	0.7466	0.063808	0.7508	-0.065098	0.6791	-0.043121	0.4587	0.0043752

Table A5. Mantel test for association between networks and attributes for the Dambwa pride												
	Greet		Groom		Play		Aggression		All Social		Pride Composition	
	P-value	Matrix Coefficient	P-value	Matrix Coefficient	P-value	Matrix Coefficient	P-value	Matrix Coefficient	P-value	Matrix coefficient	P-value	Matrix coefficient
All Social	/	/	/	/	/	/	/	/	/	/	1.0003e-13	0.31339
Greet	/	/	/	/	/	/	/	/	1.0003e-13	0.92759	0.0036	0.16947
Groom	0.589	-0.023834	/	/	/	/	/	/	0.1142	0.10186	0.0035	0.25694
Play	0.2324	0.052883	0.8012	-0.093955	/	/	/	/	0.0001	0.3519	0.0001	0.34894
Aggression	0.914	-0.11162	0.155	0.09527	0.7378	0.069799	/	/	0.7488	0.067425	0.1333	0.093763
Full sister	0.8094	-0.05818	0.208	0.072966	0.0001	0.50831	0.5593	-0.0097742	0.039	0.13293	1.0003e-13	0.70313
Half sister	0.9628	-0.14895	0.2337	0.070367	0.0004	0.38576	0.6557	-0.030388	0.4051	0.020346	0.0032	0.43402
Gender	0.8338	-0.081526	0.2677	0.067764	0.8052	-0.10892	0.4354	0.021178	0.8585	-0.085499	0.5018	-0.015247
Age	0.2726	0.027324	0.2257	0.064012	0.0021	0.28641	0.627	-0.017628	0.0218	0.1445	0.0021	0.55709
Random	0.3808	0.027525	0.2577	0.056182	0.3673	0.027052	0.786	-0.07354	0.4306	0.016736	0.6413	-0.033919

Table A6. Mantel test for association between networks and attributes for the Makhutswi pride 1

	Greet		Groom		Play		Aggression		All Social		Pride Composition	
	P-value	Matrix Coefficient	P-value	Matrix Coefficient	P-value	Matrix Coefficient	P-value	Matrix Coefficient	P-value	Matrix coefficient	P-value	Matrix coefficient
All Social	/	/	/	/	/	/	/	/	/	/	0.0385	0.27969
Greet	/	/	/	/	/	/	/	/	$1.0003e^{-13}$	0.92005	0.0680	0.20423
Groom	0.1862	0.075335	/	/	/	/	/	/	0.0372	0.19443	0.0230	0.21883
Play	0.0157	0.23668	0.5520	-0.037752	/	/	/	/	0.0001	0.40252	0.0338	0.28167
Aggression	0.7928	-0.065993	1	-0.049428	0.5488	-0.04001	/	/	0.0341	0.23533	0.4017	0.016592
Full sister	0.0146	0.18791	0.0270	0.24999	0.2217	0.094939	1	0.045999	0.0189	0.20957	$1.0003e^{-13}$	0.44677
Half sister	0.478	0.0010169	0.2155	0.082158	0.0135	0.3326	0.4005	0.00044309	0.2867	0.086259	0.0006	0.83003
Gender	0.2147	0.057428	0.0184	0.21725	0.9296	-0.13213	0.6836	-0.070348	0.291	0.039769	0.0883	0.14922
Age	0.0186	0.18791	0.0285	0.24999	0.2229	0.094939	1	-0.045999	0.0188	0.20957	$1.0003e^{-13}$	0.44677
Random	0.2441	0.063095	0.8349	-0.087261	0.721	-0.051344	0.6772	-0.052063	0.4091	0.024257	0.4366	0.009299

Table A7. Mantel test for association between networks and attributes for the Makhutswi pride 2

	Greet		Groom		Play		Aggression		All Social		Pride Composition	
	P-value	Matrix Coefficient	P-value	Matrix Coefficient	P-value	Matrix Coefficient	P-value	Matrix Coefficient	P-value	Matrix coefficient	P-value	Matrix coefficient
All Social	/	/	/	/	/	/	/	/	/	/	0.6890	-0.0610
Greet	/	/	/	/	/	/	/	/	$2.0006e^{-13}$	0.70766	0.3508	-0.09078
Groom	0.0172	0.50023	/	/	/	/	/	/	0.0030	0.67504	0.2474	-0.1381
Play	0.7396	-0.01335			/	/	/	/	0.0186	0.37141	0.1958	-0.1952
Aggression	0.0002	0.58555	0.0165	0.5848	0.4518	-0.0620	/	/	$2.0006e^{-13}$	0.80349	0.2474	-0.1381
Full sister	0.4824	-0.0923	0.8891	-0.0533	0.0203	0.3192	0.8865	-0.0533	0.0513	0.2500	0.0008	0.5369
Half sister	/	/	/	/	/	/	/	/	/	/	/	/
Gender	0.9028	0.0196	0.7086	-0.0961	0.9919	-0.0163	0.7079	-0.0961	0.7311	-0.0460	0.6133	0.0555
Age	0.4371	-0.0923	0.6424	0.1120	0.4268	0.1013	0.6560	0.1120	0.4559	0.0966	0.0668	0.4376
Random	0.1892	0.11361	0.1066	0.1630	0.3486	-0.0890	0.1146	0.1605	0.2500	0.1153	0.3120	-0.0942

References

1. Abell, J.; Kirzinger, M.W.B.; Gordon.; Kirk, J.; Kokeŝ, R.; Lynas, K.; Mandinyenya, B.; & Youldon, D. 2013a. A social network analysis of social cohesion in a constructed pride: Implications for ex situ reintroduction of the African lion (Panthera leo). *PLoS ONE*, 8, e82541.
2. Abell, J.; Kokeŝ; R; & Youldon, D. 2013b. A framework for the ex-situ reintroduction of the African lion (*Panthera leo*). *Open Sci. Repos. Nat. Resour. Conserv*. 2013b, e70081986. https://doi.org/10.7392/openaccess.70081986 (accessed on 4 August 2022).
3. Bauer, H.; Van Der Merwe, S. 2004. Inventory of free-ranging lions *Panthera leo* in Africa. *Oryx*, 38, 26–31.
4. Bauer, H.; Packer, C.; Funston, P.F.; Henschel, P.; Nowell, K. Panthera leo. 2016. The IUCN Red List of Threatened Species 2015: e.T15951A79929984. Available online: https://doi.org/10.2305/IUCN.UK.2015-4.RLTS.T15951A79929984.en (accessed on 23 February 2023).
5. Bauer, H.; Chapron, G.; Nowell, K.; Henschel, P.; Funston, P.; Hunter, L.T.B.; Macdonald, D.W.; Dloniak, S.M.; Packer, C. 2016. Reply to Riggio et al.: Ongoing lion declines across most of Africa warrant urgent action. *Proc. Natl. Acad. Sci*. USA, 113, E109.
6. Beck, B.B.; Rapaport, L.G.; Stanley Price, M.R.; & Wilson, A.C. 1994. Reintroduction of captive-born animals. In Creative Conservation; Olney P.J.S., Mace, G.M., Feistner, A.T.C., Eds.; Chapman & Hall: New York, USA, Pp. 265–286.
7. Borgatti, S.P.; Everett, M.G.; & Freeman, L.C. 2002. Ucinet for Windows: Software for Social Network Analysis; Analytic Technologies: Harvard, MA, USA. Available online: https://sites.google.com/site/ucinetsoftware/news/newbookonsna (accessed on 28 January 2022).
8. Castely, J.G.; Knight, M.H.; Mills, M.G.L.; Thouless, C. 2002. Estimation of the lion (Panthera leo) population in the southwestern Kgalagadi Transfrontier Park using a capture-recapture survey. *Afr. Zool*., 37, 27–34.
9. Cesare, M. 2011. *Man-eaters, Mambas and Marula Madness: A Game Ranger's Life in the Lowveld*; Jonathan Ball Publishing: Johannesburg, South Africa.
10. Cruickshank, K.M.; & Robinson, T.J. 1997. Inheritance of the white coat colour phenotype in African lions (Panthera leo). In A Symposium on Lions and Leopards as Game Ranch Animals; Van Heerden, J., Ed.; Wildlife Group of the South African Veterinary Association: Onderstepoort, South Africa.
11. Dicks, T. 2022. South Africa's White Lions. Wandering Through Photo Safaris and Expeditions [Website]. Available online: https://wanderingthru.com/the-white-lions-of-south-africa/ (accessed on 4 August 2022).
12. Dunston, E.; Abell, J.; Doyle, R.; Duffy, D.; Poynter, C.; Kirk, J.; Hilley, V.; Forsyth, A.; Jenkins, E.; McAllister, D.; & Freire, R. 2017. Does captivity influence territorial and hunting behaviour? Assessment for an ex-situ reintroduction program of African lions (*Panthera leo*). *Mammal Rev.* 47, 254–260.
13. Ferreira, S.M.; & Funston, P.J. 2010. Estimating lion population variables: Prey and disease effects in Kruger National Park, South Africa. *Wildl. Res*., 37, 194–206.

14. Fischer, J.; & Lindenmayer, D.B. 2000. An assessment of the published results of animal relocations. *Biol. Conserv.* 96, 1–11.
15. Funston, P.J.; Mills, M.G.L.; Biggs, H.C.; & Richardson, P.R.K. 1998. Hunting by male lions: Ecological influences and socioecological implications. *Anim Behav.* 56, 1333–1345.
16. Funston, P.J.; Mills, M.G.L.; Richardson, P.R.K.; van Jaarsveld, A.S. 2003. Reduced dispersal and opportunistic territory acquisition in male lions *Panthera Leo*. *J. Zool.*, 259, 131–142.
17. 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; Croes, B., Delongh, H.H., Bauer, H., Eds.; Institute of Environmental Sciences: Leiden, The Netherlands; Pp. 109–131.
18. Funston, P.J.; Levendal, M. 2015. Biodiversity Management Plan for Lion (Panthera leo) in South Africa; Government Gazette; Government Printing Works, Department of Government Printing Works, South Africa.
19. Funston, P.J. 2011. Population characteristics of lions (Panthera leo) in the Kgalagadi Transfrontier Park. *S. Afr. J. Wildl. Res*., 41, 1–10.
20. Hayward, M.; & Kerley, G. 2009. Fencing for conservation: Restriction of evolutionary potential or a riposte to threatening processes? *Biol. Conserv*.,142, 1–13. https://doi.org/10.1016/j.biocon.2008.09.022 (accessed 4 August 2022).
21. Hazzah, L.; Mulder, M.B.; Frank, L. 2009. Lions and warriors: Social factors underlying declining African lion populations and the effect of incentive-based management in Kenya. *Biol. Conserv.,* 142, 2428–2437.
22. Hunter, L.T.B. 1998. Behavioural Ecology of Reintroduced Lion and Cheetahs in the Phinda Resource Reserve, Kwa-Zulu Natal, South Africa. Ph.D. Thesis, Pretoria University, Pretoria, South Africa.
23. Hunter, L.T.B.; White, P.; Henschel, P.; Frank, L.; Burton, C.; Loveridge, A.; Blame, G.A.; Breitenmoser, C.; Breitenmoser, U. No science, no success and still no need for captive-origin lion reintroduction: A reply to Abell & Youldon. *Oryx* 2013, 41,27–28.
24. Jachowski, D.; & Lockhart, J. 2009. Reintroducing the black-footed ferret Mustela nigripes to the Great Plains of North America. *Small Carniv. Conserv*., 41, 58–64.
25. Jule, K.J.; Leaver, L.A.; & Lea, S.E.G. 2008. The effects of captive experience on reintroduction survival in carnivores: A review and analysis. *Biol. Conserv*. 141,355–363.
26. Kat, P. 2012. LionAid: Scientific Estimates of Lion Populations in Africa. Pieter's Blog [Available online]. Available online: https://lionaid.org/news/2012/12/lionaid-scientific-estimate-of-lion-populations-in-africa.htm (accessed on 23 February 2023).
27. Krause, J.; Croft, D.P.; James, R. 2007. Social network theory in the behavioural sciences: Potential applications. *Behav. Ecol. Sociobiol*., 62,15–27.
28. Loveridge, A.J.; Valeix, M.; Davidson, Z.; Murindagomo, F.; Fritz, H.; & Macdonald, D.W. 2009. Changes in home range size of African lions in relation to pride size and prey biomass in a semi-arid savanna. *Ecography* 32,953–962.

29. Marneweck, C.; Becker, P.; Beverley, G.; Davies-Mostert, H.; Plessis, C.; Forssman, K.; Graf, J.; Gusset, M.; Hofmeyr, M.; Kelly, C.; et al. 2019. Factors affecting the success of artificial pack formation in an endangered, social carnivore: The African wild dog. Anim. Conserv. 22, 493–502.
30. Matoba, T.; Kutsukake, N.; & Hasegawa, T. 2013. Head rubbing and licking reinforce social bonds in a group of captive African lion (*Panthera leo*). *PLoS ONE*, 8,e73044.
31. McBride, C. 1977. *The White Lions of Timbavati*; Paddington Press: New York, USA.
32. McBride, C. 1981. *Operation White Lion*; St. Martin's Press: New York, USA.
33. Miller, S.M.; Harper, C.K.; Bloomer, P.; Hofmeyr, J.; Funston, P.J. 2015. Fenced and fragmented: Conservation value of managed metapopulations. *PLoS ONE*, 10, e0144605.
34. Miller, S.M.; Funston, P.J. Rapid growth rates of lion (Panthera leo) populations in small, fenced reserves in South Africa: A management dilemma. *S. Afr. J. Wildl. Res*. 2014, 44, 43–55.
35. Mosser, A.; Packer, C. 2009. Group territoriality and the benefits of sociality in the African lion (*Panthera leo*). *Anim. Behav*., 78, 359–370.
36. Mucina, L.; & Rutherford, M.C. 2006. *The Vegetation of South Africa, Lesotho and Swaziland; Rutherford, M.C., Ed.; Strelitzia*; South African National Biodiversity Institute: Pretoria, South Africa, Volume 19.
37. Mzileni, N.; Ferreira, S.; Funston, P.; Kalala, M.; Mutombo, F.K.; & Goodall, V. 2020. Horizontal disease transmission in lions from behavioural interfaces via social network analysis. *Mammal Res*., 65, 709–718.
38. New, T.R. 2006. Conservation Biology in Australia: An Introduction; Oxford University Press: South Melbourne, Australia.
39. Nowell, K.; Jackson, P. 1996. *Wild Cats: Status Survey and Conservation Action Plan*; IUCN/SSC: Gland, Switzerland.
40. Oakleaf, J.K.; Stark, D.; Overy, P.; Smith, N. 2004. *Mexican Wolf Recovery: Technical Component of the Five-Year Program Review and Assessment*; US Fish and Wildlife Service: Washington, DC, USA.
41. Packer, C.; Pusey, A.S.; & Eberly, L.E. 2001. Egalitarianism in female African lions. *Science*, 293,690–693.
42. Packer, C.; Loveridge, A.; Canney, S.; Caro, T.; Garnett, S.T.; Pfeifer, M.; Zander, K.K.; Swanson, A.; MacNulty, D.; Balme, G; et al. 2013. Conserving large carnivores: Dollars and fence. *Ecol. Lett.*, 16, 635–641.
43. Riggio, J.; Jacobson, A.; Dollar, L.; Bauer, H.; Becker, M.; Dickman, A.; Funston, P.; Groom, R.; Henschel, P.; de Iongh, H.; et al. 2013. The size of savannah Africa: A lion's Panthera leo view. *Biodivers Conserv*., 22, 17–35.
44. Robinson, R.; & De Vos, V. 1982. Chinchilla mutant in the lion. *Genetica*, 60, 61–63.
45. Schaller, G.B. 1972. The Serengeti Lion; The University of Chicago Press: London, UK.
46. Schaller, George B. 1976. *The Serengeti Lion: A Study of Predator-Prey Relations*. Chicago: University of Chicago Press.

47. Sih, A.; Hanser, S.F.; & McHugh, K.A. 2009. Social network theory: New insights and issues for behavioural ecologists. *Behav. Ecol. Sociobiol.*, 63,975–988.
48. Slotow, R.; & 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; Hayward, M.W., Somers, M.J., Eds.; Wiley-Blackwell: Oxford, UK; Pp. 41–73.
49. Smuts, G.L. 1982. *Lion*; Johannesburg: MacMillan, South Africa.
50. Somers, M.J.; & Gusset, M. 2009. The role of social behaviour in carnivore reintroductions. In Reintroduction of Top-Order Predators; Hayward, M.W., Somers, M.J., Eds.; The University of Chicago Press: Chicago, IL, USA, Pp. 270–281.
51. Stanley Price, M.R. 1991. A review of mammal reintroductions, and the role of the re-introduction specialist group of the IUCN/SSC. In Beyond Captive Breeding: Re-Introducing Endangered Mammals to the Wild; Gipps, J.H.W., Ed.; *Symp. Zool. Soc. Lond.*; Clarendon Press: Oxford, UK, Volume 62, Pp. 9–25.
52. Stuart, S.N. Re-introductions: To what extent are they needed? *Symp. Zool. Soc. Lond*. 62, 27–37.
53. Toone, W.; & Wallace, M. 1994.The extinction in the wild and the reintroduction of the California condo Gymnogyps californianus. In Creative Conservation; Olney, P.J.S., Mace, G.M., Feistner, A.T.C., Eds.; Chapman & Hall: New York,, USA, Pp. 411–419.
54. Trinkel, M.; Funston, P.; Hofmeyr, M.; Hofmeyr, D.; Dell, S.; Packer, C.; Slotow, R. 2010. Inbreeding and density-dependent population growth in a small, isolated lion population. *Anim. Conserv.*, 13, 374–382.
55. Tucker, L. 2003. Mystery of the White Lions: Children of the Sun God; Npenvu Press: White River, South Africa.
56. Tuqa, J.H.; Funston, P.J.; Musyoki, C.; Ojwang, G.O.; Gichuki, N.N.; Bauer, H.; Tamis, W.; Dolrenry, S.; Van't Zelfde, M.; de Sno, G.R.; et al. 2014. Impact of severe climate variability on lion home range and movement patterns in the Amboseli ecosystem, Kenya. *Glob. Ecol. Conserv.*, 2, 1–10.
57. Tumenta, P.N.; Van 'TZelfde, M.; Croes, B.M.; Buij, R.; Funston, P.J.; Udo De Haes, H.A.; & De Iongh, H.H. 2010. Changes in lion (Panthera leo) home range size in Waza National Park, Cameroon. *Mamm. Biol.*, 78, 461–469.
58. Turner, J.A.; Vasicek, C.A.; Somers, M.J. 2015. Effects of a Colour Variant on Hunting Ability: The White Lion in South Africa. *Open Sci. Repos. Biol.,* e45011830. https://doi.org/10.7392/openaccess.45011830 .
59. Turner, J.A.; Dunston-Clarke, E.J.; Fabris-Rotelli, I.; de Iongh, H. 2022. Home Range and Movement Patterns of Reintroduced White Lions (Panthera leo melanochaita) in the Kruger to Canyons Biosphere Reserve, South Africa. *Animals*, 12, 2003. https://doi.org/10.3390/ani12152003.
60. Wey, T.; Blumstein, D.T.; Weiwei, S.; & Ferenc, J. 2008. Social network analysis of animal behavior: A promising tool for the study of sociality. *Anim. Behav.*, 75, 333–344.

61. Whitehead, H. 2009. SOCPROG programs: Analyzing animal social structures. Behav. Ecol. Sociobiol., 63,165–173.
62. Whitman, K.; & Packer, C. 1997. The effect of sport hunting on the social organization of the African lion (Panthera leo). In Lions and Leopards as Game Ranch Animals; Van Heerden, J., Ed.; The Wildlife Group. South African Veterinary Association: Onderstepoort, South Africa, Pp. 177–183.
63. Whitman, K.; Starfield, A.M.; Quadling, H.S.; Packer, C. 2004. Sustainable trophy hunting of African lions. *Nature*, 428, 175–178.
64. Witzenberger, K.A.; & Hochkirch, A. 2011. Ex situ conservation genetics: A review of molecular studies on the genetic consequences of captive breeding programmes for endangered animal species. *Biodivers. Conserv*. 9, 1843–1861.

Photo 3.1 White lion male on territorial patrol at Tula Tsau Wildlife Area, Greater Kruger Park Region. *© Global White Lion Protection Trust*

3 Home Range Behaviour of White Lions

Home Range and Movement Patterns of Reintroduced White Lions (*Panthera leo melanochaita*) in the Kruger to Canyons Biosphere Reserve, South Africa.

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Simple Summary: White lions are a natural colour variant of the African lion found within certain lion prides in the Greater Kruger Park Region of South Africa. Human factors led to their absence until white lions were reintroduced in 2006. This study provides the first assessment of home range and movement behaviour of white lions as an index of reintroduction success. Home range is the area where an animal spends its time and encompasses all the resources the animal requires to survive and reproduce. The home range size and average distance walked in a day were compared seasonally (wet compared to dry season) and between sexes (male compared to female) for a pride of white lions and a pride consisting of white and tawny (non-white) lions. Both prides had similar sized home ranges, walked a comparable average distance, and preferred similar types of vegetation among which to spend their time (dense woodland compared to open grassland). The white lions from both prides showed natural behaviour, similar to that of wild lions in terms of how they established and made use of their home ranges, suggesting that white lions can be successfully reintroduced into the wild.

Abstract: White lions are a colour variant of the African lion *Panthera leo melanochaita* and disappeared from the wild due to anthropogenic activities until their reintroduction to the Greater Kruger Park Region of South Africa in 2006. Natural home range behaviour is an index of reintroduction success. Therefore, the home range and movement of a pride of reintroduced white lions and a constructed pride consisting of reintroduced white lions and translocated wild tawny lionesses in small, fenced reserves was assessed. GPS data from collared adults were collected for the white lion pride in 2010-2011, and between 2018 and 2020 for the constructed pride. Home ranges were estimated using kernel density estimation and minimum convex polygon, with minimum daily distance tested for differences between sex, season, and pride. Home ranges were small and average daily movements restricted for both prides (white lion pride: 5.41 km^2 and 10.44 ± 4.82 km; constructed pride: 5.50 km^2, 11.37 ± 4.72 km) due to the small reserve size of 7 km^2. There was no difference between prides for annual and seasonal home range size, male and female home ranges, minimum daily distance travelled, or habitat selection. White lions from both prides established territories and displayed natural home ranging behaviour, suggesting that their reintroduction was successful, in the absence of anthropogenic threats.

Keywords: white lion; reintroduction; home range; movement; habitat selection

3.1 Introduction

Globally, wildlife populations are rapidly declining mainly due to human population growth and consumption (Baillie et al. 2010). Large carnivores are significantly impacted by human activity due to their ecological requirements and high conflict rate with humans (Hunter et al. 2007; Ripple et al. 2014). The increase in human populations worldwide has led to a higher incidence of conflict with many carnivorous species, resulting in population decline and local extinctions (Woodroofe 2000; Cardillo et al. 2004). The lion has experienced the greatest reduction in range since historic times out of all vertebrate species (Power 2003). Lions have recently been split into two subspecies, *Panthera leo leo* (Linneaus 1758), made up of the cats living in Asia and West, Central, and North Africa, and *Panthera leo melanochaita* (Kitchener et al. 2016), consisting of the lion populations living in East and Southern Africa (Yamaguchi et al. 2009). This reclassification is necessary to regionally ascertain the threat level of the respective subspecies of lions. In South Africa, lions have disappeared from most of their historical range (Nowell 1996; Miller et al. 2015) due to habitat loss, human-lion conflict, poaching, and trophy hunting (Miller et al. 2016). There are only three surviving historical populations at the time of this study, namely in Kruger National Park (KNP) (approximately 1700 individuals) (Ferreira & Funston 2010), Kgalagadi Transfrontier Park (KTP) (approximately 125 individuals in the South African section) (Castley et al. 2002; Funston 2011), and the Greater Mapungubwe Transfrontier Conservation Area (GMTFCA) (<50 individuals) (Funston 2010). Since the 1990s, a number of wild but managed lions have been translocated to smaller fenced reserves (<1000 km^2) across South Africa, totalling approximately 800 lions across 49 fenced reserves (Funston & Levendal 2014), being managed as a metapopulation (Miller et al. 2015; Miller & Funston 2014). The Red Data List for Mammals in South Africa, Lesotho, and Swaziland lists the conservation status of lions in South Africa as Least Concern but indicates that this species would technically qualify for Near Threatened status if the managed subpopulations in small reserves were excluded (Miller et al. 2016). These lion subpopulations are therefore a significant contribution to the conservation of lions in South Africa, forming part of the metapopulation management approach, whereby lions need to be regularly translocated to prevent inbreeding, genetic drift, and overpopulation (Miller et al. 2015).

The white lion is a rare genetic variant of the southern subspecies of the African lion (*Panthera leo melanochaita*) that has a white coat colour and either brown, blue, or green eyes, and has occurred in the Greater Timbavati Region and Central Kruger Park Region of South Africa, since 1938 (Tucker 2003). The white coat colour is not due to albinism, but rather caused by leucism, resulting from a double recessive allele or gene (Robinson & De Vos 1982; Cruckshank & Robinson 1982; Cho et al. 2013). White lions and many tawny lions carrying the recessive gene were removed from the wild and placed into captive breeding and hunting progammes, zoos, and circuses worldwide (McBride 1977; Tucker 2003; Cesare 2011; Turner et al. 2015). The anthropogenic impact of lion culling in Central Kruger National Park (Smuts 1982), trophy hunting, and removal from the wild in the Greater Timbavati Region (Tucker 2003; Cesare 2011; Turner et al. 2015) led to an absence of white lions in their natural habitat up until 2006. The recessive gene was still present in the wild population and white lion cubs were born into the Greater Timbavati Region in 2006-2009, 2011, 2014, 2015, 2018, and 2019, and in Central Kruger National Park in 2014 and 2015 (Turner et al. 2015; Dicks 2022). Only three of the 17 cubs had survived at the time of the present study due to illegal removal to breeding/hunting farms, the continued lion trophy hunting of pride males which caused infanticide, and high impact ecotourism leading to undue stress on lionesses with young cubs during regular viewings by tourist or lodge vehicles Whitman & Packer 1997; Whitman et al. 2004; Dicks 2022). The natural high mortality rate of 50% of lion cubs within the first year [30] would also have contributed to the low survival rate of white lion cubs between 2006 and 2019. The birth of white cubs in the Greater Timbavati Region and the Central Kruger Park between 2006 and 2019 is confirmation that the recessive gene was still present in the wild population (Dicks 2022). However, the distribution of the white lion gene in the Greater Timbavati Region and the Central Kruger Park Region has never been determined, nor the frequency of occurrence of the white lion gene within their natural habitat. This is beyond the scope of the present study. At the initiation of this study, there were only three free-roaming white lions within their natural habitat, largely nomadic, and none of them adults. Therefore, our study focused on a reintroduced pride of captive-origin white lions, and a free-roaming pride of captive-origin white lions constructed with wild tawny lions at the Tula Tsau Conservation Area. Turner et al. (2015) showed that there was no difference in the hunting success of the two reintroduced white lion groups compared to wild tawny lions in the same study area, Madjuma Lion Reserve (MLR), Karongwe Game Reserve (KGR), Welgevonden Game Reserve (WGR), Makalali Game Reserve (MGR), and the Associated Private Nature Reserves (APNR) in South Africa. In a recent study, Turner et al. (2022) compared the social behaviour of the reintroduced pride of captive-origin white and wild tawny lions to two captive-origin prides in Zambia and Zimbabwe respectively, and wild tawny lion prides at the Greater Makalali Private Game Reserve in South Africa. The study concluded that the white and tawny lions formed a socially cohesive pride that was more strongly bonded than either the captive-origin or wild tawny prides, a sign of successful reintroduction. In addition to the hunting success and social cohesion of a lion pride, natural home range behaviour is also an index of reintroduction success, and in the case of the white lions, an indication of whether white lions would survive in the wild in the absence of anthropogenic threats. The present study is therefore the first study to investigate the home range, movement patterns, and habitat preferences of white lions, as an index of whether reintroduced white lions show natural home range behaviour.

3.1.1 Home Range and Movements of Lions

A home range is generally defined as the area where an animal acquires resources, mates, reproduces, and takes care of its offspring (Burt 1943). Lions are the only truly social cats, generally living in prides (Schaller 1972; Packer et al. 1990). The home range of individual lions is typically confined by the pride's territory (Schaller 1972). The ranging behavior of lions is not only dependent on resource availability but also on prey availability, social interactions, habitat quality and reproductive status (Gittleman & Harvey 1982; Van Orsdol et al. 1985; Viljoen 1993; Spong 2002; Bauer & De Iongh 2005). Lion home range is directly related to prey abundance and the presence of water, thus lower availability of both resources corresponds with larger home ranges and vice versa (Van Orsdol et al. 1985; Celesia et al. 2009; Tumenta et al. 2013). However, other factors, such as social status, sex, age, season, and disturbance (e.g., human population growth and presence of livestock near reserves), may influence the home range (Schaller 1972; Loveridge et al. 2009; Tumenta et al. 2013). Group size and territoriality are social factors that also influence home range size (Packer et al. 2005), with range size increasing with group size (Van Orsdol et al. 1985). Home ranges are generally smaller in high quality habitats that have a high prey density, such as the Serengeti Plains, compared to low quality or sparse habitats with low prey availability, such as the semi-arid savannah of the Hwange National Park or the dry savannah region of the Central Kalahari in Botswana (Loveridge et al. 2009; Mosser & Packer 2009; Zehnder et al. 2018). Since rainfall determines habitat quality, structure, and density, through its influence on vegetation health, mediated through edaphic and topographic/catenary gradients, it is a key factor affecting home range size (Bell 1982; McNaughton 1983). In arid regions, lions adopt larger home ranges to locate prey, which normally occur at low densities. Stander (1991) recorded lion prides with home ranges of up to 2075 km^2 in Etosha National Park, Namibia, and Funston (2011) documented lion home ranges over 4500 km^2 in the Kgalagadi Transfrontier Park, South Africa/Botswana. In more mesic habitats, higher prey densities result in smaller home ranges. Home ranges as small as 45 km^2 were recorded for lions in the Ngorongoro Crater, Tanzania (Hanby et al. 1995). In wildlife areas that have a distinct wet and dry season, seasonal variation in home range size may therefore occur, such as in the Central Kalahari Game Reserve in Botswana (Zehnder et al. 2018).

Lioness home range is determined by suitability for having and caring for young and the availability of sufficient prey to sustain their offspring (Loveridge et al. 2009; Packer et al. 2001). Male home ranges are influenced by the distribution of females. Therefore, they are generally larger than female home ranges (Van Orsdol et al. 1985; Funston et al. 2003; Loveridge et al. 2009) and can span across numerous prides (Hunter 1998). Adult male lions maintain a territory largely contiguous with that of their home range (Bertram 1973; Van Orsdol et al. 1985; Funston et al. 1998). Large home ranges overlap extensively with those of adjacent prides, while small ranges tend to have little overlap (Van Orsdol et al. 1985).

Lions are known to move up to 20 km in 24 hours and to cover hundreds of kilometres over several months (Tuqa et al. 2014). The core of an animal's home range is defined as the most intensively used area within that animal's home range (Powell 2000). It can be quantified by a utilisation distribution that describes the frequency distribution of the locations of an animal at the landscape level (Worton 1989). The 50% utilisation distribution is often viewed as the core and most important area within the entire home range (Powell 2000).

3.1.2 Home Range and Movement Patterns of White Lions Compared to Those of Tawny Lions

Although white lions have occurred naturally in the Greater Timbavati Region since 1938 (Tucker 2003) and in the Central Kruger Park Region since 1956 (Robinson & De Vos 1982; Smuts 1982; Cruckshank & Robinson 1997), the home range and movement patterns of white lions have never been studied to determine if they differ from those of tawny lions. Since white lions are the result of a recessive gene (Robinson & De Vos 1982; Cruckshank & Robinson 1997; Cho et al. 2013), there is a perception that white lions would not survive in the wild, and that their behaviour may not be consistent with that of wild tawny lions. Turner et al. (2015) showed that there was no difference in the hunting success of white lions compared to tawny lions under managed free-roaming conditions, and the social behaviour of a constructed pride of white and tawny lions was similar to that of a pride of wild tawny lions (Turner et al. 2022). However, home range behaviour and movements of white lions has not been previously published. Home range studies have been conducted on tawny lion prides within smaller reserves in Southern Africa: a private reserve in Gweru, Zimbabawe (1.6 km^2) (Dunston et al. 2017), Dambwa Forest in Livingstone, Zambia (2.9 km^2) (Dunston et al. 2017), Madjuma Lion Reserve (15 km^2) (Power 2003), Karongwe Game Reserve, (80 km^2) (Lehmann et al. 2008), Dinokeng Game Reserve (185 km^2) (Yiu et al. 2017), and Greater Makalali Private Game Reserve (250 km^2) (Druce et al. 2004; Dunston et al. 2017) in Limpopo Province, South Africa. Dunston et al. (2017) conducted the first assessment of the spatial ecology and territorial behaviour of captive-origin lions. The study concluded that the two captive-origin prides established territories and core areas in a similar way to a wild pride in the Greater Makalali Private Nature Reserve, South Africa.

This study presents the first investigation into the home range and movement patterns of white lions. Since Hayward et al. (2008) concluded that the use of fences did not affect the natural ranging behaviour of predators, with prey abundance still being the key factor determining space use in fenced reserves, the home range and movement patterns of a reintroduced white lion pride were therefore compared to those of a free-roaming pride of white lions integrated with wild tawny lions in the same fenced study area (during different study periods), as well as the two prides of captive-origin tawny lions, and two wild prides studied by Dunston et al. (2017) in fenced reserves. Our study area was 7 km^2, a similarly small size to the Madjuma Lion Reserve (15 km^2) in Limpopo Province (South Africa), a fenced reserve that has resident wild tawny lions (see Section 2.1 below for more details on the Study Area). Our study addressed the following research questions: (i) What is the average home range size of the white lion pride and constructed pride of white and tawny lions? (ii) What is the average distance traveled within the 12 h per day monitoring period by the white lion pride and the constructed pride of white and tawny lions? (iii) Which habitat type is preferred by the white lion pride and the constructed white and tawny lion pride? and (iv) Did the white lion pride and constructed pride of white and tawny lions show natural home range behaviour, movement patterns, and habitat selection similar to that of wild tawny lions, suggesting that the reintroduction to their natural habitat was successful?

3.2 Materials and Methods

3.2.1 Study Area

The study was conducted at the Tula Tsau Conservation Area (7 km^2), a fenced wildlife area in the Kruger to Canyons Biosphere Reserve, Limpopo Province, South Africa (Figure 1). The Tula Tsau Conservation Area is located in the Lowveld of South Africa, and forms part of an important buffer area, the Greater Kruger Environmental Protection Zone (GKEPZ), between the Kruger National Park, rural communities, and the semi-urban town of Hoedspruit. The Tula Tsau Conservation Area is situated between latitude 24.374° S–24.396° E and longitude 31.106° S–31.146° E. The region experiences a dry winter season (April-September) and a wet summer season (October-March), with a mean annual rainfall of 634 mm.

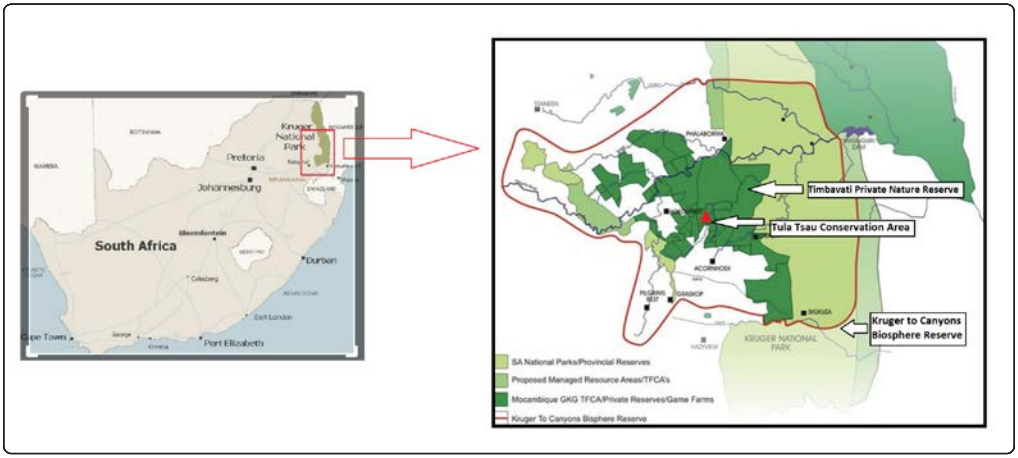

Figure 1 Location of the Tula Tsau Conservation Area, Kruger to Canyons Biosphere Reserve, South Africa.

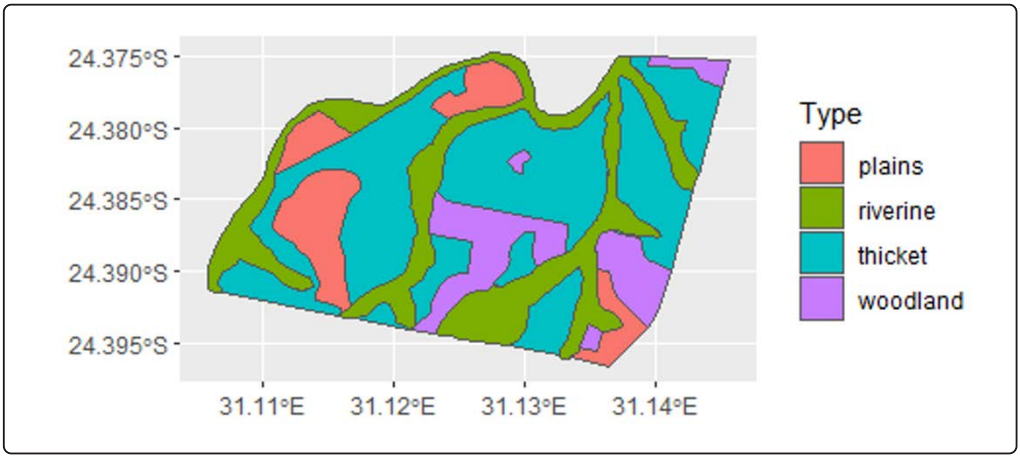

Figure 2 Vegetation map of the Tula Tsau Conservation Area Limpopo, South Africa.

The Tula Tsau Conservation Area is a natural Lowveld vegetation area that is classified as Arid Lowveld (Mucina & Rutherford 2006). The topography is undulating with plains, woodlands of various densities, thickets, and riverine vegetation (Figure 2). This wildlife area is characterised by indigenous flora and fauna, including a wide variety of mammalian prey species: Blue wildebeest (*Connochaetes taurinus*), Eland (*Taurotragus oryx*), Burchell's zebra (*Equus quagga*), Greater kudu (*Tragelaphus strepsiceros*), Nyala (*Tragelaphus angasii*), Waterbuck (*Kobus ellipsiprymnus*), Common warthog (*Phacochoerus africanus*), Bushbuck (*Tragelaphus sylvaticus*), Impala (*Aepyceros melampus*), Steenbok (*Raphicerus campestris*), and Common Duiker (*Sylvicapra grimmia*). The following small carnivores are common in the area: Black-backed jackals (*Canis mesomelas*), and caracal (*Caracal caracal*), whilst these larger carnivores are often seen but are not resident: leopard (*Panthera pardus*), spotted hyaena (*Crocuta crocuta*), African wild dog (*Lycaon pictus*), and serval (*Leptailurus serval*). A single lion pride occurred at the Tula Tsau Conservation Area: a pride of white lions from 2007 to 2013 (which were translocated to another wildlife area), and a pride of white and tawny lions from 2014 to 2020. Wild lions are present on the neighbouring wildlife areas of Kapama, Thornybush, and Timbavati Private Nature Reserve. The prey population has been replenished on an annual basis since the Tula Tsau Conservation Area is a small fenced reserve. Prey abundance and composition were therefore consistent for the period of study.

The white lion pride and the constructed pride of white and tawny lions both had a similar pride structure with one or more male lions, two or more adult lionesses, and several subadults or cubs (Table 1).

Table 1. Pride composition of the Royal pride and the Tsau pride, at the Tula Tsau Conservation Area (7 Km^2) (24°23′ S/31°98′ E).

Pride	Adult (> 4 yr)	Adult (> 4 yr)	Sub Adult (2–4 yr)	Sub Adult (2–4 yr)	Cub (< 2 yr)	Cub (< 2 yr)	Total	Observation Period
	Male	Female	Male	Female	Male	Female		
Royal	1 *	1	2	1	0	0	5	25 January 2010 – 12 December 2011
Tsau	2 *	2	2	1	0	0	7	1 January 2018 – 31 December 2020

** Indicates an individual who is of captive-bred origin.*

3.2.2 Data Collection and Sampling

The Royal pride was a reintroduced pride of white lions that comprised of an adult male, one adult female, two subadult males, and a subadult female (Table 1). The constructed pride (Tsau) of white and tawny lions comprised of two adult white lion males, two adult tawny females, two subadult tawny males, and a subadult tawny female (Table 1). All adult lions in each pride were fitted with Africa Wildlife Tracking (AWT, Pretoria, South Africa) VHF radio collars: two adults for the Royal pride (40%), and four adults for the Tsau pride (60%). Data were collected for the Royal pride for 2010 and 2011, and for the constructed white and Tsau pride between 2018 and 2020. Average rainfall was similar for the data collection periods: 655 mm for the 2010-2011 period and 608 mm for the 2018-2020 period. The average rainfall during the two study periods was also similar to the long term mean annual rainfall of 634 mm (2000 to 2020). Since there were no significant differences in climate, habitat type, prey composition or prey abundance between the two study periods (2010/2011 and 2018/2020), therefore the time difference between pride monitorings was unlikely to impact results. Using VHF radio telemetry (Communication Specialist R-1000 Receiver) and a Garmin eTrex GPS, the location and movement of the reintroduced prides were recorded daily during their peak activity periods; from dusk to dawn (1700 h to 0500 h). This was done during the following periods; for the white lion pride: 25 February 2010 to 12 October 2011; and for the constructed pride of white and tawny lions: 1 January 2018 to 31 December 2020. Additional location and movement data were recorded during the study periods by vehicle for direct observations of their hunting ability and hunting behavior, as described in Turner et al. (2015).

