Conservation biology of cheetahs *Acinonyx jubatus* (Schreber, 1775) and African wild dogs *Lycaon pictus* (Temminck, 1820) in South Africa

By
Kelly Marnewick

Submitted in partial fulfilment of the requirements for the degree

Doctor of Philosophy (Wildlife Management)

In the Faculty of Natural and Agricultural Sciences
University of Pretoria
Pretoria

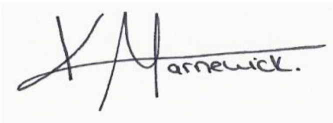
July 2015

Supervisor: Prof. M.J. Somers

DECLARATION

I, Kelly Marnewick, declare that this thesis, which I hereby submit for the degree Doctor of Philosophy (Wildlife Management) at the University of Pretoria, is my own work and has not previously been submitted by me for a degree at this or any other tertiary institution.

SIGNATURE:



DATE:

27 July 2015

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ABSTRACT

Large carnivores play a key role in regulating terrestrial ecosystems and their removal can cause effects that cascade through the lower trophic levels. Despite this, the geographic range and density of most large carnivore species are declining globally due to anthropogenic factors. Large carnivores are particularly difficult to conserve because they often come into conflict with humans, have large ranges, normally occur at low densities and are not confined to protected areas. This is particularly true for Vulnerable cheetahs *Acinonyx jubatus* and Endangered African wild dogs *Lycaon pictus* that are two of the widest ranging carnivores and are threatened by killing due to conflict, habitat fragmentation and snaring. Wild dogs are further susceptible to being killed on roads and cheetahs are often traded into captivity. Conservation planning for cheetahs and wild dogs in South Africa is hampered by a lack of information on suitable habitat for conservation action and connectivity between these habitats. Ecological niche models show that there are 21 410km^2 of suitable habitat for both species in South Africa, both inside and outside of their current distribution ranges. Key areas are identified for conflict mitigation work, reintroduction projects and range expansion. With the exception of the Kruger National Park, the current protected area network is inefficient in conserving cheetah and wild dog habitat. To supply relevant information for conservation action, the range use

of cheetahs outside of protected areas was investigated. Male home ranges ranged from 121.5 km^2 to 607 km^2 while females ranged from 14.7 km^2 to 703.3 km^2. Cheetahs utilised several ranches and mean home ranges sizes were larger than mean ranch size. This provides valuable and relevant information on cheetahs and aids conservation practitioners in mitigating human-cheetah conflict on South African farmland. The Kruger National Park is a stronghold for cheetah and wild dog conservation in South Africa thus monitoring the status of these populations is important. Tourist photographic surveys were used to obtain data for photographic-based capture-recapture analysis for open populations. Results show that 412 (329-495; SE 41.95) cheetahs and 151 (144-157; SE 3.21) wild dogs occur in the Kruger National Park. Cheetah capture probabilities were affected by time (number of entries) and sex, whereas wild dog capture probabilities were affected by the region of the park. The cheetah population of Kruger appears to be healthy, while the wild dog population size and density are of concern. Because cheetahs and wild dogs have been extirpated from most of South Africa, reintroduction programmes have resulted in cheetahs and wild dogs being introduced into fenced reserves. These are fragmented from each other and populations need to be managed to ensure demographic and genetic integrity. The survival of cheetahs introduced into reserves from the free roaming population was examined using data from 29 reserves and 189 cheetahs: 92 adults: 59 males and 33 females, plus 94 cubs born on the reserves. The Kaplan-Meier (product limit) estimator with staggered entry (Pollock *et al.* 1989) was used and the mean annual survivorship for all cheetahs, including cubs born, was 82.8%. The final survivorship value for all adult cheetahs was 0.23 and for cubs was 0.04. Cubs had significantly higher survival on reserves where other competing predators were absent. The median survival time was 38 months for adult males and more than 53 months for adult females. Cheetah and wild dog conservation needs to be addressed in three key geographically areas due to the different challenges and management interventions required: 1) free roaming populations outside of protected areas, 2) the Kruger National Park and 3) reintroduced populations in fenced reserves. Each area provides unique opportunities and challenges for conservation of these species.

Note on text

The lay out of this thesis includes: a general introduction, chapters 2-5 as stand-alone papers, of which chapters 3, 4 and 5 have been published as follows:

Chapter 3: Marnewick K, Ferreira SM, Grange S, Watermeyer J, Maputla N, *et al.* (2014) Evaluating the Status of African Wild Dogs *Lycaon pictus* and Cheetahs *Acinonyx jubatus* through Tourist-based Photographic Surveys in the Kruger National Park. PLoS ONE 9(1): e86265. doi:10.1371/journal.pone.0086265.

