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.

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

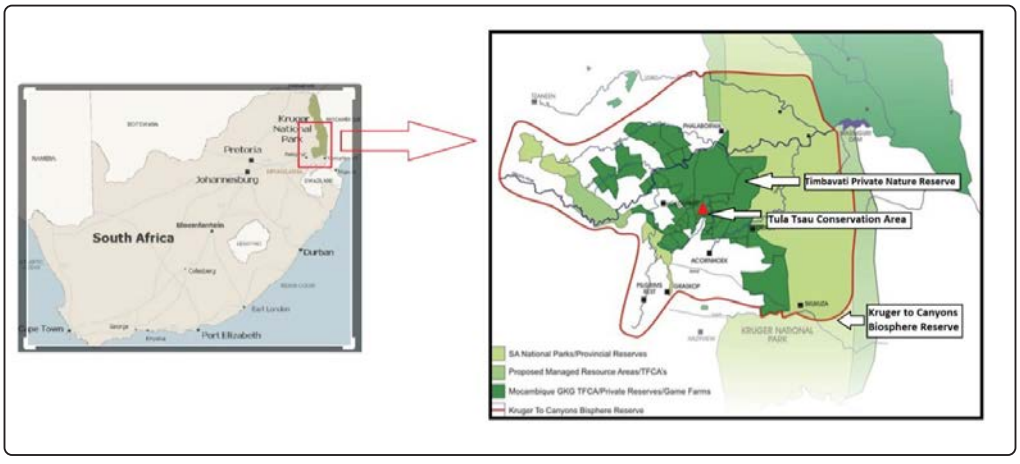

Figure 1 **Location of the Tula Tsau Conservation Area, Kruger to Canyons Biosphere Reserve, South Africa.**

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

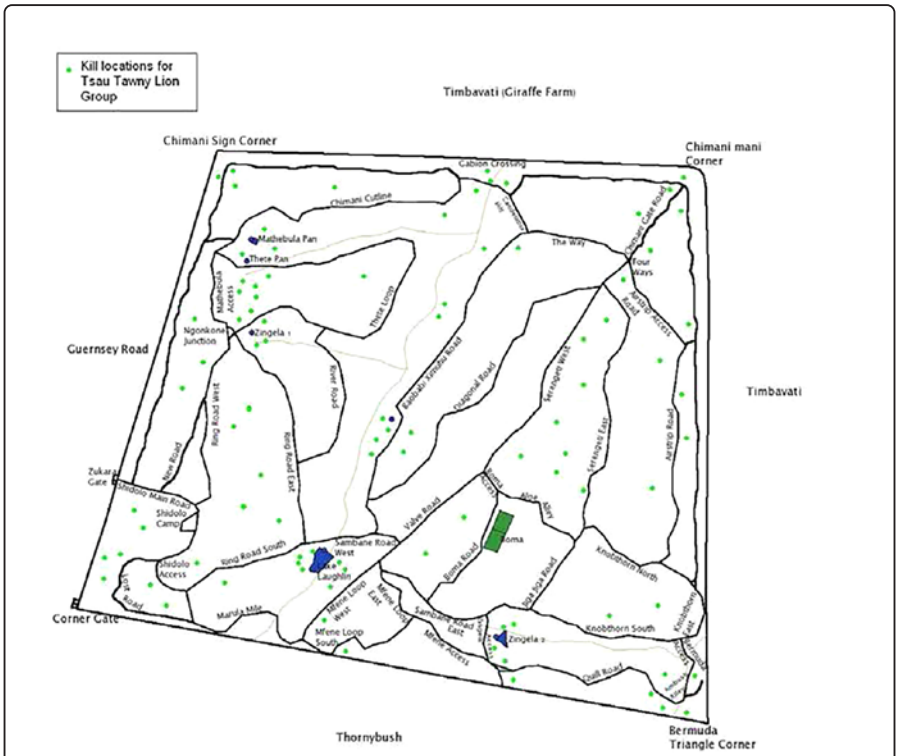

FIG 3.1 : Location of kills made by the Tsau Tawny Lion Group from August 2009 to March 2010 within the 300 ha rewilding area at the Tsau Conservancy, South Africa.