3.2.3 Data Analysis and Statistical Testing

The following statistical software packages of the programme R (R Core Team 2020) were used for data analysis and statistical testing: sf, spatstat, maptools, sp, leaflet, mapview, openair, ks, ggplot2, ggspatial, raster, rgdal, and cleangeo (Pebesma & Bivand 2005; Carslaw & Ropkins 2012; Pebesma 2018; Baddeley et al. 2015; Wickham 2016; Applehans et al. 2021; Bivand et al. 2021; Blondel 2021; Cheng et al. 2021;

Dunnington 2021; Duong & Smoothing 2021; Hijmans 2021; Bivand & Lewin-Koh 2022). For the first research question, we calculated the annual and seasonal home range of each collared lion by calculating the minimum convex polygon (MCP) and kernel density estimation (KDE) home ranges, using the programme R (R Core Team 2020). MCP is a commonly used, simple measure chosen to allow comparison with previous home range estimates. This method calculates the smallest convex polygon from all the locations available: 100% MCP for all lion locations, and 95% MCP which removes 5% of the outliers in the dataset. A more recent method is KDE, which is based on density estimations of GPS locations, by calculating the harmonic means and creating isopleths of intensity of home-range utilisation (Powell 2000). The boundary of the lion's home range is 95% KDE, and the core home range is 50% KDE (Kerley et al. 2017). Since animals utilise areas within their home range unevenly, fixed kernel density estimators were used to define the core areas (Powell & Mitchell 2012). For each home range (i.e., 50% KDE, 95% KDE, and 100% MCP) a mixed effect model was built, with sex (male/female), season (wet/dry), and pride (Royal/Tsau pride) as explanatory categorical variables. Contrary to home range studies of wild tawny lion prides, such as the work of Lesilau et al. (2021), male lions were not excluded from pride home range estimators since males were not involved in pride takeovers due to the absence of other lion prides in the small fenced (closed) system. Statistical analyses were performed using the programme R (R Core Team 2020).

To answer the second research question, the minimum potential daily distance traveled was calculated as the Euclidean distance between following GPS fixes within 12 h based on the method described by Hunter (1998). In contrast to Hunter (1998), a 12 h period rather than a 24 h period was used, due to the logistical and resource limitations of our study, and since the 12 h period was during the peak activity period for lions in the Tula Tsau Conservation Area, between dawn and dusk (1700 h to 0500 h) (Turner et al. 2015). The selection of the 12 h observation period (1700 h to 0500 h) for our study is supported by the observations of Hayward and Slotow (2009) that lion activity peaked between 2100 h to 2400 h and 0200 h to 0700 h, as well as Schaller (1972) who observed that lions are active post 1700 h, and Rudnai (1973) that lion activity increases post 1600 h. A mixed effect model was built with daily distance traveled as response variable, and with sex and season as defining categorical variables.

For the third research question, a vegetation class was assigned to each GPS fix to determine the proportion of fixes in each habitat type. The vegetation types for Tula Tsau Conservation Area were described by Mcdonald (2005). Manly's selection index was used to assess lion habitat preference (Manly et al. 2002), as described by Lesilau et al. (2021). The selection index was measured using the formula: $wi = oi/pi$, where wi = selection index for vegetation type i; oi = proportion (number) of fixes in vegetation type i; and pi = proportion of vegetation i available in the park. Values above 1.0 indicated preference, while values less than 1.0 indicated avoidance. The standardised index Bi allowed comparisons between habitat types: Bi = wi/(Σni = ŵi). Values below 0.250 (corresponding to 1/number of vegetation types) indicated relative avoidance, while values above indicated relative preference.

For the mixed effects models, a likelihood ratio test (LRT) was calculated with a Chi-squared test. The mixed effect models were built using the function lmer() from the package lmerTest (Kuznetsova et al. 2017). Lion identity and year were included as random factors for each model. Response variables for the mixed effect models met model assumptions of normality and homoscedasticity.

3.3 Results

3.3.1 Home Ranges and Movements

The individual home range size for the members of the Royal pride and Tsau pride are shown in Tables 2 and 3. The home range size was similar for the individuals of each pride, and between prides, for all sexes, ages, and seasons (Tables 2-6).

The Royal pride and Tsau pride had home ranges that extended over the majority of the reserve (77% and 80%), with the Royal pride occupying 5.41 km^2 (95% KDE) and the Tsau Pride 5.50 km^2 (95% KDE) within the 7 km^2 reserve (Figure 3). Kernel densities indicated areas most used by each pride. The Royal pride and Tsau pride both used seven core areas (50% KDE), four of them situated around a waterhole for the Royal pride, and five for the Tsau pride (Figure 3). The mean annual home range size of lions in the Tula Tsau Conservation Area was 5.53 ± 0.35 km^2 (95% KDE). Annual core home ranges (50% KDE) were on average 1.76 ± 0.10 km^2 in size, which was around 32% of the 95% KDE home range. Using 100% of the GPS fixes resulted in a mean annual home range size of 5.70 ± 0.23 km^2 (100% MCP), covering 81% of the Tula Tsau Conservation Area.
The mean annual home range size of the prides at the Tula Tsau Conservation Area (5.53 ± 0.35 km^2) did not differ significantly from the mean seasonal home range size

Table 2. Summary of individual home range size per lion (100% MCP; 95% KDE; 50% KDE) for the Royal Pride, at the Tula Conservation Area, South Africa

Lion	MCP	KDE 95%	KDE 50%
Male 1 (RM1)	6.81	5.47	1.69
Female 1 (RF1)	6.33	5.32	1.59
Subadult Male 1 (RSM1)	6.31	5.21	1.58
Subadult Male 2 (RSM2)	6.31	5.21	1.61
Subadult Female 1 (RSF1)	6.31	5.21	1.61

Table 3. Summary of individual home range size per lion (100% MCP; 95% KDE; 50% KDE) for theRoyal Pride, at the Tula Conservation Area, South Africa

Lion	MCP	KDE 95%	KDE 50%
Male 1 (TM1)	6.58	5.64	1.62
Male 2 (TM2)	6.89	5.72	1.61
Female 1 (TF1)	6.52	5.53	1.58
Female 2 (TF2)	6.79	5.61	1.61
Subadult Male 1 (TSM1)	6.51	5.37	1.61
Subadult Male 2 (TSM2)	6.51	5.37	1.61
Subadult Female 1 (RSF1)	6.51	5.37	1.58

Table 4. Annual home range size and movement metrics of lions in the Tula Tsau Conservation Area, South Africa, between 2010 to 2011 (Royal Pride) and 2018 to 2020 (Tsau Pride) (adult males: *n* = 3; adult females: *n* = 3; subadult males: *n* = 4; subadult females: *n* = 2).

Home Range	All Years	Males	Females
50% Kernel Density Estimator (km^2)	1.76 ± 0.10 (1.61–1.87)	1.85 ± 0.31 (1.48–2.24)	1.79 ± 0.32 (1.47–2.20)
95% Kernel Density Estimator (km^2)	5.53 ± 0.35 (5.50–5.64)	5.55 ± 0.21 (5.20–5.75)	5.50 ± 0.23 (5.14–5.71)
100% Minimum Convex Polygon (km^2)	5.70 ± 0.23 (5.32–6.25)	5.75 ± 0.21 (5.41–6.14)	5.63 ± 0.41) (5.60–5.66)
Daily Distance (km)	10.91 ± 4.90 (0.01–19.22)	11.54 ± 5.12 (0.01–19.30)	11.31 ± 4.94 (0.01–19.30)

Table 5. Seasonal home range size and movement metrics of lions in the Tula Tsau Conservation Area, South Africa, between 2010 to 2011 (Royal Pride) and 2018 to 2020 (Tsau Pride) (adult males: *n* = 3; adult females: *n* = 3; subadult males: *n* = 4; subadult females: *n* = 2).

Home Range	All Seasons	Summer (Wet)	Winter (Dry)
50% Kernel Density Estimator (km^2)	1.83 ± 0.28 (1.37–2.47)	1.89 ± 0.39 (1.37–2.47)	1.77 ± 0.17 (1.58–2.10)
50% Kernel Density Estimator (km^2)	5.33 ± 0.34 (5.07–5.70)	5.44 ± 0.21 (5.14–5.70)	5.21 ± 0.11 (5.07–5.35)
100% Minimum Convex Polygon (km^2)	5.57 ± 0.20 (5.15–5.98)	5.65 ± 0.21 (5.15–5.98)	5.48 ± 0.19 (5.20–5.70)
Daily Distance (km)	9.46 ± 4.59 (0.01–18.24)	9.62 ± 4.75 (0.01–18.51)	9.29 ± 4.41 (0.01–17.96)

Table 6. Pride home range size of lions in the Tula Tsau Conservation Area, South Africa, between 2010 to 2011 (Royal Pride) and 2018 to 2020 (Tsau Pride) (adult males: *n* = 3; adult females: *n* = 3; subadult males: *n* = 4; subadult females: *n* = 2).

Home Range	Royal Pride	Tsau Pride
50% Kernel Density Estimator (km^2)	1.76 ± 0.10 (1.61–1.87)	1.81 ± 0.29 (1.47–2.24)
50% Kernel Density Estimator (km^2)	5.57 ± 0.35 (5.50–5.64)	5.51 ± 0.21 (5.14–5.75)
100% Minimum Convex Polygon (km^2)	5.65 ± 0.82 (5.57–5.86)	5.70 ± 0.23 (5.32–6.25)

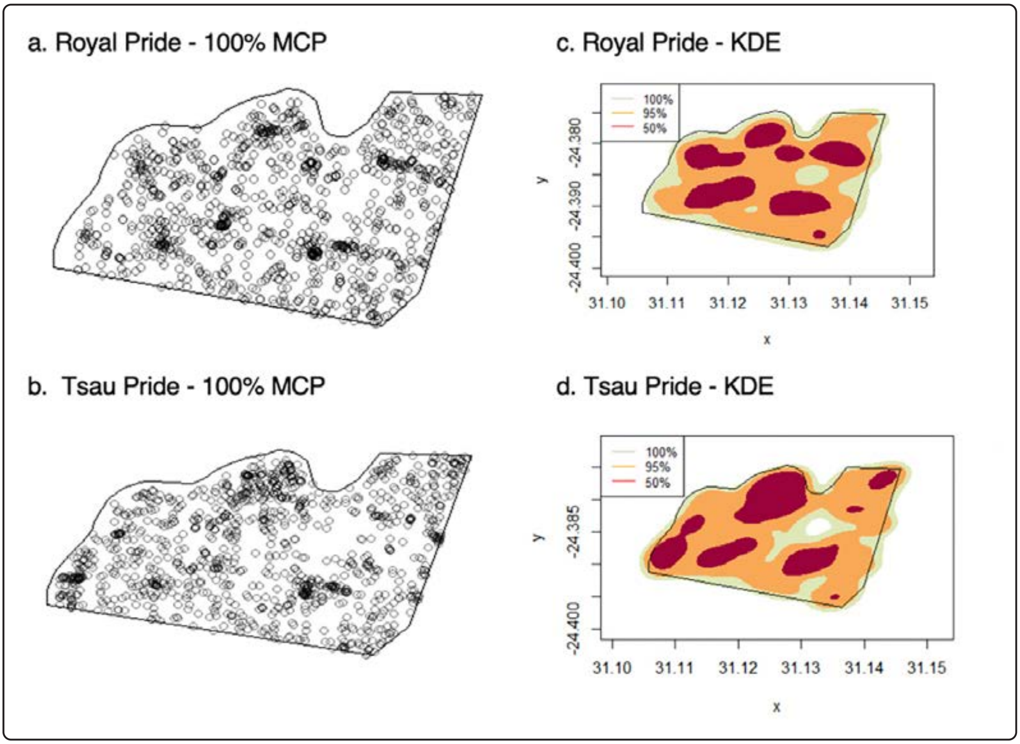

Figure 3 **Recorded locations and home range distribution for the Royal and Tsau prides, using 100% MCP(a,b), and KDE(100%, 95% and 50%) (c,d).**

(5.33 ± 0.34 km^2) (95% KDE; X^2 = 2.561, df = 1, *p*-value = 0.109). No difference in size was found between wet season home ranges and dry season home ranges for the Tula Tsau Conservation Area (Table 5; Figure 4). Seasonal home ranges (95% KDE and 100% MCP) for males and females did not differ significantly in size, or between prides (Table 5) (Figures 4-6). The home range size for the white lion males of the Royal pride was similar to that of the white lion males of the Tsau Pride (Tables 2 and 3; Figure 5). Core home ranges (50% KDE) were consistent for sex, season, and pride (Tables 4-6).

The average potential minimum distance traveled within 12 hours by lions from the Tula Tsau Conservation Area was 10.91 ± 4.90 km. There was no significant difference between the average distance traveled by the Royal pride (10.44 ± 4.82 km) and the Tsau pride (11.37 ± 4.72 km) (X^2 = 0.719, df = 1, *p*-value = 0.290). Males and females from both prides traveled similar distances (Table 4; Figure 4), with a maximum of 19.30 km traveled in 12 hours by male M and female T from the Tsau pride. The distance traveled by lions at the Tula Tsau Conservation Area was not affected by season (Table 5; Figure 4).A summary of home range size and movement metrics for the different variables tested is given in Tables 4-6 and Figure 4.

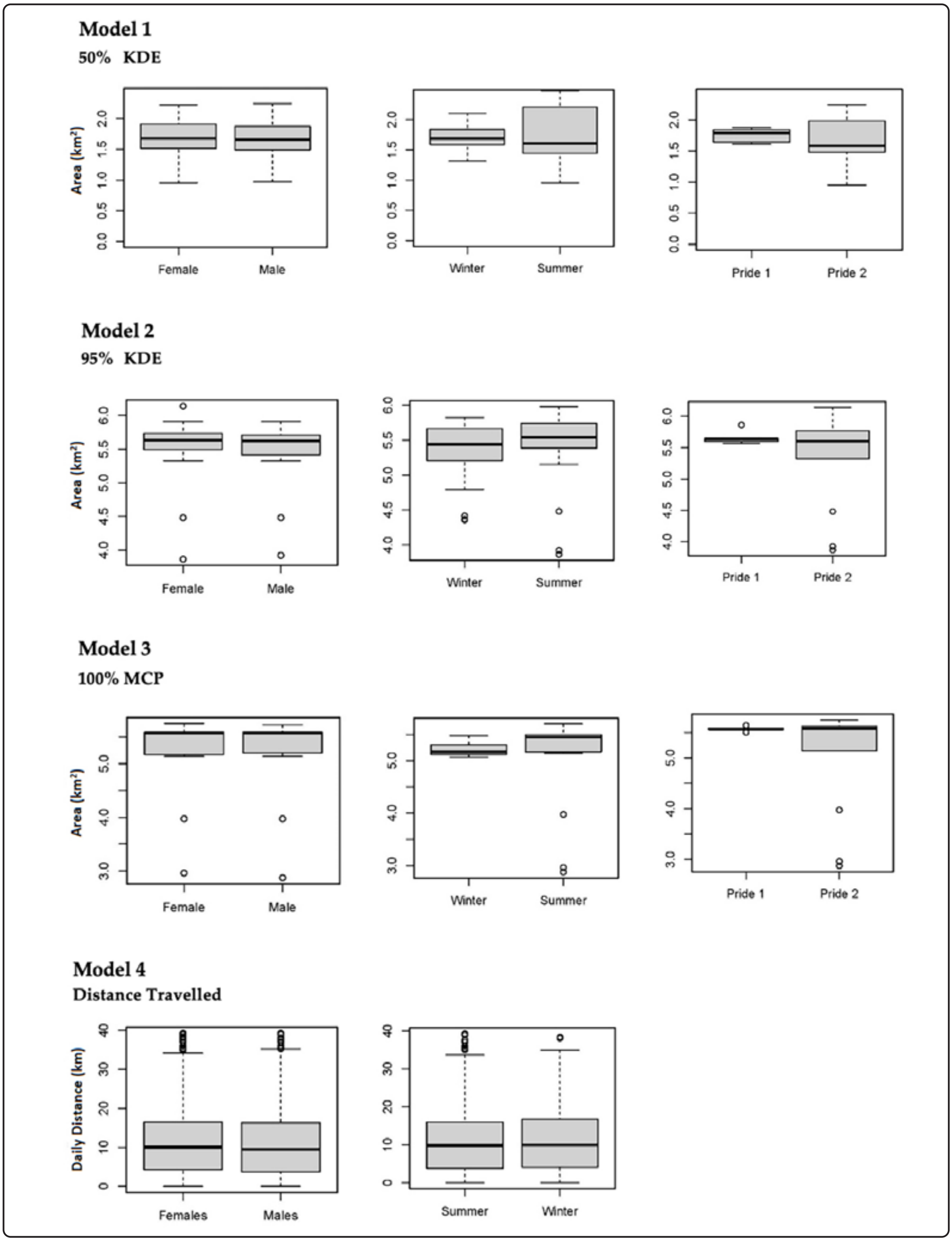

Figure 4 Differences in home range size and movement metrics for the different variables tested for lions at the Tula Tsau Conservation Area, between 2010 and 2011 (Royal Pride) [Pride 1] and 2018 and 2020 (Tsau Pride) [Pride 2]. The box plot method was used; showing upper and lower limits, the median value, and open circles indicating outlier values.

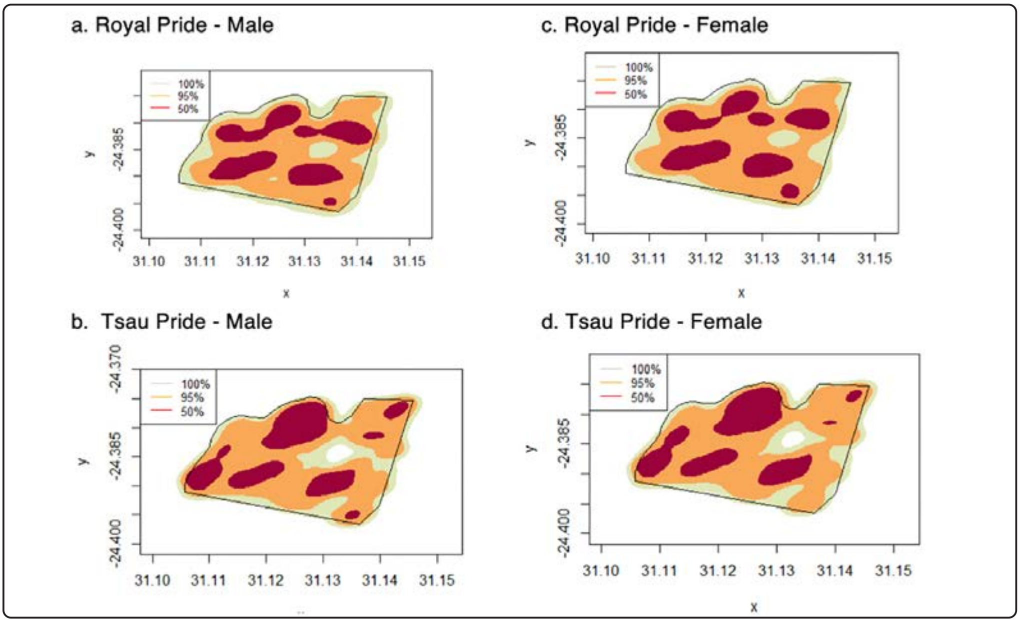

Figure 5 Home range distribution for male and female lions for the Royal and Tsau prides, using KDE (100%, 95% and 50%) (**a-d**), Tula Tsau Conservation Area, Limpopo, South Africa.

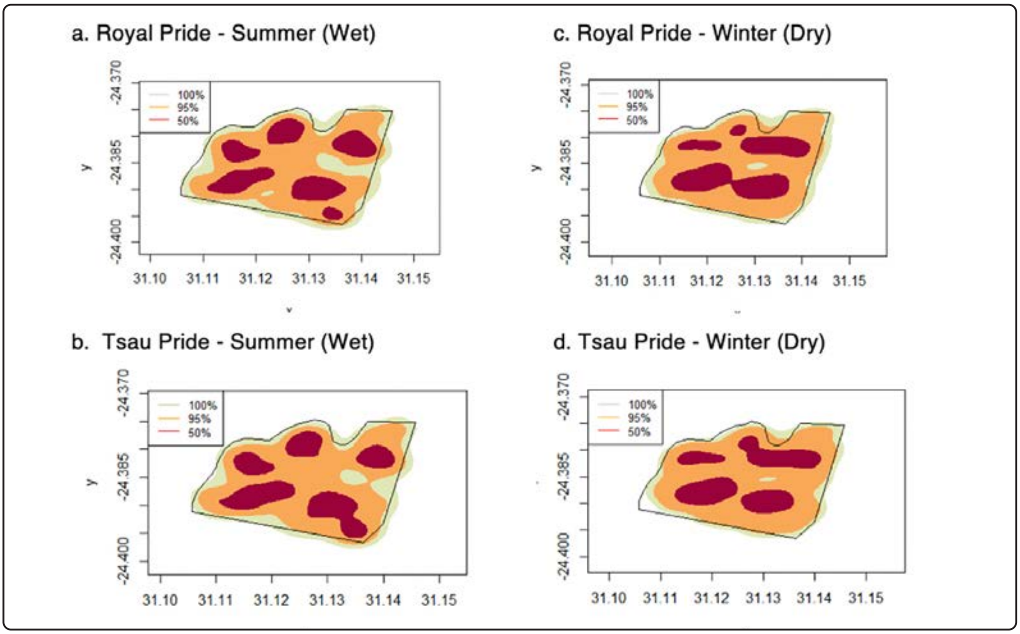

Figure 6 Seasonal home range distribution for the summer (wet) and winter (dry) seasons, for the Royal and Tsau prides, using KDE (100%, 95% and 50%) (**a-d**), at the Tula Tsau Conservation Area, Limpopo, South Africa.

Table 7. Habitat selection by the Royal and Tsau prides at Tula Tsau Protected Area (TTPA), South Africa.

Vegetation Type	Proportion of TTPA	Royal Pride	Royal Pride	Tsau Pride	Tsau Pride
Woodland	12%	1.595	0.288	1.052	0.184
Plains	13%	0.239	0.043	0.390	0.068
Riverine	27%	1.193	0.216	1.299	0.227
Thicket	48%	2.502	0.453	2.980	0.521

Wi: selection index; values above 1.0 indicate preference; values less than 1.0 indicate avoidance.

Bi: standardised selection index, which allows comparisons; values below 0.250 indicate relative avoidance; values above 0.250 indicate relative preference.

3.3.2 Habitat Selection

The habitat analysis showed that the most preferred habitat selected by both the Royal pride and the Tsau pride was thickets (Table 7). This habitat type was the largest habitat type at Tula Tsau Conservation Area. The Royal pride also showed a preference for woodland habitat, avoiding plains. The Tsau pride showed some preference for woodland, but similarly avoided plains habitat. Riverine habitat was the second largest habitat type but was avoided by both the Royal and Tsau prides.

3.4 Discussion

Establishing a home range is important for a territorial species and is therefore indicative of short-term reintroduction success. The Royal and Tsau prides occupied the Tula Tsau Conservation Area at different times, but both established home ranges and had defined movement patterns within the fenced reserve. The home range behaviour between both prides was similar. Ranging dynamics for the study prides were compared to that of previously studied captive-origin and wild tawny prides.

The home range dynamics of the reintroduced white lion pride (Royal pride) was similar to that of the constructed pride of white and tawny lions (Tsau pride) at an individual and a pride level, with a home range that extended over the majority of the reserve (Figure 3). The difference in the study period for the two prides is unlikely to have had an impact on the results since both prides existed on the same reserve, which had similar climatic conditions, prey composition, and prey abundance across all studied years. Average rainfall for both study periods was comparable and similar to the long-term average rainfall calculated between 2000 and 2020. Being a small fenced reserve with predators, including lions, spotted hyaena, and leopard, the prey population is replenished on an annual basis and maintained at the ecological carrying capacity of the reserve. Dunston et al. (2017) similarly found captive-origin tawny lion prides to establish home ranges within small reserves in Zambia and Zimbabwe. The first of these prides occupied a 1.5 km^2 territory within a 1.7 km^2 reserve (76%) and the other pride had a 2.2 km^2 territory within a 2.9 km^2 reserve (88%). The reintroduced white lion pride and constructed pride of white and tawny lions therefore established a home range in a similar way to these previously studied captive-origin tawny prides.

In larger or unfenced reserves in South Africa with a similar habitat type and prey density, wild lion prides establish larger home ranges that do not typically extend over the majority of the reserve, as was observed for wild tawny lion prides at the Phinda Resource Reserve (KwaZulu-Natal), and Greater Makalali Private Nature Reserve (Limpopo Province) [52,58]. In accordance with wild prides in other studies, the Makalali pride established larger home ranges (28.5 km^2 and 56 km^2 within a 234.8 km^2 reserve) extending over only 12 to 24% of the reserve (Dunston et al. 2017), based on prey density and factors that reflect prey availability, such as environment and season (Spong 2002; Bauer & De Iongh 2005; Loveridge et al. 2009; Davidson et al. 2012; Tuqa et al. 2014). Similar to the captive origin-prides studied by Dunston et al. (2017), the Royal and Tsau prides showed signs of natural ranging behaviour within the limited available area. Although the reserve size, and consequential lion home range size, for the Royal and Tsau prides were significantly smaller than the estimated territory sizes of wild prides; a range of 50 to 7400 km^2 (Loveridge et al. 2009; Davidson et al. 2012; Tumenta et al. 2013; Tuqa et al. 2014), and a mean territory size of 56 km^2 (a range of 15-219 km^2), nearly 20% of the wild lion population in South Africa is protected within 49 smaller fenced reserves, with several of them being significantly smaller than the Greater Makalali Private Game Reserve: Mabula Game Reserve (16.5 km^2), Thanda Private Game Reserve (70 km^2), Karongwe Game Reserve (79 km^2), Thornybush Nature Reserve (116 km^2), and Shamwari Game Reserve (139 km^2) (Miller et al. 2015). In many of these South African reserves, interventionist conservation management of territorial large carnivores has taken place, where farmland has been rehabilitated into game reserves and many species have been reintroduced (Garai et al. 2004; Gusset et al. 2008; Slotow & Hunter 2008). A restricted reserve size means the lion pride(s) need to be intensively managed to ensure overpopulation and inbreeding of lions does not occur, that a balance between all predator populations exists and that prey populations are not depleted. Regular translocation and manipulation of pride structure are often necessary (e.g., replacement of pride males with new males to promote genetic diversity or breeding control of females), disrupting the pride social structure (Kettles & Slotow 2008; Miller et al. 2013). In fenced reserves that have more than one pride present, the smaller the reserve, the higher the intraspecific and interspecific competition, territorial stress, and the more likely that lions may break out of the reserve into a neighbouring property or community-owned land, potentially becoming damage-causing animals (ie. a threat to livestock and human life) (Tumenta et al. 2012; Miller et al. 2013). A better understanding of home range behaviour and dynamics of lions in smaller reserves is therefore important for successful pride reintroduction and management. This is particularly important for the management of white lions, which were extirpated due to anthropogenic activities and are still under threat due to trophy hunting in parts of their natural habitat, meaning intensive management of these prides will be required for the near future.

The home range size of the pride males and lionesses for the Royal and Tsau prides were not significantly different due to the small and limited reserve size, and the fact that resource availability and access to females for both prides were satisfied by occupying the majority of the reserve. Abundant food and high-quality habitat allow an animal to meet its biological requirements in a relatively small home range (Gittleman & Harvey 1982; MacDonald 1983). Home ranges of male lions are often larger than those of females and may encompass two or more female prides (Funston et al. 2003; Hunter 1998; Funston 1999; Nilsen et al. 2005). The home range size and establishment of a territory by wild prides may be influenced by the presence of other prides and male coalitions (Schaller 1972), as has been observed for wild prides in Kruger National Park (Van Orsdol et al. 1985), Phinda Resource Reserve (Hunter 1998), Welgevonden Private Game Reserve (Kilian 2003), and the Greater Makalali Private Nature Reserve (Druce et al. 2004; Dunston et al. 2017). The Royal and Tsau prides were not influenced by other prides or male coalitions since the Tula Tsau Conservation Area was not large enough to support more than one pride. Although pride males and lionesses for both prides utilised the majority of the available home range, the males were often located at the reserve fence boundary in response to the territorial roaring and presence of pride males on the neighbouring Kapama, Thornybush and Timbavati Private Nature Reserves. Dunston et al. (2017) had similar observations for the males from captive-origin prides, which were regularly located close to the reserve boundary, in response to the external stimuli of large game species and roaring of lions on the other side of the boundary fence. We therefore postulate that the white lion males from the Royal and Tsau prides may establish larger home ranges in a similar way to wild lions, if the reserve size was larger. In support of our postulation, Hayward et al. (2008) concluded that the use of fences has not affected the natural ranging behaviour of predators, with prey abundance still being the key factor determining space use in fenced reserves. The white lioness from the Royal pride and white lion males from both prides therefore showed natural home range behaviour consistent with adapting to the limited reserve size, suggesting that the reintroduced captive-origin white lions and the constructed pride of white and tawny lions made optimum use of the available habitat.

The absence of seasonal variation in home range size for either the Royal or Tsau prides, or between males and females for either pride, is likely a reflection of the abundant prey availability and accessibility year-round due to the small reserve size, annual restocking with prey species, and high availability of water (Turner et al. 2015). Seasonal variation in the home range size of wild prides has been observed in regions where there is a distinct wet and dry season, such as at the Phinda Resource Reserve in KwaZulu-Natal (South Africa), Greater Makalali Private Game Reserve in Limpopo (South Africa), Dinokeng Private Game Reserve in Gauteng and Limpopo Provinces (South Africa), and the Cenral Kalahari Game Reserve in Botswana (Hunter 1998; Druce et al. 2004; Yiu et al. 2017; Zehnder et al. 2018). However, a lack of seasonal variation in home range size has also been found for wild lion prides (Van Orsdol et al. 1985; Bauer & De Iongh 2005), such as in Nairobi National Park (Kenya) (Lesilau et al. 2021), and Majete Wildlife Reserve (Malawi) (Briers-Louw & Leslie 2017), which are smaller fenced reserves (<1000 km^2) with a high prey density and availability of water. Although the Greater Makalali Private Game Reserve experienced a similar climate to the Tula Tsau Conservation Area, seasonal variation in home range size was observed for the wild prides in that reserve due to the much larger reserve size and greater incidence of pride dispersal. Our study therefore concluded that both the reintroduced white lion pride and the constructed pride of white and tawny lions showed no seasonal variation in ranging behaviour, which is consistent with natural wild prides in small reserves that have a high prey abundance and availability of artificial water sources.

The distance moved by the Royal and Tsau prides was comparable, and there was no difference in the distance moved by male lions and lionesses for either pride. The limited reserve size could support only one pride and meant pride males did not have to move between prides and females did not have to move significant distances to find potential prey. The significant variability in the size of lion home ranges, ranging between 50 and 7400 km^2 (Loveridge et al. 2009; Davidson et al. 2012; Tumenta et al. 2013; Tuqa et al. 2014) means that lions are known to move up to 20 km in 24 hours and to cover hundreds of kilometres over several months (Tuqa et al. 2014). Although the average distance traveled by the Royal and Tsau prides was calculated over 12 hours and not 24 hours as in other studies, such as those of Hunter (1998) and Lesilau et al. (2021), the level of activity of these prides during the 12 h observed was comparable to that of wild prides studied in similar woodland and plains habitats. Hanby et al. (1995) observed inactivity to occur at 79% for a pride in the Ngoronoro Crater (woodland) and 78.5% for a pride on the Serengeti Plains (plains), compared to 81.7% for the Royal pride and 84.1% for the Tsau pride, during the 12-hour observation period. The mean and maximum distance traveled by the Royal and Tsau prides (10.91 km; 19.3 km) was comparable to that observed for wild prides in the Nairobi National Park (4.5 km; 29.9 km) (Lesilau et al. 2021) and Karongwe Game Reserve (5.4 km; 24.0 km) (Lehmann et al. 2008), which also had small home ranges of 14-51 km^2 (95% KDE) and 35-69 km^2 (95% KDE), respectively. This is in agreement with Lesilau's (2019) conclusion that areas of high prey density seem to result in small home ranges and short daily distances traveled by lions, which suggests that the average distance traveled for white lions may be similar to that of tawny lions. The reintroduced white lions therefore showed natural ranging behaviour within the available sized reserve.

The habitat preference of the Royal and Tsau prides for thickets and woodland vegetation rather than open plains was not surprising since lions are ambush predators. Vegetation cover is more significant than type of terrain, since hunting lions usually use vegetation patches to stalk closer to their prey, or they wait hidden until their prey is sufficiently close to attack (Husseman et al. 2003; Gorini et al. 2012). The slight difference in preference for the selected habitat types by the Royal and Tsau prides was most likely due to the difference in pride structure, with the Tsau pride having two adult males and females, compared to one adult male and female in the Royal pride. A coalition of pride males typically spends little time with the pride, being away patrolling their territory and hunting more effectively as a coalition (Funston 1999). Within Africa, lions are found in a range of habitats from open to closed woodland and have adapted to survive in the arid outskirts of deserts bordering the dense tropical Congo forest (Riggio et al. 2013). Many lion studies have found a preference for riverine vegetation (Hayward et al. 2008; Dunston et al. 2017; Lesilau et al. 2021), which was not observed in our study. The apparent avoidance of riverine vegetation by the prides in our study was due to research vehicles being unable to access and view the lions when in this vegetation type rather than to the prides avoiding use of this habitat. The proximity to natural or artificial water sources has been found to be an important factor in lion ranging behaviour. The provision of artificially supplied water during the dry period in wildlife reserves may affect the movement patterns of ungulates (Western 1975; Mills & Retief 1984; Owen-Smith 1996), and as a result the distribution and ranging patterns of predators such as lions. This was evident at the Tula Tsau Conservation Area, where the home range of the Royal and Tsau prides were centred around the high number of artificial and natural water sources. Dunston et al. (2017) had similar observations for the captive-origin prides in Zimbabwe and Zambia, and the wild prides at the Greater Makalali Private Game Reserve. The availability of water and consequential high prey abundance have been found to be significant factors in the home range behaviour of wild lion prides at Phinda Resource Reserve, Karongwe Game Reserve, Central Kalahari Game Reserve, and Nairobi National Park (Hunter 1998; Lehmann et al. 2008; Zehnder et al. 2018; Lesilau et al. 2021). The findings for the habitat preference and home range behaviour of both the prides in our study therefore show similarities to those for wild prides, and accordingly suggest that the home range behaviour of white lions seems to be similar to that of tawny lions.

The natural home range behaviour of the Royal and Tsau prides post-release was an indication of their reintroduction being successful. We believe that the movements and home ranges of these lions may also have been influenced by the fenced areas in which they are kept. We postulate that in the absence of anthropogenic threats (artificial removal to breeding camps, culling and trophy hunting), white lions are capable of surviving in their natural habitat. This is supported by the fact that captive-origin white lions have been determined to show similar hunting success and social behaviour to wild tawny lions (Turner et al. 2015; Turner et al. 2022), and wild white lions have been observed to survive successfully and reproduce in their natural habitat (McBride 1981; Tucker 2003; Cesare 2011; Dicks 2022).

The present study has a number of limitations, namely the small size of the fenced reserve, prides, and sample size, and the difference in the time periods covered. At the time of our study, there were no adult white lions in the wild, and a future study is therefore recommended when the prides in the Timbavati Private Nature Reserve and Kruger National Park will have adult white lions. The home range behaviour of the white lion pride should ideally have been compared to that of a wild tawny pride, and not a constructed pride of white and tawny lions. Future studies should compare the home range behaviour and movements of larger prides of free-roaming white and tawny lions in big reserves or ecosystems that are at least the mean home range size for wild lions (56 km^2), and ideally within the open system of the Timbavati Private Nature Reserve or Kruger National Park. The living circumstances of the prides and vegetation differences also need to be considered when conducting comparisons between captive-origin and wild prides. We did not have a sample of truly independent samples and the conclusions should therefore be viewed as preliminary. Hence, further work in this area is recommended.

3.5 Conclusions

The present study suggests that the home ranging behaviour and movement of white lions was similar to that of tawny lions within small fenced reserves. This indicates that the reintroduction of captive-origin white lions into their natural habitat was successful, despite the limited reserve size. The reintroduction of white lions at the Tula Tsau Conservation Area is important in securing a protected subpopulation since the anthropogenic threat of trophy hunting still exists in parts of the species' natural range. This study provides critical information for the metapopulation management of lions and informs the use of reintroduced and constructed prides for lion conservation.

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Conflicts of Interest: The authors declare no conflict of interest.

References

1. Appelhans, T.; Detsch, F.; Reudenbach, C.; Woellauer, S. 2021. Mapview: Interactive Viewing of Spatial Data in R; R Package Version 2.10.0. Available online: https://CRAN.R-project.org/package=mapview (accessed on 15 July 2022).
2. Baddeley, A.; Rubak, E.; Turner, R. 2015. *Spatial Point Patterns: Methodology and Applications with R*; Chapman and Hall/CRC Press: London, UK. Available online: https://www.routledge.com/Spatial-Point-Patterns-Methodology-and-Applications-with-R/Baddeley-Rubak-Turner/9781482210200/ (accessed on 15 January 2023).
3. Baillie, J.; Collen, B.; Griffiths, J.; Loh, J.; Turvey, S. 2010. *Evolution Lost: Status and Trends of the World's Vertebrates*; Zoological Society of London: London, UK.
4. Bauer, H.; De Iongh, H.H. 2005. Lion (*Panthera leo*) home ranges and livestock conflicts in Waza National Park, Cameroon. *Afr. J. Ecol., 43*, 208–214.
5. Bell, R.H.V. 1982. The Effect of Soil Nutrient Availability on Community Structure in African Ecosystems. *Ecol. Stud., 42*, 193–216. https://doi.org/10.1007/978-3-642-68786-0_10.
6. Bertram, B. 1973. Lion population regulation. *Afr. Wildl. J.*, 2, 215–225.
7. Bivand, R.; Keitt, T.; Rowlingson, B. 2021. Rgdal: Bindings for the 'Geospatial' Data Abstraction Library; R Package Version 1.5-27. Available online: https://CRAN.R-project.org/package=rgdal (accessed on 18 July 2022).
8. Bivand, R.; Lewin-Koh, N. 2022. Maptools: Tools for Handling Spatial Objects; R Package Version 1.1-4. Available online: https://r-forge.r-project.org/projects/maptools (accessed on 5 January 2022).
9. Blondel, E. 2021. Cleangeo: Cleaning Geometries from Spatial Objects; R Package Version 0.2-4. Available online: https://CRAN.R-project.org/package=cleangeo (accessed on 18 July 2022).
10. Briers-Louw, W.; Leslie, A. 2017. Ecology of Three Apex Predators in Majete Wildlife Reserve, Malawi. Master's Thesis, University of Stellenbosch, Stellenbosch, South Africa. https://doi.org/10.13140/RG.2.2.18243.22563.
11. Burt, W.H. 1943. Territoriality and home range concepts as applied to mammals. *J. Mammal., 24*, 346–352.
12. Cardillo, M.; Purvis, A.; Sechrest, W.; Gittleman, J.L.; Biebly, J.; Mace, G.M. 2004. Human population density and extinction risk in the world's carnivores. *PLoS Biol., 2*, 909–914.
13. Carslaw, D.C.; Ropkins, K. 2012. Openair—An R package for air quality data analysis. Environ. Model. Softw., 27–28, 52–61.
14. Castley, J.G.; Knight, M.H.; Mills, M.G.L.; Thouless, C. 2002. Estimation of the lion (Panthera leo) population in the southwestern Kgalagadi Transfrontier Park using a capture-recapture survey. Afr. Zool., 37, 27–34.
15. Celesia, G.G.; Townsend Peterson, A.; Kerbis Peterhans, J.C.; Gnoske, T.P. 2009. Climate and landscape correlates of African lion (*Panthera leo*) demography. *Afr. J. Ecol., 48*, 58–71.

16. Cesare, M. 2011. *Man-Eaters, Mambas and Marula Madness: A Game Ranger's Life in the Lowveld*; Jonathan Ball Publishing: Johannesburg, South Africa, Pp. 432.
17. Cheng, J.; Karambelkar, B.; Xie, Y. 2021. Leaflet: Create Interactive Web Maps with the JavaScript 'Leaflet' Library; R Package Version 2.0.4.1. Available online: https://CRAN.R-project.org/package=leaflet (accessed on 15 July 2022).
18. Cho, Y.S.; Hu, L.; Hou, H.; Lee, H.; Xu, J.; Kwon, S.; Oh, S.; Kim, H.-M.; Jho, S.; Kim, S.; et al. 2013. The tiger genome and comparative analysis with lion and snow leopard genomes. *Nat. Commun., 4*, 2433. https://doi.org/10.1038/ncomms3433.
19. Cruickshank, K.M.; Robinson, T.J. 1997. Inheritance of the White Coat Colour Phenotype in African Lions (*Panthera leo*). In *Proceedings of a Symposium on Lions and Leopards as Game Ranch Animals*; Van Heerden, J., Ed.; Wildlife Group of the South African Veterinary Association: Pretoria, South Africa, Pp. 92–95.
20. Davidson, Z.; Valeix, M.; Loveridge, A.J.; Hunt, J.E.; Johnson, P.J.; Madzikanda, H.; Macdonald, D.W. 2012. Environmental determinants of habitat and kill site selection in a large carnivore: Scale matters. *J. Mammal., 93*, 677–685.
21. Dicks, T.; South Africa's White Lions. Wandering Through Photo Safaris and Expeditions. 2022. Available online: https://wanderingthru.com/the-white-lions-of-south-africa/ (accessed on 5 January 2023).
22. Druce, D.; Genis, H.; Braak, J.; Greatwood, S.; Delsink, A.; Kettles, R.; Hunter, L.; Slotow, R. 2004. Population demography and spatial ecology of a reintroduced lion population in the Greater Makalali Conservancy, South Africa. Koedoe, 47, 103-118.
23. Dunnington, D. 2021. Ggspatial: Spatial Data Framework for Ggplot2; R Package Version 1.1.5. Available online: https://CRAN.R-project.org/package=ggspatial (accessed on 18 July 2022).
24. Dunston, E.; Abell, J.; Doyle, R.; Duffy, D.; Poynter, C.; Kirk, J.; Hilley, V.; Forsyth AJenkins, E.; McAllister, D.; Freire, R. 2017. Does captivity influence and hunting behaviour? Assessment for an ex situ reintroduction program of African lions *Panthera leo. Mamm. Rev., 47*, 254–260. https://doi.org/10.1111/mam.12101.
25. Duong, T.; Smoothing, K. 2021. R Package Version 1.13.2. Available online: https://CRAN.R-project.org/package=ks (accessed on 15 July 2022).
26. Ferreira, S.M.; Funston, P.J. 2010. Estimating lion population variables: Prey and disease effects in Kruger National Park, South Africa. *Wildl. Res., 37*, 194–206.
27. Funston, P.J.; Mills, M.G.L.; Biggs, H.C.; Richardson, P.R.K. 1998. Hunting by male lions: Ecological influences and socioecological implications. Anim. Behav., 56, 1333–1345.
28. Funston, P.J.; Mills, M.G.L.; Richardson, P.R.K.; van Jaarsveld, A.S. 2003. Reduced dispersal and opportunistic territory acquisition in male lions *Panthera leo. J. Zool., 259*, 131–142.
29. Funston, P.J. 2010. *Greater Mapungubwe TFCA Predator Management Plan*; Unpublished report; Shashe Limpopo Predator Research Group, Bulawayo, Zimbabwe.
30. Funston, P.J. 2011. Population characteristics of lions (*Panthera leo*) in the Kgalagadi Transfrontier Park. *S. Afr. J. Wildl. Res., 41*, 1–10.