Chapter 4: Marnewick, K. & Somers, M.J. 2015. Home range size of cheetahs *Acinonyx jubatus* outside protected areas in South Africa. African Journal of Wildlife Research 45(2): 223–232.

Chapter 5: Marnewick, K., Cilliers, D., Hayward, M. & Somers, M. 2009. Survival of cheetahs relocated from ranchlands to fenced protected areas. In: Hayward, M & Somers, M. (Eds.) The re-introduction of top order predators, chapter 13. Blackwell Publishing.

Chapter 2 identifies suitable habitat and connectivity in South Africa to guide conservation action and reintroduction programmes. Chapter 3 accurately determines the size of the cheetah and wild dog populations through citizen science in the Kruger National Park as the largest protected area that houses both species. Chapter 4 quantifies the range use of free roaming cheetahs outside of protected areas in Limpopo province to assist with conflict mitigation activities. Chapter 5 examines the survival of cheetahs in fenced reserves and the implications for reintroduction programmes.

Ethics Note

All activities involving cheetah handling and research were done under the guidance of the University of Pretoria Animal Use and Care committee ref Nr EC030-09 and with permits issued by Limpopo Economic Development Environment and Tourism department (the local conservation authority).

ACKNOWLEDGEMENTS

- While only one name appears on the cover of this thesis, it definitely was not a one-woman project. Without the vast amount of support I received from so many people and organisations, this thesis would not have been possible. I would like to thank the following and apologise upfront for any omissions:
- The field work was mostly funded by the generous support of: Columbus Zoo, Cat Life Foundation, Duemke Family Trust, Scovill Zoo and Sasol Chevron.
- The University of Pretoria is thanked for a post-graduate bursary.
- Prof. Michael Somers for taking me on as a student, trusting me to complete this after repeated delays and calmly guiding me in the right direction.
- My fellow students and colleagues at the Centre for Wildlife Management at the University of Pretoria: Fred Dalerum, Lourens Swanepoel and Michelle Thorn, thank you for helping with ideas and dead ends, offering moral and academic support and generally being in the same boat. Liset 'Ma' Swanepoel for spoon feeding the admin process, for helping writing apology letters to the Dean after yet another delay and for generally looking after me.
- The Limpopo Department of Economic Development, Environment and Tourism (LEDET) for permissions to trap and collar cheetahs on farmland and SANParks for research permissions and data.
- Dr Peter Caldwell of Old Chapel Veterinary Clinic is a fantastic vet who was always on standby for any veterinary requirements and immobilised the cheetahs for the range use study and many of the relocations. He never complained about dropping everything when a cheetah was trapped and did not charge for the time he spent on the project. Without this type of veterinary support, collaring cheetahs in remote areas would not be possible.
- All the reserve mangers and staff who willingly and enthusiastically provided data for the cheetah survival study are thanked.
- Members of the Wild Dog Advisory Group of South Africa (WAG-SA) kept the pressure on at each meeting by asking for renewed deadlines for the wild dog papers. They are also thanked for the database of wild dog sightings outside protected areas.
- To all the tourists who supplied data for the Kruger Park photo surveys, it is always overwhelming to see the response that we get to our work and the passion that the general public share for cheetahs and wild dogs.
- All the co-authors on the various chapters contributed greatly to my understanding of cheetahs and wild dogs. Not only did they teach me about science, but also offered loads of

support, were always keen to throw ideas around and seldom told me I was being totally ridiculous.