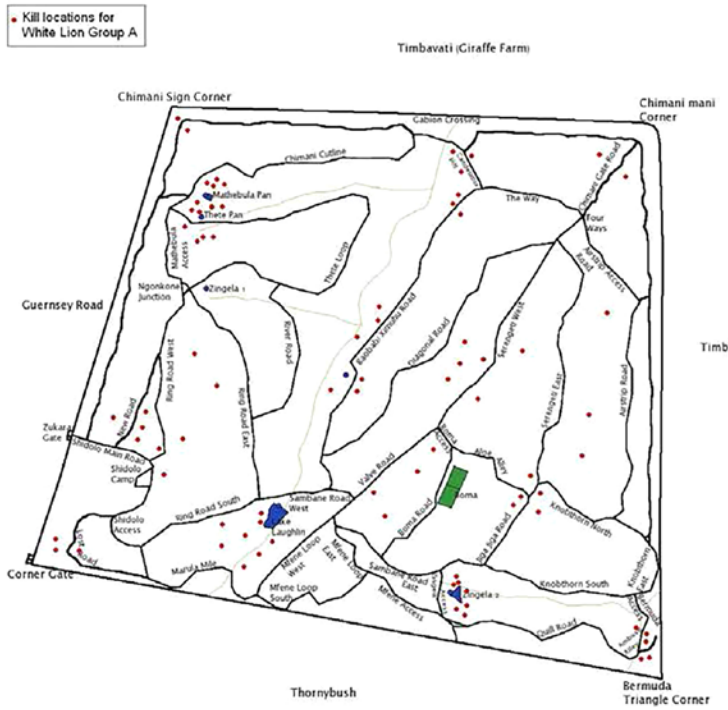

FIG 3.2 : Location of kill made by White Lion Group A from August 2005 to March 2006 within the 300 ha rewilding area at the Tsau Conservancy, South Africa.

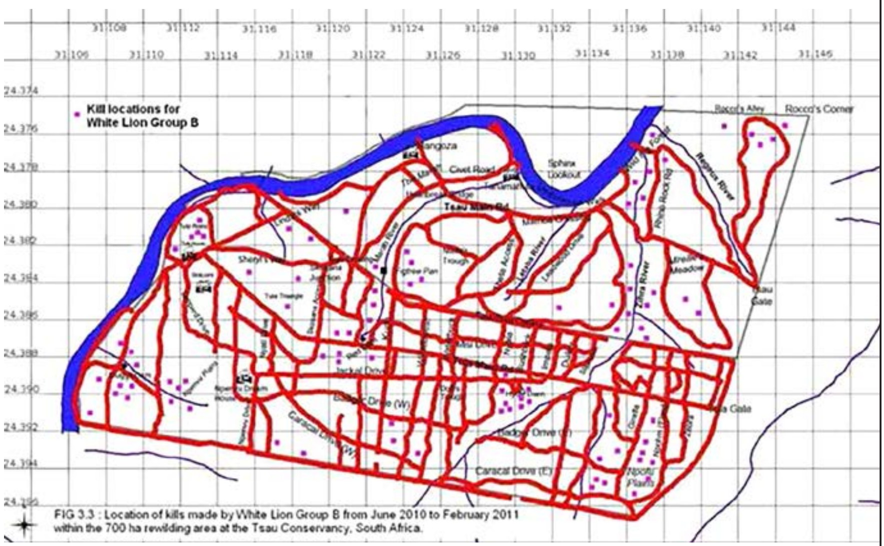

FIG 3.3 : Location of kills made by White Lion Group B from June 2010 to February 2011 within the 700 ha rewilding area at the Tsau Conservancy, South Africa.

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

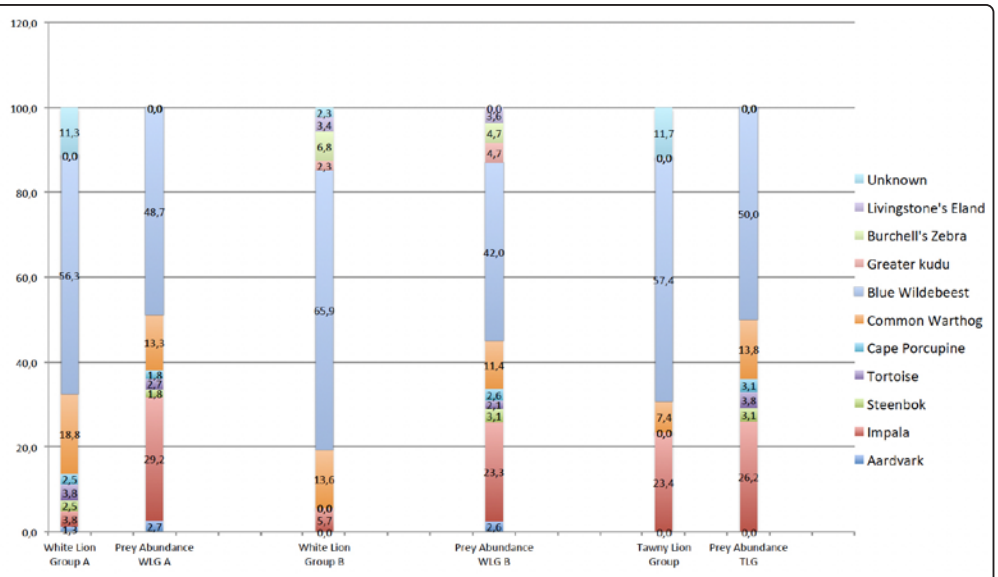

Figure 4.: Prey selection (%) of White Lion Group A, White Lion Group B, and the Tsau Tawny Lion Group under managed free-roaming conditions at the Tsau Conservancy, South Africa. The prey abundance (%) during the period of study for each lion group was taken from aerial count data and included for comparison