31. Funston, P.J.; Levendal, M. Draft Biodiversity Management Plan for the lion (*Panthera leo*) in South Africa. 2014. Available online: https://www.gov.za/sites/default/files/gcis_document/201512/39468gen1190.pdf (accessed on 27 January 2023).
32. Garai, M.E.; Slotow, R.; Reilly, B.; Carr, R.D. 2004. History and success of elephant reintroductions to small fenced reserves in South Africa. *Pachyderm*, 37, 28–36.
33. Gittleman, J.L.; Harvey, P.H. 1982. Carnivore home-ranges size, metabolic needs and ecology. *Behav. Ecol. Sociobiol., 10*, 57–63. https://doi.org/10.1007/BF00296396.
34. Gorini, L.; Linnell, J.D.C.; May, R.; Panzacchi, M.; Boitani, L.; Odden, M.; Nilsen, E.B. 2012. Habitat heterogeneity and mammalian predator-prey interactions. *Mamm. Rev., 42*, 55–77.
35. Gusset, M.; Ryan, S.J.; Hofmeyr, M.; Van Dyk, G.; Davies-Mostert, H.T.; Graf, J.A.; Owen, C.; Szykman, M.; Macdonald, D.W.; Monfort, S.L.; et al. 2008. Efforts going to the dogs? Evaluating attempts to re-introduce endangered wild dogs in South Africa. *J. Appl. Ecol., 45*, 100–108.
36. Hanby, J.P.; Bygott, J.D.; Packer, C. 1995. Ecology, Demography, and Behavior of Lions in Two Contrasting Habitats: Ngorongoro Crater and Serengeti Plains. In *Serengeti II: Dynamics, Management, and Conservation of an Ecosystem*; Sinclair, A.R.E., Arcese, P., Eds.; The University of Chicago Press: Chicago, USA, Pp. 315–331.
37. Hayward, M.; Hayward, G.; Druce, D.; Kerley, G. 2008. Do fences constrain predator movements on an evolutionary scale? Home range, food intake and movement patterns of large predators reintroduced to Addo Elephant National Park, South Africa. *Biodiv. Cons., 18*, 887–904. https://doi.org/10.1007/s10531-008-9452-y.
38. Hayward, M.W.; Slotow, R. 2009. Temporal partitioning of activity in large African carnivores: Tests of multiple hypotheses. *S. Afr. J. Wild. Res., 39*, 109–125.
39. Hijmans, R.J. 2021. Raster: Geographic Data Analysis and Modeling; R Package Version 3.4-13; 2021. Available online: https://CRAN.R-project.org/package=raster (accessed on 18 July 2022).
40. Hunter, L.T.B. 1998. Behavioural Ecology of Reintroduced Lion and Cheetahs in the Phinda Resource Reserve, Kwa-Zulu Natal, South Africa. Ph.D. Thesis, Pretoria University, Pretoria, South Africa.
41. Hunter, L.T.B.; Pretorius, K.; Carlisle, L.C.; Rickelton, M.; Walker, C.; Slotow, R.; Skinner, J.D. 2007. Restoring lions *Panthera leo* to northern KwaZulu-Natal, South Africa: Short-term biological and technical success but equivocal long-term conservation. *Oryx, 41*, 196–204.
42. Husseman, J.S.; Murray, D.L.; Power, G.; Mack, C.; Wenger, C.R.; Quigley, H. 2003. Assessing differential prey selection patterns between two sympatric large carnivores. *Oikos, 101*, 591–601.
43. Kerley, G.; Behrens, K.; Carruthers, J.; Diemont, M.; Du Plessis, J.; Minnie, L.; Richardson, P.; Somers, M.; Tambling, C.; Turpie, J.; et al. 2017. Livestock predation in South Africa: The need for and value of a scientific assessment. *S. Afr. J. Sci., 113*, 1-3. 10.17159/sajs.2017.

44. Kettles, R.; Slotow, R. 2009. Management of free-ranging lions on an enclosed game reserve. *S. Afr. J. Wild. Res., 39*, 23–33.
45. Kilian, P.J. 2003. The Ecology of Reintroduced Lions on the Welgevonden Private Game Reserve, Waterberg. Master's Thesis, University of Pretoria, Pretoria, South Africa.
46. Kitchener, A.C.; Breitenmoser-Würsten, C.; Eizirik, E.; Gentry, A.; Werdelin, L.; Wilting, A.; Yamaguchi, N.; Abramov, A.V.; Christiansen, P.; Driscoll, C.; et al. 2016. A revised taxonomy of the Felidae. The final report of the Cat Classification Task Force of the IUCN Cat Specialist Group. *Cat News Spec. Issue, 11*, 80.
47. Kuznetsova, A.; Brockhoff, P.B.; Christensen, R.H.B. 2017. lmerTest package: Tests in linear mixed effects models. *J. Stat. Softw., 82*, 1–26.
48. Lehmann, M.B.; Funston, P.J.; Owen, C.R.; Slotow, R. 2008. Home range utilisation and territorial behaviour of lions (*Panthera leo*) on Karongwe Game Reserve, South Africa. *PLoS ONE, 3*, e3998.
49. Lesilau, F. *Human–Lion Conflict around Nairobi National Park*. 2019. Ph.D. Thesis, University of Leiden, Leiden, The Netherlands, 2019.
50. Lesilau, F.; Verschueren, S.; van't Zelfde, M.; Musters, K.C.; de Snoo, G.R.; de Iongh, H.H. 2021. Spatial ecology of lions in a small, semi fenced park surrounded by dense human populations: The case study of Nairobi National Park, Kenya. *Mammalia, 85*, 198–207. https://doi.org/10.1515/mammalia-2020-0116.
51. Linnaeus, C. 1758. The system of nature through three kingdoms of nature, according to the classes, orders, genera, and species with characters, differences, synonyms, and places. *Tomus I. Tenth Ed. Reform. Holmiae*., 1, 1–4.
52. Loveridge, A.J.; Valeix, M.; Davidson, Z.; Murindagomo, F.; Fritz, H.; Macdonald, D.W. 2009. Changes in home range size of African lions in relation to pride size and prey biomass in a semi-arid savanna. *Ecography, 32*, 953–962.
53. MacDonald, D.W. 1983. The ecology of carnivore social behaviour. *Nature, 301*, 379–383.
54. Manly, B.F.; McDonald, L.; Thomas, D.; McDonald, T.L.; Erickson, W.P. 2002. *Resource Selection by Animals: Statistical Design and Analysis for Field Studies*, 2nd ed.; Springer: Dordrecht, The Netherlands.
55. McBride, C. 1981. *Operation White Lion*; St. Martin's Press: New York, NY, USA, Pp. 159.
56. McDonald, T. 2005. *Ecological Management Plan: Tsau Wildlife Area*; Unpublished Report; Monzweni Eco-Developers, Hoedspruit, South Africa.
57. McEvoy, O.K.; Ferreira, S.M.; Parker, D.M. 2021. The influence of population demographics on lion (*Panthera leo*) growth rates in small, fenced wildlife reserves. *Afr. J. Wild. Res., 51*, 75–89. https://doi.org/10.3957/056.051.0075.
58. McNaughton, S.J. 1983. Serengeti Grassland Ecology: The Role of Composite Environmental Factors and Contingency in Community Organization. Ecol. Monogr., 53, 291–320. https://doi.org/10.2307/1942533.
59. Miller, S.M.; Bissett, C.; Parker, D.M.; Burger, A.; Courtenay, B.; Dickerson, T.; Naylor, S.; Druce, D.J.; Ferreira, S.; Slotow, R.; et al. 2013. Management of reintroduced lions in small, fenced reserves in South Africa: An assessment and guidelines. *S. Afr. J. Wild. Res., 43*, 138–154. https://doi.org/10.3957/056.043.0202.

60 Miller, S.M.; 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. Res., 44*, 43–55.
61. Miller, S.M.; Harper, C.K.; Bloomer, P.; Hofmeyr, J.; Funston, P.J. 2015. Fenced and fragmented: Conservation value of managed metapopulations. PLoS ON, 10, e0144605.
62. Miller, S.; Riggio, J.; Funston, P.; Power, R.J.; Williams, V.; Child, M.F. 2016. A Conservation Assessment of *Panthera leo*. In *The Red List of Mammals of South Africa, Swaziland and Lesotho*; Child, M.F., Roxburgh, L., Do Linh San, E., Raimondo, D., Davies-Mostert, H.T., Eds.; South African National Biodiversity Institute and Endangered Wildlife Trust: Midrand, South Africa., Pp. 48.
63. Mills, M.; & Retief, P. 1984. The effect of windmill closure on the movement patterns of ungulates along the Auob riverbed. *Koedoe Afr. Prot. Area Conserv. Sci., 27*, 107–118. https://doi.org/10.4102/koedoe.v27i2.572.
64. Mosser, A.; Packer, C. 2009. Group territoriality and the benefits of sociality in the African lion *Panthera leo. Anim. Behav., 78*, 359–370.
65. Mucina, L.; Rutherford, M.C. (Eds.). 2006. *The Vegetation of South Africa, Lesotho and Swaziland*; South African National Biodiversity Institute: Pretoria, South Africa, Pp. 19.
66. Nilsen, E.B.; Herfindal, I.; Linnell, J.D.C. 2005. Can intra-specific variation in carnivore home-range size be explained using remote sensing estimates of environmental productivity? *Ecoscience, 12*, 68–75.
67. Nowell, K.; Jackson, P. 1996. *Wild Cats: Status Survey and Conservation Action Plan*; IUCN/SSC: Gland, Switzerland, Pp 1- 382.
68. Owen-Smith, R.N. 1996. Ecological guidelines for waterpoints in extensive protected areas. *S.Afr. J. Wild. Res., 26*, 107–112.
69. Packer, C.; Scheel, D.; Pusey, A.E. 1990. Why lions form groups: Food is not enough. *Am. Nat., 136*, 1–19. Available online: https://doi.org/10.1086/285079.
70. Packer, C.; Hilborn, R.; Mosser, A.; Kissui, B.; Borner, M.; Hopcraft, G.; Wilmshurst, J.; Mduma, S.; Sinclair, A.R.E. 2005. Ecological change, group territoriality, and population dynamics in Serengeti lions. *Science, 307*, 390–393.
71. Packer, C.; Pusey, A.S.; Eberly, L.E. 2001. Egalitarianism in female African lions. *Science, 293*, 690–693.
72. Pebesma, E.J.; Bivand, R.S. 2005. Classes and methods for spatial data in R. R News, 5, 9–13. Available online: https://cran.r-project.org/doc/Rnews/ (accessed on 15 July 2022).
73. Pebesma, E. 2018. Simple Features for R: Standardized Support for Spatial Vector Data. R J., 10, 439–446. https://doi.org/10.32614/RJ-2018-009.
74. Powell, R.A. 2000. Animal Home Ranges and Territories and Home Range Estimators. In *Research Techniques in Animal Ecology: Controversies and Consequences*; Boitani, L., Fuller, T.K., Eds.; Colombia University Press: New York, USA, Pp. 64–110.
75. Powell, R.A.; Mitchell, M.S. 2012. What is home range? *J. Mamm., 93*, 948–958.
76. Power, J.R. 2003. Evaluating how many lions a small reserve can sustain. *S. Afr. J. Wildl. Res., 33*, 3–11.

77. R Core Team. 2020. *R: A Language and Environment for Statistical Computing*; R Foundation for Statistical Computing: Vienna, Austria. Available online: https://www.r-project.org/ (accessed on 15 January 2023).
78. Riggio, J.; Jacobson, A.; Dollar, L.; Bauer, H.; Becker, M.; Dickman, A.; Funston, P.; Groom, R.; Henschel, P.; de Iongh, H. 2013. The size of savannah Africa: A lion's *Panthera leo* view. *Biol. Cons., 22*, 17–35.
79. Ripple, W.J.; Estes, J.A.; Beschta, R.L.; Wilmers, C.C.; Ritchie, E.G.; Hebblewhite, M.; Berger, J.; Elmhagen, B.; Letnic, M.; Nelson, M.P.; et al. 2014. Status and ecological effects of the world's largest carnivores. *Science, 343*, 1241484. https://doi.org/10.1126/science.1241484.
80. Robinson, R.; De Vos, V. 1982. Chinchilla mutant in the lion. Genetica, 60, 61–63.
81. Rudnai, J.A. 1973. *The Social Life of the Lion*; Medical and Technical Publishing Co. Ltd.: Lancaster, UK, Pp. 122.
82. Schaller, G.B. 1972. *The Serengeti Lion*; The University of Chicago Press: London, UK.
83. Slotow, R.; Hunter, L.T.B. 2008. Reintroduction Decisions Taken at the Incorrect Social Scale Devalue Their Conservation Contribution: African Lion in South Africa. In *The Reintroduction of Top-Order Predators*; Hayward, M.W., Somers, M.J., Eds.; Blackwells Publishing: Oxford, UK.
84. Smuts, G.L. 1982. *Lion*; MacMillan: Johannesburg, South Africa.
85. Spong, G. 2002. Space use in lions, *Panthera leo*, in the Selous Game Reserve: Social and ecological factors. *Behav. Ecol. Sociobiol., 52*, 303–307.
86. Stander, P. 1991. Demography of lions in the Etosha National Park, Namibia. *Madoqua, 18*, 1–9.
87. Tucker, L. 2003. *Mystery of the White Lions: Children of the Sun God*; Npenvu Press: White River, South Africa, 2003; Pp. 352.
88. Tuqa, J.H.; Funston, P.J.; Musyoki, C.; Ojwang, G.O.; Gichuki, N.N.; Bauer, H.; Tamis, W.; Dolrenry, S.; Van't Zelfde, M.; de Snoo, G.R.; et al. 2014. Impact of severe climate variability on lion home range and movement patterns in the Amboseli ecosystem, Kenya. *Glob. Ecol. Conserv., 2*, 1–10.
89. Tumenta, P.N.; de Iongh, H.H.; Funston, P.J.; Udo de Haes, H.A. 2013. Livestock depredation and mitigation methods practised by resident and nomadic pastoralists around Waza National Park, Cameroon. *Oryx, 47*, 237–242.
90. Tumenta, P.N.; Visser, H.D.; van Rijssel, J.; Müller, L.; de Iongh, H.H.; Funston, P.J.; de Haes, H.A.U. 2012. Lion predation on livestock and native wildlife in Waza National Park, northern Cameroon. *Mammalia, 77*, 247–251.
91. Turner, J.A.; Vasicek, C.A.; Somers, M.J. 2015. Effects of a colour variant on hunting ability: The white lion in South Africa. *Open Sci. Reposi. Biol.*, e45011830; https://doi.org/10.7392/openaccess.45011830.
92. Turner, J.A.; Iongh, H.d.; Dunston-Clarke, E.J. 2022. Assessing the Social Cohesion of a Translocated Pride of White Lions Integrated with Wild Tawny Lions in South Africa, Using Social Network Analysis. *Animals, 12*, 1985. https://doi.org/10.3390/ani12151985.

93. Van Orsdol, K.G.; Hanby, J.P.; Bygott, J.D. 1985. Ecological correlates of lion social organisation (*Panthera leo*). *J. Zool., 206*, 97–112.
94. Viljoen, P.C. 1993. The effects of change in prey availability in lion predation in a large natural ecosystem in northern Botswana. *Symp. Proc. Zool. Soc., 65*, 1–15.
95 Western, D. 1975. Water availability and its influence on the structure and dynamics of the savanna large mammal community. *E. Afr. Wild. J., 13*, 265.
96. Whitman, K.; Packer, C. 1997. The effect of sport hunting on the social organisation of the African lion (Panthera leo). In *Proceedings of a Symposium on Lions and Leopards as Game Ranch Animals*; Van Heerden, J., Ed.; The Wildlife Group, South African Veterinary Association: Pretoria, South Africa, Pp. 177–183.
97. Whitman, K.; Starfield, A.M.; Quadling, H.S.; Packer, C. 2004. Sustainable trophy hunting of African lions. *Nature, 428*, 175–178.
98. Wickham, H. 2016. Ggplot2: Elegant Graphics for Data Analysis. Springer: New York, USA.
99. Woodroffe, R. 2000. Predators and people: Using human densities to interpret decline of large carnivores. *Anim. Cons., 3*, 165–173.
100. Worton, B.J. 1989. Kernel methods for estimating the utilization distribution in home-range studies. *Ecology, 70*, 164–168.
101. Yamaguchi, N.; Kitchener, A.; Driscoll, C.; Macdonald, D. 2009.Divided infraorbital foramen in the lion (*Panthera leo*): Its implications for colonisation history, population bottlenecks, and conservation of the Asian lion (P. l. persica). *Contrib. Zool., 78*, 77–83. https://doi.org/10.1163/18759866-07802004.
102. Yiu, S.-W.; Parrini, F.; Karczmarski, L.; Keith, M. 2017. Home range establishment and utilization by reintroduced lions (*Panthera leo*) in a small South African wildlife reserve. *Integr. Zool., 12*, 318–332. https://doi.org/10.1111/1749-4877.12243.
103. Zehnder, A.; Henley, S.; Weibel, R. 2018. Home ranges of lions in the Kalahari, Botswana exhibit vast sizes and high temporal variability. *Zoology, 128*, 46–54. https://doi.org/10.1016/j.zool.2018.04.001.

Photo 4.1 White lion males stalking prey, showing camouflage at Tula Tsau Wildlife Area. The present study was the first to investigate whether the white lions' coat colour could prevent lions from hunting successfully and therefore reduce survival in the wild. This perception has never been tested scientifically and is not based on any quantifiable data.
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4 White Lion Hunting Success

Effects of a Rare Colour Variant on Hunting Ability: The White Lion (*Panthera Leo Melanochaita*) in South Africa.

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4.1 Abstract

Background

Coat colour variation has been recorded in several mammalian taxa, including large felid species. White lions are a rare colour variant of the African lion, *Panthera leo,* that have only ever been recorded in the wild in the Timbavati Private Nature Reserve and Central Kruger National Park, South Africa. The frequency of occurrence of white lions in their natural habitat was increasing until 1994, after which there was an absence of white lions in the wild until 2006. This absence is thought to be due to either a lack of camouflage that prevents white lions from hunting successfully and therefore surviving in the wild, or the impact of anthropogenic activities. The present study was the first to investigate whether a white coat colour has an effect on hunting ability in lions. This hypothesis was tested under managed free-roaming conditions in two fenced areas since no adult white lions existed in the wild at the time. Two separate groups of white lions were rewilded and their hunting success evaluated. Prey density, availability of preferred prey and habitat type were similar to that of the white lions' natural habitat of Timbavati Private Nature Reserve. As a means of direct comparison, wild tawny lions were released into the study area and their hunting success recorded. The two white lion groups and the tawny lion group were located three times per day respectively using radio telemetry, and all kill data were compared to that of wild tawny lions in other small wildlife reserves in South Africa.

Results

There was no significant difference between the mean kill rate or mean consumption rate of the two white lion groups and the tawny lion group in the same study area. Similarly, there was no significant difference between the mean kill rate or the mean consumption rate of the white lion groups and wild tawny lions at the Madjuma Lion Reserve (MLR), Karongwe Game Reserve (KGR), Welgevonden Game Reserve (WGR), Makalali Game Reserve (MGR) and the Associated Private Nature Reserves (APNR) in South Africa.

Conclusions

Our data shows that white lions are capable of surviving and hunting self-sufficiently under managed free-roaming conditions in a small fenced area (17 km^2), and suggests that white coat colour does not prevent free-roaming white lions from hunting successfully in their natural habitat. We suggest therefore that the absence of adult white lions in their natural habitat was not due to an inability to hunt, and recommend that the hunting behaviour of white lions be studied under truly free-roaming conditions. This is supported by historical and recent observations of wild white lions hunting self-sufficiently and having cubs in the Timbavati Private Nature Reserve (65 000 ha) in 2006-2009, 2011, 2014, 2015, 2018, and 2019, in Central Kruger National

Park in 2014, 2015 and 2022, and in the Ngala Lodge traversing area (Timbavati Private Nature Reserve) in 2018 and 2019.

Key words
White Lion, Colour Variant, Leucism, Rewilding, Hunting Success, Timbavati, Kruger National Park.

4.2 Background

Coat colour variation, resulting from gene mutations, is present in several mammalian taxa and has been detected in mammals as far back as 14 000 years ago (Searle 1968; Römpler et al. 2006). Natural intraspecific coat colour variation has been observed in a number of mammalian species including deer mice (*Peromyscus spp*.), black bear (*Ursus americanus*), cheetah (*Acinonyx jubatus*), leopard (*Panthera pardus*), Bengal tiger (*Panthera tigris tigris*) and African lion (*Panthera leo*) (Searle 1968; Marshall & Ritland 2002; Kaelin et al. 2012; Xu et al. 2013). Natural selection determines which coat colour will persist based on whether the colour is a benefit or not to the survival of that species (Darwin 1904-1914; Hoekstra 2010) . Common colour mutations in big cats are albinism (pure white), chinchilla (white with pale markings), leucism (partial albinism / cream) and melanism (black) (Searle 1968).

The white lion is a rare phenotype or colour variant of the African lion *Panthera leo* that has a white coat colour (Figure 1) with either yellow, blue or green eyes, and has only ever been recorded in the wild in the Timbavati Private Nature Reserve (TPNR) and central Kruger National Park (KNP) – the Greater Timbavati Region – in South Africa (McBride 1977; McBride 1982; Robinson & De Vos 1982; Cruickshank & Robinson 1997; Tucker 2003; Cesare 2011). The white coat colour is not due to albinism (Robinson & De Vos 1982), but rather leucism resulting from a double recessive allele (Cruickshank & Robinson 1997). The presence of white lions was documented for the first time in the Central KNP in 1959 Robinson & De Vos 1982), and in the Timbavati Private Nature Reserve (TPNR) in 1975 (McBride 1977). The frequency of occurrence of white lions in their natural endemic habitat was increasing (Robinson & De Vos 1982) until there was an absence of white lions in the wild from 1994 to 2006. The possible reasons for this absence are thought to be either a lack of camouflage that prevents white lions from hunting successfully and therefore surviving in the wild, or the anthropogenic impact of lion culling (white and tawny) in Central Kruger National Park (Smuts 1982), trophy hunting of white lions (Cadman 2006), and removal from the wild in the Greater Timbavati Region (Tucker 2003; Cesare 2011; Turner et al. 2015) into captive breeding and hunting farms (Cadman 2006). The natural high mortality rate of 50% of wild lion cubs (white and tawny) within the first year may also have contributed to the low survival rate of white lion cubs (Funston et al. 2003). Although the recessive gene (allele) was still present in the wild population and white lion cubs were born into the Greater Timbavati Region in 2006-2009, 2011, 2014, 2015, 2018, and 2019, in Central Kruger National Park in 2014, 2015 and 2022, and in the Ngala Lodge traversing area (Timbavati Private Nature Reserve) in 2018 and 2019 (Turner et al. 2015; Dicks 2022), only three of the 17 'white' cubs in the wild population had survived at the time of writing (2023). This is considered and discussed in detail in Chapter 5.

Here we investigate the hunting ability of white lions in their natural habitat using the following hypotheses and predictions:-

Hypothesis a: the hunting success of white lions in their natural habitat is similar to that of wild tawny lions, suggesting that white lions can survive in the wild;
Hypothesis b: the hunting success of white lions in their natural habitat is lower than that of wild tawny lions, suggesting that white lions cannot survive in the wild

For the present study, this translates into two predictions:

Prediction a: white lions show similar hunting success to other wild lions
Prediction b: white lions show lower hunting success than other wild lions

At the time of the present study there were no adult white lions in the Greater Timbavati Region. Two groups of captive-born white lions were therefore rewilded by using a soft release (Van Dyk 1997) approach, and their hunting behaviour was studied. Rewilding is the process by which captive bred animals are reintroduced into the wild. Due to high failure rates and high costs, rewilding is generally discouraged (Griffith et al. 1989; Snyder et al. 1996; Miller et al. 1999; Jule et al. 2008). Additionally, there is a perception that certain captive felids, particularly lions, cannot survive in the wild (Jule et al. 2008). However, the use of captive-born individuals becomes necessary when no wild representatives remain or when the surviving wild population is no longer viable Stuart 1991). Soft release is more successful than hard release (Stanley Price 1991) because it involves a period of captivity at the release site during which the animal can adjust to its surroundings (Moore & Smith 1990; Linnell et al. 1997) and other possible animals or conspecifics that may be released at the same time (Brocke et al. 1990; Van Dyk 1997). After the soft release of the white lion groups, their hunting behaviour was recorded and compared to that of (i) a pair of wild tawny lionesses that were observed in the same study area, and (ii) other scientifically documented wild and reintroduced lions in South Africa.

4.3 Materials and methods

4.3.1 Study Area

The rewilding took place in two rehabilitation areas within the Tsau Wildlife Area, a 1700 ha wildlife area. The rehabilitation areas were 300 ha and 700 ha in size respectively. The Tsau Wildlife Area is located in the Lowveld of South Africa, bordering the Timbavati Private Nature Reserve (TPNR), the natural distribution range of the white lions (Figure 2). The Tsau Wildlife Area consists of natural bushveld that is classified as Arid Lowveld (Mucina & Rutherford 2006). It is an undulating landscape consisting of plains, woodlands of various densities and riverine vegetation.

There are several permanent water points as well as numerous seasonal water points and streams in each of the rehabilitation areas. In accordance with the *IUCN Guidelines for Reintroduction* (IUCN 1998), the rehabilitation area was used to provide the lions with the opportunity to gain the skills needed to survive self-sufficiently. The rewilding took place under managed free-roaming conditions to enable the lions to roam freely whilst being protected from poachers, conspecifics and large dangerous prey species. The managed conditions also ensured the disease-free status of both the lions and their prey. The area is populated by indigenous flora and fauna and contains the following mammalian prey species: blue wildebeest (*Connochaetes taurinus*), common warthog (*Phacochoerus africanus*), Cape porcupine (*Hystrix africaeaustralis*), impala (*Aepyceros melampus*), steenbok (*Raphicerus campestris*), aardvark (*Orycteropus afer*), bushbuck (*Tragelaphus scriptus*) and grey duiker (*Sylvicapra grimmia*). Conspecifics and large prey animals such as African buffalo (*Syncerus caffer*) and giraffe (*Giraffa camelopardalis*), which are dangerous for inexperienced lions to hunt, were excluded from the

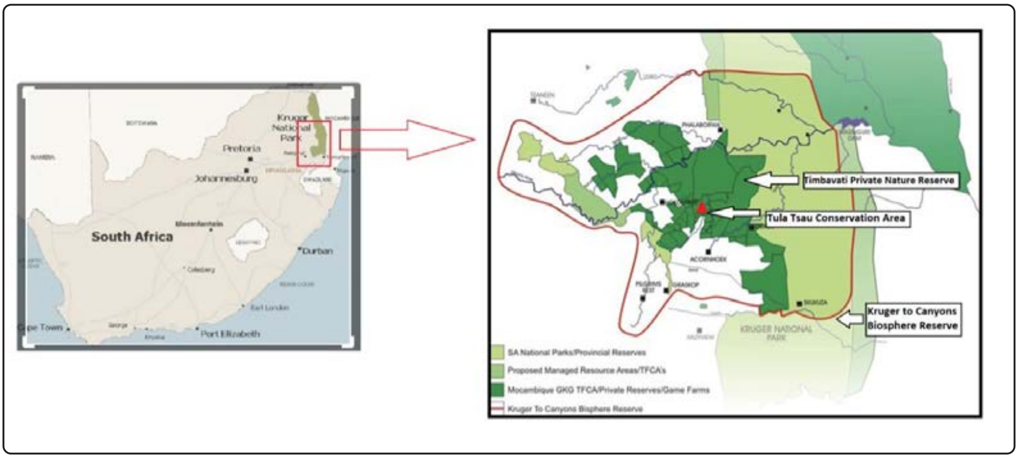

Figure 1 Location of the Tula Tsau Conservation Area, Kruger to Canyons Biosphere Reserve, South Africa.

rehabilitation area. Black-backed jackals (*Canis mesomelas*) and caracal (*Caracal caracal*) occur in the rehabilitation area, and both leopard (*Panthera pardus*) and spotted hyaena (*Crocuta crocuta*) have been seen, but are not considered resident in the area. Wild lions occur on neighbouring properties that border three of the four boundary fences of the rehabilitation area. The entire rehabilitation area is surrounded by an electrified (9000 V) double predator-proof fence that is 2.4 m high. The double fence minimised the risk of conflict with the lions from the three neighbouring private nature reserves, and also reduced the risks of the lions escaping the area if a prey animal ran into the fence whilst being hunted by the lions.

An aerial game count was conducted prior to releasing the lions, to determine the prey density within the rehabilitation areas. Additional aerial game counts were conducted annually at the same time of year, to monitor prey population trends. The smaller rehabilitation area (300 ha) had a limited number of prey species due to its small size: blue wildebeest, warthog, impala, common duiker, and steenbok. The larger rehabilitation area (700 ha) could sustain a wider variety of prey species: blue wildebeest, warthog, impala, waterbuck, bushbuck, Burchell's zebra, Livingstone's eland, nyala, greater kudu, common duiker, steenbok and porcupine. The prey populations were replenished on an annual basis, typically in March or April, to ensure the prey density was similar to that of the white lions' natural habitat of the TPNR. The exception was in October 2006 when the blue wildebeest population in the 300 ha area was replenished. Prey density estimates for the TPNR were obtained from Turner (2005). The annual replenishment of prey is in accordance with other small reserves that have free-roaming lions, such as Madjuma Lion Reserve in the Limpopo Province of South Africa (Power 2002), which similarly replenish prey on an annual basis.
The size of the rehabilitation areas was optimal for the rewilding process and this preliminary study, but the long-term objective is to study wild white lions within the open system of the Greater Timbavati-Kruger Park Region.

4.3.2 Lion Particulars

Captive-born lions were utilised for the initial part of the study on white lions (August 2005 to March 2006) because there were no adult white lions in the wild at the time, and it was surmised that the white lion had become extinct in the wild in their natural endemic habitat. Moreover, it was uncertain whether the gene responsible for the white coat colour still existed in the wild. At the time that the hunting success of white lions was being studied (2015), nine white lions had been recorded in four different prides in the Timbavati Private Nature Reserve, neighbouring Umbabat Private Nature Reserve, and Central Kruger National Park, but no scientific study had been done on their ecology or hunting behaviour. Although free-roaming white lions were also reported in two wildlife reserves in the Western Cape (Sanbona Wildlife Reserve) (Gomersall 2015) and Eastern Cape (Pumba Private Game Reserve) (Howarth 2022) in South Africa, these reserves are not in the natural endemic range of the white lions and no scientific evidence was available on their hunting behaviour. The white lions used for this study comprised of two rewilded white lion groups and a wild introduced tawny lion group. Rewilding is the process by which captive bred animals are reintroduced into the wild when no wild representatives remain or when the surviving wild population is no longer viable. Using the soft release technique, the two white lion groups were released into separate (fenced) rewilding areas of natural bushveld within the greater endemic range of the white lion. The founder white lion group (White Lion Group A) consisted of a white lioness and her three white offspring (two males and one female) that were acquired from the Johannesburg Zoo when the cubs were three months old, to be rehabilitated and introduced to managed free-roaming conditions. The lioness had the highest genetic integrity (lineage traceable back to the wild) of any white lion in existence at the time, originating from two different bloodlines, with the mother of the lioness being wild-born. Though the white lioness was hand-reared, her cubs were not. A stringent protocol with no human contact or activity on foot, and minimal human imprinting during monitoring was applied to rehabilitate the lions. A soft release approach was taken, whereby the founder group was held temporarily in a 1.5 ha acclimation boma (enclosure) before been released into the managed free-roaming conditions. This approach is in accordance with the principles outlined in the *National Norms and Standards for the Sustainable Use of Large Predators in South Africa (section 9 (1) of the National Environmental Management Biodiversity Act 10 of 2004).* The adult lioness was six years old and her three white offspring were three years old at the time of release into the rewilding area. The second white lion group, White Lion Group B, was studied three years later (June 2010 to February 2011), and consisted of the rewilded daughter of the founder lioness (six years old), together with a captive-born adult white male (12 years old) and their three wild-born offspring (1.3 years old) which were released into the managed free-roaming conditions of a 700 ha rewilding area. The wild tawny lion group, Tsau Tawny Lion Group, was comprised of two adult lionesses (four years old) that were released into the same 300 ha rewilding area as the founder white lion group, in August 2009, three years after the founder white lion group had been relocated to a new area at the Tsau Wildlife Area.

4.3.3 Monitoring

The adult lions were fitted with VHF radio tracking collars (148 to 152 MHZ), and two of the cubs were fitted with internal VHF tracking transponders (148 to 152 MHZ), prior to release. The lions were monitored daily, in the rewilding area from a closed vehicle to minimise conditioning. Radio telemetry was used to locate each of the lion groups, three times a day at sunset, midnight and sunrise. These were times that coincided with the lions' peak activity periods. The lions were monitored for one to five hours, depending on how active the lions were during each monitoring session. Constant monitoring was deemed counter-productive to the rewilding process of the white lions, as the vehicle may have alerted potential prey and hindered the hunting success of the lions. Whenever possible, the lions were located visually during every monitoring session. The lions were approached up to a distance of 15 to 20 m, close enough to observe if a kill had taken place but distant enough not to disturb them. At each monitoring session the lions' physical well-being was assessed and data on the date, time, location, and activity of the lions were collected, as well as the species, age and sex of the prey killed, and a subjective belly score (Bertram 1975). If, due to distended stomachs and/or evidence of blood on the lions' bodies, it was obvious that they had made a kill but no remains were found, then it was recorded as an unknown kill. Each of the lion groups were studied at a similar time of year, and for a similar duration to ensure that the data were as comparable as possible.

4.3.4 Data analysis

Data were collected for an eight-month observation period for each of the three lion groups studied. The observation period for the white lion groups was started once the white lions were hunting without human intervention. The white lion groups were considered to be self-sufficient once it was no longer necessary to supplement them with a carcass to sustain them, two months after release into the rewilding area. No correction factor was applied to the kill data to account for the smaller sized kills that may have been consumed entirely and therefore not recorded, since this is probably balanced out by the fact that aerial counts are biased towards larger sized animals (Hayward & Kerley 2005). Due to the non-invasive monitoring approach used it can be assumed that smaller kills such as impala were missed and the number of kills recorded is therefore a minimum.

The GPS (Global Positioning System) location of kills were recorded and imported into an Arcview Global Information System package (Arcview 3.2) (Hooge 1999), from which a map was generated showing the kill locations within the study area and allowing a comparison between the three lion groups studied.

Although the age of prey animals was recorded in the kill data when possible, the present study only compared these data with that of the Tsau Tawny Lion Group, since the same observation technique was used and data were therefore comparable. Data were combined for White Lion Group A and B to make the data more robust. The Mann-Whitney Test was used to compare the age selection of the White Lion Groups with that of the Tsau Tawny Lion Group. There were too many unknowns to include a meaningful analysis of the sex selection by the lion groups. The live prey number of a species at any one time was calculated by deducting the recorded number of killed individuals and natural mortalities from that provided by the aerial game count.

Overall dietary preferences were calculated by using the data from observed kills and applying Jacob's Index (1974), a modified version of Ivlev's electivity index ($D = r - p \div [r + p]$

– 2rp) in which r is the proportion of each type of prey killed by the founder lion pride and p is the proportion of each prey species available in the rewilding area. The standardised values for Jacob's Index range from +1.0 to -1.0, where +1.0 indicates the maximum preference by the lions for a particular prey species (ie. a lion killing frequency greater than the relative abundance of the prey animal), whereas a Jacob's Index of -1.0 indicates the maximum avoidance by the lion group for a particular prey species (ie. a lion killing frequency less than the relative abundance of the prey animal). The Jacob's Index was calculated for the most frequently killed prey species of the lion groups studied, for a period of eight months of hunting self-sufficiently (Jacob's 1974). However, the increase in blue wildebeest numbers (to achieve the correct prey density) two months after white lion group A had been hunting self-sufficiently, necessitated the calculation of the weighted mean of the Jacob's Index of the first two months and the following six months. Utilising the kill data collected during the eight-month study period, the mean food consumption rate (kg/LFU / day) and kill rate (days / kill) were calculated for the two rewilded white lion groups and the Tsau Tawny Lion Group. In accordance with Van Orsdol (1982) [33] and Power (2002) the food consumption rate was calculated per adult lioness or lion feeding unit (LFU), with the age and size of the lions in each pride being taken into account when determining the mean daily consumption rate. This classification assumes that adult males eat 1.5 times as much as females and are therefore 1.5 LFU, and large cubs (2–3 years) are 0.75 LFU, medium cubs (1–2 years) are 0.5 LFU, and small cubs are 0.25 LFU.

In order to determine if the kill rate and food consumption rate of the rewilded white lions was statistically different from that of wild tawny lion prides, data collected during the 8 month period were compared with data for: (i) Tsau Tawny Lion Group at the Tsau Wildlife Area, (ii) wild tawny lions in the neighbouring APNR (Turner 2005), (iii) wild reintroduced lions in the Madjuma Lion Reserve (MLR), adjacent to Mabula Game Reserve (MGR) (Power 2002), (iv) wild reintroduced lions in the Welgevonden Private Game Reserve (WGR) (Kilian 2003), and (v) wild reintroduced lionesses (alone or in a pair with or without cubs) in the Karongwe Game Reserve (KGR) (Lehmann et al. 2008). The MLR, WGR and KGR are all small fenced reserves (<1000 km^2) within the Limpopo Province that have lions, and the APNR is a large conservancy open to the Kruger National Park, within both the Limpopo and Mpumulanga Provinces of South Africa. The Kruskal-Wallis (KW) Analysis of Variance (ANOVA) was utilised to compare the mean kill rate and mean food consumption rate of the two white lion groups with that of the corresponding rates for the wild tawny lions in the Tsau Wildlife Area, APNR, MLR, WGR, MGR and KGR, when available. A non-parametric statistical test was used since the distribution of the data did not conform to the assumptions of normality (Kolmogorov-Smirnov test) (Palomares et al. 2001). Even when the data were transformed using the square root, reciprocal and log function, the data failed the normality test. The statistical analyses were performed using GraphPad Prism version 4.00 for Windows (GraphPad Software, San Diego California USA, www.graphpad.com).

4.4 Results

A total of 80 kills were recorded for White Lion Group A, 88 kills for White Lion Group B, and 94 kills for the Tsau Tawny Lion Group, during the eight-month period of observation on each lion group. Figures 3.1, 3.2 and 3.3 show the location of kills made by the three lion groups, indicating that the majority of kills were made close to waterpoints, drainage lines and open plains, and a relatively low number of kills were made at the boundary fence.

Table 1 and Figure 4 indicates the kill frequency by the three lion groups for the 10 prey species recorded during this study, compared to the prey abundance (%) for each lion group during the period of study.

Of the ten prey species White Lion Group A selected seven types, White Lion Group B six types, and the Tsau Tawny Lion Group selected three types of prey. The two prey species that were killed by all three lion groups were the blue wildebeest and common

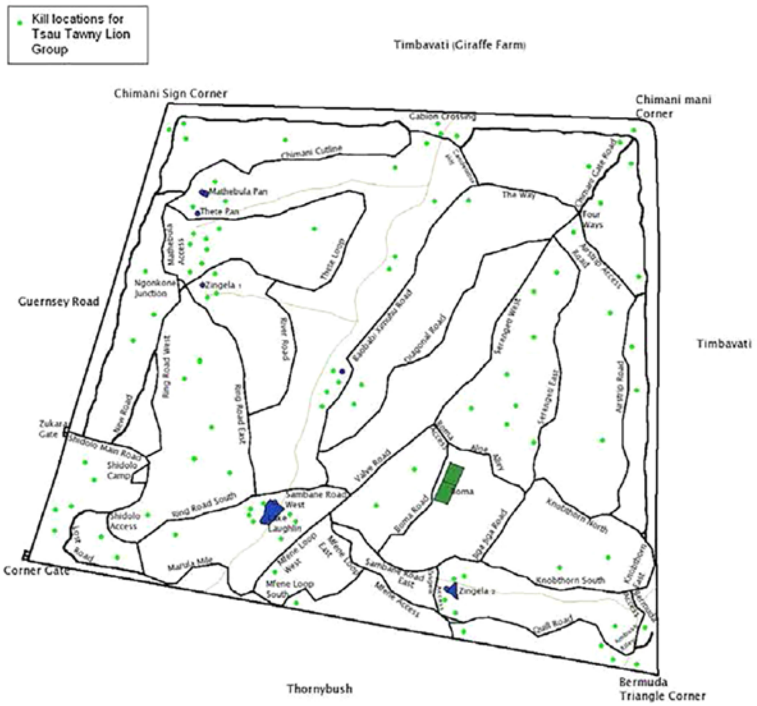

FIG 3.1 : Location of kills made by the Tsau Tawny Lion Group from August 2009 to March 2010 within the 300 ha rewilding area at the Tsau Conservancy, South Africa.

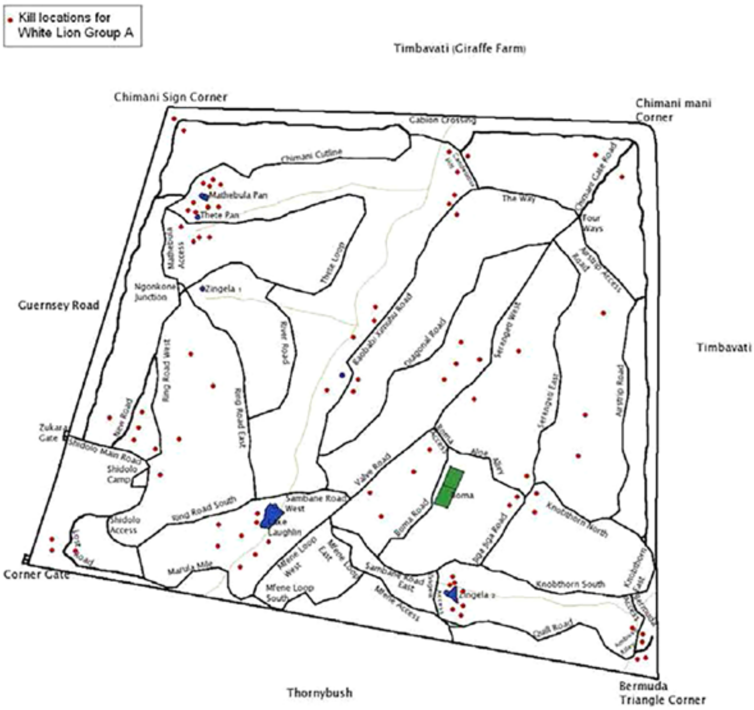

FIG 3.2 : Location of kill made by White Lion Group A from August 2005 to March 2006 within the 300 ha rewilding area at the Tsau Conservancy, South Africa.