- The many landowners in Thabazimbi, Limpopo who were curious and brave enough to allow a researcher to catch, collar and release cheetahs on their properties. Willem Engelbrecht, the Jeurissen family of Silent Valley Safaris, staff on Atherstone Nature Reserve and the owners of Mabulskop are thanked for their contribution to our knowledge of cheetahs outside reserves. All the many other landowners who allowed access to their properties to set traps and look for signs of cheetahs are also thanked for trusting me with access and for general support of the project.
- Grant Beverley, Luke Strugnell and Deon Cilliers assisted with field logistics, support and company in Thabazimbi. Thank you – it would have been a lonely journey without you all.
- The Carnivore Conservation Programme team at the Endangered Wildlife Trust. You guys have been fantastic. Grant Beverley, thank you for helping me trawl through thousands of cheetah photos to identify individuals and for spending many late nights and frustrating hours trying to get the database finalised. Brendan Whittington-Jones, for always being there to bounce ideas off and for a balanced opinion. Vincent van der Merwe, for taking over the reins of the cheetah metapopulation and making a huge success of it. Derek van der Merwe, for sharing my passion for free-roaming cheetahs and wild dogs and for forging on with the farmers.
- The senior management at the Endangered Wildlife Trust, CEO Yolan Friedmann for supporting my studies, being understanding about leave to complete this thesis and for keeping the pressure on for finalisation. Harriet Davies-Mostert who was always keen to throw data analysis ideas around, help me learn about wild dogs and share a glass or two of wine to make it all better.
- My family and friends, who have not heard the end of this, have had to reschedule things around my travels and studies and who have been horribly neglected. Thank you for still being there. My mom, Geraldine Wilkins, for supporting me in my career choice when you would have preferred a ballerina! My husband, Daniel thank you for understanding and support. My china Shannon McKay for helping me train my Staffie, Diesel, to sniff for cheetah scat when I was over looking for the stuff and who has always cheered me on. “The Aunties” Melanie and Lee-Anne your support is invaluable. My friend, Jeanetta Selier, for being in the same boat!
- Liam – the ultimate deadline. Thank you.

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CHAPTER 1: General Introduction

Large carnivores play a key role in regulating terrestrial ecosystems (Estes *et al.* 2011) and removing large carnivores can cause effects that cascade through the lower trophic levels (Terborgh *et al.* 2002; Ripple & Beschta 2004; Estes *et al.* 2011), for example mesocarnivore release has caused changes in predation patterns that affect prey populations (Berger *et al.* 2008) and habitats (Estes *et al.* 2011).

Despite this, the geographic range and density of most large carnivore species are declining globally due to anthropogenic factors (Weber & Rabinowitz 1996; Treves 2009). Large carnivores are particularly difficult to conserve because they often come into conflict with humans (e.g. Woodroffe *et al.* 2007), have large ranges (e.g. Marnewick & Cilliers 2006) and normally occur at low densities (e.g. Fuller *et al.* 1992). Furthermore, formal protected areas are generally ineffective in conserving large carnivores because they are vulnerable to edge effects and stochastic processes that act on small populations (Woodroffe & Ginsberg 1998) and because the areas are general too small to maintain viable populations of large carnivores. Therefore effective large carnivore conservation needs to be addressed at a landscape level rather than at a local reserve or park level.

This is particularly true for cheetahs *Acinonyx jubatus* and African wild dogs *Lycaon pictus* that are two of the widest ranging carnivores and as such require large areas for their survival (IUCN/SSC 2007). Both species have undergone extensive declines in their geographic range in southern Africa with resident populations of wild dogs occurring in only 12% of their former range and cheetahs in 21% (IUCN/SSC 2007). While formal protected areas are important for cheetah and wild dog conservation, a large proportion of the populations of both species occur outside of protected areas (IUCN/SSC 2007).

A key threat to cheetah and wild dog survival in South Africa is conflict with land owners (Marnewick *et al.* 2007; Thorn *et al.* 2013). Cheetahs particularly have most of their distribution range outside protected areas which makes them vulnerable to persecution (Marnewick *et al.* 2007). South Africa has few large protected areas that can hold self-sustaining populations of cheetahs and wild dogs. The Kruger National Park is the stronghold for cheetah and wild dog conservation and Kgalagadi National Park is of secondary importance for cheetahs. Several smaller national parks and provincial protected areas are present throughout South Africa, but their effectiveness in contributing to conserving cheetahs and wild dogs is unknown.

To date, national level conservation action for both species has been guided by the National Action Plan for Cheetahs and African Wild Dogs (Lindsey & Davies-Mostert 2009) but implementation has been done geographically on an ad-hoc basis. The benefits of these conservation actions could be maximised and resources more effectively utilised if key areas important for cheetahs and wild dogs can be identified for concentrated effort (e.g. Karanth *et al.* 2012) but conservation planning is limited by a lack of information, at national and provincial levels.

Currently, conservation action for cheetahs and wild dogs is geographically focussed on three key areas due to the different challenges and management interventions required: 1) free roaming populations outside of protected areas, 2) the Kruger National Park and 3) reintroduced populations in fenced reserves. Each area provides unique opportunities and challenges for conservation of these species and as such is discussed separately here.