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

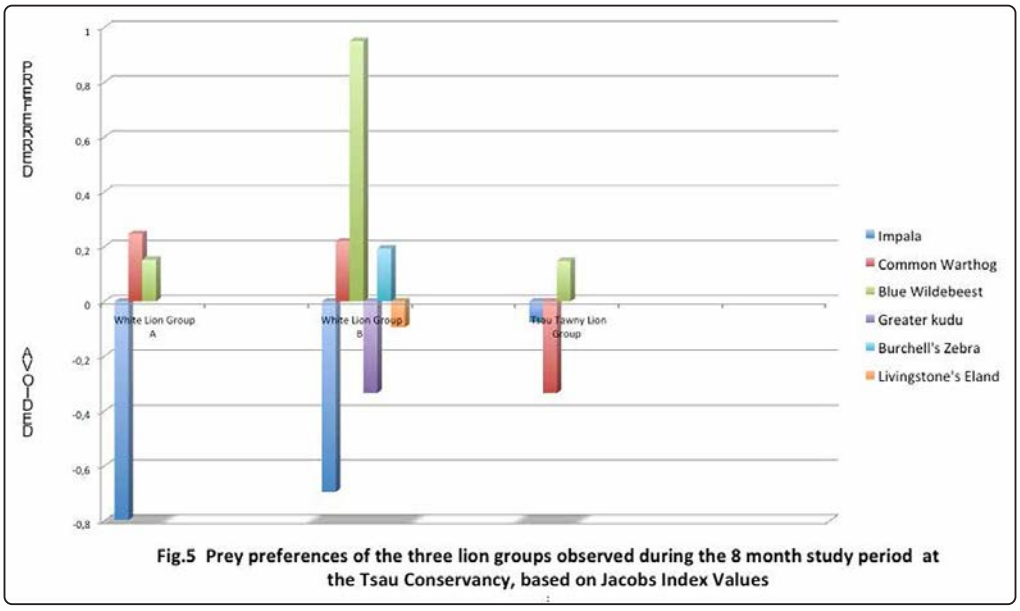

Fig.5 Prey preferences of the three lion groups observed during the 8 month study period at the Tsau Conservancy, based on Jacobs Index Values

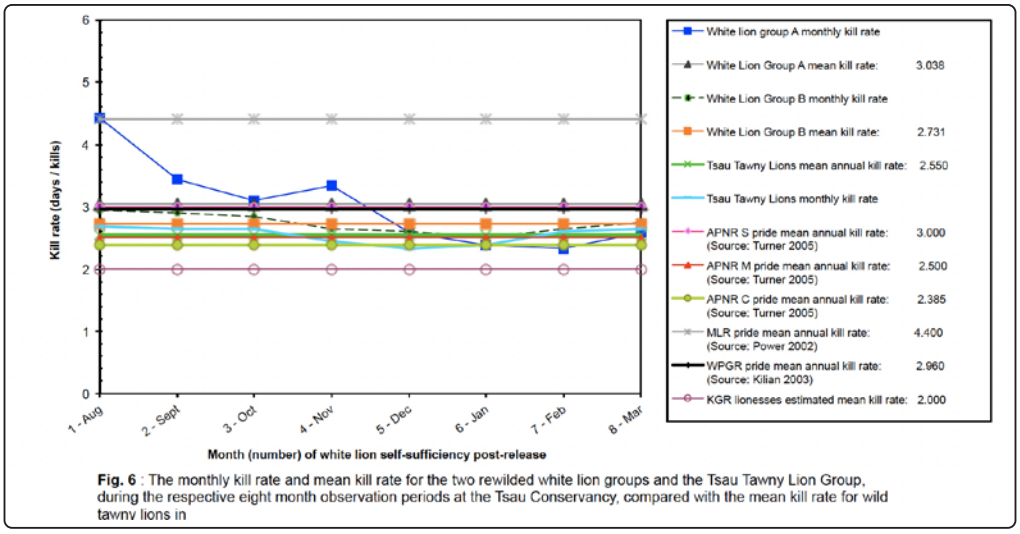

Fig. 6 : The monthly kill rate and mean kill rate for the two rewilded white lion groups and the Tsau Tawny Lion Group, during the respective eight month observation periods at the Tsau Conservancy, compared with the mean kill rate for wild tawny lions in

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 APNR Male Coalition APNR Mixed Group	17 31 13	4.3 to 11.5	1570 to 4197
KARONGWE Lionesses Alone KARONGWE Male Coalition KARONGWE 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.

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