FIG 3.3 : Location of kills made by White Lion Group B from June 2010 to February 2011 within the 700 ha rewilding area at the Tsau Conservancy, South Africa.

Table 1. The hunting success of White Lion Group A and B compared to Tsau Wild Tawny Lion Group

Common Name	Scientific Name	Total kills White lion group A 8 month period		Prey Availability		Total kills White lion group B 8 month period		Prey Availability		Total kills Tsau Tawny lions 8 month period		Prey Availability	
		No.	%	No.	%	No.	%	No.	%	No.	%	No.	%
Aardvark	*Orycteropus afer*	1	1.3	**3**	**2.7**	0	0.0	**5**	**2.6**	0	0.0	**0**	**0.0**
Impala	*Aepyceros melampus*	3	3.8	**33**	**29.2**	5	5.7	**45**	**23.3**	22	23.4	**34**	**26.2**
Steenbok	*Raphicerus campestris*	2	2.5	**2**	**1.8**	0	0.0	**6**	**3.1**	0	0.0	**4**	**3.1**
Tortoise	Spp. not specified	3	3.8	**3**	**2.7**	0	0.0	**4**	**2.1**	0	0.0	**5**	**3.8**
Cape Porcupine	*Hystrix africaeaustralis*	2	2.5	**2**	**1.8**	0	0.0	**5**	**2.6**	0	0.0	**4**	**3.1**
Common Warthog	*Phacochoerus africanus*	15	18.8	**15**	**13.3**	12	13.6	**22**	**11.4**	7	7.4	**18**	**13.8**
Blue Wildebeest	*Connochaetes taurinus*	45	56.3	**55**	**48.7**	58	65.9	**81**	**42.0**	54	57.4	**65**	**50.0**
Greater kudu	*Tragelaphus strepsiceros*	0	0.0	**0**	**0.0**	2	2.3	**9**	**4.7**	0	0.0	**0**	**0.0**
Burchell's Zebra	*Equus burchelli*	0	0.0	**0**	**0.0**	6	6.8	**9**	**4.7**	0	0.0	**0**	**0.0**
Livingstone's Eland	*Tragelaphus oryx livingstonii*	0	0.0	**0**	**0.0**	3	3.4	**7**	**3.6**	0	0.0	**0**	**0.0**
Unknown	-	9	11.3	**0**	**0.0**	2	2.3	**0**	**0.0**	11	11.7	**0**	**0.0**
Total		**80**	**100.0**	113	**100**	**88**	**100.0**	193	**100**	**94**	**100.0**	130	**100**

The number and percentage of kills made by the two rewilded white lion groups over an eight month period of hunting self-sufficiently, was compared to that of the Tsau Tawny Lion Group and the prey availability during each respective 8 month study period, at the Tsau Conservancy

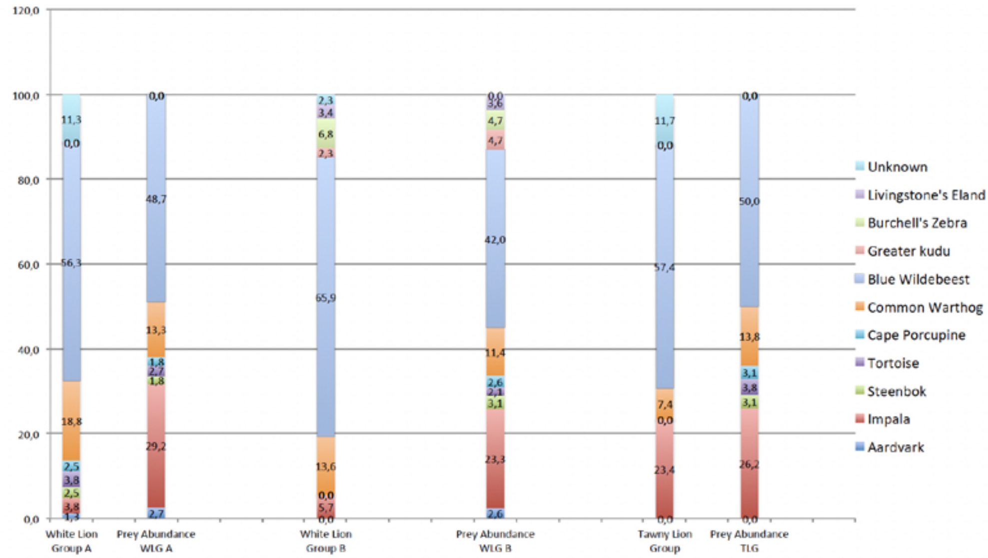

Figure 4.: Prey selection (%) of White Lion Group A, White Lion Group B, and the Tsau Tawny Lion Group under managed free-roaming conditions at the Tsau Conservancy, South Africa. The prey abundance (%) during the period of study for each lion group was taken from aerial count data and included for comparison

warthog. The prey species selected at the highest frequency by the three lion groups was the blue wildebeest. Common warthog was the second most frequently killed prey species for the two white lion groups, and the third most frequently killed by the Tsau Tawny Lion Group. The impala was the second most frequently killed prey species by the Tsau Tawny Lion Group. By contrast, impala was the least frequently killed prey by the white lion groups. The Jacob's Index values confirm that the white lion groups avoided hunting impala and indicate White Lion Group A showed a preference for warthog whilst White Lion Group B preferred blue wildebeest. The Tsau Tawny Lion Group selected blue wildebeest and impala in accordance with their availability but killed warthog less frequently than expected by their abundance (Figure 5).

The White Lion Groups A and B selected 84% adults and 16% subadults, and similarly the Tsau Tawny Lion Group showed a greater selection for adults (80%) compared to subadult (20%) prey animals. There was no significant difference between the age selection of the White Lion Groups and the Tsau Tawny Lion Group (Mann-Whitney U = 10.000, df = 4, P = 0.675).

The mean kill rate for White Lion Group A (1 kill every 3.038 days) and White Lion Group B (1 kill every 2.731 days) during the eight-month period lies between that observed

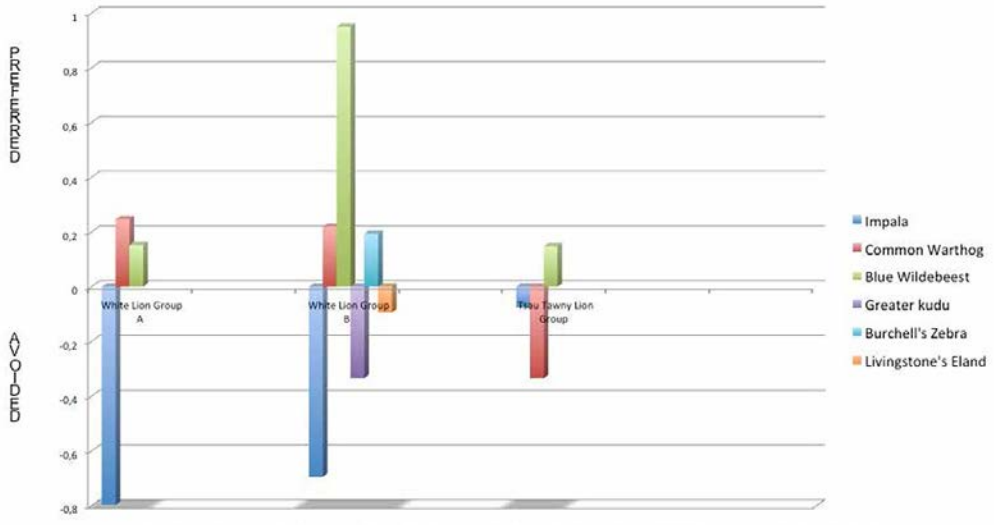

Fig.5 Prey preferences of the three lion groups observed during the 8 month study period at the Tsau Conservancy, based on Jacobs Index Values

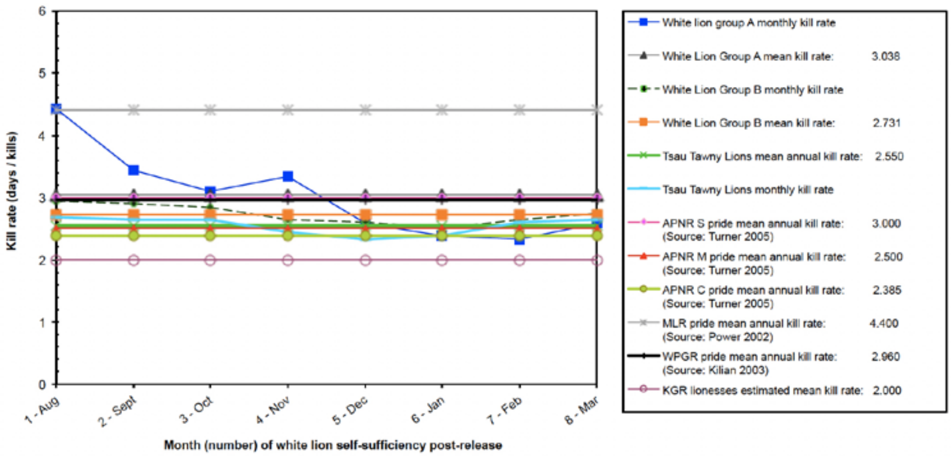

Fig. 6 : The monthly kill rate and mean kill rate for the two rewilded white lion groups and the Tsau Tawny Lion Group, during the respective eight month observation periods at the Tsau Conservancy, compared with the mean kill rate for wild tawny lions in

for the wild tawny lionesses at Karongwe and the wild tawny lions reintroduced to the Madjuma Lion Reserve (Figure 6). No significant differences (KW = 6.776, n = 9, P = 0.561) were found between the mean kill rate for the white lions and the kill rates of the wild tawny lionesses (1 kill every 2.550 days) at the Tsau Wildlife Area, the three wild tawny lion prides of the nearby APNR, the reintroduced wild tawny lion prides in the MLR and WGR, and the reintroduced lionesses in KGR. Similarly, the mean kill rate of the two white lion groups displayed no statistical difference to that of the Tsau Tawny Lion Group (KW = 0.225, n = 9, P = 0.894).

The mean food consumption rate of the two white lion groups displayed no statistical difference to that of the Tsau Tawny Lion Group, or the lion prides of the Associated Private Nature Reserves (APNR), Mabula Lion Reserves (MLR), Welgevonden Game Reserve (WGR), Makalali Game Reserve (MGR) and the Karongwe Game Reserve (KGR) (KW = 12.573, P = 0.083) (Table 2). The results of Dunn's Multiple Comparison test [37]

Table 2: Number of kills per lion feeding unit (LFU) and food consumption rate per day (kg/LFU/day) and per year (kg/LFU/year) for the Tsau White Lion Groups A & B,Tsau Tawny Lion Group, and the lion groups from the APNR, Karongwe, Makalali, Mabula, and Welgevonden Game Reserves, in South Africa.

LION GROUP	NUMBER OF KILLS PER LION FEEDING UNIT (kills / LFU)	FOOD CONSUMPTION RATE	
		kg/LFU/day	kg/LFU/year
TSAU WHITE LION GROUP A	37	8.6	3142
TSAU WHITE LION GROUP B	38	14.9	5468
TSAU TAWNY LION GROUP	66	14.8	3235 5383
APNR Lionesses Alone Male Coalition Mixed Group	17 31 13	4.3 to 11.5	1570 to 4197
KARONGWE Lionesses Alone Male Coalition Mixed Group	64 32 42	6.9 to 12.1	2530 to 4419
MAKALALI GAME RESERVE	Not Available	3.0 to 3.2	1095 to 1168
MABULA LION RESERVE	47	4.6	2263
WELGEVONDEN GAME RESERVE	27	6.1	2219

indicated that no significant difference exists between the food consumption rate of any of the lion groups compared.

4.5 Discussion

This study suggests that if a strict rewilding protocol is followed with minimal human habituation, captive-born lions can be successfully introduced to managed free-roaming conditions. We also show that rewilded lions can be efficient hunters, in the controlled conditions we provided. Despite our small sample size and the small size of the lion territories, our data indicate that the white lions studied were as efficient hunters as the tawny lions observed in the same study area. Both historical and recent observations of wild white lions in the Timbavati Private Nature Reserve (65 000 ha) support these findings (Cesare 2011; White Lions 2012).

4.5.1 Prey species selection

Lions are highly adaptable in terms of their prey selection, hunting strategy, killing technique, activity pattern, and use of different habitat types. They eat any suitable food that is abundant and accessible, and their diet is more varied throughout their geographic range than that of any other large cat (Frankham 1995). In the KGR lions have been recorded to select 21 different prey species (Lehmann et al. 2008), and in the KNP, over 37 prey species (Mills & Biggs 1993). The white lion group preyed on just seven prey species, but this number cannot be directly compared to that of the KGR and KNP due to the controlled conditions of the rewilding area where the lions' prey base was managed and the number of potential prey species was purposely limited when compared to lions in fully free-roaming conditions. Additionally, the white lions' situation was different in terms of group composition and founder members being captive-born. However, several studies have shown that generally less than five medium-sized to large ungulate species constitute 75% of the diet of lions (Schaller 1972; Rudnai 1974; Power 2002; Druce et al. 2004; Funston 1999).

Numerically, blue wildebeest were the white lions' preferred prey (61% of total kills) followed by warthog (16% of total kills). This is consistent with findings for the Tawny Lion Group and the wild prides in the MLR and KGR (Power 2002; Lehmann et al. 2008), but opposite to the observations in the Greater Makalali Conservancy, Limpopo Province, where the lions' main prey was warthog, making up 30% of their diet, followed by wildebeest (18%) (Druce et al. 2004). By contrast, warthog and wildebeest are not amongst the two most preferred lion prey in the APNR, although both warthog and wildebeest were hunted at a frequency greater than their relative abundance (Turner 2005). Two further studies also observed that lion tend to kill both wildebeest and warthog with greater frequency than their abundance (Schaller 1972; Power 2002).

Although both the white lion groups and the Tsau Tawny Group showed a selection for blue wildebeest and warthog, these lion groups similarly showed no significant preference or avoidance for any of the available prey species. The latter is most probably due to the controlled (managed) circumstances of the study area. Consistent with the findings of numerous other lion studies in similar habitat types, impala were clearly not the most preferred prey of the white lion groups (Schaller 1972; Mills & Biggs 1993; Power 2002; Kilian 2003; Turner 2005; Lehmann et al. 2008). The impala was the second most frequently killed prey species of the Tsau Tawny Lion Group probably because it was likewise the second most abundant prey species. Additionally, studies show that lionesses tend to select impala more frequently than male lions due to the evasive speed of the impala (Schaller 1972). A similar reasoning is possible for the inexperienced white lion groups which were still perfecting their hunting technique, and therefore selected easier prey. However, the more experienced and successful White Lion Group B still avoided selecting impala.

4.5.2 Prey age selection

The white lion groups selected larger prey as they honed their hunting technique, as did the Tsau Tawny Lion Group. This observation is also consistent with that observed for a pair of rewilded tawny lions released in the Luangwa Game Reserve in 1961 (Carr 1962). Despite being at a disadvantage in having to learn to hunt, the white lion groups preferred to hunt adult prey animals. This is consistent with the findings of other studies (Power 2002; Turner 2005; Lehmann et al. 2008), though these studies point out that the methodology may have biased this finding toward large adult kills, as small kills, which are consumed rapidly, are more difficult to detect. Additionally, independent of their availability, medium to large prey species (190 to 550 kg) are preferred by lions (Druce et al. 2004). With a mean weight of 215 kg an adult female blue wildebeest in the KNP (Funston 1999) fits into the lower limit of this range. This is consistent with our observation for White Lion Group B, for which several equally sized or larger prey species, such as greater kudu, waterbuck, and eland, were available, yet this lion group selected blue wildebeest at the highest frequency. By contrast, the predilection of White Lion Group A and the Tsau Tawny Lion Group for adult blue wildebeest as well as adults of any of the smaller prey, is better explained by the fact that the blue wildebeest was the largest and most abundant prey species available.

4.5.3 Hunting success

Within two months of being released into managed free-roaming conditions both white lion groups attained hunting self-sufficiency, and within three months of being released both groups displayed a kill rate that was consistently similar to that of lions in the APNR (Turner 2005), MLR (Power 2002), WGR (Kilian 2003) and KGR (Lehmann et al. 2008). This was the case despite the number of kills that may have been missed due to the non-invasive methodology applied in the present study, making the white lion kill

rate an absolute minimum. By comparison, the five lion studies with which this study is being compared either monitored the lions continuously or used a correction factor to account for kills that may have been missed.
The mean daily food consumption rate of lions may vary considerably in both fenced ecosystems (KGR) (Lehmann et al. 2008), and open ecosystems (APNR) (Turner 2005). The study in KGR observed lion kill rates varying from one kill every 1.6 days to one kill every 16.4 days, depending on group composition and season [35]. As the kill rate of the white lion groups was similar to that of the Tsau Tawny Lion Group and the wild tawny prides in the aforementioned reserves, it is not surprising that the number of days between kills was also similar. The kill data show that both white lion groups hunted successfully with a kill rate and food consumption rate comparable to the Tsau Tawny Lion Group in the same study area. Although the number of kills made per LFU by the Tsau Tawny Lionesses was much higher than the White Lion Groups, the food consumption rate per LFU was comparable for White Lion Group B. Similar to the lionesses at KGR, the Tsau Tawny lionesses selected smaller prey (ie. impala) and a high percentage of juveniles, whilst the Tsau White Lion Groups selected larger prey (ie. blue wildebeest) and a greater percentage of adult prey. The lionesses therefore made smaller kills more frequently. The findings from this study indicate that the white lions survived as successfully as the tawny lions studied.

It is acknowledged that certain factors in the study area may have facilitated the white lions' hunting conditions by comparison to the conditions during the other lion studies, but the conditions were the same for the Tsau Tawny Lion Group and the hunting success of the aforementioned was comparable with both White Lion Group A and B. Some of the factors that were different in the study area were; the prey species and numbers were controlled, no other large predators and conspecifics were resident in the study area, apart from some transient leopard or spotted hyaena, and the small size of the area may have ensured the presence of prey within a certain proximity. Despite the small size of the rewilding area, the number of fence kills was minimal, and all three lion groups studied made kills randomly across the entire study area (Figures 3.1, 3.2, and 3.3). Subsequent to the completion of this study White Lion Group A has been released into a larger area where there are large dangerous prey including giraffe and buffalo, and the two male lions were observed killing adult buffalo. Furthermore, in 2010 the adult male lion from White Lion Group B (13 years old) was confronted by a wild tawny male lion (eight years old) that broke through the boundary fence from the neighbouring Kapama Game Reserve, and the white lion male successfully fended him off the intruder. Additionally, in 2014, one of the adult white lionesses in the Timbavati Private Nature Reserve defended herself against a rival group of four adult lionesses, further signs suggesting that white lions are capable of surviving in the wild in their natural habitat.

There were other factors that may well have made hunting conditions more difficult for the white lion group. The small sized area may have increased the vigilance of prey, thus making stalking and successful hunting more difficult (Power 2002). Moreover, the captive-born white lioness and her offspring (White Lion Group A) were learning to hunt and the lioness in particular had to overcome the negative factors associated with being hand-reared in captive conditions and being the only adult (capable hunter) in the founder group. Although there were two adult lions in White Lion Group B the male lion was often separate on a territorial patrol, as is typical behaviour for pride males (Smuts 1982). Additionally, the two introduced groups of white lions were all white and should therefore have been even more conspicuous than the naturally occurring white lions that were integrated in tawny prides. As approximately 30% of the white lion groups' successful hunts took place during daylight or on moonlit nights, further strengthens the case. However, as discussed for the lions of MLR (Power 2002), some of the daylight and moonlight success may be ascribed to the camouflage provided by the vegetation and/or the presence of the diurnal warthog. Additionally, tall grass, dense vegetation and dark moon conditions have been identified as the most important environmental factors that determined lion hunting success of medium-sized prey, such as blue wildebeest, in the KNP (Funston 1999). Because lions hunt mostly at night (Smuts 1982) and most lion prey see poorly at night (Goldsmith 2006), it is postulated that the white coat colouration in lions is less significant for hunting success than previously perceived. Evidence in support of this hypothesis is the self-sufficient hunting and survival of an adult white lioness in the Timbavati Private Nature Reserve in the 1990's (Cesare 2011). This lioness was observed hunting and surviving alone after her tawny sister was killed by nomadic male lions, and she successfully raised three litters of cubs. This adult white lioness survived despite the extreme human intervention of snaring, lion trophy hunting, consequent pride disruption and infanticide (Cesare 2011). Further evidence of the hunting ability of white lions is the occurrence of two adult white lionesses surviving and hunting on their own in the Timbavati Private Nature Reserve in 2015 (White Lions 2012; Patrick O'Brien personal communication). Additionally, a pride of white lions has been surviving in the wild for more than five years at the Pumba Game Reserve in the Eastern Cape of South Africa (Howarth 2022).

The adaptation of the released white lions to managed free-roaming conditions and their hunting success in the rewilding area gives preliminary evidence that white lions can hunt self-sufficiently, with a kill rate and a food consumption rate that is comparable to wild tawny lions in the same environment and study area. These findings put into question the postulation that white lions cannot hunt successfully in the wild due to a lack of camouflage (McBride 1977), confirming *prediction a* that white lions show similar hunting success to other wild lions, and therefore supporting *hypothesis a* that white lions can survive in the wild. This prediction is supported by the earlier findings of this study (Chapter 2 and 3) which suggest that white lions display natural behaviour similar to wild tawny lions in terms of their social behaviour, home range dynamics, and movement patterns. Due to the absence of conclusive scientific study on the ecology of wild white lions in an open system such as the Associated Private Nature Reserves or the Kruger National Park, the findings of this study are preliminary, and suggest that further study is necessary.

4.6 Conclusions

Having determined that white lions can hunt successfully under managed free-roaming conditions, with a kill rate and a food consumption rate that is comparable to wild tawny lions, we suggest therefore that white lions are capable hunters and are able to survive in their natural habitat. Since white lions occurred in their natural habitat both historically and recent to the writing of this article (1938; 1975 to 1980; 1994; 2006 to 2022), we propose therefore that the disappearance of white lions from the natural ecosystem was not due to an inability to hunt, but instead due to other factors most likely anthropogenic related. The anthropogenic activities that are likely to have impacted wild white lions historically, causing an absence of white lions in the wild from 1994 to 2006, and subsequently, leading to a low survival rate of white cubs from 2006 to 2022, is discussed in detail in the next chapter. However, to conclusively investigate this postulation we recommend that the hunting behaviour and ecology of white lions be studied under truly free-roaming conditions.

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Author's contributions
J.A.T. conceived of the study, coordinated the field research, and drafted the manuscript. C.V. assisted with field research and data analysis and helped to draft the initial manuscript. M.J.S. advised on the data analysis and reviewed the manuscript. All authors read and approved the final manuscript.

References

1. Bertram, B.C.R. 1975. Weights and measures of lions. *East African Wildlife Journal*, 13: 141 – 143.
2. Bothma, J. du P., Walker, C.H. 1999. *Larger carnivores of the African savannas.* Pretoria: J.L. van Schaik Publishers.
3. Brocke, R.H., Gustafson, K.A., Major, A.R. 1990. Restoration of lynx in New York: biopolitical lessons. *Transactions of the North American Wildlife and Natural Resources Conference*, 55: 590-598.
4. Cadman, M. 2006. First wild white lions born in Timbavati area for 12 years. In: *The Sunday Independent*, 26: 1.
5. Carr, N. 1962. *Return to the Wild: A story of two lions.* St James' Place: Collins Publishers.
6. Cesare, M. 2011. *Man-eaters, Mambas and Marula Madness: A Game Ranger's Life in the Lowveld*. Johannesburg: Jonathan Ball Publishing.
7. Cruickshank, K.M., Robinson, T.J. 1997. Inheritance of the white coat colour phenotype in African lions (Panthera leo). In: *Proceedings of a Symposium on Lions andLeopards as Game Ranch Animals.* Edited by Van Heerden J. Onderstepoort: Wildlife Group of the South African Veterinary Association.
8. Darwin, C.R. 1909-14. *The Origin of Species*. Vol. XI. The Harvard Classics. New York: PF Collier & Son.
9. Druce, D., Genis, H., Greatwood, S., Delsink, A., Hunter, L., Slotow, R., Braak, J.,Kettles, R. 2004. Prey selection by a reintroduced lion population in the Greater Makalali Conservancy, South Africa. *African Zoology*, 39: 273-284.
10. Dunn, O.J. 1964.*Technometrics*, 5: 241 – 252.
11. Frankham, R. 1995. Conservation genetics. *Annual Review of Genetics,* 29:305-327.
12. Funston, P.J. 1999. *Predator-prey relationships between lions and large ungulates in the Kruger National Park*. PhD thesis. University of Pretoria, Mammal Research Institute.
13. Goldsmith, T.H. 2006. What birds see. *Scientific American*, 295: 68–75.
14. Gomersall, W. 2015. *The cat's whiskers: Wild about white lions and charmed by cheeky cheetahs at South Africa's feline-friendly conservation reserve.* Available online: *http://www.dailymail.co.uk/travel/article-1307465/South-Africa-safari-Wild-white-lions-sensational-Sanbona.html* (Accessed on 23 February 2023).
15. Griffith, B., Scott, J.M., Carpenter, J.W., Reed, C. 1989. Translocation as a species conservation tool: status and strategy. *Science*, 345: 447–480.
16. Hayward, M.W., Kerley, G.I.H. 2005. Prey preferences of the lion *(Panthera leo). Journal of Zoology*, 267: 309-322.
17. Hoekstra, H.E. 2010. From Darwin to DNA: The Genetic Basis of Colour Variations. In: *In the Light of Evolution: Essays from the Laboratory and Field*. Edited by Losos, J:Roberts and Company Publishers. Pp 277-295.
18. Hooge, P.N. 1999. Animal movement analysis Arcview Extension, USGS-BRD, Alaska Biological Science Centre, Glacier Bay Field Station, Gustavus.

19. Howarth, D. (2022). *History of the White Lion.* [Website]. Available online: 10 February 2023 from, https://www.pumbagamereserve.co.za/pages/history-of-the-white-lion/ (Accessed on 10 February 2023).
20. Hunter, L.T.B. 1998.*The behavioural ecology of reintroduced lions and cheetahs in the Phinda Resource Reserve, Kwazulu-Natal, South Africa*. PhD thesis. University of Pretoria, Mammal Research Institute.
21. IUCN. 1998. *IUCN guidelines for reintroduction*. Switzerland: IUCN/SSC Reintroduction Specialist Group.
22. Jacobs, J. 1974. Quantitative measurement of food selection - a modification of the forage ratio and Ivlev's electivity index. *Oecologia*, 14:413-417.
23. Jule, K.R., Leaver, L.A., Lea, S.E.G. 2008. The effects of captive experience in reintroduction survival in carnivores: a review and analysis. *Biological Conservation*, 141(2): 355-363.
24. Kaelin, C.B., Xu, X., Hong. L.Z. , David, V.A., McGowan, K.A. et al. 2012. Specifying and Sustaining Pigmentation Patterns in Domestic and Wild Cats. *Science*, 337(6101):1536–1541.
25. Kilian, P.J. 2003. *The ecology of reintroduced lions on the Welgevonden Private Game Reserve, Waterberg*. MSc thesis. University of Pretoria, Centre for Wildlife Management.
26. Lehmann, M.B., Funston, P.J., Owen, C.R., Slotow, R. 2008. Feeding behaviour of lions *(Panthera leo)* on a small reserve. *South African Journal of Wildlife Research*, 38: 66-78.
27. Linnell, J.D.C., Aanes, R., Swenson, J.E., Odden, J., Smith, M.E. 1997. Translocation of carnivores as a method for managing problem animals: a review. *Biodiversity. Conservation* 1997, 6: 1245-1257.
28. Marshall, H.D., Ritland, K. 2002. Genetic diversity and differentiation of Kermode bear populations. *Molecular Ecology*, 11(685-697).
29. McBride, C. 1977. *The White Lions of Timbavati*. New York: Paddington Press.
30. McBride, C. 1981. *Operation White Lion.* New York: St. Martin's Press.
31. Miller, B., Ralls, K., Reading, R.P., Scott, J.M., Estes, J. 1999. Biological and technical considerations of carnivore translocation: a review. *Animal Conservation*, 2: 59-68.
32. Mills, M.G.L., Biggs, H.C. 1993. Prey apportionment and related ecological relationships between large carnivores in Kruger National Park. *Symposia of the Zoological Society of London*, 65: 253– 268.
33. Moore, D.E., Smith, R. 1990. The red wolf as a model for carnivore reintroductions. *Symposia of the Zoological Society of London*, 62: 263-278.
34. Mucina, L.; & Rutherford, M.C. (Ed). 2006. The vegetation of South Africa, Lesotho and Swaziland. *Strelitzia* Volume 19. Pretoria: South African National Biodiversity Institute.
35. Palomares, F., Delibes, M., Revilla, E., Calzada, J., Fedriani, J.M. 2001. Spatial ecology of the Iberian lynx and abundance of European Rabbit in southwestern Spain. *Wildlife Monographs*,148, 1-36.
36. PBS Nature Series. 2012. *The White Lions*. Available online: https://www.pbs.org/wnet/nature/white-lions-introduction/7663/ (Accessed on 21 February 2023)

37. Power, R.J. 2002. Prey selection of lions *Panthera leo* in a small, enclosed reserve. *Koedoe*, 45: 67-75.
38. Robinson, R., De Vos, V. 1982. Chinchilla mutant in the lion. *Genetica*, 60: 61-63.
39. Römpler, H., Rohland, N., Lalueza-Fox, C., Willerslev, E., Kuznetsova, T., Rabede, G., Bertranpeti, J., Schöneberg, T., Hofreiter, M. 2006. Nuclear gene indicates coat-colour polymorphism in mammoths. *Science,* 313(5783): 62.
40. Rudnai, J. 1974. The pattern of lion predation in Nairobi Park. *East African Wildlife Journal,*12: 213–225.
41. Schaller, G.B. 1972. *The Serengeti Lion: A Study of Predator–Prey Relations,* University of Chicago Press, Chicago.
42. Searle, A.G. 1968. *Comparative Genetics of Coat Color in Mammals*. New York: Academic Press.
43. Skinner, J.D., Chimimba, C.T. 2005. *The Mammals of the Southern African Subregion*. Cape Town: Cambrige University Press.
44. Smuts, G.L. 1982. *Lion*. Johannesburg: MacMillan South Africa.
45. Snyder, N.F.R., Derrickson, S.R., Beissinger, S.R., Wiley, J.W., Smith, T.B., Toone, W.D., Miller, B. 1996. Limitations of captive breeding in endangered species recovery. *Conservation Biology*, 10:338-348.
46. Stanley Price, M.R. 1991. A review of mammal re-introductions, and the role of the Re-Introduction Specialist Group of IUCN/SSC. *Symposia of the Zoological Society of London*, 62: 9-25.
47. Stuart, S.N. 1991. Re-introductions: to what extent are they needed? *Symposia of the Zoological Society of London*, 62: 27-37.
48. Tucker, L. 2003. *Mystery of the White Lions: Children of the Sun God.* White River: Npenvu Press.
49. Turner, J. 2005. *The impact of lion predation on the large ungulates of the Associated Private Nature Reserves, South Africa.* MSc thesis. University of Pretoria, Centre for Wildlife Management.
50. Van Dyk, G. 1997. Reintroduction techniques for lion (Panthera leo). In: *Proceedings of a Symposium on Lions and Leopards as Game Ranch Animals.* Edited by Van Heerden J. Onderstepoort: Wildlife Group of the South African Veterinary Association.
51. Van Orsdol, K.G. 1982. Ranges and food habits of lions in Rwenzori National Park, Uganda. *Symp. Zool. Soc. Lond*. 49: 325–340.
2. Xu, X., Dong, G-X., Hu, X-S., Miao, L., Zhang, X-L., Zhang, D-L., Yang, H-D., Zhang, T-Y., Zou, Z., Zhang, et al. 2013. The Genetic Basis of White Tigers. *Current biology*, CB. 23. 10.1016/j.cub.2013.04.054.

Photo 5.1 White lion male in an acclimation boma (enclosure) before being reintroduced into free-roaming area at Tula Tsau Wildlife Area. © *Global White Lion Protection Trust*

5 White Lion Conservation

Reintroduction, Anthropogenic Impact and Conservation Management in the Greater Kruger Park Region.

Summary: The reintroduction and conservation management of white lions in the Greater Kruger Park Region by the Global White Lion Protection Trust is described for the first time. Although white lions are a natural occurrence in the Greater Kruger Park Region, and the frequency of occurrence increased historically, there was an absence from 1994 to 2006. The reason was proposed to be either a lack of camouflage preventing white lions from hunting successfully in the wild, or the impact of anthropogenic activities. Between 2006 and 2022 white lion cubs (17) were born to seven lion prides in the Greater Kruger Park Region, confirming that the recessive gene is still present in the wild lion population. However, at the time of writing (2023) only three adult white lions had survived in the wild, and the Global White Lion Protection Trust proposed that this was due to anthropogenic activities. In 2006 the Global White Lion Protection Trust reintroduced a pride of white and tawny lions to free-roaming condition and initiated a study to compare the ecology of white lions to wild tawny lions, and to consider the anthropogenic activities that could have had an impact on white lions, historically and at the time of this study. White lions showed natural behaviour similar to wild tawny lions in terms of their social behaviour, home range dynamics, movement patterns, habitat selection, and hunting success (Chapter 2, 3, and 4). The key anthropogenic activities that are likely to have affected wild white lions historically and at the time of this study were in accordance with those identified in the draft conservation policies being developed by the South Africa Government at the time of writing (2023): illegal removal from the wild into captive breeding (hunting) farms, trophy hunting of captive and wild lions, targeted poaching of lions for their body parts, and human-lion conflict. In conclusion, the conservation management of white lions in the Greater Kruger Park Region by the Global White Lion Protection Trust is an important contribution to the metapopulation approach to lions in South Africa, and in particular through the establishment that the cultural significance of the white lion to local Tsonga and Sepedi communities is a possible way to reduce poaching, trade in lion parts, and human-lion conflict.

Keywords: white lion; human threats; reintroduction; lion conservation policy; South Africa

5.1 Introduction

As outlined in the earlier chapters of this study, white lions are a natural occurrence in the Greater Kruger Park Region of South Africa, and do not occur naturally anywhere else. From 1994 to 2006, white lions were absent from the wild due to anthropogenic impact. An organisation called the Global White Lion Protection Trust (GWLPT)[3] therefore initiated a reintroduction programme to return white lions to free-roaming conditions in the region of their natural occurrence. The white lion is a natural colour variant, or leucistic form, of the southern subspecies of the African lion (*Panthera leo melanochaita*) that has only ever been recorded in the wild in the Timbavati, Klaserie and Umbabat Private Nature Reserves (Greater Timbavati Region) and the Central Kruger National Park (KNP) – the Greater Kruger Park Region – in South Africa (Robinson & De Vos 1982; McBride 1977; McBride 1981; Cruickshank & Robinson 1997; Tucker 2003; Cesare 2011; Turner et al. 2015; Dicks 2022). Although white lions occur within the wild lion population in the Greater Kruger Park Region, due to the rarity of white lions (only 13 wild-managed lions and three wild adult white lions) (Turner et al. 2022b; Dicks 2022), the anthropogenic activities that affect the wild tawny lion population may have a more significant impact on wild and wild-managed white lions in that region. These anthropogenic activities will be considered in this chapter. Human-lion conflict being one of the anthropogenic threats that has been identified for wild lions (eg. Bauer et al. 2015; Bauer et al. 2020), I will also discuss the long-standing cultural significance of white lions amongst the local Tsonga and Sepedi populations in the Greater Kruger Park Region that has led white lions to be referred to as a 'living cultural heritage' that may help to mitigate human-lion conflict and lion poaching for body parts (Tucker 2003; Meyerhoff Hieronimus 2017: 82-120;Turner & Wels 2023).

The conservation of white lions in South Africa is an indistinguishable part of the broader conservation efforts for tawny lions (*Panthera leo melanchaita*) since, according to taxonomic studies, white lions themselves are not a subspecies of *Panthera leo*, but instead belong to the southern subspecies *Panthera leo melanochaita* (Bertola et al. 2015; Kitchener et al. 2017). Conservation management seeks to minimise the direct and indirect negative impacts on species, by regulating human activities, with the goal of sustaining the existence of specific species or of biodiversity in general (Sale 2002). The conservation management of lions and other wildlife species in South Africa is guided and regulated by the conservation policies promulgated by the Department

[3] The Global White Lion Protection Trust is a non-profit conservation trust that was founded in 2002 after ten years of research into both the conservation and cultural significance of white lions (Tucker 2003; 2013; Turner et al. 2015), in order to re-establish white lions in the wild in their natural habitat and ensure their long-term protection as an important contribution to the biodiversity of the Greater Kruger Park Region and Kruger to Canyons Biosphere Reserve (www.whitelions.org).

of Forestry, Fisheries, and Environment (DFFE) in that country. The key conservation policies in South Africa were under review at the time of writing: the 'Draft Policy Position on the Conservation and Ecologically Sustainable Use of Elephant, Lion, Leopard and Rhinoceros' (Government Gazette 45160), 'The National Environmental Management Biodiversity Act (10/2004): Biodiversity Management Plan for the African Lion (*Panthera leo*)' (Government Gazette 39468), the 'Draft African Lion Biodiversity Management Plan Review Report' (DFFE & NLWG 2022), and the more overarching South African 'Revised Draft White Paper on Conservation & Sustainable use of Biodiversity in South Africa (Government Gazette 46687). Since white lions were absent from the wild in 2006, and there were no adult white lions in the wild at that time, the Global White Lion Protection Trust (GWLPT) reintroduced a pride of white and tawny lions to free-roaming conditions within a small fenced wildlife area (Tula Tsau Wildlife Area), in the Greater Kruger Park Region.

In Chapter 2, 3 and 4 the ecology of white lions was found to be similar to that of wild tawny lions in terms of their genetics, social behaviour, hunting success, home range dynamics and movement patterns (for more on the genetics of white lions and *Panthera leo melanochaita* see Robinson & De Vos 1982; Cruickshank & Robinson 1997; Bertola et al. 2015; Kitchener et al. 2017; and Cho et al. 2013). This is supported by historical and recent observations of white lions as part of socially cohesive prides in the wild (Cesare 2011; Gomersall 2015; Howarth 2022; Dicks 2022).

This conclusion supports the postulation by the Global White Lion Protection Trust that the absence of white lions from the wild from 1994 to 2006 is not due to white lions lacking camouflage and not being able to hunt, but may be due to anthropogenic activities. This chapter is therefore focused on the reintroduction and conservation management of white lions in the Greater Kruger Park Region by the Global White Lion Protection Trust in context of the anthropogenic activities that affect lions (white and tawny) in the Greater Kruger Park Region, and the metapopulation management approach to lions in South Africa. The chapter is structured as follows:

1. Firstly, the significance of white lions is discussed in terms of their genetics, hunting success, home range behaviour, social structure and general lion behaviour, as shown through current scientific research, including a discussion about their conservation and cultural importance.

2. Secondly, a review is provided of the reintroduction and conservation management efforts by the Global White Lion Protection Trust with regard to white lions (as part of wild tawny prides).

3. Next, the anthropogenic threats to wild and captive white lions in South Africa are summarised and put into context by considering the anthropogenic threats to wild tawny lions in the Greater Kruger Park Region, defined by the draft conservation policies in South Africa ('Draft Policy Position on the Conservation and Ecologically Sustainable Use of Elephant, Lion, Leopard and Rhinoceros') and recent scientific studies.

4. Finally, the conservation role of the white lion reintroduction by the Global White Lion Protection Trust is discussed, in the context of the anthropogenic threats to (white and tawny) lions, and the existing conservation management principles for the metapopulation approach to lion conservation in South Africa.

5.2 Theoretical Background

5.2.1 White Lion Significance as Members of the Southern Subspecies of the African Lion (*Panthera leo melanochaita*) in the Greater Kruger Park Region

Lions were eradicated from most of their range in South Africa by the 1900s, with historic populations remaining in only Kruger National and Kgalagadi Transfrontier Parks. Today just over 3500 wild lions are well protected in these and other large national parks and game reserves, with all populations either stable or increasing (Bauer et al. 2015; Miller et al. 2015; Miller et al. 2016). This managed lion metapopulation network comprises free-roaming populations and those maintained in smaller fenced reserves and protected areas across South Africa's provinces (Miller et al. 2016). Over the last three decades lions have also been reintroduced into over 49 smaller reserves with a total population of what are termed the 'managed-wild' lions of about 800 individuals (Miller et al. 2015; Government Gazette 39468). In addition to the wild and managed-wild lion populations there are also significant numbers of captive-bred lions in South Africa – the latest estimate is more than 8500 captive lions (Coals et al. 2019; Hutchinson & Roberts 2020; Green et al. 2021). At least 300 to 500 of these captive lions were estimated to be white lions, mainly bred for trophy hunting or the lion bone trade (Tucker 2013). Due to the unethical and unregulated nature of the majority of the captive breeding farms, the number of lions in captivity can only be estimated (Green et al. 2020; Government Gazette 45160).

I have already established earlier in this chapter that white lions are naturally-occurring members of the southern subspecies of the African lion *Panthera leo melanochaita*, in terms of their genetics (Bertola et al. 2015; Kitchener et al. 2017). The findings from my earlier scientific research in this doctoral study suggest that white lions show similar natural behaviour to wild tawny lions in terms of their hunting success, home range behaviour, social structure and general lion behaviour (Chapter

2, 3 and 4; Turner et al. 2015; 2022a; 2022b). To elaborate further on this point, in their study, Turner et al. (2015) found that there was no significant difference between the mean kill rate or mean consumption rate of white and tawny lions, concluding that white lions are capable of hunting self-sufficiently under managed free-roaming conditions in their natural habitat. Turner et al. (2022b) determined that the annual and seasonal home range size, male and female home ranges, potentially minimum daily distance travelled, and habitat selection of white lions were found to be similar to that of wild tawny lions, concluding that white lions established territories and displayed natural home ranging behaviour. Also, the social behaviour of white lions was observed to be similar to that of tawny lions by Turner et al. (2022a), and in fact the level of social cohesion between pride members was stronger for white lions than for the captive or wild tawny lion prides with which they were compared. As such, white lions show natural behaviour similar to that of wild tawny lions and are therefore relevant members of the Southern African lion subspecies (*Panthera leo melanochaita*) and, consequently, reporting on their reintroduction and conservation management should be a worthwhile contribution.