1.1 FREE ROAMING POPULATIONS

1.1.1 Description of study area

The land use system in South Africa is unique in Africa in that land and wildlife can be privately owned and utilized for commercial purposes (Benson 1991; Lindsey *et al.* 2009). This has resulted in more than 100 000 km^2 of land being fenced to form more than 5 000 wildlife ranches that are stocked with various wildlife species for the main purpose of sport hunting (Eloff 2002). Wildlife is therefore consumptively utilized for economic gain by landowners, which provides concomitant habitat conservation (Hayward 2005). Lions *Panthera leo* and spotted hyaenas *Crocuta crocuta* have been extirpated from most ranchlands in South Africa, but leopards *Panthera pardus*, cheetahs, brown hyaenas *Hyaena brunnea* and African wild dogs still persist (Wilson 2006). The Thabazimbi district in Limpopo is a typical wildlife ranching area and here, the mean ranch size is 18 km^2 and the ranches are enclosed in game fencing, which is not predator proof (Wilson 2006), allowing predators to move either under or over the fences.

In some areas, cheetahs and wild dogs may fare better outside than inside conservation areas, owing to the lack of intra-guild competition (Laurenson 1995; Mills & Gorman 1997). Additionally, prey species on wildlife ranches are often maintained at artificially high densities (van der Waal & Dekker 2000) by means of supplementary feeding and water provisioning, which further improves conditions for cheetahs and wild dogs in these areas. Populations on ranches may also provide important connectivity with cheetah and wild dog populations in other parts of southern Africa as these populations are contiguous and form the southernmost extent of the distribution range for cheetahs and wild dogs on the continent.

1.1.2 Key threats to free roaming populations of cheetahs and wild dogs

While ecological conditions may theoretically favour cheetahs and wild dogs outside reserves, conflict with landowners frequently occurs owing to the perceived threat that carnivores pose to ungulate populations and domestic stock (Woodroffe & Ginsberg 1998; Marker 2002; Wilson 2006). This is exacerbated when ranchers stock expensive rare or endangered antelope or rare colour variations, e.g. black impala *Aepyceros melampus* or white blesbok *Damaliscus pygargus phillipsi* (unpublished data). This often results in landowners illegally removing cheetahs and wild dogs from their land (unpublished data). Cheetahs are mostly removed through shooting or live capture. Because cheetahs have a financial value in the captive market, they are reportedly (Marnewick *et al.* 2007) sold from the free ranging population into captive facilities. Wild dogs are mostly removed through shooting as they are difficult to trap in cages. Additionally, wild dogs are susceptible to being killed on roads and in snares. Conserving carnivores outside protected areas is challenging because of scale of the areas, the multiple stakeholders involved and the difficulties associated with policing and enforcement.

A compensation–relocation programme for 'problem' cheetahs was initiated in South Africa by landowners, conservation officials and biologists. This programme allowed landowners to legally capture 'damage-causing' cheetahs on their property for relocation into fenced protected areas. Landowners were compensated for the live cheetah. This ran from 2000 until 2006 when it was terminated (Marnewick *et al.* 2009; see chapter 5). This compensation–relocation programme was not initiated as a long-term solution to conflict, but rather as a short-term method of buying time while other mitigation measures, such as education, improved livestock husbandry practices, research and non-lethal damage prevention were implemented. The project has since been terminated because it was felt that enough time had passed to allow for the implementation of mitigation measures, some landowners were trapping specifically for the financial gain, the impact on the free roaming population was of concern and removals did not appear to be alleviating the conflict (unpublished data).

1.1.3 What is known about free roaming populations of cheetahs and wild dogs

The distribution of cheetahs and wild dogs in South Africa is well known though field studies and expert opinion (Friedmann & Daly 2004; Lindsey *et al.* 2005, Marnewick *et al.* 2007). But their status is generally poorly understood outside protected areas. Cheetah numbers are only known for a few key areas in Limpopo from questionnaire surveys (Wilson 2006) and camera trapping (Marnewick *et al.* 2007); while wild dogs have been surveyed through questionnaires (Lindsey *et al.* 2005) and as well as reports to conservation NGOs (Endangered Wildlife Trust unpublished data; see chapter 2)

Generally attitudes towards cheetahs and wild dogs are negative (Lindsey *et al.* 2005; Wilson 2006; Thorn *et al.* 2013) and they are often shot to protect livestock or game species (Thorn *et al.* 2013). However, wild dogs hold potential as ecotourism attractions and the income obtained through ecotourism related ventures can offset the costs of conserving dogs outside protected areas (Lindsey *et al.* 2005).

