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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

Turner, J.A.

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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*, Linnaeus 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 km², 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*, Linnaeus, 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 pictus*) (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 Trust¹ 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 Kitsoo 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 longh & 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 km²) 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 reserve² 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.

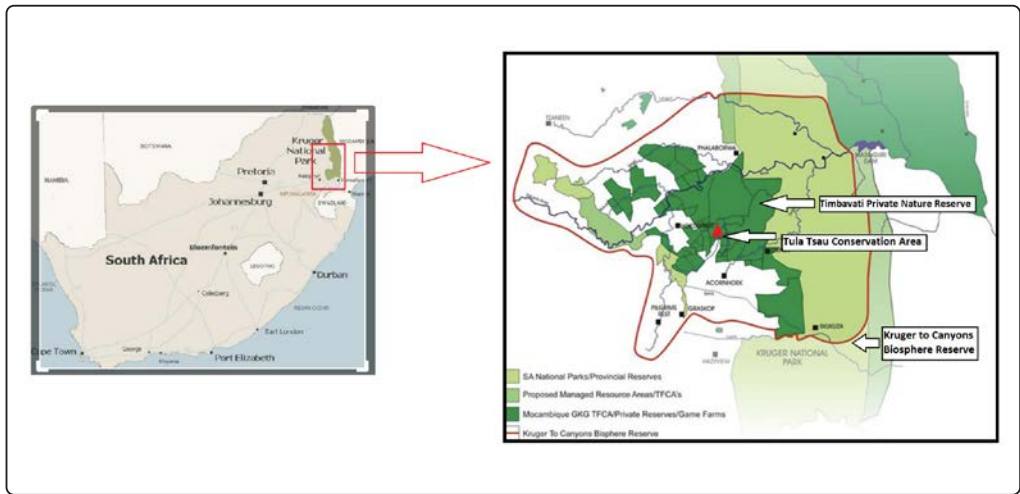


Figure 1 Map showing the Tula Tsau Conservation Area, Kruger National Park, and Timbavati Private Nature Reserve, within the Kruger to Canyons Biosphere Reserve, South Africa.

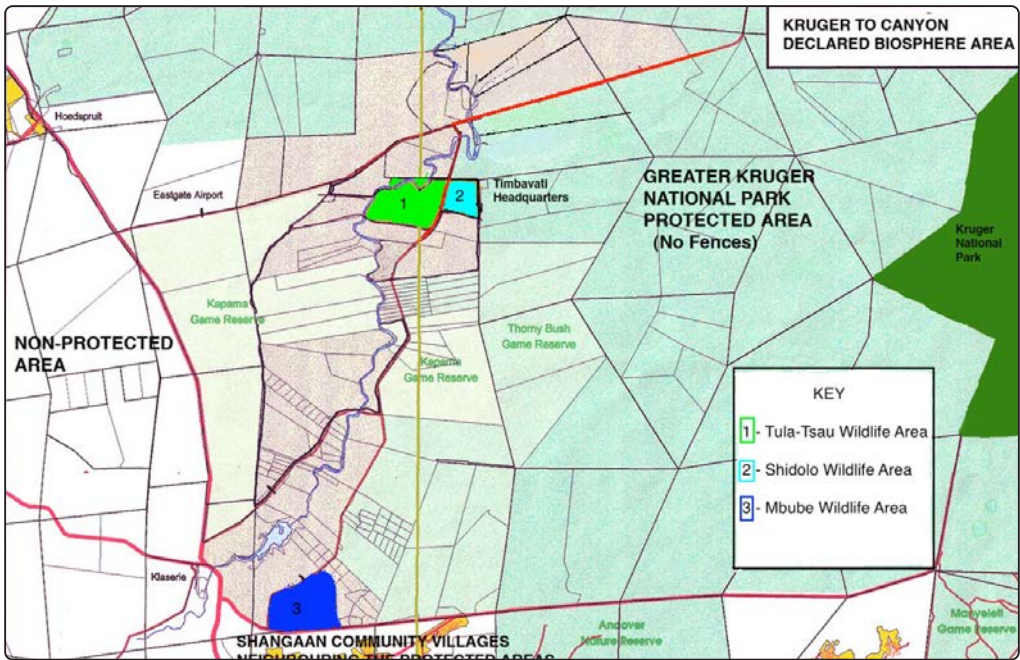


Figure 2 Map showing the wildlife areas that comprise the Tsau Wildlife Area – (1) Tula Tsau, (2) Shidolo and (3) Mbube Wildlife Areas - within the Kruger to Canyons Biosphere Reserve, South Africa.

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 subordinated mafic 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.