5.2.2 White Lion Reintroduction and Conservation Management in the Greater Kruger Park Region

The conservation and protection of all natural heritage is critical since the rate of global change in nature during the past 50 years is unprecedented in human history (IPBES 2019). The Global White Lion Protection Trust (GWLPT) was established in 2002 with the aim to reintroduce white lions to the wild in their natural habitat, as members of wild tawny lion prides, in the way that white lions occurred naturally (McBride 1978; McBride 1981; Cesare 2011). The frequency of occurrence of white lions in the region was increasing in the 1980s, with 12 recorded sightings in nine different prides in the Timbavati Private Nature Reserve and Central Kruger National Park (Robinson & De Vos 1982; Cruickshank & Robinson 1997). As a natural occurrence in the Greater Kruger Park Region of South Africa that has never occurred in the wild anywhere else, it has been suggested that the reason white lions were absent in the wild from 1994 to 2006 was due to anthropogenic impact. The proposed anthropogenic activities were removal (unauthorised or illegal translocation) of white lions from the wild in the Timbavati Private Nature Reserve to small fenced captive breeding farms, and trophy hunting of the pride males of lion prides in which the white cubs were born, leading to infanticide of the white (and tawny) cubs from those prides (Cadman 2006; Tucker 2003; Cesare 2011; Turner et al. 2015; Pinnock 2018). In 2006, the Global White Lion Protection Trust therefore initiated the first reintroduction of white lions to free-roaming conditions within a small fenced wildlife area in the Greater Kruger Park Region. Between 2006 and 2022 white lion cubs (17) were born in the Greater Kruger Park Region, confirming that the recessive gene is still present in the wild lion population (Dicks 2022). Since in 2006 there were no adult white lions in the wild, no study had been done to investigate the ecology of white lions compared with free-roaming tawny lions. Although free-roaming white lions have been introduced to two fenced wildlife reserves in the Western Cape (Sanbona Wildlife Reserve: Gomersall 2015) and Eastern Cape (Pumba Private Game Reserve: Howarth 2022) of South Africa these reserves are not within the region of natural occurrence of white lions, and to my knowledge no published scientific studies have been done on the introduced white lions. The findings of this doctoral study could therefore be of benefit to the conservation management of the white lions in these reserves. My study is the first to compare the ecology of white lions in relation to wild tawny lions, to see if white lions show natural behaviour similar to wild tawny lions, suggesting that white lions can survive in the wild (see Chapter 2, 3, and 4). Prior to this study, the perception was that the white colouration led to a lack of camouflage in white lions such that they could not hunt successfully or survive in the wild. The earlier findings of this doctoral study (Chapter 2, 3, and 4; Turner et al. 2015; 2022a; 2022b), do suggest that white lions behave naturally in a similar way to wild tawny lions, and could therefore survive in the wild. This is supported by previous observations of wild white lions forming socially cohesive prides with wild tawny lions in the Greater Kruger Park Region and at Sanbona Wildlife Reserve and Pumba Private Nature Reserve (Cruickshank & Robinson 1997; Cesare 2011; Gomersall 2015; Dicks 2022; Howarth 2022). Notably, at the time of writing (2023), of the 17 white lion cubs that had been born in the wild in the Greater Kruger Park Region between 2006 and 2022, only 3 adult white lions had survived. Because the earlier findings of this doctoral study, historical observations, and anecdotal observations at Sanbona and Pumba Private Game Reserves, suggest that white lions are capable of surviving in the wild as part of wild tawny prides, it is proposed that the reason for the low survival rate of white lion cubs in the Greater Kruger Park Region was due to anthropogenic activities – i.e. the on-going trophy hunting of pride males of lion prides with white cubs leading to cub mortality due to consequential infanticide, and the high impact of ecotourism vehicles, viewing prides when white lion cubs are still very young, causing high levels of stress on the mother of the cubs and leading her to move the cubs prematurely or leave them unattended for long periods of time (Pinnock 2018; Tucker 2013; Turner et al. 2015; Gomersall 2015; Dicks 2022; Howarth 2022). These anthropogenic activities could have had a significant effect on white lion survival, in addition to the fact that the natural mortality rate of lion cubs (white and tawny) that do not survive to reach adulthood can be as high as 50% (Schaller 1972).

The Global White Lion Protection Trust initiated the following steps in its conservation efforts towards achieving its goal of reintroducing white lions to their natural home range, and protecting them from the anthropogenic impact thought to have led to their absence (cf. Turner et al. 2015):

1 Translocation of white lions of high genetic integrity (i.e. individuals that are genetically diverse and with a lineage that is traceable back to a wild origin within two or three generations) from captive hunting operations to a reintroduction enclosure (boma) in their natural habitat;
2. Rewilding of translocated white lions;
3. Integration of translocated white lions with wild tawny (non-white) lions;
4. Reintroduction of prides of rewilded captive-origin white and wild tawny lions to a wild-managed conservation area (fenced wildlife areas where lions hunt self-sufficiently but the prey population is replenished when necessary: definition from Government Gazette 39468);
5. Facilitating the birth of white and tawny cubs carrying the recessive white gene, in a wild-managed conservation area;
6. Introduction of individuals with different genetics when necessary to ensure genetic diversity and prevent inbreeding (Kitchener et al. 2017) - in accordance with the metapopulation management approach to lions in South Africa (as described by Miller et al. 2015);
7. Expansion of conservation areas belonging to the Global White Lion Protection Trust to include more suitable habitat and territory for the reintroduced lion prides and their offspring, as well as opening up important wildlife corridors within larger conservation areas;
8. Strategies to mitigate the anthropogenic threats to white lions: trophy hunting, trade in lion bones, poaching, disease (especially Bovine Tuberculosis bTB), and human-lion conflict.

The Global White Lion Protection Trust reintroduction of white lions within their natural habitat in 2006 was done by applying and advancing existing successful lion reintroduction techniques such as outlined by Van Dyk (1997) and Kilian (2003) (Turner et al. 2015). The rewilded offspring of reintroduced white lions of captive-origin were integrated with wild tawny lions from the region and released through a phased reintroduction technique and a 'soft' release approach. A pride of high genetic diversity (ie. a pride that is not inbred and has genetics that can be traced back to the wild) was established, which hunted self-sufficiently in their natural habitat, at a predation rate comparable to that of the wild tawny lions in the same habitat (Chapter 4; Turner et al. 2015). The lion prides reintroduced by the Global White Lion Protection Trust were translocated to a fenced wildlife reserve that is managed in a similar way to that of the 49 other fenced reserves that are part of the metapopulation management approach to lions in South Africa (Miller et al. 2016). As a unique and natural occurrence to the UNESCO-declared Kruger to Canyons Biosphere Reserve (Tucker 2003; Dicks 2022), the Global White Lion Protection Trust poses that the white lions are a contribution to the biodiversity of the Kruger to Canyons Biosphere Reserve. As apex predators responsible for regulating prey populations ('trophic cascading': Hairston et al. 1960[4]), white lions (as part of wild tawny prides) play a role within the ecosystem of the Greater Kruger Park Region. In addition to the role that white lions potentially play within the ecosystem, the Global White Lion Protection Trust also points out that white lions are important due to their cultural meaning to local communities (Tucker 2003). According to the Global White Lion Protection Trust the cultural meaning of white lions to the Tsonga and Sepedi communities living on the boundary of the Tula Tsau Wildlife Area, is encouraging these communities to have a positive attitude towards protecting white lions and their habitat, helping to reduce human-lion conflict, and the targeted poaching of lions for their bones in that region (Tucker 2003). The Global White Lion Protection Trust has implemented the following strategies to reduce the impact of these anthropogenic activities: (i) Prohibition of trophy hunting in Global White Lion Protection Trust wildlife areas; (ii) Establishment of anti-poaching teams, and electrified fences with alarms on all Global White Lion Protection Trust wildlife areas; (ii) Replenishment of the prey population on Global White Lion Protection Trust wildlife areas with disease-free prey herds whenever it is necessary; (iii) Development of environmental education programmes in local Tsonga and Sepedi schools (the StarLion Programme: https://whitelions.org/starlion-education-initiative/), to help reduce human-lion conflict and poaching of lions for their bones. (iv) Creation of public awareness, through public campaigns, lobbying and partnering with other like-minded organisations, in order to change conservation policies in South Africa to better protect wild populations of white and tawny lions in their natural habitat by stopping captive lion hunting (so called 'canned hunting'[5]), and the trade in lion bones. The Global White Lion Protection Trust has therefore focused on the co-existence between Lions, Land and People: a conservation model that creates mutual benefits for people and their natural environment, thereby protecting white lions as a natural and cultural heritage.

For seven years, the Global White Lion Protection Trust led collaborative research projects together with five other countries, comparing the genetics of white lions with snow leopards, tigers, and the white 'Kermode' bear of British Columbia, which finally led to the discovery of the genetic marker (allele) TYR260G>A, a specific recessive gene responsible for white colouration in white lions, in October 2013 (Cho et al. 2013). As part

[4] 'In a trophic cascade, ecological processes and consequences initiated by a change at the top of the food chain work their way down to lower trophic levels and eventually rebalance the ecological relationships of numerous species.' Trophic cascade in Yellowstone National Park - AccessScience from McGraw-Hill Education, accessed 29 January 2021.

[5] '(A) Canned hunt would be any hunt where the target animal is unfairly prevented from escaping the hunter through either physical (fencing) or mental (habituated to humans) constraints' (Pearce 2018: 137). See also Campaign Against Canned Hunting (CACH) - Campaign Against Canned Hunting Home Page (cannedlion.org), accessed 29 January 2021, and a documentary made to protest against canned hunting practices in South Africa, Blood Lions – A Call to Stop Canned Lion Hunting, accessed 29 January 2021.

of a strategy to help protect *Panthera leo melanochaita* in the Greater Kruger Park Region, the Global White Lion Protection Trust aims to utilise the white lion genetic marker (allele) to ensure the genetic diversity of the reintroduced lion prides and ultimately to determine the frequency of occurrence of the rare white lion gene in the wild population.

Subsequent to the lion reintroduction programme of the Global White Lion Protection Trust, white cubs started being born in the Timbavati, Klaserie, and Umbabat Private Nature Reserves in 2006 to 2009, 2011, 2014, 2015, 2018, and 2019, in neighbouring Nwanetsi Area of Kruger National Park in 2014, 2015 and 2022, and in the Ngala Lodge traversing area (Timbavati Private Nature Reserve) in 2018 and 2019. This reoccurrence of white lions in the wild, has confirmed that the recessive gene is still present in the wild population of the Kruger to Canyons Biosphere Reserve and that white lions are a natural occurrence and part of the biodiversity of this ecosystem (Tucker 2003; Cesare 2011; Turner et al. 2015; Ngala Lodge[6]; Dicks 2022). The Global White Lion Protection Trust advocates that the restoration of white lions to their natural distribution range has conservation importance as well as cultural heritage benefits for the Greater Kruger Park Region, and the Kruger to Canyons Biosphere Reserve. White lions, as members of the subspecies *Panthera leo melanochaita*, are an apex predator and could be considered a 'keystone species' (Mills et al. 1993; Simberloff (1998). In the Greater Kruger Park Region the lion population has been negatively impacted by human interventions such as historical culling (cropping) programmes (Smuts 1982) and commercial trophy hunting activities (in the neighbouring buffer reserves) (Tucker 2003; Cesare 2011; Pinnock 2018), along with illegal poaching, trade in lion parts (Miller et al. 2014) (Government Gazette 45160), and the spread of diseases such as bTB (bovine tuberculosis) (Government Gazette 39468). The Global White Lion Protection Trust therefore ensured that the white lion reintroduction to their natural habitat was part of a restoration strategy for the biodiversity of the region, and a possible way to help mitigate human-lion conflict and targeted lion poaching for their body parts.

The approach of the Global White Lion Protection Trust to protect a charismatic apex predator that has significant cultural meaning within the greater ecosystem is based on other international precedents, such as that used to protect the Kermode Bear (*Ursus americanus kermodei*) in British Columbia (Western Canada), whereby this rare white variant of the Black Bear (*Ursus americanus*) has been declared Critically Endangered due to its conservation and cultural value. As with the Kermode Bear, which is being used as a keystone animal for protecting a 4000,000 ha wilderness area (Russell 2017; Marshall & Ritland 2002), it is hoped and envisioned by the Global

[6] https://www.andbeyond.com/magazine/the-rare-white-lions-of-ngala/, accessed 13 January 2023.

White Lion Protection Trust that protecting the white lions as a keystone animal for the Kruger to Canyons Biosphere Reserve, could ultimately help to ensure that the entire lion population and all naturally occurring species within their area of occurrence will be protected.[7]

5.2.3 Anthropogenic Threats to White Lions in the Greater Kruger Park Region

As naturally-occurring members of the southern subspecies of the African lion *Panthera leo melanochaita*, and more specifically the lion population in the Greater Kruger Park Region, the wild and managed-wild white lions face similar threats to the wild tawny lions in that region. Although the lion population in South Africa is regarded as being stable, and anthropogenic activities are therefore regarded as not having a significant impact, since there are only 13 wild-managed white lions and three wild lions in the Greater Kruger Park Region, white lions are more vulnerable to anthropogenic impact (Riggio et al. 2013; Turner et al. 2015; Turner et al. 2022a; 2022b). The downlisting of the conservation status of lions in South Africa by the Department of Fisheries, Forestry, and the Environment (DFFE)[8] from Regionally Vulnerable to Regionally Least Concern on the global IUCN Red List (Hutchinson & Roberts 2020), as well as the demand for lion bones for traditional and cultural use, could in the long term put the chances of survival of white lions in the Greater Kruger Park Region under threat. The downlisting could increase the demand for wild lion trophies and especially lion bones, increasing poaching and illegal hunting and threatening the future of wild lion populations in South Africa[9]. Equally, if not more concerning from a conservation perspective, is the reclassification of 32 South African wild species (which includes lions) as farm animals by the South African Government (Somers et al. 2020). The reclassification as farm animals means that these wild species are open to a higher level of consumptive utilisation and therefore possible commercial exploitation.

The specific human threats to wild and captive lions (white and tawny) in South Africa are summarised (2.3.1 and 2.3.2) based on the draft lion conservation policies under review by the South African Government: 'Draft policy position on the conservation and ecologically sustainable use of Elephants, Leopard, Lion and Rhinoceros', 'The National Environmental Management Biodiversity Act (10/2004): Biodiversity Management Plan for the African Lion (Panthera leo)', and the 'Draft African Lion Biodiversity Management Plan Review Report' (Government Gazette 45160; Government Gazette 39468; DFFE & NLWG 2022):

[7] Kruger to Canyons | Biosphere Region (kruger2canyons.org), accessed 12 January 2023

[8] Now the Department of Forestry, Fisheries and the Environment (DFFE).

[9] http://whitelions.org/2015/05/22/sa-proposed-biodiversity-management-plan-to-put-lions-at- greater-risk/, accessed 28 January 2023.

5.2.3.1 Anthropogenic Threats to Wild and Wild-Managed White Lions

Trophy-hunting: Trade-related practices such as trophy-hunting have been recognised as risk factors for lions (Bauer et al. 2018). White lions are specifically sought for by trophy hunters and this may lead to selective hunting and dilution of the white gene pool (Cadman 2006; Tucker 2003; 2013; Turner et al. 2015; Dickinson 2021). The trophy hunting of lions in the privately-owned Associated Private Nature Reserves (APNR) that are open to the Kruger National Park, has often removed pride male lions, that may or may not be carrying the white lion recessive gene, and led to consequential infanticide and long-term disruption of natural lion pride and population structure (Whitman et al. 2007; Turner et al. 2015; Pinnock 2018; Dickinson 2021).

Lion bone trade: The legalisation of the international trade in lion body parts and derivatives from captive lions in South Africa to South East Asia by CITES in 2016, has subsequently led to a concern that this could prompt an increase in poaching and most likely illegal trade (Williams et al. 2017; EWT 2017). According to the same authors, a concern exists that this illegal trade could become a serious threat to wild-ranging lion populations in South Africa. Legal international trade in bones that were reported as being from captive-bred lions, could serve as a cover-up for illegally wild-sourced lion parts (Nowell & Pevushina 2014; Coals et al. 2022). The international trade in lion body parts and derivatives from captive lions in South Africa to South East Asia was therefore stopped by the South African government in 2021 (Government Gazette 45160). In response to a relative paucity of evidence-based research into trade in wild lion body parts, the International Union for Conservation of Nature (IUCN) in its Resolution 059 at the World Conservation Congress (WCC) in Marseille in 2020 -'Combatting the illegal trade in lion body parts and derivatives' - calls for further consideration of drivers of poaching, illegal trade in lion parts and understanding of value-driven incentives for lion conservation (IUCN World Conservation Congress 2020). Detailed studies and investigations into the lion bone trade have therefore been done by several authors, including Williams et al. (2017a; 2017b), Coals et al. (2021), Williams et al. (2021), Coals et al. (2022), and Mbongwa et al. (2022). The following important points were taken from the abovementioned studies. Until recently, the focus has been on legal trade in lion bones to Southeast Asia (Williams et al. 2017a; 2017b; 2021), whereas in Southern Africa lion bones and body parts are also sourced and traded domestically for cultural purposes, including zootherapeutic or traditional medicines, clothing, ornamentation, bushmeat, and curios, involving intra-continental supply chains (Lindsey et al. 2012; Williams et al. 2017a; 2021). Although domestic trade and use of lion body parts is common in Southern Africa, traditional and local uses are often overlooked in terms of their potential impact on wild lion exploitation, poaching and even population decline in regions of low density (Coals et al. 2020; Williams et al. 2021; Arias et al. 2022), probably due to cultural-political sensitivities associated with the policing of traditional practices (Bauer et al. 2018; Naude et al. 2020). There are many cultural beliefs regarding lions, including attributes of power, strength, and fear, and the lion therefore often denotes status and respect amongst kings, chiefs, and traditional healers (Thornton 2009; Williams et al. 2015; Williams et al. 2021). Despite the number of ethnographic studies that have been done on wildlife use in traditional and cultural practices (Mokgobi 2014), very little is known about the impact that traditional and cultural use and trade in lion body parts in South Africa for traditional medicine may have on wild lion populations (Coals et al. 2022). According to Tucker (2003), the white lions have a long history of being regarded as culturally and spiritually significant by several population groups in South Africa and other parts of Africa. In accordance with ancient African tradition in which clans had specific totem animals that were revered and protected, the white lion was regarded as sacred and protected as a totem animal by specific Tsonga, Sepedi, Swazi, and Khoi San (Bushmen) local communities, dating back centuries. The knowledge passed down through this oral tradition indicates that the white lions appeared over 400 years ago during the reign of Queen Numbi, in the area known today as Timbavati Private Nature Reserve. The Global White Lion Protection Trust has therefore suggested that the cultural meaning of white lions to the Sepedi and Tsonga communities bordering on the Tula Tsau Wildlife Area is helping to mitigate against lion poaching and trade in lion body parts in that wildlife area.

However, the recent legalisation of the trade in lion bones from captive lions in South Africa in 2016 has led to concerns that it could prompt an increase in poaching and most likely illegal trade (Williams et al. 2017; EWT 2017). According to the same authors, this illegal trade could become a serious threat to wild-ranging lion populations in South Africa. Legal international trade in bones from captive-bred lions could serve as a cover-up for illegally wild-sourced lion parts (Nowell & Pevushina 2014; Coals et al. 2022). The international trade in lion body parts and derivatives from captive lions in South Africa to South East Asia was therefore stopped by the South African government in 2021 (Government Gazette 45160). The impact of traditional trade on wild lion populations remains largely under-considered and unquantified, although some authors suggest that the impact may be larger than that of international (legal and illegal) trade (Williams et al. 2017; EWT 2017). Nevertheless, the results of a study by Coals et al. (2022) indicate that South African muthi (i.e. traditional, or cultural medicine) trade in lion parts within southern Africa has a trade footprint with international dimensions. This includes a trade in body parts from white lions which are sought after due to their cultural meaning and rarity, since they are only found in the Greater Kruger Park Region in South Africa (Tucker 2003). It has been suggested that due to their rarity (three wild and 13 wild-managed) white lions are particularly at risk of poaching for their body parts (Tucker 2013; Dickinson 2021). In response to a relative lack of evidence-based research into the illegal trade in wild lion body parts, the International Union for Conservation of Nature (IUCN), in its Resolution 059 adopted at the World Conservation Congress

(WCC) in Marseille in 2020 - 'Combatting the illegal trade in lion body parts and derivatives' - calls for further consideration of drivers of poaching, illegal trade in lion parts and an understanding of value-driven incentives for lion conservation (IUCN World Conservation Congress 2020). There is also concern that wild lion body parts from eastern and southern Africa could be drawn into the large illegal wildlife trade to Asia centred around elephant ivory and rhino horn (IUCN 2016). Coals et al. (2022) suggest that, in order to protect wild lion populations from illegal exploitation, there is a need for effective and socially just law enforcement and trade regulation engagement with stakeholders in culturally traditional lion trade systems.

Poaching for the bushmeat trade[10]: (White) lions often end up in snares intended for other species such as buffalo, zebra and wildebeest, targeted for the trade in bushmeat (Becker et al. 2022). Despite the daily snare patrols by anti-poaching teams on the Global White Lion Protection Trust wildlife areas, sometimes animals still end up in snares.

Bovine tuberculosis (bTB): In the Kruger National and Hluhluwe-iMfolozi Parks, Bovine tuberculosis (bTB) has spread throughout these parks by the movements of the buffalo, as maintenance hosts for bTB and a primary prey of lions, and over 80% of lions in some areas of the Kruger National Park are infected by bTB (Radloff & Du Toit 2004; Owen-Smith & Mills 2008a; 2008b; Funston et al. 1998; Keet et al. 2009). Since African buffalo and blue wildebeest are primary prey of lions in the Greater Kruger Park Region, lions (tawny and white) are at risk to the spill-over effects of bTB. With the existing shifts in climate towards drier conditions, lions, and all animal species, are likely to be under greater environmental stress, reducing their immunity, and making them more susceptible to diseases such as bTB (Government Gazette 39468).[11]

Human-lion conflict: Poor management of the boundary fences of wildlife reserves and national parks often leads to a high occurrence of human-lion conflict for communities bordering on the Greater Kruger National Park, with lions (tawny and white) being killed as damage-causing animals (Government Gazette 45160). Since certain tawny lions in the Kruger National Park have the recessive gene that causes the white colouration, potential gene carriers are at risk of being killed through human-lion conflict.

[10] 'The term 'bushmeat' is originally an African term for wildlife species that are hunted for human consumption, and usually refers specifically to the meat of African wildlife (Bennett et al. 2007).

[11] SANParks is presently planning to conduct a comprehensive study to investigate the incidence of bTB in the lion population in the Kruger National Park, and the correlation with the stress levels of lions, in relation to environmental conditions. The outcome of this study will be important for managing this threat to wild lion populations, which was introduced to African buffalo when European cattle were imported into South Africa in the 1950s or early 1960s (Bengis et al. 1996; Michel et al. 2006; Keet et al. 2009).

Policy concerns: (i) No national policy exists to enforce a minimum level of regulation for lion management in the 49 fenced wildlife reserves; instead, at the time of writing it is based on voluntary membership and adherence to management principles defined by the Lion Management Forum (LiMF) and adaptive management (Government Gazette 45160; Government Gazette 39468); (ii) Corruption and involvement of national park personnel in lion and rhino poaching has been identified within certain of South Africa's national parks and a number of the wildlife reserves (Bloom 2021); (iii) Trophy hunting of lions (white and tawny) is still an accepted practice within the private wildlife reserves that form part of the Greater Kruger Park ecosystem. In addition to the negative effects on the lion pride and population structure, trophy hunting in South Africa is opposed by many tourists and is a threat to the significant income source derived from ecotourism (Pinnock 2022); (iv) Poorly managed fence lines between the national parks and community areas leads to human-lion conflict and often the shooting of lions that escape into the community areas (Bloom 2021).

5.2.3.2 Anthropogenic Threats to the Captive White Lion Population in South Africa

The rarity of white lions and their spiritual and cultural significance to certain Sepedi and Tsonga communities in South Africa, and Asian communities in South East Asia, has made them highly sought after and therefore bred extensively in captivity in South Africa (Tucker 2003; Tucker 2013). The following are anthropogenic activities that affect captive white and tawny lions in South Africa:

Trade in lion parts: Since the international trade in captive lion bones and derivatives was legalised in South Africa in 2016, captive-bred lions (white and tawny) have been seen simply as a commodity, compromising the conditions under which captive lions are kept, with no regard for their fundamental living conditions or the prevention of inbreeding (Green et al. 2020; Dickinson 2021; Coals et al. 2022). Although the international lion bone trade from captive lions in South Africa was stopped in May 2021 due to the concerns raised by a high-level panel of experts (Government Gazette 45160; Green et al. 2021), the impact on illegal trade is not yet well understood (Williams et al. 2021; Coals et al. 2022). The controversial practice of lion 'farming' and associated industries of captive-bred or 'canned' trophy hunting linked to intercontinental lion bone trade throughout Southeast Asia brought issues of lion trade to the fore in both conservation and public discourse (Coals et al. 2019). Considerable debate focused on South African lion farming, particularly on how supplies of captive-bred lion products may influence trade dynamics and impact the few remaining wild lion populations (Williams et al. 2017a; Coals et al. 2019; Williams et al. 2021; Becker et al. 2022). Combatting the illegal trade in lion body parts and derivatives is critical to provide evidence-based research into drivers of wild lion overexploitation for trade, and the development of novel methods for the investigation and monitoring of trade in lion parts (IUCN World Conservation Congress 2020). A key to monitoring the trade in lion parts will be to distinguish between captive-bred and wild lion bones, and as yet there is no effective technique for achieving this (Coals et al. 2021). The Global White Lion Protection Trust suggests that since lion bone parts from white lions are highly sought after, and there are so few wild (3) and wild-managed white lions (13), white lions are particularly at risk of poaching for their parts (Tucker 2013; Dickinson 2021).

Trophy hunting: although proposed in the 'Draft Policy on the Conservation and Sustainable Use of Elephants, Leopard, Lion and Rhinoceros' (Government Gazette 45160), it remains to be seen whether the hunting of captive-bred lions (white and tawny) will be banned by the South African conservation authority (DFFE); especially with the opposition from the captive lion breeding industry and lion bone traders, who are threatening with court action against the South African Government if the stricter policy measures are implemented.

Inbreeding and disease: In the more than 300 captive lion breeding operations (Government Gazette 45160), inbreeding of white and tawny lions is common, as well as poor hygiene within the lion enclosures, and the consequential spread of disease (Green et al. 2022).

Policy concerns: A number of policy concerns have been listed in 'The National Environmental Management Biodiversity Act (10/2004): Biodiversity Management Plan for the African Lion (*Panthera leo*)'(Government Gazette 39468) and the 'Draft African Lion Biodiversity Management Plan Review Report' (DFFE & NLWG 2022): (i) There is a lack of regulation of captive lion operations by conservation authorities due to insufficient resources, capacity, and funds to conduct regular inspections of permits, enclosure conditions, and lion numbers in the more than 300 captive breeding operations (Government Gazette 39468; DFFE & NLWG 2022); (ii) There is often a lack of compliance to policy requirements, and enforcement of regulations, at captive lion operations due to the respective South African provinces implementing different Ordinances, as well as the absence of a standard permit system (DFFE & NLWG 2022).

From the description above (2.3.1 and 2.3.2), it is apparent that the Global White Lion Protection Trust and draft conservation policies in South Africa (Government Gazette 39468; DFFE & NLWG 2022) have identified anthropogenic activities that could have an impact on lions (white and tawny) in the Greater Kruger Park Region. The rarity of free-roaming white lions in the Greater Kruger Park Region suggests that particular attention should be given to mitigating the anthropogenic activities that could put free-roaming white lions at risk.

5.2.4 Conservation Role of the GWLPT in the Reintroduction of White Lions to the Greater Kruger Park Region

According to the Global White Lion Protection Trust, the key objectives forreintroducing white lions to the Greater Kruger Park Region are: to return white lions to their natural habitat as part of wild tawny prides, as a natural occurrence of that region; to protect white lions from the anthropogenic activities that led to their absence (1994 to 2006) and low survival rate (2006 to 2022); and to better protect lions (white and tawny) in that region through the cultural significance of white lions to the local Sepedi and Tsonga communities that could reduce human-lion conflict, and poaching of lions for their parts. The long-term objective of the Global White Lion Protection Trust is that the reintroduced prides of white and tawny lions at the Global White Lion Protection Trust wildlife areas will contribute to the metapopulation management approach to wild lions in the Greater Kruger Park Region, and therefore South Africa.

5.3 Discussion and Conclusions

In Chapter 5 the reintroduction and conservation management of white lions in the Greater Kruger Park Region is outlined for the first time, and discussed in relation to the anthropogenic activities that could have had an impact on lions (white and tawny) historically, and at the present time in that region. The possible conservation role of the white lion reintroduction is then discussed in context of the metapopulation management approach to lions (white and tawny) in South Africa.

Since there were no adult white lions in the wild in 2006, the Global White Lion Protection Trust conducted the first reintroduction of white lions to free-roaming conditions in their natural habitat, which was reviewed for the first time in this chapter. The reintroduction methodology used by the Global White Lion Protection Trust was based on the reintroduction guidelines of the IUCN (IUCN / SSC 2013), and the conservation principles applied were aimed at protecting and managing the reintroduced lions in accordance with the principles of the metapopulation approach to lions in South Africa. The earlier findings of this doctoral study (Chapter 2, 3 and 4), showed that white lions are similar to wild tawny lions in terms of their genetics, hunting success, home range behaviour, social structure and general lion behaviour, and are therefore significant members of *Panthera leo melanochaita*. These findings agree with historical observations and reports that in the wild, white lions form socially cohesive prides with wild tawny lions, are able to hunt successfully, and to survive in the wild (Cesare 2011; Tucker 2015). I therefore agree with the postulation by the Global White Lion Protection Trust (GWLPT) that the most likely reason that white lions were absent from the wild from 1994 to 2006, was due to anthropogenic impact: illegal removal to breeding and hunting farms, the continued lion trophy hunting of pride males which caused infanticide, and high impact ecotourism leading to undue stress on lionesses with young cubs during regular viewings by tourist or lodge vehicles (McBride 1977; McBride 1981; Whitman et al. 1997; 2004; Cadman 2006; Turner et al. 2015; Dicks 2022). Although 17 white lion cubs were born in the Greater Kruger Park Region between 2006 and 2022, only three survived. The natural high mortality rate of 50% of wild lion cubs within the first year was likely a contributing factor to the low survival rate (Funston et al. 2003), but a growing anthropogenic threat to lions (white and tawny) in South Africa, including the Greater Kruger Park Region, is the poaching of lions for their body parts for cultural and traditional use, as indicated by Coals et al. (2022) and the 'Revised Draft White Paper on Conservation and Sustainable Use of Elephants, Lion, Leopard and Rhinoceros in South Africa' (Government Gazette 46687). Until recently, the focus has been on legal trade in lion bones to Southeast Asia (Williams et al. 2017a; Williams et al. 2017b; Williams et al. 2021), whereas in Southern Africa lion bones and body parts are also sourced and traded domestically for cultural purposes, including zootherapeutic or traditional medicine, clothing, ornamentation, bushmeat, and curios, involving intra-continental supply chains (Lindsey et al. 2012; Williams et al. 2017a; Williams et al. 2021). Although domestic trade and use of lion body parts is common in Southern Africa, traditional and local uses are often overlooked in terms of their potential impact on wild lion exploitation, poaching and even population decline in low density regions (Coals et al. 2020; Williams et al. 2021; Arias et al. 2022). This includes a trade in body parts of white lions which are sought after due to their cultural meaning and rarity, since they can only be found in the Greater Kruger Park Region in South Africa (Tucker 2003). It has been suggested that due to their rarity (three wild and 13 wild-managed) white lions are particularly at risk of poaching for their body parts (Tucker 2013; Dickinson 2021).The Global White Lion Protection Trust proposes that the fact that the white lion is regarded as a living cultural heritage by local communities in the Greater Kruger Park Region, could in fact help to mitigate human-lion conflict and lion poaching for their body parts (Tucker 2003; Lagendijk & Gusset 2008; Evans 2018: pp. 155-8 and 243-7; Somerville 2020: pp. 196-8). The low incidence of lion poaching at the wildlife areas of the Global White Lion Protection Trust over the past 20 years, suggests that the Tsonga and Sepedi communities that border on the Global White Lion Protection Trust wildlife areas do have a positive attitude towards the conservation of white lions in the Tula Tsau Wildlife Area and the conservation of wildlife in general. The creating of jobs by the Global White Lion Protection Trust, its environmental outreach programme, and its school leadership programme may have contributed to this positive attitude. Recognition of the cultural and spiritual value of wildlife and the natural environment is also reflected in the mission statement of the conservation authority that manages South Africa's national parks (SANParks), which reads as follows: "To acquire and manage a system of national parks that represents the indigenous wildlife, vegetation, landscapes and associated cultural assets of South Africa, for the joy and benefit and spiritual well-being of the nation and the people of the world." (McKeown 2015). Therefore, wildlife forms a key part of the heritage of South Africa, having cultural and political value, as well as potential economic value from tourist revenue[12]. On a broader scale the Global White Lion Protection Trust hopes that the cultural meaning of the white lion to local communities, will be supportive to protecting the Greater Kruger Park Region, just like the Kermode Bear (*Ursus americanus kermodei*) has been for protecting the 4000,000 ha Great Bear Rainforest in British Columbia (Western Canada).

Within the South African context, the aim of the Global White Lion Protection Trust is to contribute to the metapopulation management approach to wild lions in South Africa, in accordance with the management principles outlined in Miller et al. (2015) and by the Lion Management Forum (LiMF 2020:1), since the area where the white lion reintroduction took place (Tula Tsau Wildlife Area) is a fenced wildlife area bordering on other fenced wildlife areas (such as Kapama and Thornybush Private Nature Reserves) within the Greater Kruger Park Region. In light of the significant decline in the lion population on the African continent (Riggio et al. 2013; Miller et al. 2016), the high growth rate of lions achieved by the 49 fenced wildlife reserves in South Africa can certainly be considered a conservation achievement. However, rapidly growing lion populations in enclosed, albeit extensive, systems can very quickly result in significantly depleted prey numbers (Power 2003; Tambling et al. 2005; Hayward et al. 2007; Lehmann et al. 2008) and sometimes even localised extinctions of ungulates (Slotow & Hunter 2009) if left unmanaged. The adaptive management[13] principles defined by the metapopulation management approach to lions in South Africa (Miller et al. 2015; LiMF 2020:1) is therefore critical, and even more importantly that these principles are reflected in the final policy on lion conservation and management in South Africa. It is therefore important that the Global White Lion Protection Trust inspires similar organisations by continuing to apply the conservation management approach towards regulating and managing the prides of white and tawny lions on its wildlife areas going forward, in accordance with the ecological carrying capacity of the habitat, the natural pride social structure, and promoting genetic diversity.

[12] Marie-Christine Cormier-Salem and Thomas J. Bassett, "Nature as Local Heritage in Africa: Longstanding Concerns, New Challenges," Africa 77, no. 1 (2007): 1-17].

[13] Adaptive management: An iterative process of interventions to achieve management plan objectives in the face of uncertainty through development of an expectation of how the system may respond to a considered and planned intervention. Implementation thereof, monitoring the outcomes, adapting management interventions, and /or expectations, thereby allowing continual improvement through learning (definition from: Government Gazette 46687).

References

1. Arias, M.; Coals, P.G.; Ardiantiono; Powell, J.; Bell Rizzolo, J.; Ghoddousi, A.; Boron, V.; Da Silva, M.; Naude, V.N.; Poudel, S.; et al. 2022. Guarding against simplistic conceptions of illegal trade in big cats. *Conserv. Sci. Pract*. in review.
2. Bauer, H.; Van Der Merwe, S. 2004. Inventory of free-ranging lions *Panthera leo* in Africa. *Oryx* 38: 26-31.
3. Bauer, H.; Chapron, G.; Nowell, K.; Henschel, P.; Funston, P.; Hunter, L.T.B.; Macdonald, D.W.; Packer, C. 2015. Lion (*Panthera leo*) populations are declining rapidly across Africa, except in intensively managed areas. *Proc. Natl. Acad. Sci*. USA. 112, 14894–14899.
4. Bauer, H.; Packer, C.; Funston, P.F.; Henschel, P.; Nowell, K. *Panthera leo*. 2016. The IUCN Red List of Threatened Species 2015: e.T15951A79929984. Available online: https://doi.org/10.2305/IUCN.UK.2015-4.RLTS.T15951A79929984.en (accessed on 31 January 2023).
5. Bauer, H., Nowell, K., Sillero, C. & Macdonald, D. 2018. Lions in the modern arena of CITES. *Conserv. Lett.* 11. E12444. 10.1111/conl.12444.
6. Bauer, H., Dickman, A., Chapron, G., Oriol-Cotterill, A., Nicholson, S. K., Sillero-Zubiri, C., et al. 2020. Threat analysis of more effective lion conservation. *Oryx* 56(1) 108–115. Doi: 10.1017/S0030605320000253.
7. Becker, M., Almeida, J., Begg, C., Bertola, L., Breitenmoser, C., Breitenmoser, U., Coals, P., Funston, P., Gaylard, A., Groom, R., Henschel, P., Ikanda, D., Jorge, A., Kruger, J., Lindsey, P., Maimbo, H., Mandisodza-Chikerema, R., Maude, G., Mbizah, M., Becker, A. (2022). Guidelines for evaluating the conservation value of African lion (*Panthera leo)* translocation. *Frontiers in Conservation Science*. 3. 963961. 10.3389/fcosc.2022.963961.
8. Bennett, E. L.; Blencowe, E.; Brandon, K.; Brown, D.; Burn, R. W.; Cowlishaw, G.; Davies, G.; Dublin, H.; Fa, J. E.; Milner- Gulland, E. J.; Robinson, J. G.; Rowcliffe, J. M.; Underwood, F. M. & Wilkie, D. S. 2007. Hunting for consensus: Reconciling bushmeat harvest, conservation, and development policy in West and Central Africa, *Conservation Biology* 21 (3): 884–887, doi:10.1111/j.1523-1739.2006.00595.x
9. Bengis, R.G.; Kriek, N.P.J.; Keet, D.F.; Raath, J.P.; de Vos, V. & Huchzermeyer, H.F.K.A. 1996. An outbreak of bovine tuberculosis in a free-living African buffalo (Syncerus caffer) population in the Kruger National Park – A preliminary report. *Onderstepoort Journal of Veterinary Research*, 63: 15-18.
10. Bertola, L.D.; Tensen, L.; van Hooft, P.; White P.A.; Driscoll C.A.; Henschel P.; et al. 2015. Autosomal and mtDNA Markers Affirm the Distinctiveness of Lions in West and Central Africa. *PLoS ONE* 10(10): e0137975. Pmid:26466139.
11. Bloom, K. 2021. Communities, corruption and carcasses: when the Kruger National Park, the bushmeat trade and the Mthimkulu's complex history collide. Daily Maverick, 2 December 2021. Available online: https://www.dailymaverick.co.za/article/2021-12-02-communities-corruption-and-carcasses-when-the-kruger-national-park-the-bushmeat-trade-and-the-mthimkulus-complex-history-collide/ (accessed on 31 January 2023).

12. Cadman, M. 2006. First wild white lions born in Timbavati area for 12 years. In: *The Sunday Independent* 2006, 26: 1.
13. Cesare, M. 2011. *Man-Eaters, Mambas and Marula Madness: A Game Ranger's Life in the Lowveld*; Jonathan Ball Publishing: Johannesburg, South Africa, Pp. 432.
14. Cho, Y.S.; Hu, L.; Hou, H.; Lee, H.; Xu, J.; Kwon, S.; Oh, S.; Kim, H.-M.; Jho, S.; Kim, S.; et al. 2013. The tiger genome and comparative analysis with lion and snow leopard genomes. *Nat. Commun*. 4, 2433. [Google Scholar] [CrossRef]
15. Coals, P.; Burnham, D.; Johnson, P.J.; Loveridge, A.; Macdonald, D.W.; Williams, V.L.; Vucetich, J.A. 2019. Deep uncertainty, public reason, the conservation of biodiversity and the regulation of markets for lion skeletons. *Sustainability* 11, 5085.
16. Coals, P.; Dickman, A.; Hunt, J.; Grau, A.; Mandisodza-Chikerema, R.; Ikanda, D.; Macdonald, D.W.; Loveridge, A. 2020. Commercially driven lion part removal: What is the evidence from mortality records? Glob. Ecol. Conserv. 24, e01327.
17. Coals, Peter G.R., Nolwazi S. Mbongwa, Vincent N. Naude, and Vivienne L. Williams. 2022. "Contemporary cultural trade of lion body parts" *Animals* 12, no. 22: 3169.
18. Cruickshank, K.M.; Robinson, T.J. Inheritance of the white coat colour phenotype in African lions (*Panthera leo*). In *A Symposium on Lions and Leopards as Game Ranch Animals*; Van Heerden, J., Ed.; Wildlife Group of the South African Veterinary Association: Onderstepoort, South Africa, 1997.
19. De Cleene, M & De Keersmaeker, J.P. 2012. *Compendium van dieren als dragers van cultuur [Compendium of animals as carriers of culture*], Gent: Mens & Cultuur Uitgevers.
20. Dicks, T. 2022. South Africa's White Lions. Wandering Through Photo Safaris and Expeditions. Available online: https://wanderingthru.com/the-white-lions-of-south-africa/ (accessed on 5 August 2022).
21. Everatt, K. Moore, J. & Kerley, G. 2019. Africa's apex predator, the lion, is limited by interference and exploitive competition with humans. *Glob. Ecol. Cons.* 20. e00758. 10.1016/j.gecco.2019.e00758.
22. Everatt, K.T; Kokes, R, & Lopez Pereira, C. 2019. Evidence of a further emerging threat to lion conservation; targeted poaching for body parts. Biodiversity and Conservation 28: 4099. https://doi.org/10.1007/s10531-019-01866-w
23. DFFE & NLWG 2022. Draft African Lion Biodiversity Management Plan Review Report. Sub-Directorate: Conservation Management of the Department of Forestry, Fisheries, and the Environment DFFE) in consultation with National Lion Working Group (NLWG). South Africa. Pp. 1-13.
24. Dickinson, I. 2021. White Lions Face New Extinction Threat as Trophy Hunters Offered Cut-price Deals. The Daily Star, UK. Available online: https://www.dailystar.co.uk/news/latest-news/white-lions-face-new-extinction-23891371 (Accessed on 01 February 2023).
25. Funston, P.J.; Mills, M.G.L.; Biggs, H.C.; Richardson, P.R.K. 1998. Hunting by male lions: Ecological influences and socioecological implications. Anim. Behav. 56, 1333–1345.
26. Gewald, J.B., Spierenburg, M.J. and Wels, H. (Eds). 2018. *Nature conservation in*

southern Africa. Morality and marginality: Towards sentient conservation? Leiden: Brill Academic Publishers. 16: Pp. 1–292.