The use of space and thus impact of cheetahs and wild dogs on a particular property is only known though one limited study on cheetahs (Marnewick & Cilliers 2006). Areas of suitable and connecting habitat are unknown making it difficult to guide conservation interventions outside protected areas in geographically important areas. As a result, interventions are often centred in the areas where the landowners complain the most and not necessarily in the most important areas.

1.1.4 Key gaps in knowledge on free roaming populations of cheetahs and wild dogs

In this thesis I attempt to address some of the gaps in knowledge related to cheetahs and wild dogs outside of protected areas that will help with conservation planning and interventions. The range use of cheetahs outside protected areas is addressed in chapter 4. This shows that cheetahs move over large areas despite the lack of intraguild competition and the high density, sedentary prey base.

Suitable habitat and connectivity for cheetahs and wild dogs outside protected areas are evaluated in chapter 2. This aids in spatial conservation planning for both species ensuring that conservation interventions can now be done in areas of key conservation value to both species.

A gap remains in our knowledge of both species in that population estimates are unknown and habitat selection is not understood outside protected areas. Further studies are required to address these gaps.

1.2 THE KRUGER NATIONAL PARK

1.2.1 Description of study area

The 21 353 km^2 Kruger National Park (hereafter Kruger) and its neighbouring conservation areas represent an important core area for cheetah and wild dog conservation on South Africa (Woodroffe *et al.* 2004; Lindsey *et al.* 2005). There is a decrease in gradient from south to north in prey biomass, density of roads and infrastructure, and tourist volumes. As South Africa's largest protected area that holds the only potentially viable, unmanaged populations of cheetahs and wild dogs, it is important to understand both the status and trends of the populations of both species. While the park is large in size, cheetahs and wild dogs are wide ranging and often leave the borders of the park where they are vulnerable to anthropogenic threats.

1.2.2 Key threats to cheetahs and wild dogs in the Kruger National Park

The narrow north-south orientation of the Kruger National Park, makes it vulnerable to edge effects and makes it easier for cheetahs and wild dogs to leave the boundaries of the park. While edge effects are seldom directly responsible for population declines, they may reduce chances of recovery following disturbances (Woodroffe & Ginsberg 1998) particularly where the populations are small in relation to the scale of their movements (Woodroffe *et al.* 2004), as in cheetahs and wild dogs.

1.2.3 What is known about cheetahs and wild dogs in the Kruger National Park

The wild dog and cheetah populations in Kruger have been monitored in various ways since 1964 when the parks register system to deduce an estimate of 335 wild dogs and 263 cheetahs present in the park (Pienaar 1969). In 1980 an estimate of more than 70 wild dogs was given for the southern section of the park using direct observations (Reich 1981). Thereafter wild dog estimates were obtained using photographic surveys in 1989 (Maddock & Mills 1994), 1994/5 (Wilkinson 1995), 1999/2000 (Davies 2000), 2004/5 (Kemp & Mills 2005) and 2008/9 (Marnewick & Davies-Mostert 2012). Cheetah census data were obtained from photographic surveys in 1990/1 (Bowland 1994), 2004/5 (Kemp & Mills 2005) and 2008/9 (Marnewick & Davies-Mostert 2012). All photographic surveys gave a population estimate of the minimum number of animals alive on 1 January of the survey period (Maddock & Mills 1994). Results showed that estimated wild dog numbers declined from 434 in 1994/5 to 132 in 2008/9, and cheetah numbers are low with 172 estimated between 1990/1 and 2008/9. The drivers of the decline in wild dogs numbers is unknown and currently under investigation.

The home range and habitat use of cheetahs in Kruger has been studied (Broomhall *et al.* 2009) as well as factors affecting the density and distribution of wild dogs (Mills & Gorman 1997).

1.2.4 Key gaps in knowledge on populations of cheetahs and wild dogs in the Kruger National Park

While the Kruger cheetah and wild dog numbers have been monitored using minimum counts through citizen science surveys, there have been no attempts to obtain more statistically robust population estimates with confidence intervals. There has also been no attempt to develop effective monitoring protocols. These issues are addressed in chapter 3.

1.3 FENCED RESERVES

1.3.1 Description of study area

Because cheetahs and wild dogs have been extirpated from most of their historical range in South Africa several reintroductions have been done into smaller fenced protected areas (Davies-Mostert *et al.* 2009; Marnewick *et al.* 2009). In these small, isolated populations dispersals between reserves have to be simulated through a managed metapopulation approach (Davies-Mostert *et al.* 2009). This is done through management interventions to ensure demographic and genetic integrity of the population.

