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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

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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 km²), 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 (<1000km²), 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 longh 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 $10.44 \pm 4.82 \text{ km}$; constructed pride: 5.50 km^2 , $11.37 \pm 4.72 \text{ km}$), 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 km²) 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 longh 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 km²) 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 ($>56\text{km}^2$) instead of to a pride of both white and tawny lions in a small fenced area ($<17\text{km}^2$). 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 ($<1000\text{ km}^2$) 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.