27. Government Gazette, 45160 (675), Pp. 1-83, 14 September 2021. Draft Policy Position on the Conservation and Ecologically Sustainable Use of Elephant, Lion, Leopard and Rhinoceros: Minister of Forestry, Fisheries and the Environment of South Africa, 2021.
28. Government Gazette, 46687 (685), Pp. 1-76, 8 July 2022. Revised Draft White Paper on Conservation and Sustainable Use of Elephants, Rhino, Lion, and Leopard: Minister of Forestry, Fisheries and the Environment of South Africa, 2022:7.
29. Government Gazette, 39468 (606), Pp. 1-76, 2 December 2015. National Environmental Management Biodiversity Act (10/2004): Biodiversity Management Plan for the African Lion (*Panthera leo*): Minister of Forestry, Fisheries and the Environment of South Africa, 2015:1
30. Government Gazette, 44229 (171), Pp. 1-79, 5 March 2021. Draft Revised National Biodiversity Framework Published for Public Comment in terms of the National Environmental Management: Biodiversity Act, 2004 (Act No.10 of 2004): Minister of Forestry, Fisheries and the Environment of South Africa, 2021:3.
31. Green, J.; Jakins, C.; Asfaw, E.; Bruschi, N.; Parker, A.; de Waal, L.; et al. 2020. African Lions and Zoonotic Diseases: implications for Commercial Lion Farms in South Africa. *Animals* 10:1692. doi: 10.3390/ani10091692
32. Green, J.; Jakins, C.; Waal, L.; de, D.; and Cruze, N. 2021. Ending Commercial Lion Farming in South Africa: a Gap Analysis Approach. *Animals* 11:1717. doi: 10.3390/ani11061717
33. Green, J.; Jakins, C.; Asfaw, E.; Parker, A.; Waal, L. & D'Cruze, N. 2022a. Welfare concerns associated with captive lions (*Panthera leo*) and the implications for commercial lion farms in South Africa. *Animal welfare* (South Mimms, England) Pp. 209-218. 10.7120/09627286.31.2.005.
34. Green, J.; Hankinson, P.; Waal, L.; Coulthard, E.; Norrey, J.; Megson, D.; D'Cruze, N. 2022b. Wildlife Trade for Belief-Based Use: Insights From Traditional Healers in South Africa. *Frontiers in Ecology and Evolution*. 10. 906398. 10.3389/fevo.2022.906398.
35. Hairston, N.G.; Smith, F.E.; & Slobodkin, L.B. 1960. Community structure, population control and competition, *American Naturalist* 94: 421-425.
36. Hayward, M.W.; Adendorff, J.; O'Brien, J.; Sholto-Douglas, A.; Bissett, C.; Moolman, L.C.; Bean, P.; Fogarty, A.; Howarth, D.; Slater, R.; Kerley, G.I.H. 2007. The reintroduction of large carnivores to the Eastern Cape, South Africa: An assessment. *Oryx* 41: 205-214.
37. Hazzah, L.; Mulder, M.B.; Frank, L. 2009. Lions and warriors: Social factors underlying declining African lion populations and the effect of incentive-based management in Kenya. *Biol. Conserv*. 142: 2428-2437.
38. Hiller, C.; Davies-Mostert, H.T.; Friedmann, Y.; Taylor, W.A.; MacMillan, D.C. 2022. Understanding South Africa's captive lion sector and the trade in captive lions (*Panthera leo*). EWT Research & Technical Paper No. 2, Endangered Wildlife Trust, South Africa.
39. Hunter, L.T.B. 1998. *Behavioural Ecology of Reintroduced Lion and Cheetahs in the Phinda*

Resource Reserve, Kwa-Zulu Natal, South Africa. Ph.D. Thesis, Pretoria University, Pretoria, South Africa.

40. Hutchinson, A., and Roberts, D. L. 2020. Differentiating captive and wild African lion (*Panthera leo*) populations in South Africa, using stable carbon and nitrogen isotope analysis. *Biodivers. Conserv.* 29, 2255–2273.
41. Intergovernmental Science-Policy Platform on Biodiversity and Ecosystem Services (IPBES). 2019. Global Assessment Report on Biodiversity and Ecosystem Services of the Intergovernmental Science-Policy Platform on Biodiversity and Ecosystem Services, E.Z. Brondizio, J. Settele, S. D.az and H.T. Ngo (eds). Bonn: IPBES Secretariat.
42. 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) Reintroduction Specialist Group). Available at: https://portals.iucn.org/library/efiles/documents/2013-009.pdf
43. IUCN World Conservation Congress 2020. Combatting the Illegal Trade in Lion Body Parts and Derivatives; IUCN World Conservation Congress: Gland, Switzerland. Available online: https://www.iucncongress2020.org/motion/072/57715 (accessed on 31 January 2023).
44. Kat, P. 2012. LionAid: Scientific Estimates of Lion Populations in Africa. Pieter's Blog. Available online: https://lionaid.org/news/2012/12/lionaid-scientific-estimate-of-lion-populations-in-africa.htm (accessed on 31 January 2023).
45. Keet, D.F.; Davies-Mostert, H.; Bengis, R.G.; Funston, P.; Buss, P.; et al. (Eds.). 2009. Lion (*Panthera leo*) Bovine tuberculosis disease risk assessment (Workshop report). Skukuza, South Africa: Conservation Breeding Specialist Group (CBSG SSC / IUCN), CBSG Southern Africa, Endangered Wildlife Trust.
46. Kitchener, A.C.; Breitenmoser-Würsten, C.; Eizirik, E.; Gentry, A.; Werdelin, L.; Wilting, A.; Yamaguchi, N.; Abramov, A.V.; Christiansen, P.; Driscoll, C.; et al. 2017. A revised taxonomy of the Felidae. The final report of the Cat Classification Task Force of the IUCN Cat Specialist Group. *Cat News Spec. Issue* 11: Pp80.
47. Lagendijk, D.D.G. and Gusset, M. 2008. Human-carnivore coexistence on communal land bordering the greater Kruger area, South Africa. *Environmental Management* 42, 971-976.
48. Lehmann, M.B.; Funston, P.J.; Owen, C.R.; & Slotow, R. Home range utilisation and territorial behaviour of lions (*Panthera leo*) on Karongwe Game Reserve, South Africa. *PLoS ONE* 2008, 3, e3998.
49. LiMF. 2020. LiMF Research Summary 2020:1 - A review of past lion management interventions in 16 small, fenced reserves from 1992 - 2018; Unpublished Report, Lion Management Forum of South Africa.
50. Lindsey, P.,; Balme, G.; Midlane, N.; Alexander, R.; & Craig, J. 2012. Possible relationships between the South African captive-bred lion hunting industry and the hunting and conservation of lions elsewhere in Africa: Research article. *S. Afr. J.Wildl.* Res. 42, 11–22.

51. Marshall H. D., & Ritland K. 2002. Genetic diversity and differentiation of Kermode bear populations. *Molecular Ecology* 11(685-697).
52. McBride, C. *The White Lions of Timbavati*; Paddington Press: New York, NY, USA, 1977.
53. McBride, C. *Operation White Lion*; St. Martin's Press: New York, NY, USA, 1981.
54. McKeown, Kathleen. 2015. Tracking Wildlife Conservation in Southern Africa: Histories of Protected Areas in Gorongosa and Maputaland. Retrieved from the University of Minnesota Digital Conservancy, https://hdl.handle.net/11299/175690 (Accessed on 15 January 2023).
55. Michel, A.L.; Bengis, R.G.; Keet, D.F.; Hofmeyr, M.; de Klerk, L.M.; Cross, P.C.; et al. 2006. Wildlife tuberculosis in South African conservation areas: Implications and challenges. *Veterinary Microbiology,* 112: 91–100.
56. Miller S.M., Harper C.K., Bloomer P., Hofmeyr J., Funston P.J. 2014. Evaluation of microsatellite markers for population studies and forensic identification of African lions (*Panthera leo*). *J Hered.,* 105, 762–72. doi: 10.1093/jhered/esu054 PMID: 25151647.
57. Miller, S.M.; Harper, C.K.; Bloomer, P.; Hofmeyr, J.; Funston, P.J. 2015. Fenced and fragmented: Conservation value of managed metapopulations. *PLoS ONE* 10, e0144605.
58. Miller, S.; Riggio, J.; Funston, P.; Power, R.J.; Williams, V.; Child, M.F. 2016. A Conservation Assessment of *Panthera leo*. In *The Red List of Mammals of South Africa, Swaziland and Lesotho*; Child, M.F., Roxburgh, L., Do Linh San, E., Raimondo, D., Davies-Mostert, H.T., Eds.; South African National Biodiversity Institute: Pretoria, South Africa; Endangered Wildlife Trust: Midrand, South Africa, Pp. 48.
59. Mills, L. Soulé, M.; Doak, D. 1993. The Keystone-Species Concept in Ecology and Conservation. *BioScience*. 43. 219-224. 10.2307/1312122.
60. Mokgobi, M.G. Understanding traditional African healing. 2014. *Afr. J. Phys. Health Educ. Recreat. Danc*. 20, 24–34.
61. Naude, V.N.; Balme, G.A.; Rogan, M.S.; Needham, M.D.; Whittington-Jones, G.; Dickerson, T.; Mabaso, X.; Nattrass, N.; Bishop, J.M.; Hunter, L.; et al. 2020. Longitudinal assessment of illegal leopard skin use in ceremonial regalia and acceptance of faux alternatives among followers of the Shembe Church, South Africa. *Conserv. Sci. Pract*. 2, e289.
62. Nieman, W. A.; Leslie, A. J.; & Wilkinson, A. 2019. Traditional medicinal animal use by Xhosa and Sotho communities in the Western Cape Province, South Africa. *J. Ethnobiol. Ethnomed*. 15, 1–14. doi: 10.1186/s13002-019-0311-6.
63. Nowell, K & Pervushina, N. 2014. Review of implementation of Resolution Conf. 12.5(Rev.CoP16) on Conservation and trade in tigers and other Appendix-I Asian big cats. IUCN and TRAFFIC report prepared for the CITES Secretariat, 65th meeting of the CITES Standing Committee, Geneva, 7-11 July. Geneva. Available at: https://cites.org/sites/default/files/eng/com/sc/65/E-SC65-38-A01_0.pdf (accessed on 31 January 2023).
64. Owen-Smith, N. & Mills, M.G.L. 2008a. Predator-prey size relationships in an African large-mammal food web. *Journal of Animal Ecology* 77: 173-183.

65. Owen-Smith, N. & Mills, M.G.L. 2008b. Shifting prey selection generates contrasting herbivore dynamics within a large-mammal predator–prey web. *Ecology*, 89: 1120–1133.
66. Pinnock, D. 2018. A lion too far. Daily Maverick, 17 June 2018. Available online: https://conservationaction.co.za/recent-news/10491/ (accessed on 31 January 20223).
67. Pinnock, D. 2022. End trophy hunting in South Africa, or we won't visit your country, say tourists. Daily Maverick, 31 August 2022. Available online: https://www.dailymaverick.co.za/article/2022-08-31-end-trophy-hunting-in-south-africa-or-we-wont-visit-your-country-say-tourists/ (accessed on 31 January 2023).
68. Power, J.R. 2003. Evaluating how many lions a small reserve can sustain. S. Afr. *J. Wildl. Res.* 33, 3-11. [Google Scholar].
69. Radloff, F.G.T. & du Toit J.T. 2004. Large predators and their prey in a southern African savanna: a predator's size determines its prey size range. Journal of *Animal Ecology*, 73: 410-423.
70. Riggio, J.; Jacobson, A.; Dollar, L.; Bauer, H.; Becker, M.; Dickman, A.; Funston, P.; Groom, R.; Henschel, P.; de Iongh, H. 2013. The size of savannah Africa: A lion's *Panthera leo* view. *Biodivers. Conserv*. 2013, 22, 17–35.
71. Robinson, R.; De Vos, V. 1982. Chinchilla mutant in the lion. *Genetica* 60, 61–63.
72. Russell, C. 2017. *Spirit bear. Encounters with the white bear of the western rainforest,* Toronto: House of Anansi.
73. Sale, P.F. 2002. The Science We Need to Develop for More Effective Management. In: Sale, P.F (Ed), *Coral Reef Fishes: Dynamics and Diversity in a Complex Ecosystem*. Academic Press. Pp. 527-549. ISBN 9780126151855. Available online: https://doi.org/10.1016/B978-012615185-5/50021-9.
74. Simberloff D. 1998. Flagships, umbrellas and keystones: Is a single-species management passe n the landscape era? *Biol. Cons*. 83:247-257.
75. Slotow, R. & Hunter, L.T.B. 2009. Reintroduction decisions taken at the incorrect social scale devalue their conservation contribution: African lion in South Africa. In: M.W. Hayward & M.J. Somers (Eds.), *Reintroduction of top-order predators*. Oxford, U.K.: Wiley-Blackwell. Pp. 43–71.
76. Smuts, G.L. 1982. *Lion*; Johannesburg: MacMillan, South Africa. [Google Scholar]
77. Somers, M.J.; Walters, M.; Measey, J.; Strauss, W.M.; Turner, A.A.; Venter, J.A.; et al. 2020. The implications of the reclassification of South African wildlife species as farm animals. *S Afr J Sci*. 116(1/2), Art. #7724, 2 pages. https://doi.org/10.17159/sajs.2020/7724.
78. Somerville, K. 2020 Humans and lions. Conflict, conservation and coexistence, Oxon: Routledge, specifically referring to Pp. 196-198.
79. Evans, S. (2018). *When the last lion roars. The rise and fall of the king of the beasts,* London: Bloombury, Pp. 155-158 and 243-247
80. Tambling, C.J. & du Toit, J. Modelling wildebeest population dynamics: implications of predation and harvesting in a closed system. 2005. *J. of Appl. Ecol.* 42(3), 431–441. DOI: 10.1111/j.1365-2664.2005.01039.x

81. Tucker, L. 2013. *Saving the White Lions: One Woman's Battle for Africa's Most Sacred Animal*. Berkeley, CA: North Atlantic Books.
82. Tucker, L. 2003. *Mystery of the White Lions: Children of the Sun God*; Npenvu Press: White River, South Africa.
83. Turner, J.A.; Vasicek, C.A.; Somers, M.J. 2015. Effects of a colour variant on hunting ability: The white lion in South Africa. *Open Sci. Repos. Biol*. e45011830.
84. Turner, J.A.; Wels, H. Chapter 10. White Lions in South Africa: A Living Heritage. In: *Calling on the Community: Understanding Participation in the Heritage Sector, an Interactive Governance Perspective*. Edited by Rodenberg J., Wagenaar, P., and Gert-Jan Burgers. Berghahn Books, New York, 2023; Pp 1–297.
85. Turner, J.A.; Iongh, H.d.; Dunston-Clarke, E.J. 2022a. Assessing the Social Cohesion of a Translocated Pride of White Lions Integrated with Wild Tawny Lions in South Africa, Using Social Network Analysis. *Animals* 12: 1985. https://doi.org/10.3390/ani12151985
86. Turner, J.A.; Dunston-Clarke, E.J.; Fabris-Rotelli, I.; de Iongh, H. 2022b. Home Range and Movement Patterns of Reintroduced White Lions (*Panthera leo melanochaita*) in the Kruger to Canyons Biosphere Reserve, South Africa. *Animals* 12:2003. https://doi.org/10.3390/ani12152003
87. Van Dyk G. 1997. Reintroduction techniques for lion (*Panthera leo*). In: *Proceedings of a Symposium on Lions and Leopards as Game Ranch Animals*. Edited by Van Heerden J. Onderstepoort: Wildlife Group of the South African Veterinary Association.
88. Williams, V.L.; Newton, D.J.; Loveridge, A.J.; Macdonald, D.W. 2015. Bones of Contention: An Assessment of the South African Trade in African Lion *Panthera leo* Bones and other Body Parts; TRAFFIC: Cambridge, UK; WildCRU: Oxford, UK. Available online: https://www.traffic.org/publications/reports/bones-of-contention-south-african-trade-in-african-lion-bones-and-other-body-parts/ (accessed on 31 January 2023).
89. Williams, V.L.; Loveridge, A.J.; Newton, D.J. & Macdonald, D.W. 2017. A roaring trade? The legal trade in *Panthera leo* bones from Africa to East-Southeast Asia. *PLOS ONE* 12, e0185996.
90. Williams, V.L.; Coals, P.G.; de Bruyn, M.; Naude, V.N.; Dalton, D.L.; Kotzé, A. 2021. Monitoring compliance of CITES lion bone exports from South Africa. *PLoS ONE*, 16, e0249306.

Photo 6.1 Subadult white lioness feeding on an adult blue wildebeest she hunted successfully.
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6 Synthesis of Thesis

6.1 Introduction

This doctoral study is the first study to investigate the ecology and conservation management of white lions in comparison to non-white (tawny) lions. It is also the first study to consider the anthropogenic activities that may have led to the absence of white lions in the wild historically, and caused the low survival rate of white cubs in recent times. The conservation management of white lions in the Greater Kruger Park Region is discussed in the context of the metapopulation management of lions in South Africa.

A key part of the study was to determine whether having a white coat colour has caused white lions to differ in their ecology compared to wild tawny lions. Coat colour variation, resulting from gene mutations, is present in several mammalian taxa and has been detected in mammals as far back as 14000 years ago (Searle 1968). Natural intraspecific coat colour variation has been observed in a number of mammalian species including deer mice (*Peromyscus spp.*), black bear (*Ursus americanus*), cheetah (*Acinonyx jubatus*), leopard (*Panthera pardus*), Bengal tiger *(Panthera tigris tigris*) and African lion (*Panthera leo*) (Searle 1968; Marshall & Ritland 2002; Kaelin et al. 2013; Xu et al. 2013; Cruickshank & Robinson 1997). Natural selection determines which coat colour will persist based on whether the colour is a benefit or not to the survival of that species (Darwin 1904-1914; Hoekstra 2010). Common colour mutations in big cats are albinism (pure white), chinchilla (white with pale markings), leucism (partial albinism/cream) and melanism (black) (Searle 1968; Schneider et al. 2015].

The white lion is a rare genetic variant of the southern subspecies of the African lion (*Panthera leo melanochaita*) that has a white coat colour and either brown, blue, or green eyes, and has occurred in the Greater Timbavati Region and Central Kruger Park Region of South Africa, since 1938 (Tucker 2003). The white coat colour is not due to albinism, but rather leucism resulting from a double recessive allele or gene (Robinson & De Vos 1982; Cruickshank & Robinson 1997; Cho et al. 2013). White lions and many tawny lions carrying the recessive gene were removed from the wild and placed into captive breeding and hunting programmes, zoos, and circuses worldwide between 1975 and 2006 (McBride 1981; Tucker 2003; Cesare 2011). The anthropogenic impact of lion culling (white and tawny) in Central Kruger National Park (Smuts 1982), trophy hunting of white lions, and removal from the wild in the Greater Timbavati Region (Tucker 2003; Cesare 2011; Turner et al. 2015) led to a total absence of white lions in their natural habitat up until 2006. However the recessive gene was still present in the wild population and white lion cubs were born into the Greater Timbavati Region in 2006–2009, 2011, 2014, 2015, 2018, and 2019, and in Central Kruger National Park in 2014, 2015 and 2022, and in the Ngala Lodge traversing area (Timbavati Private Nature Reserve in 2018 and 2019 (Turner et al. 2015; Dicks 2022). Only three of the 17 white cubs in the wild population had survived at the time of the present study, due to illegal removal to breeding/hunting centres, the continued lion trophy hunting of pride males which caused infanticide, and high impact ecotourism leading to undue stress on lionesses with young cubs during regular viewing by tourist or lodge vehicles (Whitman et al. 1997; Whitman et al. 2004; Cadman 2006; Turner et al. 2015; Dicks 2022). The natural high mortality rate of 50% of wild lion cubs within the first year may also have contributed to the low survival rate of white lion cubs between 2006 and 2022 (Funston et al. 2003). The birth of white cubs in the Greater Timbavati Region and the Central Kruger Park between 2006 and 2022 confirmed that the recessive gene was still present in the wild population (Dicks 2022). However, the distribution of the white lion allele in the Greater Timbavati Region and the Central Kruger Park Region has never been determined, nor the frequency of occurrence of the white lion allele within their natural habitat (Turner et al. 2015). This genetic aspect was beyond the scope of the present study, but there is a strong need to investigate this. At the initiation of this study, there were only three free-roaming white lions within their natural habitat, largely nomadic, and none of them adults. Therefore, our study focused on a reintroduced pride of captive-origin white lions, and a free-roaming pride of captive-origin white lions with wild tawny lions at the Tula Tsau Wildlife Area.

White lions are an important contribution to the biodiversity of the Greater Kruger Park Region, and the Kruger to Canyons Biosphere Reserve. They also have a cultural and spiritual value to local Tsonga and Sepedi communities. In addition they have also an increasingly important ecotouristic value (Tucker 2003). The Global White Lion Protection Trust (GWLPT) is a non-profit conservation organisation in South Africa that was established in 2002. At the time of this study it had been involved in the reintroduction and the conservation of white lions for nearly 20 years. In 2006 the Global White Lion Protection Trust started the reintroduction of white lions to managed and fenced free-roaming conditions. Simultaneously there was a (re) birth of white lions in the wild in Timbavati Private Nature Reserve (Limpopo Province, South Africa) in 2006 (Cadman 2006). Also several private nature reserves in South Africa have introduced white lions as a draw-card for ecotourism: Sanbona Private Game Reserve and Aquila Private Game Reserve in the Western Cape (Gomersall 2015), and Pumba Private Game Reserve in the Eastern Cape (Howarth 2022). These reserves are both outside the region of natural occurrence for white lions: the Greater Timbavati Region and Central Kruger Park. It was my intention that the results of this study would contribute to the conservation management knowledge of white lions for these private reserves and the wildlife reserves in the Greater Kruger Park Region. The reintroduction of white lions to managed free-roaming conditions and their conservation management by the Global White Lion Protection Trust was investigated with consideration of the anthropogenic activities that may have led to the absence of white lions in the wild, and could be an ongoing threat. The conservation management of white lions by the Global White Lion

Protection Trust is put into context by referring to the draft policies for the conservation and sustainable use of lions (and other iconic species) in South Africa: (Government Gazette 45160; Government Gazette 46687; DFFE & NLWG 2020). The implications of the findings of this study for the conservation of lions (white and tawny) in the Greater Kruger Park Region is discussed in Chapter 5, in context of the lion conservation policies for the management and regulation of lions in South Africa which were under review at the time of writing, and the metapopulation management approach to lions in South Africa. According to these policies and recent studies, the prevailing anthropogenic activities affecting wild lion populations in Africa are poaching, trophy hunting, mortalities of lions due to persecution associated with human-lion conflict, snaring by-catch and increasingly, targeted poaching of lions for their body parts (Government Gazette 45160; Government Gazette 39468; 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).

The aim of this study was to determine whether the reintroduction, social structure, home range, movement patterns, and hunting success of the white lion is similar to that of tawny (non-white) lions, and displayed natural behaviour of wild lions, thereby advancing existing knowledge about wild white lions, the anthropogenic activities that impact them, and the role of white lion conservation as part of the metapopulation management approach to lions in South Africa.

6.1.1 Hypotheses

Based on a literature review, I defined the following hypotheses:

Hypothesis a

There is no difference in social cohesion between prides dominated by white lions and prides dominated by non-white (tawny) lions, because the social behaviour of white lions is similar to that of wild tawny lions;

Hypothesis b

There is no difference between home ranges and movement patterns of white lions and tawny lions, because white lions display natural home ranging behaviour similar to that of wild tawny lions.

Hypothesis c

There is no difference in the hunting success of white lions and tawny lions due to a lack of camouflage, because white lions show natural hunting behaviour similar to that of wild tawny lions

6.1.2 Research Questions

The following research questions were addressed in this doctoral study:

1. What is the social cohesion of prides dominated by white lions compared to that of prides dominated by non-white (tawny) lions
2. Can a pride comprised of white lions and tawny lions form a socially cohesive unit, and do they show natural pride social behaviour?
3. What are the home ranges, movement patterns and habitat selection of white lions, and are they comparable to those of non-white lions, and to natural wild lion behaviour?
4. What is the prey selection and hunting success of white lions compared to that of non-white lions?
5. Does the white lion reintroduction and conservation management by the Global White Lion Protection Trust provide insight into the anthropogenic activities that may have led to the absence of white lions in the wild from 1994 to 2006, and the low survival rate of white lions in the wild from 2006 to 2022, and does it contribute to the metapopulation management approach to lions in South Africa?

6.1.3 Research Methods

In order to test the listed hypotheses the following methods were used:

6.1.3.1 Social Behaviour of White Lions

Assessing the Social Cohesion of a Translocated Pride of White Lions Integrated with Wild Tawny Lions in South Africa, Using Social Network Analysis

Social Network Analysis (SNA) was used to compare the social behaviour of a pride consisting of captive-origin white and wild tawny lions with that of captive-origin and wild tawny lion prides, to determine similarities and differences in the social behaviour of the prides. Statistical analysis of the social interaction data was based on the approach used by Abell et al. (2013) and Dunston et al. (2017). Social interactions and pride compositions were analysed at an individual (degree and betweenness centrality) and pride level (density and clique) for each of the five prides. The SNA statistical programmes UCINET version 6.543, NETDRAW version 2.1476, and SOCPROG version 2.4, were used to analyse the data (Borgatti et al. 2002; Wey et al. 2008; Whitehead 2009).

6.1.3.2 Home Range and Movement Patterns of White Lions

Home Range and Movement Patterns of Reintroduced White Lions (Panthera leo melanochaita) in the Kruger to Canyons Biosphere Reserve, South Africa

The home range and movement of a pride of reintroduced white lions and a constructed pride consisting of reintroduced white lions and translocated wild tawny lionesses in small, fenced reserves was assessed. GPS data from collared adults were collected for the white lion pride between 2010 and 2011, and between 2018 and 2020 for the reintroduced pride. Home ranges were estimated using kernel density estimation and minimum convex polygon, with minimum daily distance tested for differences between sex, season, and pride. The annual and seasonal home ranges, minimum daily distance travelled, and habitat preferences were determined and compared per pride and between males and females.

6.1.3.3 Feeding Ecology of White Lions

Effects of a Colour Variant on Hunting Ability: The White Lion in South Africa

The hypothesis that white coat colour prevents free-roaming lions from hunting successfully and therefore surviving in the wild was tested in this chapter. This hypothesis was tested under managed free-roaming conditions in two fenced areas since no adult white lions existed in the wild at the time. Two separate groups of white lions were rewilded and their hunting success was evaluated. Prey density, availability of preferred prey and habitat type were similar to that of the white lions' natural habitat of Timbavati Private Nature Reserve. As a means of direct comparison, wild tawny lions were released into the study area and their hunting success was recorded. Radio telemetry was used to locate each of the lion groups, three times a day at sunset, midnight and sunrise. The two white lion groups and the tawny lion group were located three times per day respectively using radio telemetry, and all kill data were compared to that of wild tawny lions in other small wildlife reserves in South Africa.

6.1.3.4 White Lion Conservation

Reintroduction, Anthropogenic Impact and Conservation Management in the Greater Kruger Park Region

In Chapter 5, a descriptive study was conducted to outline for the first time the reintroduction and conservation management of white lions in the Greater Kruger Park Region by the Global White Lion Protection Trust. The anthropogenic activities suggested to have led to the absence of white lions in the wild from 1994 to 2006, and to be responsible for the high mortality rate of wild white lions from 2006 to 2022, were discussed. These anthropogenic activities were discussed in context of the draft lion conservation management policies in South Africa which were under review at the time of the present study. The cultural meaning of the white lion to Tsonga and Sepedi communities was discussed as a possible way to reduce human-lion conflict and trade in lion parts. Finally, the conservation role of the reintroduction and conservation management of white lions by the Global White Lion Protection Trust was discussed in relation to the existing metapopulation management approach to lions in South Africa.

6.2 Synthesis For Each Chapter

6.2.1 Social Behaviour of White Lions

Assessing the Social Cohesion of a Translocated Pride of White Lions Integrated with Wild Tawny Lions in South Africa, Using Social Network Analysis

The hypothesis I defined was supported by the data of my study, indicating that there is no difference in social cohesion between prides dominated by white lions and prides dominated by non-white (tawny) lions, because the social behaviour of white lions is similar to that of wild tawny lions.

In accordance with the metapopulation approach to lions in South Africa which requires translocation between smaller reserves (<1000 km^2), the successful translocation and reintroduction of white lions at Tula Tsau Wildlife Area to form a socially cohesive pride, within the Kruger to Canyons Biosphere Reserve, is a first in the region and is therefore a relevant contribution. Since white lions were absent in the wild for nearly 12 years (from 1994 to 2006), and there were no adult white lions at the time this study was initiated, the focus of this study was on the social cohesion of a reintroduced captive-origin pride of white lions and a pride of rewilded white and wild tawny lions under managed free-roaming conditions in a small fenced wildlife area.

Typically, the African lion (*Panthera leo*) lives in a 'fission–fusion' social unit (pride) of 4-12 related adult females together with their young. Pride males form coalitions of, on average, two to three adult males originating from different prides (Schaller 1972). The lion pride is the largest social unit and the core of lion social organisation (Schaller 1972; Bauer et al. 2003). The social cohesion of the released pride of captive-origin white and wild tawny lions (Tsau Pride) was more evenly distributed, and in a number of ways stronger when compared with two captive-origin and wild prides of tawny lions, an index of reintroduction success. The Tsau pride was found to display natural social behaviours, with similarities to both the captive-origin and wild prides. For all prides, there was a strong connection between adult and subadult pride males and between pride females and their cubs. This is typical of wild lion prides and is fundamental to the role that males and females play in prides and overall pride cohesion (Schaller 1972). Similar to the wild and captive-origin prides, for the reintroduced pride of white and tawny lions, cubs and subadults were central to the play network, while adults received the most social interactions. Play behaviour is typical of cubs, as they hone the skills necessary to hunt prey successfully and defend themselves from attack by conspecifics or other carnivores (Schaller 1972), indicating that the cubs from the Tsau Pride were behaving naturally as wild cubs do. Notably, the white lion males, along with wild tawny adult males, initiated more social interactions than captive-origin tawny males, which was probably due to the presence of cubs in the reintroduced and wild prides, which often results in more frequent social interaction (Schaller 1972; Funston et al. 1998). Each of the five prides had a keystone adult female that was involved in the majority of the social networks and played a critical role in connecting peripheral members to the rest of the pride. The role of a keystone female is critical to pride structure and stability within wild prides, and similar to the study of Dunston et al. (2017) our findings suggest that a captive history did not prevent this role from being fulfilled. The social behaviour observed for both captive-origin white males and their offspring showed no indications of being impaired by captive origin or human impact. Another important finding from this study is the fact that the two adult lionesses in the Tsau pride were unrelated and translocated from different reserves, yet were highly connected to each other and formed a socially cohesive pride, indicating that such human management and intervention can be successful.

Our study is the first to demonstrate that captive-origin white and wild tawny lions formed a socially functional pride that displayed natural home range behaviour, movement patterns and hunting success, suggesting that white lions would survive in the wild in the absence of anthropogenic threats (see Chapter 5 for a detailed description of the anthropogenic activities that affect white and tawny lions in South Africa). This finding is particularly important for the metapopulation management approach to lions in South Africa, where about 20% of the wild lion population occurs within 49 smaller fenced reserves (<1000km^2), and reintroduction or translocation of unrelated lions is often required to promote genetic diversity and regulate lion populations. A recent study by McEvoy et al. (2022) found that cub and territory defence are key drivers of sociality in wild lion prides, and the absence of intraspecific competition in many of the smaller fenced reserves in South Africa disrupts the natural pride structure and cohesion, with pride males and other members spending less time with the pride, often leading to a higher predation impact on prey populations. It is therefore relevant to note the level of pride cohesion for the reintroduced pride of white and tawny lions, and the fact that the pride males spent more time with the pride than either the captive or wild tawny males, suggesting that the correct reintroduction protocol and management intervention could promote a more natural sociality within the prides in smaller reserves that are part of the metapopulation approach to lions in South Africa.

6.2.2 Home Range and Movement Patterns of White Lions

Home Range and Movement Patterns of Reintroduced White Lions (*Panthera leo melanochaita*) in the Kruger to Canyons Biosphere Reserve, South Africa

The hypothesis I defined was supported by the data of my study. The reintroduced white lions showed natural ranging behaviour and habitat selection within the available sized reserve, similar to wild lions under similar environmental and habitat conditions.

In Chapter 3, we compared the home range dynamics and movements of a pride of reintroduced white lions (Royal pride) to that of a constructed pride consisting of reintroduced white lions and translocated wild tawny lionesses (Tsau pride) in small, fenced reserves. Since natural home range behaviour is an index of reintroduction success, this study was an important indication whether white lions can survive in the wild in the absence of anthropogenic activities. A home range is defined as the area used by an individual animal for its regular activities of food gathering, mating and caring for its young (Burt 1943). Lion home ranges vary substantially, depending on habitat and season, prey abundance, interaction with lions from neighbouring home ranges, human presence and geographical boundaries (Bauer & De Iongh 2005; Davidson et al. 2012; Loveridge et al. 2009; Oriol-Cotterill et al. 2015). The home range dynamics of white lions had never been studied or compared to those of non-white lions until the present study. There was no difference between prides for annual and seasonal home range size, male and female home ranges, minimum daily distance travelled, or habitat selection. White lions from both prides established territories and displayed natural home ranging behaviour, suggesting that their reintroduction was successful. Home ranges were small and average daily movements restricted for both prides (white lion pride: 5.41 km^2 and 10.44 ± 4.82 km; constructed pride: 5.50 km^2, 11.37 ± 4.72 km), as expected due to the small reserve size of 7 km^2. This finding was consistent with that of the captive-origin and wild tawny prides studied by Dunston et al. (2017), and that of wild tawny lions at the small fenced reserve of Nairobi National Park (40 km^2). Although the reserve size, and consequential lion home range size, for the study prides were significantly smaller than the estimated territory sizes of wild prides; a range of 50 to 7400 km^2 (Loveridge et al. 2009; Davidson et al. 2012; Tumenta et al. 2013; Tuqa et al. 2014), and a mean territory size of 56 km^2 (range of 15-219 km^2), nearly 20% of the wild lion population in South Africa is protected within 49 smaller fenced reserves, with several of them being significantly smaller than the Greater Makalali Private Game Reserve (Miller et al. 2015). A key finding of our study concurred that for wild tawny lions in smaller fenced reserves, areas of high prey density seem to result in small home ranges often near an artificial waterhole, and short daily distances travelled by lions.

The findings of our study agreed with other studies that have found that the sex of an individual is an important factor for home range size and movement patterns. Females prefer territories where they can deliver and care for newborn cubs and that harbor sufficient prey to sustain their offspring (Loveridge et al. 2009; Packer et al. 2001). Male home ranges are generally larger than female home ranges (Van Orsdol 1985; Funston et al. 2003; Loveridge et al. 2009). The home range size of the pride males and lionesses for the Royal and Tsau prides were not significantly different, due to the small and limited reserve size, and the fact that resource availability and access to females for both prides were satisfied by occupying the majority of the reserve. Abundant food and high-quality habitat allow an animal to meet its biological requirements in a relatively small home range (Gittleman & Harvey 1982; MacDonald 1983). In agreement with the observations of Dunston et al. (2017), although pride males and lionesses for both prides utilised the majority of the available home range, the males were often located at the reserve fence boundary in response to the territorial roaring and presence of pride males on the neighbouring reserves. The white lioness from the Royal pride and white lion males from both prides therefore showed natural home range behaviour consistent with adapting to the limited reserve size, suggesting that the reintroduced captive-origin white lions and constructed pride of white and tawny lions made optimum use of the available habitat. Fences have been found to have an influence on lion movement and home range dynamics for wild lions at the Nairobi National Park, Kenya, (Lesilau et al. 2019).

The absence of seasonal variation in home range size for either the Royal or Tsau prides, or between males and females for either pride, was likely a reflection of the abundant prey availability and accessibility year-round, due to the small reserve size, annual restocking with prey species, and high availability of water (Turner et al. 2015). This is consistent with natural wild prides in small reserves (<1000 km^2) that have a high prey abundance and availability of artificial water sources, such as in Nairobi National Park (Kenya) (Lesilau et al. 2021), and Majete Wildlife Reserve (Malawi) (Briers-Louw & Leslie 2017).

Within Africa, lions are found in a range of habitats from open to closed woodland and have adapted to survive in the arid outskirts of deserts to the borders of the dense tropical Congo forest (Riggio et al. 2013). The habitat preference of both the pride of reintroduced white lions and the constructed pride consisting of reintroduced white lions and translocated wild tawny lionesses was for thickets, while riverine vegetation was avoided, indicating that white lions showed similar habitat selection even in the constructed pride of white and tawny lions. This is a sign that the habitat selection of the white lions was in accordance with the available habitat. Since the natural habitat of wild lions in the Greater Kruger Park Region is dominated by thickets (Turner 2005), our findings suggest that white lions are adapted to surviving in the wild of that region.

Our study concluded that the reintroduced white lions showed natural ranging behaviour and habitat selection within the available sized reserve, similar to that of wild lions under similar environmental and habitat conditions. This indicates that the reintroduction of captive-origin white lions into their natural habitat was successful, despite the limited reserve size. The reintroduction of white lions at the Tula Tsau Conservation Area is important in securing a protected subpopulation, since the anthropogenic threat of trophy hunting still exists in parts of the species' natural range.

Our study had a number of limitations: the small size of the fenced reserve, the limited number of white lions in the study prides, the small sample size, and the difference in the time periods of the data collected for the respective prides that were compared. The findings are therefore preliminary and require further study, but they do provide new information about white lion ranging behaviour and habitat selection, which is similar to that of wild tawny lions on smaller reserves. The findings inform the use of reintroduced and constructed prides for lion conservation and are therefore relevant for the metapopulation management of lions in South Africa.

6.2.3 Feeding Ecology of White Lions

Effects of a Colour Variant on Hunting Ability: The White Lion in South Africa

In Chapter 4, the hunting success of the white lion was investigated, with a particular focus on the effect of colouration on the hunting ability, which had never been tested scientifically until this study. The perception that white coat colour prevents free-roaming lions from hunting successfully and therefore surviving in the wild was tested.

The data of my study supported the hypothesis that there would be no difference in the hunting success of white lions and tawny lions due to a lack of camouflage, because white lions show natural hunting behaviour similar to that of wild tawny lions, which was investigated under managed free-roaming conditions in two smaller fenced areas, since no adult white lions existed in the wild at the time. The prey selection and hunting success of the reintroduced white lions was similar to that of wild non-white (tawny) lions in the same study area, and lion prides in other South African wildlife reserves. There was no significant difference between the mean kill rate or mean consumption rate of the two white lion groups and (i) the tawny lion group in the same study area; (ii) wild tawny lions at the Madjuma Lion Reserve (MLR), Karongwe Game Reserve (KGR), Welgevonden Game Reserve (WGR), Makalali Game Reserve (MGR) and the Associated Private Nature Reserves (APNR) in South Africa.

Our study confirmed that white lions are similar to tawny lions in being diet generalists. They feed on a wide variety of small to large animals depending on region, species vulnerability, species availability, season, and protective vegetation, similar to the prey animals described by other authors (Bauer & De Iongh 2005; Hayward & Kerley 2005; Tumenta et al. 2013). The preferred prey of the white lion group (blue wildebeest and warthog) was similar to that of the wild prides in the Greater Makalali Private Nature reserve, Mabula Lion Reserve, and Karongwe Game Reserve. The white lion groups preferred to hunt adult prey animals. This is consistent with the findings of other studies (Power 2002; Turner 2005; Lehmann 2008). Additionally, independent of their availability, medium to large prey species (190 to 550 kg) are preferred by lions (Druce et al. 2004). With a mean weight of 215 kg, an adult female blue wildebeest in the Kruger National Park fits into the lower limit of this range (Funston 1999). This is consistent with our observation for White Lion Group B, for which several equally sized or larger prey species, such as greater kudu, waterbuck and eland, were available, yet this lion group selected blue wildebeest at the highest frequency. By contrast, the predilection of White Lion Group A and the Tsau Tawny Lion Group for adult blue wildebeest, as well as adults of any of the smaller prey, is better explained by the fact that the blue wildebeest was the largest and most abundant prey species available. Medium-sized and water-dependent prey such as African buffaloes (*Syncerus caffer*), kudu (*Tragelaphus strepsiceros*), and blue wildebeest (*Connochaetes taurinus*) are vulnerable to depredation by lions, especially during the dry season when water points become scarce (Druce et al. 2004; Hayward & Kerley 2005; De Boer et al. 2010). A recent study by Loveridge et al. (2006) revealed that lions even prey on elephant calves in the dry season. A similar observation was reported by Tuqa (2015). This was not the case in our study, since elephants were not present at the study sites. Lion hunting success for herbivores is increased when vegetation is available to provide cover, and prey abundance is high (Davidson et al. 2012), whilst lion hunting success is limited by prey anti-predatory strategies (such as grouping by African buffalo) and prey morphology (horns). Our findings for both White Lion Groups and the Tawny Lion Group were in agreement with these observations, with all lion groups hunting more successfully in denser habitat, when prey abundance is greater, and when selecting less dangerous prey (eg. blue wildebeest rather than African buffalo).

The white lions were capable of hunting self-sufficiently under managed free-roaming conditions in a small fenced area, suggesting that white coat colour does not prevent free-roaming white lions from hunting successfully in their natural habitat. Since white lions occurred in their natural habitat both historically and recent to the writing of this dissertation (1938; 1975 to 1980; 1994; 2006 to 2022), I propose that the disappearance of white lions from the natural ecosystem was not due to an inability to hunt, but instead due to other, most likely anthropogenic, factors. Indeed, anthropogenic activities are increasingly threatening carnivores worldwide (Belden & Hagendorn 1993; Schmidt-Posthaus et al. 2002; Davies & Du Toit 2004; Wear, Eastridge & Clark 2005; Thatcher, Van Manen & Clark 2006; Loveridge et al. 2007). In Chapter 5, more detail is given regarding the anthropogenic activities that are proposed to have affected white lions historically and at the time of writing.