These reserves provide an important population of cheetahs and wild dogs that are protected outside of the Kruger National Park. However, management of these populations is intensive, expensive, involves long-term commitments and is challenging.

Wild Dogs have been reintroduced into small fenced reserves across South Africa for more than 30 years. This was partially driven over the last 10 years by the observed decline in wild dog numbers in Kruger and guided through a wild dog Population and Habitat Viability Analysis (PHVA) (Mills *et al.* 1998). Currently over 150 wild dogs occur in 16 packs in nine reserves throughout South Africa (Wild Dog Advisory Group of South Africa unpublished data). These reintroductions are carried out through continuous, proactive liaison with conservation community and commercial stakeholders by the KwaZulu-Natal Wild Dog Advisory Group (KZN-WAG) and the national Wild Dog Advisory Group of South Africa (WAG-SA) (www.wagsa.org).

Cheetahs have been reintroduced into 52 reserves for tourism and ecological reasons and currently more than 300 cheetahs occur in fenced reserves in South Africa (EWT unpublished data). These cheetahs were sourced from the free-roaming populations in South Africa (see above on the free roaming population) and Namibia and the reintroductions and their management were undertaken haphazardly with no larger conservation plan in mind. This has in some cases resulted in in-breeding and local over-populations. This limits the conservation potential of these cheetahs and reserves. A cheetah PHVA (Lindsey *et al.* 2009) identified the need for a national management plan for these cheetahs to attempt to maximise the conservation benefit of these small isolated populations. This is currently in the early stages of implementation.

While conserving cheetahs and wild dogs in small fenced reserves may not seem like the ideal way forward for conservation, it does play a role in the South African context. Both species have been extirpated from large areas of South Africa and these reintroductions are the only way to develop populations on these reserves. Similar strategies are in place for black rhinoceroses *Diceros bicornis* and a national management plan is currently being developed for lions in small fenced reserves. Recently this management reigime for lions has shown to be effective in that fenced reserves can maintain lions at near the upper limits of their potential densities (Packer *et al.* 2013a). While the conservation benefit of fenced reserves is debated (Creel *et al.* 2013, Packer *et al.* 2013b) and it is clear that fenced popualtions are not the answer in all situtations. In some areas, however, this is an effective management regime that allows for populations of carnviores to exist in areas where they would otherwise be absent.

1.3.2 Key threats to cheetahs and wild dogs in fenced reserves

Due to the restricted size of fenced protected areas, each reserve can only hold a small population of cheetahs or wild dogs (e.g. 4-10 cheetahs and one pack of wild dogs). Small subpopulations are vulnerable to extinction through stochastic processes (Lande 1988) and large ranging carnivores are even more vulnerable to extinction as they often leave the confines of reserves and come into conflict with humans (Woodroffe & Ginsberg 1998). This means that each subpopulation of animals inside a reserve is highly susceptible to extinction. While localised extinction is a natural process in metapopulations, in the managed metapopulation it complicates management and makes the population as a whole less stable. Additionally, because large carnivores are management intensive and expensive to hold on reserves, the success of the project is often related to the individual manager or owner and the amount of support they give the project. As a result, changes in management or ownership can result in the removal of the subpopulation of cheetahs or wild dogs.

Fenced reserves often keep lions at high densities (Creel *et al.* 2013) which can compromise the success of cheetah and wild dog reintroductions. In some reserves snaring is a threat although this is localised. The high value of cheetahs on the captive market often results in cheetahs being sold from metapopulation reserves into the captive breeding industry and being lost to conservation.

1.3.3 What is known about populations of cheetahs and wild dogs in fenced reserves

Wild dogs in fenced reserves have been well studied including the post-release use of space and prey (Andreka *et al.* 1999; Krüger *et al.* 1999; Van Dyk & Slotow 2003), demography of reintroduced populations (Maddock 1999; Somers *et al.* 2008) and the role of social structure in reintroduction success (Gusset *et al.* 2006; Somers *et al.* 2009; Graf *et al.* 2009). Demographic models have been used to evaluate and plan reintroductions (Gusset *et al.* 2009) and reintroduction attempts have been critically evaluated (Gusset *et al.* 2008a) as has the entire managed metapopulation strategy (Davies-Mostert *et al.* 2009).

Attitudes of various stakeholders towards reintroductions of wild dogs have been assessed and found that communities bordering parks are often negative towards wild dogs (Gusset *et al.* 2008b) which can have consequences for the fate of dogs dispersing from parks. Thus routes used by wild dogs dispersing from protected areas have been identified to aid in developing strategies to increase survival of dispersers (Whittington-Jones 2011). Isolation by fences is detrimental to the survival of wild dogs unless periodic translocations are done between populations (Somers *et al.* 2012) even though inbreeding avoidance is effective even in small isolated populations (Becker *et al.* 2012).