The findings for Chapter 4 were consistent with those of the rest of the study, i.e. with the overall conclusion that white lions display natural behaviour similar to that of wild lions in terms of their social interaction, home range behaviour, movement patterns, and hunting behaviour. We do however suggest that the findings are preliminary and that the ecology and behaviour of white lions should be studied under fully free-roaming conditions.

6.2.4 White Lion Conservation

Reintroduction, Anthropogenic Impact and Conservation Management in the Greater Kruger Park Region

In Chapter 5, the reintroduction and conservation management of white lions in the Greater Kruger Park Region were discussed, in addition to the anthropogenic activities that may have led to the absence of white lions in the wild from 1994 to 2006, and to the low survival rate of white cubs between 2006 and 2022. The long-term aim of the reintroduction was to return white lions to free-roaming conditions in their natural habitat, to conduct the first study comparing the ecology of white lions to that of wild tawny lions, and to better protect wild white and tawny lions, as an important contribution to the biodiversity of the Greater Kruger Park Region, and the metapopulation management of lions in South Africa.

The preliminary findings of this study suggest that the social behaviour, home range dynamics, movement patterns, and hunting success of white lions are similar to those of wild tawny lions, suggesting that white lions can survive in the wild and that anthropogenic activities may have led to their absence from 1994 to 2006, and to the low survival rate of white cubs between 2006 and 2022. In accordance with the concerns raised in the Revised Draft White Paper on 'Conservation and Sustainable Use of Elephants, Lion, Leopard and Rhinoceros in South Africa' (Government Gazette 46687), and by the Global White Lion Protection Trust, the present study postulates that trophy hunting, snaring-by catch, and targeted poaching for body parts are anthropogenic activities that could impact lions (white and tawny) in the Greater Kruger Park Region. A number of recent studies are in support of this postulation, identifying that the targeted poaching for lion body parts for the illegal international trade in South East Asia, and local trade for cultural and traditional use which is common in Southern Africa, may be of concern to wild lion populations (Williams et al. 2015; Williams et al. 2017; 2021; Lindsey et al. 2017; Everatt et al. 2019; Jacobsen et al. 2020; Coals et al. 2022). Of additional concern is that the lion population in South Africa is regarded as stable (Riggio et al. 2013; Kitchener et al. 2017), and therefore not significantly impacted by anthropogenic activities. The international trade in lion body parts and derivatives from captive lions in South Africa to South East Asia that was legalised in 2016 by CITES, was stopped by the South African Government in 2021 (Government Gazette 45160), due to a relative lack of evidence-based research into trade in wild lion body parts, and the impact on wild lion populations (Williams et al. 2017; Coals et al. 2022). Due to the low number of wild-managed white lions at the Global White Lion Protection Trust wildlife area (13) and wild white lions (3) in the Greater Kruger Park Region, I agree with the Global White Lion Protection Trust that anthropogenic impact may be of concern to the future survival of free-roaming white lions (Dicks 2022; Turner et al. 2022b). The 'Draft Policy Position on the Conservation and Ecologically Sustainable Use of Elephant, Lion, Leopard and Rhinoceros' (Government Gazette 45160), and 'The National Environmental Management Biodiversity Act (10/2004): Biodiversity Management Plan for the African Lion (*Panthera leo*)' (Government Gazette 39468), were under review at the time of writing, and it is important that stricter regulations be implemented through these policies to better protect wild lion populations in South Africa.

At the present time, although the conservation management principles are being applied by the Global White Lion Protection Trust at a small-scale (17 km^2) fenced wildlife area, it has the highest number of wild-managed white lions within their natural habitat and is therefore an important contribution to the conservation of free-roaming (wild-managed) white lions in the Greater Kruger Park Region. The following conservation principles applied by the Global White Lion Protection Trust may therefore be of benefit to wildlife managers managing lion prides with white lions: (i) land expansion that increases conservation corridors and available lion habitat; (ii) minimizing the incidence of poaching by means of high security double predator-proof electric fences with a zoned alarm system, 24/7 anti-poaching patrols and snare sweeps, and working closely with local communities (eg. job creation, community conservation partnership); (iii) a no hunting policy; and (iv) an environmental education programme in local Tsonga and Sepedi communities, to help reduce human-lion conflict and targeted lion poaching for their body parts, by using the fact that white lions have cultural meaning to these communities. The Global White Lion Protection Trust postulation that the white lion is regarded as a living cultural heritage by local communities in the Greater Kruger Park Region, which may help to reduce human-lion conflict and lion poaching for their body parts, seems to be having a positive effect for the Tula Tsau Wildlife Area (Tucker 2013; Turner et al. 2015). Other studies have had similar observations for community areas bordering wildlife areas that have wild lions, that are more tolerant of lions if they enter the communal areas to kill cattle or livestock (Lagendijk & Gusset 2008; Evans 2018: pp. 155-8 and 243-7; Somerville 2020: pp. 196-8). The low incidence of lion poaching at the wildlife areas being managed by the Global White Lion Protection Trust over the past 20 years, suggests that the Tsonga and Sepedi communities that border on these wildlife areas now generally have a positive attitude towards the conservation of white lions (and other wildlife) in the Tula Tsau Wildlife Area. The creation of jobs by the Global White Lion Protection Trust, its environmental outreach programme, and its school leadership programme may have contributed to this positive attitude (https://whitelions.org/starlion-education-initiative/). Since wildlife is a key a part of the heritage of South Africa, having cultural and political value, as well as potential economic value from tourist revenue (McKeown 2015), on a broader scale the conservation approach of the Global White Lion Protection Trust, and specifically the cultural meaning of white lions to local communities, may be supportive in protecting the Greater Kruger Park Region in the same way that the Kermode Bear (*Ursus americanus kermodei*) has been helpful in protecting the

4000,000 ha Great Bear Rainforest in British Columbia (Western Canada) (Marshall & Ritland 2002), and could therefore be an important contribution to the metapopulation management of lions in South Africa.

6.3 Research Recommendations

A number of limitations exist in the present study on the ecology and conservation management of the white lion in the Greater Kruger Park Region, namely the small size of the fenced reserve, the small number of animals in the prides, and the small sample size. At the time of our study, there were no adult white lions in the wild, only three white cubs - although 17 white lions were born between 2006 and 2022 in the Greater Kruger Park Region, only three survived due to anthropogenic activities. A future study is therefore recommended when the prides in the Timbavati Private Nature Reserve and Kruger National Park have adult white lions. The ecology of the white lion pride should ideally have been compared to that of a wild tawny pride, in a larger fenced area (>56km^2) instead of to a pride of both white and tawny lions in a small fenced area (<17km^2). The living circumstances of the prides and vegetation differences also need to be considered when conducting comparisons between captive-origin and wild ranging prides. Future studies could compare the social cohesion, home range behaviour, movement patterns, and hunting success of larger prides of free-roaming white and tawny lions in big reserves or ecosystems that are at least the mean home range size for wild lions (56 km^2), and ideally within the open system of the Timbavati Private Nature Reserve or Kruger National Park. A study on a larger pride(s) of white and tawny lions to investigate whether the level of social cohesion is as strong as observed for the prides in this study would be particularly relevant in light of the recent concern identified by McEvoy et al. (2022) that there is a lack of intraspecific competition within the prides in the smaller reserves (<1000 km^2) that comprise the metapopulation in South Africa, which disrupts pride sociality and can lead to a high predation impact on prey populations.

It is also recommended that future research should focus on testing the frequency of occurrence of the white lion allele in the two historical areas where white lions occurred naturally: the Greater Timbavati Region (GTR) and the Central Kruger National Park (CKNP). The GTR is an area of 180 000 ha, whilst the CKNP is a vast area of 573 894 ha with more than 650 lions in 60 prides, and the frequency of occurrence study will therefore require a significant amount of time, finances, and resources, which were beyond the scope of this study. The relevance of testing the frequency of occurrence of the white lion allele is in accordance with the motivation by Henson et al. (2022) for collecting genetic, geographic, and ecological data on the Kermode bear (*Ursus americanus kermodei*): to inform locally relevant, long-term, and precautionary wildlife management, in an era in which the resurgence of indigenous governance fosters decentralised decision-making. At the time of writing, a collaborative study between the Global White Lion Protection Trust, Greater Timbavati Region and Kruger National Park (SANParks) had been proposed, to establish the frequency of occurrence of the white lion allele in the wild.

6.4 Recommendations to Reserve Managers

Despite the limitations of this study, the findings are supported by historical records that indicate that white lions were observed as fully functional, socially connected members of wild tawny prides in the Timbavati Private Nature Reserve (McBride 1978; 1981; Tucker 2003; Cesare 2011; Turner et al. 2015), and Kruger National Park (Robinson & De Vos 1982; Smuts 1982; Cesare 2011). The conclusion of this study that the ecology of white lions is similar to that of wild tawny lions suggests that the conservation management of white lions should be similar to that of wild tawny lions, a valuable contribution to reserve managers that are managing lion prides with white lions – this includes the Associated Private Nature Reserves (APNR), Sanbona Private Nature Reserve, and Pumba Private Game Reserve. Furthermore, reserve managers are recommended to be aware of the potential poaching risk to white lions for their body parts, for both international and local (legal and illegal) trade, cultural and traditional use. Finally, reserve managers in the Greater Kruger Park Region can potentially use the cultural meaning of white lions to the Tsonga and Sepedi communities to reduce human-lion conflict and targeted poaching for the lions' body parts.

Photo 6.2 Reintroduced adult white lioness with her cub at Tula Tsau Wildlife Area. *© Global White Lion Protection Trust*

Summary

This is the first study to investigate the ecology and conservation management of the white lion (Panthera leo melanochaita). The white lion is a natural colour variant, or leucistic form, of the southern subspecies of the African lion (Panthera leo melanochaita) that has only ever been recorded in the wild in the Timbavati, Klaserie and Umbabat Private Nature Reserves (Greater Timbavati Region) and the Central Kruger National Park (KNP) – the Greater Kruger Park Region – in South Africa. The frequency of occurrence of white lions in the region was increasing in the 1980s, with 12 recorded sightings in nine different prides in the Timbavati Private Nature Reserve and Central Kruger National Park. From 1994 to 2006, there was an absence of white lions in the wild, the perception being that white lions cannot survive in the wild due to a lack of camouflage preventing them from hunting successfully.

In 2006 a non-profit conservation organisation, the Global White Lion Protection Trust, therefore initiated the first reintroduction of white lions to free-roaming conditions within a small fenced wildlife area in the Greater Kruger Park Region. The results of this doctoral study suggest that the reintroduced white lions show natural behaviour, similar to wild tawny lions, in terms of their social interactions, home range and movement patterns, and their hunting success. These findings are supported by historical observations at the Timbavati Private Nature Reserve, and recent observations at Sanbona and Pumba Private Game Reserves. these observations suggest that white lions are capable of surviving in the wild as part of wild tawny prides. Based on these findings it is concluded that the reason for the low survival rate of white lion cubs in the Greater Kruger Park Region was due to anthropogenic activities And not due to lack of competitive capacity of white lions. Between 2006 and 2022 white lion cubs (17) were born in the Greater Kruger Park Region, confirming that the recessive gene is still present in the wild lion population. Although white lions occur within the wild lion population in this region, due to the rarity of white lions (only 13 wild managed lions and 3 wild adult white lions), the anthropogenic activities that affect the wild tawny lion population may have had a more significant impact on wild and managed white lions in that region. Human-lion conflict and trade in lion body parts for traditional and cultural use are two of the anthropogenic activities that have been identified as a major threat to wild lions in South Africa. The long-standing cultural significance of white lions amongst the local Tsonga and Sepedi communities in the Greater Kruger Park Region led white lions to be referred to as a 'living cultural heritage'. According to the Global White Lion Protection Trust, this cultural belief may help to mitigate human-lion conflict and prevent lion poaching for body parts. The low incidence of lion poaching and human-lion conflict over the past 20 years at the wildlife areas managed by the Global White Lion Protection Trust suggests that a positive attitude of local Tsonga and Sepedi communities towards the conservation of white lions has contributed to the conservation of white lions in the bordering wildlife areas.

The present study had a number of limitations, namely: the small size of the prides and small number of prides studied, the restricted size of the fenced wildlife area included in the study and the captive-origin of the white lions studied. The findings of the study are therefore preliminary, but they do indicate that white lions display natural behaviour similar to wild tawny lions, and they can therefore survive in the wild. This finding is supported by historical observations. The implications of the study are therefore expected to advance the existing knowledge of the ecology of the white lion, may contribute to reintroduction techniques and translocation success for white lions. The results of this study may also contribute to the conservation management of white lions in relation to the metapopulation approach for lions in South Africa. The findings suggest the potential role of the white lion in lion conservation in the Greater Kruger Park Region, in terms of their economic, eco-touristic and cultural significance.

Samenvatting

Dit is de eerste studie die de ecologie en het behoud en beheer van de witte leeuw (*Panthera leo melanochaita*) onderzoekt. De witte leeuw is een natuurlijke kleurvariant, of leucistische vorm, van de zuidelijke ondersoort van de Afrikaanse leeuw (*Panthera leo melanochaita*), die alleen in het wild is waargenomen in de particuliere natuurreservaten Timbavati, Klaserie en Umbabat (in de regio Timbavati), en in het Central Kruger National Park (KNP) – in de Krugerparkregio – in Zuid-Afrika. In de jaren tachtig van de vorige eeuw nam het aantal witte leeuwen in de regio toe, met twaalf geregistreerde waarnemingen binnen negen verschillende troepen in het Timbavati Private Nature Reserve en het Central Kruger National Park. Van 1994 tot 2006 kwamen er geen witte leeuwen in het wild voor, wat leidde tot het idee dat witte leeuwen niet in het wild kunnen overleven vanwege een gebrek aan camouflage, waardoor ze niet succesvol kunnen jagen.

In 2006 startte een natuurbeschermingsorganisatie zonder winstoogmerk, de Global White Lion Protection Trust, daarom met een eerste herintroductie van witte leeuwen, die in vrijheid leven binnen een klein omheind natuurgebied in de Krugerparkregio. Uit dit proefschrift blijkt dat de opnieuw geïntroduceerde witte leeuwen een natuurlijk gedrag vertonen dat vergelijkbaar is met dat van wilde geelbruine leeuwen wat betreft hun sociaal gedrag, leefgebied en bewegingspatronen, en, belangrijker nog, hun jachtsucces. Deze bevindingen worden ondersteund door historische waarnemingen in het particuliere natuurreservaat Timbavati en recente waarnemingen in de particuliere wildreservaten Sanbona en Pumba, wat erop wijst dat witte leeuwen in het wild kunnen overleven als onderdeel van wilde geelbruine leeuwentroepen.
De bevindingen van deze studie suggereren daarom dat de reden voor het lage overlevingspercentage van witte leeuwenwelpen in de Krugerparkregio te wijten was aan menselijke activiteiten. Tussen 2006 en 2022 werden 17 witte leeuwenwelpjes geboren in de Krugerparkregio, wat bevestigt dat het recessieve gen nog steeds aanwezig is in de wilde leeuwenpopulatie. Hoewel witte leeuwen voorkomen binnen de wilde leeuwenpopulatie in deze regio, zou het kunnen dat menselijke activiteiten die van invloed zijn op de wilde leeuwenpopulatie in het algemeen, een grotere invloed hebben op wilde en wildbeheerde witte leeuwen in de regio vanwege de zeldzaamheid van witte leeuwen (slechts 13 wildbeheerde en drie wilde witte leeuwen).

Conflicten tussen mens en leeuw en de handel in lichaamsdelen van leeuwen voor traditioneel en cultureel gebruik zijn twee van de menselijke activiteiten waarvan is vastgesteld dat ze invloed hebben op wilde leeuwen in Zuid-Afrika. De van oudsher bestaande culturele betekenis van witte leeuwen onder de lokale Tsonga- en Sepedi-gemeenschappen in de Krugerparkregio heeft ertoe geleid dat witte leeuwen worden bestempeld als 'levend cultureel erfgoed'. Volgens de Global White Lion Protection Trust zou dit kunnen helpen om conflicten tussen mens en leeuw en het stropen van leeuwen voor lichaamsdelen te verminderen.

Het lage aantal gevallen van leeuwenstroperij en mens-leeuwconflicten in de natuurgebieden van de Global White Lion Protection Trust in de afgelopen twintig jaar, geeft aan dat de Tsonga- en Sepedi-gemeenschappen die aan de grenzen van deze natuurgebieden wonen, een positieve houding hebben tegenover het behoud van witte leeuwen in de Tula Tsau Wildlife Area en tegenover het behoud van wilde dieren in het algemeen.

Dit proefschrift kent een aantal beperkingen, namelijk: de kleine omvang van de troepen, het kleine aantal bestudeerde troepen, de beperkte omvang van het natuurgebied en het feit dat de onderzochte witte leeuwen in gevangenschap geboren zijn. De bevindingen van het onderzoek zijn daarom voorlopig, maar geven wel aan dat witte leeuwen een natuurlijk gedrag vertonen dat vergelijkbaar is met dat van wilde geelbruine leeuwen, en daarom in het wild kunnen overleven, wat ook wordt ondersteund door historische observaties. De resultaten van de studie zullen daarom naar verwachting de bestaande kennis vergroten van zowel de ecologie van de witte leeuw, alsook van herintroductietechnieken en translocatiesucces voor leeuwen, en het behoud en beheer van leeuwen in relatie tot de metapopulatiebenadering van leeuwen in Zuid-Afrika. De bevindingen geven aan dat de witte leeuw mogelijk een rol kan spelen bij het behoud van leeuwen in de Krugerparkregio, dankzij hun economische, ecotoeristische en culturele betekenis.

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Lastly, a tribute to the subject of this doctoral study, the lions, and specifically the white lions, that I had the privilege of spending so many days and nights with, experiencing all of their trials and tribulations.

Curriculum Vitae

Jason Andrew Turner was born on 14 May 1973 in Johannesburg, South Africa. From 1978 to 1990 he attended primary and secondary school at De La Salle College in Johannesburg, South Africa. From 1990-1994 he completed a BSc Zoology and Grassland Science at the University of KwaZulu Natal, Pietermartizburg, South Africa. This degree provided a solid theoretical and practical grounding in the discipline of Zoology and Botany, and Grassland Science. In 1995-1996 he completed a BSc Honours Wildlife Management at the University of Pretoria (South Africa), providing an introduction to specialist theory and skills in wildlife management in South Africa. From 2000 to 2005 he completed a MSc Wildlife Management at the Centre for Wildlife Management, in Pretoria, South Africa, specializing in lion predation and predator-prey relationships in the Greater Kruger Park Region. Whilst completing his MSc, in 2004 he was asked by the Global White Lion Protection Trust (GWLPT), a NPO conservation trust, to help initiate the first rewilding and reintroduction program of white lions to their natural habitat. In 2013, Turner initiated the collaborative international study that identified the genetic marker for the white lion in September 2013 (see Cho et al. 2013). In 2018 he became a member of the African Lion Working Group (ALWG), responsible for the management of wild lions in Africa, and the Lion Management Forum (LiMF). From 2018 to 2023, Turner conducted Environmental Consulting and Conservation Management in South Africa, whilst also being registered as a PhD candidate at Leiden University (Netherlands) focused on the Conservation Management and Ecology of the white lion (Panthera leo melanochaita Hamilton Smith 1842) in the Greater Kruger Park Region, South Africa. In 2023, Jason Turner was appointed as a Protected Area Manager for the King Salman Bin Abdulaziz Royal Reserve in Saudi Arabia.

References

1. Abade L., Macdonald D.W., Dickman A.J. (2014). Assessing the relative importance of landscape and husbandry factors in determining large carnivore depredation risk in Tanzania's Ruaha landscape. *Biol. Conser.* 180: 241-248.
2. Abell, J., Kirzinger, M.W.B., Gordon.; Kirk, J., Kokeŝ, R., Lynas, K., Mandinyenya, B., Youldon. (2013). A social network analysis of social cohesion in a constructed pride: Implications for ex situ reintroduction of the African lion (*Panthera leo*). *PLoS ONE* 8, e82541.
3. Acocks, J.P.H. (1988). Veld types of South Africa. *Mem. Bot. Surv*. S. Afr. 57: 1-146.
4. Angelici, F. M. (2016). Problematic Wildlife at the Beginning of the Twenty-First Century: Introduction. Pages 3–18. *Problematic Wildlife*. Cham: Springer International Publishing.
5. Anthony, B., Scott, P. & Antypas, A. (2010). Sitting on the fence? Policies and practices in managing human-wildlife conflict in Limpopo Province, South Africa. *Conservation & Society*. 8. 10.4103/0972-4923.73812.
6. Arias, M.; Coals, P.G.; Ardiantiono; Powell, J.; Bell Rizzolo, J.; Ghoddousi, A.; Boron, V.; Da Silva, M.; Naude, V.N.; Poudel, S.; et al. 2022. Guarding against simplistic conceptions of illegal trade in big cats. *Conserv. Sci. Pract*.
7. Baker, P. J., Boitani, L., Harris, S., Saunders, G., and White, P. C., L. (2008). Terrestrial carnivores and human food production: impact and management. *Mamm. Rev*. 38, 123–166. doi: 10.1111/j.1365-2907.2008. 00122.x Bank, W. (2009).
8. Bauer, H., de Iongh, H.H., Princée, F.P.G. & Ngantou, D. (2003). Research needs for lion conservation in West and Central Africa. *Comptes Rendus Biologies*, 326, 112–118. DOI: 10.1016/S1631-0691(03)00047-7
9. Bauer H., Van der Merwe S. (2004). Inventory of free-ranging lions Panthera leo in Africa. *Oryx* 38:26-31.
10. Bauer, H.; De Iongh, H.H. 2005. Lion (*Panthera leo*) home ranges and livestock conflicts in Waza National Park, Cameroon. *Afr. J. Ecol*. 43, 208–214.
11. Bauer, H., Chapron, G., Nowell, K., Henschel, P., Funston, P., Hunter, L.T., Macdonald, D.W., Packer, C., (2015). Lion (Panthera leo) populations are declining rapidly across Africa, except in intensively managed areas. *Proc. Natl. Acad. Sci.* U. S. A. 112, 14894–14899.
12. Bauer, H.; Packer, C.; Funston, P.F.; Henschel, P.; Nowell, K. *Panthera leo*. (2016). *The IUCN Red List of Threatened Species 2015*: e.T15951A79929984. Available online: https://doi.org/10.2305/IUCN.UK.2015-4.RLTS.T15951A79929984.en (accessed on 31 January 2023).
13.. Bauer, H., Nowell, K., Sillero, C. & Macdonald, D. (2018). Lions in the modern arena of CITES. *Conserv. Lett.* 11. E12444. 10.1111/conl.12444.

14. Bauer, H., Dickman, A., Chapron, G., Oriol-Cotterill, A., Nicholson, S. K., Sillero-Zubiri, C., et al. (2020). Threat analysis of more effective lion conservation. *Oryx* 56(1) 108–115. Doi: 10.1017/S0030605320000253.
15. Beck B.B., Rapaport L.G., Stanley Price M.R., Wilson A.C. (1994). Reintroduction of captive-born animals. In: Olney PJS, Mace GM, Feistner ATC, editors. *Creative Conservation*. The Netherlands: Springer, 265-286.
16. Becker, M., Almeida, J., Begg, C., Bertola, L., Breitenmoser, C., Breitenmoser, U., Coals, P., Funston, P., Gaylard, A., Groom, R., Henschel, P., Ikanda, D., Jorge, A., Kruger, J., Lindsey, P., Maimbo, H., Mandisodza-Chikerema, R., Maude, G., Mbizah, M., Becker, A. (2022). Guidelines for evaluating the conservation value of African lion (*Panthera leo)* translocation. *Frontiers in Conservation Science*. 3. 963961. 10.3389/fcosc.2022.963961.
17. Belden, R. C. & B. W. Hagedorn. (1993). Feasibility of translocating panthers into northern Florida. *Journal of Wildlife Management,* 57:388-397.
18. Belinda, R., 2013. Conserving Biodiversity Outside Protected Areas, Editor(s): S. A Levin, *Encyclopedia of Biodiversity (Second Edition)*, Academic Press, Pp. 289-305, ISBN 9780123847201, https://doi.org/10.1016/B978-0-12-384719-5.00359-2. Available online: https://www.sciencedirect.com/science/article/pii/B9780123847195003592 (Accessed on 06 February 2023).
19. Bengis, R.G.; Kriek, N.P.J.; Keet, D.F.; Raath, J.P.; de Vos, V. & Huchzermeyer, H.F.K.A. (1996). An outbreak of bovine tuberculosis in a free-living African buffalo (Syncerus caffer) population in the Kruger National Park – A preliminary report. *Onderstepoort Journal of Veterinary Research* 63: 15-18.
20. Bennett, E. L.; Blencowe, E.; Brandon, K.; Brown, D.; Burn, R. W.; Cowlishaw, G.; Davies, G.; Dublin, H.; Fa, J. E.; Milner-Gulland, E. J.; Robinson, J. G.; Rowcliffe, J. M.; Underwood, F. M. & Wilkie, D. S. (2007). Hunting for consensus: Reconciling bushmeat harvest, conservation, and development policy in West and Central Africa, *Conservation Biology* 21 (3): 884–887, doi:10.1111/j.1523-1739.2006.00595.x
21. Berkes, F. (1999). *Sacred ecology: Traditional ecological knowledge and resource management.* Philadelphia: Taylor & Francis.
22. Bertola, L.D.; Tensen, L.; van Hooft, P.; White P.A.; Driscoll C.A.; Henschel P.; et al. (2015). Autosomal and mtDNA Markers Affirm the Distinctiveness of Lions in West and Central Africa. *PLoS ONE* 10(10): e0137975. Pmid:26466139.
23. Bertola, L.D. (2016). *Genetic diversity in the lion (Panthera leo Linnaeus 1758): unravelling the past and prospects for the future.* PhD Thesis. Leiden University, Netherlands.
24. Bertram, B. (1973). Lion population regulation. *E. Afr. Wildl. J.,* 2: 215-225.
25. Bloom, K. (2021). Communities, corruption and carcasses: when the Kruger National Park, the bushmeat trade and the Mthimkulu's complex history collide. Daily Maverick, 2 December 2021. Available online: https://www.dailymaverick.co.za/article/2021-12-02-communities-corruption-and-carcasses-when-the-kruger-national-park-the-bushmeat-trade-and-the-mthimkulus-complex-history-collide/ (accessed on 31 January 2023).

26. Böer, M., Hodenhagen, J. Reklewski, Izabelin, J. Smielowski, P. Tyrala. (2000). Reintroduction of the European lynx (Lynx lynx) to the Kampinoski National Park/ Poland – a field experiment with zooborn individuals part III: demographic development of the population from December 1993 until January 2000. *Der Zoologische Garten*, 70: 304-312.
27. Borgatti S.P., Evertt M.G., Freeman L.C, (2002). Ucinet 6 for Windows: software for social network analysis. Harvard (MA): Analytic Technologies. Available online: https://sites.google.com/site/ucinetsoftware/news/newbookonsna (accessed on 31 January 2023).
28. Born Free Foundation. (2018). Cash before conservation: An overview of the breeding of lions for hunting and bone trade. [Website] Available: https://www.bornfree.org.uk/publications/cash-before-conservation (Accessed on 11 February 2023).
29. Bouman I. (2000). The reintroduction of Prezalski horses in the Hustain Nuruu mountain forest steppe reserve in Mongolia; an integrated conservation development project. *Gazella* 27:27-52.
30. Breitenmoser, U., C. Breitenmoser-Würsten, H. Okarma, T. Kaphegyi, U. Kaphegyi-Wallman, & U. M. Müller. (2000). Action Plan for the Conservation of the Eurasian Lynx In Europe (*Lynx lynx*). Convention on the Conservation of European Wildlife and Natural Habitats.
31. Briers-Louw, W. & Leslie, A. (2017). *Ecology of three apex predators in Majete Wildlife Reserve, Malawi*. MSc thesis, University of Stellenbosch, Department of Conservation Ecology and Entomology. South Africa. 10.13140/RG.2.2.18243.22563.
32. Briers-Louw, W. D., Verschueren, 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
33. Brocke, R. H., K. A. Gustafson, & A. R. Major. (1990). Restoration of lynx in New York: biopolitical lessons. *Transactions of the North American Wildlife and Natural Resources Conference,* 55: 590-598.
34. Burt, W.H. (1943). Territoriality and home range concepts as applied to mammals*. J. Mammal.* 24: 346–352.
35. Cadman M. (2006). First wild white lions born in Timbavati area for 12 years. In: *The Sunday Independent* 2006, 26: 1.
36. Carr, N. (1962). *Return to the Wild: A story of two lions*. Collins, St James' Place, London. UK.
37. Carruthers, J. 1995. *The Kruger National Park: A Social and Political History*. Pietermaritzburg: University of Natal Press.
38. Carvalho, A.M. & Frazão-Moreira, A. (2011). Importance of local knowledge in plant resources management and conservation in two protected areas from Trás-os-Montes, Portugal. *Journal of Ethnobiology and Ethnomedicine*, 7, 36.
39. Castley, J.G., Knight, M.H., Mills, M.G.L. & Thouless, C. 2002. Estimation of the lion (Panthera leo) population in the southwestern Kgalagadi Transfrontier Park using a capture-recapture survey. *Afr. Zool*. 37(1): 27–34.

40. Cesare M. (2011). *Man-eaters, Mambas and Marula Madness: A Game Ranger's Life in the Lowveld.* Johannesburg: Jonathan Ball Publishing.
41. Chapron G., Kaczensky P., Linnell J.D.C., Manuela von A., Huber C. et al. (2014). *Recovery of large carnivores in Europe's modern human-dominated landscapes. Science, 346(6216): 1517-1519.*
42. Cho,Y.S., Hu, L., Hou, H., Lee, H., Xu, J. Kwon, S. Oh, S. Kim, H., ... *et al.* (2013). The tiger genome and comparative analysis with lion and snow leopard genomes. *Nature Communications* 4: 2433, DOI: 10.1038/ncomms3433.
43. Coals, P.; Burnham, D.; Johnson, P.J.; Loveridge, A.; Macdonald, D.W.; Williams, V.L.; Vucetich, J.A. 2019. Deep uncertainty, public reason, the conservation of biodiversity and the regulation of markets for lion skeletons. *Sustainability* 11, 5085.
44. Coals, P.; Burnham, D.; Loveridge, A.; Macdonald, D.W.; 't Sas-Rolfes, M.; Williams, V.L.; Vucetich, J.A. (2019). The ethics of human–animal relationships and public discourse: A case study of lions bred for their bones. *Animals*, 9:52.
45. Coals, P.; Dickman, A.; Hunt, J.; Grau, A.; Mandisodza-Chikerema, R.; Ikanda, D.; Macdonald, D.W.; Loveridge, A. (2020). Commercially driven lion part removal: What is the evidence from mortality records? *Glob. Ecol. Conserv*. 24, e01327.
46. Coals, Peter G.R., Nolwazi S. Mbongwa, Vincent N. Naude, and Vivienne L. Williams. 2022. "Contemporary cultural trade of lion body parts". *Animals* 12, no. 22: 3169.
47 Crandall, K. A., Bininda-Emonds, O. R. P., Mace, G. M., & Wayne, R. K. (2000). Considering evolutionary processes in conservation biology. *Trends in Ecology & Evolution*, 15(7), 290–295
48. Croft D.P., James R., Krause J. (2008). *Exploring Animal Social Networks*. Princeton (NJ): Princeton University Press.
49. Cruickshank, K. M., & T. J. Robinson. (1997). Inheritance of the white coat colour phenotype in African lions (Panthera leo). In: van Heerden, J. (ed.). *Proceedings of a Symposium on Lions and Leopards as Game Ranch Animals.* Wildlife Group of the South African Veterinary Association, Onderstepoort, RSA.
50. Cumming, D. H. M. (2004). Performance of Parks in a Century of Change. In B. Child (Ed.), *Parks in Transition: Biodiversity, Rural Development and the Bottom Line.* Pp. 105–124. London: Earthscan.
51. Darwin, C. R.: The Origin of Species. (1909 -14). Vol. XI. *The Harvard Classics*. New York: PF Collier & Son.
52. Davidson, Z.; Valeix, M.; Loveridge, A.J.; Hunt, J.E.; Johnson, P.J.; Madzikanda, H.; Macdonald, D.W. *(*2012).Environmental determinants of habitat and kill site selection in a large carnivore: Scale matters. *J. Mammal. 93*, 677–685.
53. Davies, H. T. & J. T. Du Toit. (2004). Anthropogenic factors affecting wild dog Lycaon pictus reintroductions: A case study in Zimbabwe. *Oryx*, 38: 32-39.
54. De Boer, W.F., Vis, M.J.P, De Knegt, H. J., Rowles, C., Kohi, E. M., *et al.* (2010). Spatial distribution of lion kills determined by the water dependency of prey species. *Journal of Mammalogy* 91: 1280–1286.

55. De Cleene, M & De Keersmaeker, J.P. (2012). *Compendium van dieren als dragers van cultuur* [Compendium of animals as carriers of culture], Gent: Mens & Cultuur Uitgevers.
56. DeRoy, B. C., Darimont, C. T., & Service, C. N. (2019). Biocultural indicators to support locally led environmental management and monitoring. *Ecology and Society*, 24(4), 21.
57. Dickman, A. J., Hazzah, L., Carbone, C., and Durant, S. M. (2014). Carnivores, culture and "contagious conflict": multiple factors influence perceived problems with carnivores in Tanzania's Ruaha landscape. *Biol. Conserv.* 178, 19–27. doi: 10.1016/j.biocon.2014.07.011
58. Dickman, A. J., Macdonald, E. A., and Macdonald, D. W. (2011). A review of financial instruments to pay for predator conservation and encourage human-carnivore coexistence. *Proc. Natl. Acad. Sci*. U.S.A. 108, 13937–13944. doi: 10.1073/pnas.1012972108
59 Dicks, T. 2022. South Africa's White Lions. Wandering Through Photo Safaris and Expeditions. Available online: https://wanderingthru.com/the-white-lions-of-south-africa/ (accessed on 5 August 2022).
60. DFFE & NLWG 2022. Draft African Lion Biodiversity Management Plan Review Report. Sub-Directorate: Conservation Management of the Department of Forestry, Fisheries, and the Environment DFFE) in consultation with National Lion Working Group (NLWG). South Africa. p. 1-13.
61. Dickinson, I. (2021). White Lions Face New Extinction Threat as Trophy Hunters Offered Cut-price Deals. The Daily Star, UK. Available online: https://www.dailystar.co.uk/news/latest-news/white-lions-face-new-extinction-23891371 (Accessed on 01 February 2023).
62. Druce, D., H. Genis, S. Greatwood, A. Delsink, L. Hunter, R. Slotow, J. Braak & R. Kettles. (2004). Prey selection by a reintroduced lion population in the Greater Makalali Conservancy, South Africa. *African Zoology*, 39: 273-284.
63. Dunston, E. (2016). *Assessment of functionality of two captive-origin and a wild pride of African lions (Panthera leo): pre-release evaluation for an ex-situ reintroduction program*. PhD Thesis. Charles Stuart University, Australia.
64. Dunston, E.; Abell, J.; Doyle, R.; Duffy, D.; Poynter, C.; Kirk, J.; Hilley, V.; Forsyth, A.; Jenkins, E.; McAllister, D.; Freire, R. 2017. Does captivity influence territorial and hunting behaviour? Assessment for an ex-situ reintroduction program of African lions *Panthera leo*. *Mammal Rev. 47*, 254–260.
65. Elliot, N. B., & Gopalaswamy, A. M. (2017). Towards accurate and precise estimates of lion density. Conservation Biology, 31, 934–943. https://doi.org/10.1111/cobi.12878
66. Endangered Wildlife Trust. (2017). Conservation Matters. Issue 5 – The Trade Edition August - September 2017; pp 4. Available: https://www.ewt.org.za/magazine.html
67. Evans, S. (2018) *When the last lion roars. The rise and fall of the king of the beasts*, London: Bloombury, pp. 155-158 and 243-247.
68. Everatt, K.T., Kokes, R. & Pereira, L. (2018). The targeted poaching of lions for body

parts in Mozambican National Parks; evidence of a further emerging threat to lion conservation. *Biodiversity and Conservation*. 28. 10.1007/s10531-019-01866-w.

69. Everatt, K. Moore, J. & Kerley, G. (2019). Africa's apex predator, the lion, is limited by interference and exploitive competition with humans. *Glob. Ecol. Cons*. 20. e00758. 10.1016/j.gecco.2019.e00758.
70. Everatt, K.T; Kokes, R, & Lopez Pereira, C. (2019). Evidence of a further emerging threat to lion conservation; targeted poaching for body parts. *Biodiversity and Conservation* 28: 4099. https://doi.org/10.1007/s10531-019-01866-w
71. Ferreira, S. (2014). 50/50 Nature Program: White lions. [Website] https://www.youtube.com/watch?v=F5CPbr8PA3k.
72. Ferreira S.M. & Funston P.J. (2010). Estimating lion population variables: prey and disease effects in Kruger National Park, South Africa. *Wildl. Res*.; 37(3):194–206.
73. Ferreira, S.M. & Hofmeyr, M. (2014). Managing charismatic carnivores in spatially restricted areas: large felids in South Africa. *S. Afr. J. Wildl. Res*.
74. Fischer, J. & D. B. Lindenmayer. (2000). An assessment of the published results of animal relocations. *Biological Conservation*, 96: 1-11.
75. Funston, P.J. (1999). Predator-prey relationships between lions and large ungulates in the Kruger National Park. Ph.D thesis, University of Pretoria, Pretoria.
76. Funston, P.J. (2010). Greater Mapungubwe TFCA predator management plan. Unpublished report, Shashe Limpopo Predator Research Group.
77. Funston, P.J., M. Levendal, & Department of Environmental Affairs. (2014). Draft Biodiversity Management Plan for the lion (Panthera leo) in South Africa. [Website] Available https://www.dffe.gov.za/sites/default/files/gazetted_notices/nemba10of2014_biodiversitymanagementplan_africanlion39468_gen1190.pdf
78. Funston, P.J. (2008). Conservation and management of lions in southern Africa: status, threats, utilization and the restoration option. In: B. Croes, H.H. De Iongh & H. Bauer (Eds), *Management and conservation of large carnivores in West and Central Africa* (pp. 109–131). Institute of Environmental Sciences, Leiden.
79. Funston, P., Henschel, P., Hunter, L., Lindsey, P/, Nowak, K., Vallianos, C. & Wood, K. 2017. Panthera / WildAid / WildCRU: *Beyond Cecil: Africa's Lions in Crisis*. Retrieved from https://www.panthera.org/cms/sites/default/files/Beyond%20Cecil%20Africa%27s%20Lions%20in%20Crisis.pdf
70. Funston, P.J. (1999). *Predator-prey relationships between lions and large ungulates in the Kruger National Park***.** PhD thesis. University of Pretoria, Mammal Research Institute.
80. Funston P.J., Mills M.G.L., Biggs H.C., Richardson P.R.K. (1998). Hunting by male lions: ecological influences and socioecological implications. *Anim Behav* 56: 1333–1345.
81. Funston, P.J.; Mills, M.G.L.; Richardson, P.R.K.; van Jaarsveld, A.S. (2003). Reduced dispersal and opportunistic territory acquisition in male lions *Panthera leo*. *J. Zool.* 259, 131–142.
82. Garibaldi, A., & Turner, N. (2004). Cultural keystone species: Implications for ecological conservation and restoration. Ecology and Society, 9(3), 1.

83. Gavin, M. C., Mccarter, J., Mead, A., Berkes, F., Stepp, J. R., Peterson, D., & Tang, R. (2015). Defining biocultural approaches to conservation. *Trends in Ecology and Evolution*, 30(3), 140–145.

84. Gewald, J.B., Spierenburg, M.J. and Wels, H. (eds). (2018). *Nature conservation in southern Africa. Morality and marginality: Towards sentient conservation?* Leiden: Brill Academic Publishers. 16: Pp. 1–292.

85. Girma, E., Girmay, T., Hans B., Zealealem T.A., Iongh, H.H. de & Jorgelina, M. (2015). Community Resource Uses and Ethiopian Wolf Conservation in Mount Abune Yosef. *Environmental Management*, 56: 684-694.

86 Gittleman, J.L., Harvey, P.H. (1982). Carnivore home-range size, metabolic needs and ecology. *Behav. Ecol. Sociobiol*. 10 (1), 57–63. Available online: https://www.dailymail.co.uk/travel/article-1307465/South-Africa-safari-Wild-white-lions-sensational-Sanbona.html (Accessed on 23 February 2023).

87. Gomersall, W. 2015. *The cat's whiskers: Wild about white lions and charmed by cheeky cheetahs at South Africa's feline-friendly conservation reserve.* [Available online] *http://www.dailymail.co.uk/travel/article-1307465/South-Africa-safari-Wild-white-lions-sensational-Sanbona.html* (Accessed on 23 February 2023).

88. Government Gazette, 45160 (675). 2021. Draft Policy Position on the Conservation and Ecologically Sustainable Use of Elephant, Lion, Leopard and Rhinoceros: Minister of Forestry, Fisheries and the Environment of South Africa, 2021. Pp 1-83.

89. Government Gazette, 46687 (685). 2022. Revised Draft White Paper on Conservation and Sustainable Use of Elephants, Rhino, Lion, and Leopard: Minister of Forestry, Fisheries and the Environment of South Africa, 2022:7. Pp 1-76.

90. Government Gazette, 39468 (606). 2015. National Environmental Management Biodiversity Act (10/2004): Biodiversity Management Plan for the African Lion (*Panthera leo*): Minister of Forestry, Fisheries and the Environment of South Africa, 2015:. Pp 1-76.

91. Government Gazette, 44229 (171). 2021. Draft Revised National Biodiversity Framework Published for Public Comment in terms of the National Environmental Management: Biodiversity Act, 2004 (Act No.10 of 2004): Minister of Forestry, Fisheries and the Environment of South Africa, 2021:3. Pp 1-79.