Cheetahs in fenced reserves are less studied than wild dogs with most studies focussing on the use of space and prey in individual reserves or clusters of reserves (e.g. Bissett 2004; Bissett & Bernard 2007; Bissett 2007). Indicative of the management intensity required to maintain cheetahs and wild dogs on fenced reserves, effort has been made to quantify the minimum amount of space and prey required to house both species in closed systems.

Fenced reserves as small as 131 km^2 with a high prey density can supply enough prey to meet the energetic requirements of wild dogs; given the prey profile related to prey abundance (Lindsey *et al.* 2004). The minimum reserve size required to hold a pack of wild dogs is known for different regions of South Africa and is primarily dependent on the prey biomass of the area (Lindsey *et al.* 2004). Methods have also been devised to predict the carrying capacity of individual reserves for cheetahs and wild dogs through the relationship between preferred prey species and weight range and population densities of predator (Hayward *et al.* 2007). Wild dogs are likely to be limited by factors other than prey density (Pole 1999) but the minimum reserve size approach offers a good starting point for planning reintroductions of wild dogs.

The prey base in fenced reserves in South Africa can support a population of 10 cheetahs on reserves between 48–466 km^2 in the absence of lions, with larger areas needed when lions and other competing carnivores are present (Lindsey *et al.* 2011). Achieving long-term viability of the cheetah population in fenced reserves is challenging due to the large space requirements needed to maintain sub-populations of cheetahs without exceeding the capacity of the reserve (Lindsey *et al.* 2011).

The challenge with cheetahs and wild dogs in fenced reserves is now to manage these subpopulations under one managed metapopulation to ensure long-term genetic and demographic sustainability. While this has largely been managed for wild dogs, for cheetahs this process is in its early phases and is presented with many challenges.

1.3.4 Key gaps in knowledge on populations of cheetahs and wild dogs in fenced reserves

Identification of new reserves for both species is done on an availability basis in what is considered historical distribution range, without the luxury of prior spatial planning. A better understanding of suitable habitat and connectivity can aid in guiding these reintroductions into areas that are suitable and that could in the future allow for natural connectivity to be developed between these small isolated populations. These areas have been identified through ecological niche models and circuit flow models in Chapter 2. Additionally, the survival of reintroduced cheetahs is quantified in Chapter 5.

This thesis aims to address the above mentioned gaps in knowledge on cheetahs and African wild dogs in South Africa. The various scales at which the research was done and the different study areas ensure that cheetah and wild dog conservation issues are tacked from various angles from localised on-the-ground action to national-level conservation planning. A variety of data types from various sources are used to answer pertinent questions that make a meaningful contribution to the conservation of cheetahs and African wild dogs.

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CHAPTER 2: Habitat suitability and connectivity for cheetahs *Acinonyx jubatus* and African wild dogs *Lycaon pictus* in South Africa

Marnewick, K., Jackson, C.R., Dalerum, F. Somers, M.J. & Swanepoel, L.H.

For submission to Biological Conservation

2.1 ABSTRACT

Despite large carnivores playing an important role in regulating terrestrial ecosystems, their global range and density continue to decline due to anthropogenic threats. Cheetahs *Acinonyx jubatus* and African wild dogs *Lycaon pictus* have experienced large decreases in their ranges and numbers and neither are limited to protected areas. In South Africa, conservation planning for these two most threatened large carnivores is hampered by a lack of national-level information on suitable habitat and connectivity. Ecological niche models were used in MaxEnt and current flow models in Circuitscape to; 1) quantify current suitability habitat for cheetahs and wild dogs within South Africa and to identify important areas for their conservation and assisted range expansion; 2) identify important areas of connectivity between suitable habitat patches and 3) evaluate how effective the current protected network is in conserving suitable habitat for cheetahs and wild dogs. I found that a greater proportion of South Africa had suitable habitat for wild dogs than cheetahs. Overall about 21 410km^2 of South Africa had suitable habitat for both species. While the Kruger National Park and its bordering reserves were important for conserving suitable habitat for both species, the rest of the protected area system in South Africa was ineffective in capturing suitable habitat for both species. Through connectivity analysis I identified important areas of connectivity in the Limpopo province, along the western boundary of the Kruger National Park and in the Eastern Cape. Key areas for conservation action, range expansion and reintroduction included areas of Limpopo, KwaZulu-Natal and the Eastern Cape Provinces. Dispersal areas between fenced populations were identified that could allow for decreased management intensity and increased long-term sustainability of small isolated populations of both species.