92. Gratwicke B, Mills J, Dutton A, Gabriel G, Long B, Seidensticker J, et al. (2008). Attitudes toward consumption and conservation of tigers in China. *PLoS ONE*; 3: e2544. Available: http://dx.plos.org/10.1371/ journal.pone.0002544. https://doi.org/10.1371/journal.pone.0002544 PMID: 18596926/

93. Green, J.; Jakins, C.; Asfaw, E.; Bruschi, N.; Parker, A.; de Waal, L.; et al. (2020). African Lions and Zoonotic Diseases: implications for Commercial Lion Farms in South Africa. *Animals* 10:1692. doi: 10.3390/ani10091692

94. Green, J.; Jakins, C.; Waal, L.; de, D.; and Cruze, N. (2021). Ending Commercial Lion Farming in South Africa: a Gap Analysis Approach. *Animals* 11:1717. doi: 10.3390/ani11061717

95. Green, J.; Jakins, C.; Asfaw, E.; Parker, A.; Waal, L. & D'Cruze, N. (2022a). Welfare concerns associated with captive lions (*Panthera leo*) and the implications for commercial lion farms in South Africa. *Animal welfare* (South Mimms, England) pp. 209-218. 10.7120/09627286.31.2.005.
96. Green, J.; Hankinson, P.; Waal, L.; Coulthard, E.; Norrey, J.; Megson, D.; D'Cruze, N. (2022b). Wildlife Trade for Belief-Based Use: Insights From Traditional Healers in South Africa. *Frontiers in Ecology and Evolution*. 10. 906398. 10.3389/fevo.2022.906398.
97. Griffith, B., J. M. Scott, J. W. Carpenter & C. Reed. (1989). Translocation as a species conservation tool: status and strategy. *Science* 345: 447–480.
98. Gusset, M., Stewart, G., Bowler, D., & Pullin, A. (2010). Wild dog reintroductions in South Africa: A systematic review and cross-validation of an endangered species recovery programme. *Journal for Nature Conservation*. 18. 230–234. 10.1016/j.jnc.2009.11.001.
99. Hanby, J.P., Bygott, J.D., & C. Packer. (1995). Ecology, demography and behaviour of lions in two contrasting habitats: Ngorongoro Crater and the Serengeti Plains. Pp. 315 – 331. In: A.R.E Sinclair and P. Arceses (Eds.) *Serengeti II: Dynamics, management and conservation of an ecosystem.* University of Chicago Press.
100. Hairston, N.G.; Smith, F.E.; & Slobodkin, L.B. (1960). Community structure, population control and competition, *American Naturalist* 94: 421-425.
101. Hayward, M.W., & Kerley, G.I.H. (2005). Prey preferences of the lion *(Panthera leo)*. *Journal of Zoology* 267: 309-322.
102. Hayward, M. W., J. Adendorff, J. O'Brien, A. Sholto-Douglas, C. Bissett, L. Moolman, P. Bean, A. Fogarty, D. Howarth, R. Slater & G. I. H. Kerley. (2007a). The reintroduction of large, terrestrial, mammalian predators to the Eastern Cape, South Africa. *Oryx*, 41:205-214.
103. Hayward, M.W., Adendorff, J., O'brien, J., Sholto-Douglas, A., Bissett, C., Moolman, L.C., Bean, P., Fogarty, A., Howarth, D., Slater, R. & Kerley, G.I.H. (2007b). Practical considerations for the reintroduction of large, terrestrial, mammalian predators based on reintroductions to South Africa's Eastern Cape Province. *Open Conserv. Biol*. J. 11:1–11.
104. Hayward, M. & Kerley, G. (2009). Fencing for conservation: restriction of evolutionary potential or a riposte to threatening processes? *Biol. Conserv*. 142: 1–13
105. Hayward M.W., Hayward G.J., Druce D.J., Kerley G.I.H. (2009). Do fences constrain predator movements on an evolutionary scale? Home range, food intake and movement patterns of large predators reintroduced to Addo Elephant National Park, South Africa. *Biodiversity and Conservation* 18, 887–904.
106. Hazzah L, Mulder MB, Frank L, 2009. Lions and warriors: social factors underlying declining African lion populations and the effect of incentive-based management in Kenya. *Biological Conservation* 142:2428-2437.
107. Hemson G. (2003). *The ecology and conservation of lions: human-wildlife conflict in semi arid Botswana*. PhD Dissertation, University of Oxford.
108. 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

109. Henson, Lauren & Service, Christina & Stronen, Astrid & Moody, Jason & Housty, William & Reece, Donald & vonHoldt, Bridgett & Darimont, Chris. (2022). Genetic evidence to inform management of rare genetic variants and gene flow: Balancing the conservation of the rare "Spirit bear" allele and population genetic diversity across a complex landscape. Conservation Science and Practice. 4. 10.1111/csp2.12769.
110. Hiller, C.; Davies-Mostert, H.T.; Friedmann, Y.; Taylor, W.A.; MacMillan, D.C. (2022). Understanding South Africa's captive lion sector and the trade in captive lions (*Panthera leo*). EWT Research & Technical Paper No. 2, Endangered Wildlife Trust, South Africa.
111. Hoare, R. E., & J. Williamson. (2001). Assisted re-establishment of a resident pride of lions from a largely itinerant population. *South African Journal of Wildlife Research*, 31: 179-182.
112. Hoekstra, H. E.: From Darwin to DNA (2010). The Genetic Basis of Colour Variations. In: *In the Light of Evolution: Essays from the Laboratory and Field.* Edited by Losos, J.: Roberts and Company Publishers; 277-295.
113. Howarth, D. (2022). *History of the White Lion.* [Website]. Available online: 10 February 2023 from, https://www.pumbagamereserve.co.za/pages/history-of-the-white-lion/ (Accessed on 10 February 2023).
114. Hopcraft, J.G.C., Sinclair, A.R.E. & Packer, C. (2005). Planning for success: Serengeti lions seek prey accessibility rather than abundance. *Journal of Animal Ecology*, 74:559-566.
115. Hunter, L. (1998). *The behavioural ecology of reintroduced lions and cheetahs in the Phinda Resource Reserve, Kwazulu-Natal, South Africa*. Ph.D. thesis, University of Pretoria, Pretoria.
116. Hutchinson, A., and Roberts, D. L. (2020). Differentiating captive and wild African lion (*Panthera leo*) populations in South Africa, using stable carbon and nitrogen isotope analysis. *Biodivers. Conserv*. 29, 2255–2273.
117. Intergovernmental Science-Policy Platform on Biodiversity and Ecosystem Services (IPBES). (2019). Global Assessment Report on Biodiversity and Ecosystem Services of the Intergovernmental Science-Policy Platform on Biodiversity and Ecosystem Services, E.Z. Brondizio, J. Settele, S. D.az and H.T. Ngo (eds). Bonn: IPBES Secretariat.
118. IUCN. (2016). *The IUCN Red List of Threatened Species: African lion (Panthera leo)*. [Website] Available online 15 January 2023: http://dx.doi.org/10.2305/IUCN.UK.2016-3.RLTS.T15951A107265605.en
119. IUCN/SSC (2013). *Guidelines for Reintroductions and Other Conservation Translocations*. Version 1.0. Gland, Switzerland: IUCN Species Survival Commission, viiii + 57 pp.
120. IUCN/SSC (2014). Guidelines on the Use of Ex Situ Management for Species Conservation. Version 2.0. Gland, Switzerland: IUCN Species Survival Commission.
121. IUCN World Conservation Congress 2020. *Combatting the Illegal Trade in Lion Body Parts and Derivatives*; IUCN World Conservation Congress: Gland, Switzerland. Available online: https://www.iucncongress2020.org/motion/072/57715 (accessed on 31 January 2023).

122. 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.
123. Jule, K. R., Leaver, L. A., and S.E.G. Lea. (2008). The effects of captive experience in reintroduction survival in carnivores: a review and analysis. *Biol. Conserv.* 141(2): 355-363.
124. Jones J.P.G., Andria M., Hockley N. (2008). The importance of taboos and social norms to conservation in Madagascar. *Conservation Biology*, 22(4): 976-986.
125. Johnsingh, A. J. T., S. P. Goyal & Q. Qureshi. (2007). Preparation for the reintroduction of Asiatic lion Panthera leo persica into Kuno Wildlife Sanctuary, Madhya Pradesh, India. *Oryx,* 41: 93-96.
126. Kaelin, C. B., Xu X., Hong L. Z. , David V. A., McGowan K. A. *et al.* (2013). Specifying and Sustaining Pigmentation Patterns in Domestic and Wild Cats. *Science* 2012, 337(6101):1536–1541.
127. Kat P, 2012. LionAid: scientific estimates of lion populations in Africa. [cited 2 March 2016]. Pieter's Blog [Online]. [Website] Available online 7 February 2023: http://www.lionaid.org/news/2012/12/lionaid-scientific-estimator-of-lion-populations-in-africa.htm(2012)/12/lionaid-scientific-estimate-of-lion-populations-in-africa.htm (7 February 2023)
128. Keet, D.F.; Davies-Mostert, H.; Bengis, R.G.; Funston, P.; Buss, P.; et al. (Eds.). (2009). Lion (*Panthera leo*) Bovine tuberculosis disease risk assessment (Workshop report). Skukuza, South Africa: Conservation Breeding Specialist Group (CBSG SSC / IUCN), CBSG Southern Africa, Endangered Wildlife Trust.
129. Kerley, G. I., K. G. Behrens, J. Carruthers, M. Diemont, J. Du Plessis, L. Minnie, P. R. Richardson, M. J. Somers, C. J. Tambling, J. Turpie, H. N. Van Niekerk, and D. Balfour. (2017). Livestock predation in South Africa: the need for and value of a scientific assessment. *South African Journal of Science* 113:1–3.
130. Kilian, P.J. (2003). *The ecology of reintroduced lions on the Welgevonden Private Game Reserve, Waterberg*. MSc thesis. University of Pretoria, Centre for Wildlife Management.
131. Kissui, B. M. (2008). Livestock predation by lions, leopards, spotted hyenas, and their vulnerability to retaliatory killing in the Maasai steppe, Tanzania. *Anim. Conserv.* 11, 422–432. doi: 10.1111/j.1469-1795.2008.00199.
132. Kitchener, A.C.; Breitenmoser-Würsten, C.; Eizirik, E.; Gentry, A.; Werdelin, L.; Wilting, A.; Yamaguchi, N.; Abramov, A.V.; Christiansen, P.; Driscoll, C.; et al. (2017). A revised taxonomy of the Felidae. The final report of the Cat Classification Task Force of the IUCN Cat Specialist Group. *Cat News Spec. Issue* 11: pp80.
133. Kolipaka, S.S., Persoon, G.A., De Iongh, H.H &Srivastava, D.P. (2015). The Influence of People's Practices and Beliefs on Conservation: A Case Study on Human-Carnivore Relationships from the Multiple Use Buffer Zone of the Panna Tiger Reserve, India. J. *Hum. Ecol.,* 52(3): 192-207.
134. Krause J., Croft D.P., James R. (2007). Social network theory in the behavioural sciences: potential applications. *Behavioral Ecology and Sociobiology* 62:15-27

135. Krebs, C.J. (1999). *Ecological Methodology*. Addison-Wesley Educational Publishers, Inc., Menlo Park, Canada

136. Kuznetsova, A., Brockhoff, P. B., and Christensen, R. H. B. (2017). lmerTest package: tests in linear mixed effects models. *J. Stat. Softw*. 82: 1–26.

137. Lagendijk, D.D.G. and Gusset, M. (2008). Human-carnivore coexistence on communal land bordering the greater Kruger area, South Africa. *Environmental Management* 42, 971-976.

138. Lehmann, M.B., Funston, P.J., Owen, C.R., Slotow, R. 2008. Feeding behaviour of lions (*Panthera leo*) on a small reserve. *South African Journal of Wildlife Research* 2008, 38: 66-78.

139. Lesilau, F. (2019). *Human–lion conflict around Nairobi National Park*. Ph.D thesis. Leiden, University of Leiden.

140. Lesilau, F., Verschueren, S., van't Zelfde, M., Musters, Kees C. J. M., de Snoo, G. R. and de Iongh, H. H. (2021). Spatial ecology of lions in a small, semi fenced park surrounded by dense human populations: the case study of Nairobi National Park, Kenya. *Mammalia*, vol. 85, no. 3, pp. 198-207. <https://doi.org/10.1515/mammalia-2020-0116>.

141. LiMF. 2020. LiMF Research Summary 2020:1 - A review of past lion management interventions in 16 small, fenced reserves from 1992 - 2018; Unpublished Report, Lion Management Forum of South Africa.

142. Linden, Helaine M. (2017). *Development and Application of a 30-year Vegetation Dataset to Assess the Impacts of Fence Removal within the Kruger to Canyons Biosphere Reserve, South Africa.* Master's Theses. 1091. [Website] Available online (7 February 2023): http://digitalcommons.uconn.edu/gs_theses/1091

143. Lindsey, P.,; Balme, G.; Midlane, N.; Alexander, R.; & Craig, J. 2012. Possible relationships between the South African captive-bred lion hunting industry and the hunting and conservation of lions elsewhere in Africa: Research article. *S. Afr. J.*Wildl. Res. 42, 11–22.

144. 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), 137–1149. doi: 10.1016/j.biocon.2017.01.011

145. Linnell, J., & Breitenmoser, U., Breitenmoser, C., Odden, J. & von Arx, M. (2009). *Recovery of Eurasian Lynx in Europe: What Part has Reintroduction Played?* .10.1002/9781444312034.ch4.

146. Linnell, J. D. C., R. Aanes, J. E. Swenson, J. Odden, & M. E. Smith. (1997). Translocation of carnivores as a method for managing problem animals: a review. *Biodiversity and Conservation*, 6: 1245-1257.

147. Loveridge, Andrew & Hunt, J. & Murindagomo, F. & Macdonald, David. (2006). Influence of drought on predation of elephant (Loxodonta africana) calves by lion (Panthera leo) in an African wooded savannah. *Journal of Zoology*. 270. 523 - 530. 10.1111/j.1469-7998.2006.00181.x.

148. Loveridge, A. J., A. W. Searle, F. Murindagomo & D. W. Macdonald. (2007). The impact of sport hunting on the population dynamics of an African lion population in a protected area. *Biological Conservation,* 134: 548-558.

149. Loveridge, A. J., Valeix, M., Elliot, N. B., and Macdonald, D. W. (2016). The landscape of Anthropogenic mortality: how African lions respond to spatial variation in risk. J. Appl. Ecol. 54, 815–825. doi: 10.1111/1365-2664.12794
150. Loveridge A.J., Valeix M., Davidson Z., Murindagomo F., Fritz H., Macdonald D.W. (2009). Changes in home range size of African lions in relation to pride size and prey biomass in a semi-arid savanna. *Ecography* 32:953-962.
151. MacDonald D.W. (1983), The ecology of carnivore social behaviour. *Nature* 301: 379–383.
152. Macdonald, D. W. (2016). Animal behaviour and its role in carnivore conservation: examples of seven deadly threats. *Anim. Behav*. 120, 197–209. doi: 10.1016/j.anbehav.2016.06.013
153. Macdonald, E., Burnham, D., Hinks, A., Dickman, A. J., Malhi, Y., and Macdonald, D. W. (2015). Conservation inequality and the charismatic cat: *Felis felicis. Glob. Ecol. Conserv.* 3, 851–866. doi: 10.1016/j.gecco.2015. 04.006 Madden, F.
154. Macdonald, D., & Chapron, G. (2017). Outbreeding ideas for conservation success. *Oryx*. 51:206. doi: 10.1017/S0030605317000151
155. Macdonald, D. W., Loveridge, A. J., and Rabinowitz, A. (2010). "*Felid futures: crossing disciplines, borders, and generations*," in Biology and Conservation of Wild Felids, (Eds) D.W. Macdonald and A. J. Loveridge (Oxford, UK: Oxford University Press), 599–649.
156. Manly, B. McDonald, L. & Thomas, D. (1993). Resource selection by animals. Statistical design and analysis for field studies. Chapman and Hall, London, UK.
157. Manly, B.F.; McDonald, L.; Thomas, D.; McDonald, T.L.; Erickson, W.P. (2002). *Resource Selection by Animals: Statistical Design and Analysis for Field Studies*, 2nd ed.; Springer: Dordrecht, The Netherlands.
158. Marshall H. D., & Ritland K. 2002. Genetic diversity and differentiation of Kermode bear populations. *Molecular Ecology* 11(685-697)
159. Matoba T, Kutsukake N, Hasegawa T. (2013). Head rubbing and licking reinforce social bonds in a group of captive African lion *Panthera leo*. *PloS ONE* 8:e73044.
160. McBride, C. (1977). *The White Lions of Timbavati*; Paddington Press: New York, NY, USA.
161. McBride, C. (1981). *Operation White Lion*; St. Martin's Press: New York, NY, USA.
162. McDonald, T. 2005. *Ecological Management Plan: Tsau Wildlife Area*; Unpublished Report; Monzweni Eco-Developers, Hoedspruit, South Africa.
163. McEvoy, Orla & Ferreira, Sam & Parker, Daniel. (2022). The impacts of management interventions on the sociality of African lions (Panthera leo): Implications for lion conservation. *Ecological Solutions and Evidence*. 3. 10.1002/2688-8319.12135.
164. McNeely, J. A. (2000). Practical approaches for including mammals in biodiversity conservation. *Conserv. Biol*. Ser. 32000, 355–367.
165. McKeown, Kathleen. 2015. Tracking Wildlife Conservation in Southern Africa: Histories of Protected Areas in Gorongosa and Maputaland. Retrieved from the University of Minnesota Digital Conservancy, https://hdl.handle.net/11299/175690.
166. Michel, A.L.; Bengis, R.G.; Keet, D.F.; Hofmeyr, M.; de Klerk, L.M.; Cross, P.C.; et al. (2006). Wildlife tuberculosis in South African conservation areas: Implications and challenges. *Veterinary Microbiology*, 112: 91–100.

167. Miller, B., K. Ralls, R. P. Reading, J. M. Scott, & J. Estes. (1999). Biological and technical considerations of carnivore translocation: a review. Animal Conservation, 2:59-68

168. Miller S.M., Bissett C., Burger A., Courtenay B., Dickerson T., Druce D.J., Ferreira S., Funston P.J., Hofmeyr D., Kilian P.J., Mathews W., Naylor S., Parker D.M., Slotow R., Toft M., Zimmermann D. (2013). Management of reintroduced lions in small, fenced reserves in South Africa: An assessment and guidelines. *South African Journal of Wildlife Research* 43:138-154.

169. Miller S.M., Harper C.K., Bloomer P., Hofmeyr J., Funston P.J. (2014). Evaluation of microsatellite markers for population studies and forensic identification of African lions (*Panthera leo*). *J Hered*., 105, 762–72. doi: 10.1093/jhered/esu054 PMID: 25151647.

170. 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): 1-16.

171. Miller, S.; Riggio, J.; Funston, P.; Power, R.J.; Williams, V.; Child, M.F. (2016). A Conservation Assessment of Panthera leo. 2016. In The Red List of Mammals of South Africa, Swaziland and Lesotho; Child, M.F., Roxburgh, L., Do Linh San, E., Raimondo, D., Davies-Mostert, H.T., Eds.; South African National Biodiversity Institute: Pretoria, South Africa; Endangered Wildlife Trust: Midrand, South Africa, Pp. 48.

172. Mills, M.G.L and T.M. Shenk. (1992). Predator-prey relationships: the impact of lion predation on wildebeest and zebra populations. *Journal of Animal Ecology* 61: 693 - 702.

173. Mills, L. Soulé, M.; Doak, D. (1993). The Keystone-Species Concept in Ecology and Conservation. *BioScience*. 43. 219-224. 10.2307/1312122.

174. Milupi, Inonge & Somers, Michael & Ferguson, Willem. (2017). Local ecological knowledge and community based management of wildlife resources: a study of the Mumbwa and Lupande Game Management areas of Zambia. *Southern African Journal of Environmental Education*. 33. 25. 10.4314/sajee.v.33i1.3.

175. Mokgobi, M.G. Understanding traditional African healing. (2014). *Afr. J. Phys. Health Educ. Recreat. Danc*. 20, 24–34.

176. Montgomery R.A., Elliott K.C., Hayward M.W., Gray S.M., Millspaugh J.J., Riley S.J., Kissui B.M., Kramer D.B., Moll R.J., Mudumba T., Tans E.D., Muneza A.B., Bade L., Beck J.M., Hoffmann C.F., Booher C.R. and Macdonald D.W. (2018). Examining Evident Interdisciplinarity Among Prides of Lion Researchers. *Front. Ecol. Evol.* 6:49 doi:10.3389/fevo.2018.00049

177. Moore, D. E. & R. Smith. (1990). The red wolf as a model for carnivore re-introductions. *Symposia of the Zoological Society of London*, 62: 263-278

178. Mucina, L.; Rutherford M.C. (Eds) (2006). The vegetation of South Africa, Lesotho and Swaziland. *Strelitzia* 19, South African National Biodiversity Institute, Pretoria, South Africa.

179. Nieman, W. A.; Leslie, A. J.; & Wilkinson, A. (2019). Traditional medicinal animal use by Xhosa and Sotho communities in the Western Cape Province, South Africa. *J. Ethnobiol. Ethnomed*. 15, 1–14. doi: 10.1186/s13002-019-0311-6.

180. New T.R. (2006). *Conservation Biology in Australia: an Introduction*. South Melbourne: Oxford University Press

181. Naude, V.N.; Balme, G.A.; Rogan, M.S.; Needham, M.D.; Whittington-Jones, G.; Dickerson, T.; Mabaso, X.; Nattrass, N.; Bishop, J.M.; Hunter, L.; et al. (2020). Longitudinal assessment of illegal leopard skin use in ceremonial regalia and acceptance of faux alternatives among followers of the Shembe Church, South Africa. *Conserv. Sci. Pract.* 2, e289.
182. News24 Correspondent. (2013, October 2). White Lion cubs born at Pumba Game Reserve. [Website]. Available online (10 February 2023): https://www.news24.com/Travel/MyTravels/White-Lion-cubs-born-at-Pumba-Game-Reserve-20131001
183. News24. (2017, June 26). Lion bones export quota is a done deal. [Website] Available https://www.news24.com/Green/News/lion-bone-export-quota-in-sa-a-done-deal-20170626/
184. Nowell, K. & Jackson, P. (1996) Wild Cats. Status Survey and Conservation Action Plan. IUCN/SSC Cat Specialist Group. IUCN, Gland, 382 p.
185. Nowell, K & Pervushina, N. (2014). Review of implementation of Resolution Conf. 12.5(Rev.CoP16) on Conservation and trade in tigers and other Appendix-I Asian big cats. IUCN and TRAFFIC report prepared for the CITES Secretariat, 65th meeting of the CITES Standing Committee, Geneva, 7-11 July. Geneva. Available at: https://cites.org/sites/default/files/eng/com/sc/65/E-SC65-38-A01_0.pdf (accessed on 31 January 2023).
186. Ogutu J.O., Dublin H.T. (2002). Demography of lions in relation to prey and habitat in the Maasai Mara National Reserve, Kenya. *African Journal of Ecology* 40(2): 120-129.
187. Oriol-Cotterill, A., Macdonald, D.W., Valeix, M., Ekwanga, S., & Frank, L.G. (2015). Spatiotemporal patterns of lion space use in a human-dominated landscape. *Anim. Behav*. 101:27–39.
188. Owen, G.T. (2014). Qualitative methods in higher education policy analysis: Using interviews and document analysis. *The Qualitative Report*, 19(26), 1–19
189. Owen-Smith, N. & Mills, M.G.L. (2008a). Predator-prey size relationships in an African large-mammal food web*. Journal of Animal Ecology* 77: 173-183.
190. Owen-Smith, N. & Mills, M.G.L. (2008b). Shifting prey selection generates contrasting herbivore dynamics within a large-mammal predator–prey web. *Ecology*, 89: 1120–1133.
191. Packer, C., Hilborn, R., Mosser, A., Kissui, B., Borner, M., Hopcraft, G., Wilmshurst, J., Mduma, S. & Sinclair, A.R.E. (2005). Ecological change, group territoriality, and population dynamics in Serengeti lions. *Science*. 307: 390–393.
192. Packer C. (1986). The ecology of sociality in felids. *Ecological Aspects of Social Evolution*: 429–451.
193. Packer, C., & Pusey. A.E. (1983). Adaptations of female lions to infanticide by incoming males. *The American Naturalist* 121:716–728
194. Packer C., Pusey A.S., Eberly L.E. (2001). Egalitarianism in female African lions. *Science* 293:690-693.
195. Peel, M. J. S. (2010). The impact of fences within the Kruger to Canyons Biosphere Reserve. In K. Ferguson & J. Hanks (Eds.), *Fencing Impacts: A review of the environmental,*

social, and economic impacts of game and veterinary fencing in Africa with particular reference to the Great Limpopo and Kavango-Zambezi Transfrontier Conservation Areas. Pretoria: Mammal Research Institute.

196. Pienaar, U. de V. (1969). Predator-prey relationships amongst the larger mammals of the Kruger National Park. *Koedoe* 12: 108 - 184

197. Pinnock, D. (2018). A lion too far. Daily Maverick, 17 June 2018. Available online: https://conservationaction.co.za/recent-news/10491/ (accessed on 31 January 20223).

198. Pinnock, D. (2022). End trophy hunting in South Africa, or we won't visit your country, say tourists. Daily Maverick, 17 June 2018. Available online: https://www.dailymaverick.co.za/article/2022-08-31-end-trophy-hunting-in-south-africa-or-we-wont-visit-your-country-say-tourists/ (accessed on 31 January 2023).

199. Pooley, S. (2016). An interdisciplinary review of current and future approaches to improving human-predator relations. *Conserv. Biol.* 31, 513–523. doi: 10.1111/cobi.12859

200. Pool-Stanvliet R. (2013). A history of the UNESCO Man and the Biosphere Programme in South Africa. *S Afr J Sci*.;109(9/10), Art. #a0035, 6 pages. http:// dx.doi.org/10.1590/sajs.2013/a0035/

201. Power, R.J. 2002. Prey selection of lions *Panthera leo* in a small, enclosed reserve. *Koedoe*, 45: 67-75.

202. Power, J.R. 2003. Evaluating how many lions a small reserve can sustain. *S. Afr. J. Wildl. Res.* 33, 3-11.

203. Radloff, F.G.T. & du Toit J.T. (2004). Large predators and their prey in a southern African savanna: a predator's size determines its prey size range. *Journal of Animal Ecology*, 73: 410-423.

204. Ray, J.C. (2005). Large carnivorous animals as tools for conserving biodiversity: assumptions and uncertainties. In: Ray, J. C., K. H. Redford, R. S. Steneck, & J. Berger (eds). *Large Carnivores and the Conservation of Biodiversity*. Island Press, Washington, D.C. USA.

205. R Core Team (2016). R: A language and environment for statistical computing. R Foundation for Statistical Computing, Vienna, Austria. URL http://www.R-project.org/

206. R Core Team. 2020. R: A Language and Environment for Statistical Computing; R Foundation for Statistical Computing: Vienna, Austria, Available online: https://www.r-project.org/ (accessed on 31 December 2022).

207. Redpath, S. M., Bhatia, S., and Young, J. (2015). Tilting at wildlife: reconsidering human-wildlife conflict. *Oryx* 49, 222–225. doi: 10.1017/S0030605314000799.

208. Riggio J., Jacobson A., Dollar L., Bauer H., Becker M., Dickman A., Funston P., Groom R., Henschel P., de Iongh H. (2013). The size of savannah Africa: a lion's *Panthera leo* view. *Biological Conservation* 22:17-35.

209. Ripple, W. J., Estes, J. A., Beschta, R. L., Wilmers, C. C., Ritchie, E. G., & Hebblewhite, M. (2014). Status and ecological effects of the world's largest carnivores. *Science* 343:1241484. doi: 10.1126/science.1241484.

210. Robinson R., De Vos V. (1982). Chinchilla mutant in the lion. *Genetica*, 60: 61-63.
211. Römpler H., Rohla nd N., Lalueza-Fox C., Willerslev E., Kuznetsova T., Rabede G., Bertranpeti J., Schöneberg T., Hofreiter M. (2006). Nucleargene indicates coat-colour polymorphism in mammoths. *Science*, 313(5783): 62.
212. Russell, C. (2017) *Spirit bear. Encounters with the white bear of the western rainforest*, Toronto: House of Anansi.
213. Sale, P.F. (2002). The Science We Need to Develop for More Effective Management. In: Sale, P.F (Ed), *Coral Reef Fishes: Dynamics and Diversity in a Complex Ecosystem*. Academic Press. Pp. 527-549. ISBN 9780126151855. Available online: https://doi.org/10.1016/B978-012615185-5/50021-9.
214. Sarrazin F., and Barbault R. (1996). Reintroductions: challenges and lessons for basic ecology. *Trends in Ecology and Evolution* 11:474-478.
215. Saunders, N. J. (1998). *Icons of power: Feline symbolism in the Americas*. London, UK: Routledge.
216. Schmidt-Posthaus, H., C. Breitenmoser Wursten, H. Posthaus, L. Bacciarini & U. Breitenmoser. (2002). Causes of mortality in reintroduced Eurasian lynx in Switzerland. *Journal of Wildlife Diseases,* 38: 84-92.
217. Schneider A, Henegar C, Day K, Absher D, Napolitano C, Silveira L, *et al.* (2015). Recurrent Evolution of Melanism in South American Felids. *PLoS Genet* 10(2): e1004892. doi:10.1371/journal.pgen.1004892
218. Schaller, G.B. 1972. *The Serengeti Lion: A Study of Predator–Prey Relations,* University of Chicago Press, Chicago.
219. Schaller, G. B. (1976). The Serengeti Lion: A study of predator-prey relations. *Wildlife and Ecology Series*. University of Chicago Press, Chicago, IL. USA.
220. Searle, A.G. (1968). *Comparative Genetics of Coat Color in Mammals*. New York: Academic Press.
230. Shenk, T. (2005). *Lynx update*. Colorado Division of Wildlife, Colorado. USA.
231. Sih A., Hanser S.F., McHugh K.A. (2009). Social network theory: new insights and issues for behavioural ecologists. *Behavioural Ecology and Sociobiology* 63:975-988.
232. Simberloff D. (1998). Flagships, umbrellas and keystones: Is a single-species management passe n the landscape era? *Biol. Cons*. 83:247-257.
233. Slotow, R. & Hunter, L.T.B. 2009. Reintroduction decisions taken at the incorrect social scale devalue their conservation contribution: African lion in South Africa. In: M.W. Hayward & M.J. Somers (Eds.), *Reintroduction of top-order predators*. Oxford, U.K.: Wiley-Blackwell. Pp. 43–71.
234. Smuts G. L. (1982). *Lion*. Johannesburg: MacMillan South Africa.
235. Snyder, N. F. R., S. R. Derrickson, S. R. Beissinger, J. W. Wiley, T. B. Smith, W. D. Toone, & B. Miller. (1996). Limitations of captive breeding in endangered species recovery. *Conservation Biology*, 10: 338-348.
236 Sogbohossou E.A., Iongh H.H.de, Sinsin B., Snoo G.R. de, Funston P.J. (2011). Human–carnivore conflict around Pendjari Biosphere Reserve, northern Benin, *Oryx*, 45 (04), 569-578.

237. Soh, Y. H., Carrasco, L. R., Miquelle, D. G., Jiang, J., Yang, J., and Rao, M. (2014). Spatial correlates of livestock depredation by Amur tigers in Hunchun, China: relevance of prey density and implications for protected area management. *Biol. Conserv*. 169, 117–127. doi: 10.1016/j.biocon.2013.10.011
238. Somers, M. & Gusset, M. (2009). The Role of Social Behaviour in Carnivore Reintroductions. *Reintroduction of Top-Order Predators*. 270–281. 10.1002/9781444312034.ch12.
239. Somers, M.J.; Walters, M.; Measey, J.; Strauss, W.M.; Turner, A.A.; Venter, J.A.; et al. (2020). The implications of the reclassification of South African wildlife species as farm animals. *S Afr J Sci.* 116(1/2), Art. #7724, 2 pages. https://doi.org/10.17159/sajs.2020/7724.
240. Somerville, K. (2020) *Humans and lions. Conflict, conservation and coexistence*, Oxon: Routledge, pp. 196-198.
241. South African Department of Environmental Affairs. (2017). 2017 Export Quota for Lion Bones in Place. [Website] Available: http://www.sabinetlaw.co.za/environmental-affairs and-water/articles/2017-export-quota-lion-bones-place/
242. South African National Parks. (2018). *Kruger National Park Management Plan* (2018 to 2028). Published document for stakeholder participation process. PO Box 787, Pretoria, 0001.
243. Spong, G. (2002). Space use in lions, Panthera leo, in the Selous Game Reserve: social and ecological factors. *Behavioural Ecology and Sociobiology*, 52:303-307.
244 Stander, P. Demography of lions in the Etosha National Park, Namibia. (1991). *Madoqua* 18, 1–9.
245. Stanley Price, M. R. (1991). *A review of mammal re-introductions, and the role of the Re-introduction Specialist Group of IUCN/SSC*. Symposia of the Zoological Society of London, 62: 9-25.
246. Stevenson-Hamilton, James. (1937). *South African Eden: The Kruger National Park 1902-1946.* Struik Publishers, 1993.
247. Stuart, S. N. 1991. Re-introductions: to what extent are they needed? *Symposia of the Zoological Society of London*, 62: 27-37.
248. Sunquist, M. & F. Sunquist. (2002). *Wild Cats of the World*. University of Chicago Press, Chicago, IL. USA.
249. Suryawanshi, K. R., Bhatnagar, Y. V., Redpath, S., and Mishra, C. (2013). People, predators and perceptions: patterns of livestock depredation by snow leopards and wolves. *J. Appl. Ecol*. 50, 550–560. doi: 10.1111/1365-2664
250. Tambling, C.J. & du Toit, J. (2005). Modelling wildebeest population dynamics: implications of predation and harvesting in a closed system. *J. of Appl. Ecol*. 42(3), 431–441. DOI: 10.1111/j.1365-2664.2005.01039.x
251. Thatcher, C. A., F. T. Van Manen & J. D. Clark. (2006). Identifying suitable sites for Florida Panther reintroduction. *Journal of Wildlife Management,* 70: 752-763.
252. Toone W., Wallace M. (1994). The extinction in the wild and the reintroduction of the California condo Gymnogyps californianus. In: Olney PJS, Mace GM, Feistner ATC, editors. *Creative Conservation*. The Netherlands: Springer. 411-419.

253. Trinkel, M., Ferguson, N., Reid, A, Reid, C., Somers, M., Turelli, L., Graf, J., Szykman, M., Cooper, D., Haverman, P., Kastberger, G., Packer, C. & Slotow, R. 2008. Translocating lions into an inbred lion population in the HluhluweiMfolozi Park, South Africa. *Anim. Conserv*. 11: 138–143.
254. Tucker, L. (2003). Mystery of the White Lions: Children of the Sun God. White River: Npenvu Press.
255. Tucker, L. (2013). *Saving the White Lions: One Woman's Battle for Africa's Most Sacred Animal*. Berkeley, CA: North Atlantic Books.
256. Tuqa, J.H., Funston, P., Musyoki, C., Ojwang, G.O., Gichuki, N.N., Bauer, H., Tamis, W., Dolrenry, S., Van't Zelfde, M., de Snoo, G.R., et al. (2014). Impact of severe climate variability on lion home range and movement patterns in the Amboseli ecosystem, Kenya. *Glob. Ecol. Conserv*. 2: 1–10.
257. Tuqa, J. H., Funston, P. J., Musyoki, C., Ojwang, G. O., Gichuki, N. N., Bauer, H., Tamis, W., Dolreny, S., Van't Zelfde, M., de Snoo, G. R., de Iongh, H. H. (2015). Impact of severe climate variability on lion home range and movement patterns in the Amboseli ecosystem, Kenya. *Global Ecology and Conservation*. 2: 1-10.
258. Tumenta, P.N., van't Zelfde, M., Croes, B.M., Buij, R., Funston, P.J., Udo de Haes, H.A., and De Iongh, H.H. (2013). Changes in lion (Panthera leo) home range size in Waza National Park, Cameroon. *Mamm. Biol.* 78: 461–469.
259. Turner J. (2005). *The impact of lion predation on the large ungulates of the Associated Private Nature Reserves, South Africa*. MSc thesis. University of Pretoria, Centre for Wildlife Management.
260. Turner, J. A., Vasicek, C. A., & Somers, M. J. (2015). Effects of a colour variant on hunting ability: the white lion in South Africa. *Open Science Repository Biology*, Online(open-access), e45011830. doi:10.7392/openaccess.45011830.
261. Turner, J.A.; Iongh, H.d.; Dunston-Clarke, E.J. (2022a). Assessing the Social Cohesion of a Translocated Pride of White Lions Integrated with Wild Tawny Lions in South Africa, Using Social Network Analysis. *Animals*, *12*, 1985. https://doi.org/10.3390/ani12151985
262. Turner, J.A.; Dunston-Clarke, E.J.; Fabris-Rotelli, I.; de Iongh, H. (2022b).Home Range and Movement Patterns of Reintroduced White Lions (*Panthera leo melanochaita*) in the Kruger to Canyons Biosphere Reserve, South Africa. *Animals*, *12*, 2003. https://doi.org/10.3390/ani12152003.
263. Turner, J.A.; Wels, H. (2023). Chapter 10. White Lions in South Africa: A Living Heritage. In: *Calling on the Commnity: Understanding Participation in the Heritage Sector, an Interactive Governance Perspective*. Edited by Rodenberg J., Wagenaar, P., and Gert-Jan Burgers. Berghahn Books, New York. Pp 1–297.
264. United Nations General Assembly. (2007). United Nations declaration on the rights of indigenous people. New York, NY: United Nations
265. Valeix, M. (2015). Review of Effects of a colour variant on hunting ability: the white lions in South Africa. [Website] Available: http://www.open-science-repository.com/review-of-the-article-effects-of-a-colour-variant-on-hunting-ability-the-white-lion-in-south-africa.html (Accessed on 23 February 2023).

266. Van Aarde, R.J. & Van Dyk, A. (1986). Inheritance of the king coat colour pattern in cheetahs Acinonyx jubatus. *J. Zool., Lond*. 209, 573-578.
267. Van Dierendonck M.C., Wallis de Vries M.F. (1996). Ungulate reintroductions: experiences with the Takhi or Przewalski horse Equus ferus przewalskii in Mongolia. *Conservation Biology* 10:728-740.
268. Van Dyk G. (1997). Reintroduction techniques for lion (*Panthera leo*). In: *Proceedings of a Symposium on Lions and Leopards as Game Ranch Animals*. Edited by Van Heerden J. Onderstepoort: Wildlife Group of the South African Veterinary Association.
269. Van Orsdol, K.G., Hanby, J.P. & Bygott, J.D. (1985). Ecological correlates of lion social organisation (*Panthera leo*). *J. Zool., Lond*., 206: 97-112.
270. Viljoen, P.C. (1997). Ecology of lions in Northern Botswana. Pp. 37 - 46. In: *Proceedings of a Symposium on Lions and Leopards as Game Ranch Animals*. Edited by Van Heerden J. Onderstepoort: Wildlife Group of the South African Veterinary Association.
271. VSN International. (2014). *GenStat for Windows*. Hemel Hempstead: VSN International.
272. Vucetich J.A., Bruskotter J.T., Nelson M.P.(2015). Evaluating whether nature's intrinsic value is an axiom of or anathema to conservation. *Conservation Biology*, 1-12.
273. Wasserman S., Faust K. (1994). *Social Network Analysis: Methods and Applications*. New York: Cambridge University Press.
274. Wear, B. J., R. Eastridge & J. D. Clark. (2005). Factors affecting settling, survival, and viability of black bears reintroduced to Felsenthal National Wildlife Refuge, Arkansas. *Wildlife Society Bulletin,* 33: 1363-1374.
275. Wey, T.; Blumstein, D.T.; Weiwei, S.; Ferenc, J. 2008. Social network analysis of animal behavior: A promising tool for the study of sociality. *Anim. Behav.* 75, 333–344.
276. White, P. C. L., and Ward, A. I. (2010). Interdisciplinary approaches for the management of existing and emerging human – wildlife conflicts. *Wildlife Res.* 37, 623–629. doi: 10.1071/WR10191.
277. Whitehead, H. (2009). SOCPROG program: Analyzing animal social structures. *Behav. Ecol. Sociobiol*. 63, 165–173.
278. Whitman, K.; Packer, C. (1997). The effect of sport hunting on the social organization of the African lion (Panthera leo). In *Lions and Leopards as Game Ranch Animals*; Van Heerden, J., Ed.; The Wildlife Group, South African Veterinary Association: Onderstepoort, South Africa, Pp. 177–183.
279. Whitman, K.; Starfield,A.M.;Quadling,H.S.; Packer, C. (2004). Sustainable trophy hunting of African lions. *Nature*, 428, 175–178
280. Williams, V.L.; Newton, D.J.; Loveridge, A.J.; Macdonald, D.W. (2015). Bones of Contention: An Assessment of the South African Trade in African Lion *Panthera leo* Bones and other Body Parts; TRAFFIC: Cambridge, UK; WildCRU: Oxford, UK. Available online:https://www.traffic.org/publications/reports/bones-of-contention-south-african-trade-in-african-lion-bones-and-other-body-parts/ (accessed on 31 January 2023).
281. Williams, V.L.; Loveridge, A.J.; Newton, D.J. & Macdonald, D.W. (2017). A roaring trade? The legal trade in *Panthera leo* bones from Africa to East-Southeast Asia. *PLOS ONE* 12, e0185996.

282. Williams, V.L.; Coals, P.G.; de Bruyn, M.; Naude, V.N.; Dalton, D.L.; Kotzé, A. (2021). Monitoring compliance of CITES lion bone exports from South Africa. *PLoS ONE*, 16, e0249306.

283. Witzenberger K.A., Hochkirch A. (2011). Ex situ conservation genetics: a review of molecular studies on the genetic consequences of captive breeding programmes for endangered animal species. Biodiversity Conservation 9:1843-1861.

284. World Wilderness Congress 2009. (2009). Resolution 33: Protection of white, non-albino animals / Protección de animales blancos no albinos. Available: https://www.wild.org/wild-congress/wild9/wild9-resolutions/ (Accessed on 23 February 2023).

285. Xu *et al.* (2013). The Genetic Basis of White Tigers, *Current Biology*, 23: 1-5; doi: 10.1016/j.cub.2013.04.054.

287. Yirga, G., Ersino, W., De Iongh, H.H., Leirs, H., Gebrehiwot, K., Deckers, J. & Bauer, H. (2013). Spotted hyena (Crocuta Crocuta) coexisting at high density with people in Wukro district northern Ethiopia. *Mammalian Biology* 78: 193-197.

288. Yiu, S.W., Parrini, F., Karczmarski, L., Keith, M. (2017). Home range establishment and utilization by reintroduced lions (Panthera leo) in a small South African wildlife reserve. *Integrative Zoology 2017*; 12: 318–332.

Above
Young white and tawny lion siblings in the Timbavati Private Nature Reserve, South Africa.
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Front cover
White lion male free-roaming at the Tsau Conservation Area, South Africa
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