2.2 INTRODUCTION

2.2.1 Conserving large carnivores

Large carnivores play a key role in regulating terrestrial ecosystems (Estes *et al.* 2011) and removing large carnivores can cause effects that cascade through the lower trophic levels (Terborgh *et al.* 2002; Ripple & Beschta 2004; Estes *et al.* 2011). For example the removal of apex predators can facilitate a mesocarnivore release that can cause changes in predation patterns affecting prey populations and habitats (Berger *et al.* 2008; Estes *et al.* 2011), which can have consequences for biodiversity.

Despite this, the geographic range and density of most large carnivore species are declining globally due to anthropogenic factors (Weber & Rabinowitz 1996; Treves 2009). Large carnivores are particularly difficult to conserve because they often come into conflict with humans (e.g. Woodroffe *et al.* 2007a), have large ranges (e.g. Marnewick & Cilliers 2006) and normally occur at low densities (e.g. Fuller *et al.* 1992). Furthermore, formal protected areas are generally ineffective in conserving large carnivores because they are vulnerable to edge effects and stochastic processes that act on small populations (Woodroffe & Ginsberg 1998). Effective large carnivore conservation therefore needs to be addressed at a landscape level rather than at a local reserve or park level.

This is particularly true for cheetahs *Acinonyx jubatus* and African wild dogs *Lycaon pictus* that are two of the widest ranging carnivores and as such require large areas for their survival (IUCN/SSC 2007). Both species have undergone extensive declines in their geographic range in southern Africa with resident populations of cheetahs occurring in only 21% of their former range and wild dogs 12% (IUCN/SSC 2007). While formal protected areas are important for cheetah and wild dog conservation, a large proportion of the populations of both species occur outside of protected areas (IUCN/SSC 2007).

2.2.2 The South African Context

In South Africa, conservation planning for cheetahs and wild dogs is limited by a lack of information, at national and provincial levels, on which areas are important and which should be prioritised. Understanding habitat suitability and connectivity in South Africa at a country scale would help with several aspects of conservation planning including: land use planning, conflict mitigation and identification of reintroduction and range expansion sites. To date the large carnivore guild has not been considered in this planning. As both cheetahs and wild dogs are wide ranging, occur at low densities and face similar threats, it is feasible to include both species under one conservation plan (e.g. South African Action Plan Cheetahs and African Wild Dogs [Lindsey & Davies-Mostert 2009] and Regional Conservation Strategy for the Cheetah and African Wild Dog in Southern Africa [IUCN/SSC 2007]). Additionally, owing to their large space requirements, it is likely that conservation plans for these two species will benefit other taxa.

A key threat to cheetah and wild dog survival in South Africa is conflict with land owners (Marnewick *et al.* 2007; Lindsey & Davies-Mostert 2009; Thorn *et al.* 2013). Cheetahs particularly have most of their distribution range outside protected areas which makes them vulnerable to persecution (Marnewick *et al.* 2007). South Africa has few large protected areas that can hold self-sustaining populations of cheetahs and wild dogs. The Kruger National Park is the stronghold for cheetah and wild dog conservation and Kgalagadi National Park is of secondary importance for cheetahs. Several smaller national parks and provincial protected areas are present throughout South Africa, but their effectiveness in contributing to conserving cheetahs and wild dogs is unknown.

Because cheetahs and wild dogs have been extirpated from most of their historical range in South Africa several reintroductions have been done into fenced protected areas (Davies-Mostert *et al.*

2009; Marnewick *et al.* 2009). These small isolated populations are managed artificially by simulating dispersals between reserves as a managed metapopulation (Davies-Mostert *et al.* 2009). Identification of new reserves for both species is generally done on an availability basis in what is considered historical distribution range, without the luxury of prior spatial planning. A better understanding of suitable habitat and connectivity can aid in guiding these reintroductions into areas that are suitable and that could in the future allow for natural connectivity to be developed between these small isolated populations.

To date national level conservation action for both species has been guided by the National Action Plan for Cheetahs and African Wild Dogs (Lindsey & Davies-Mostert 2009) but implementation has been done geographically on an ad-hoc basis. The benefits of these conservation actions could be maximised and resources more effectively utilised if key areas important for cheetahs and wild dogs can be identified for concentrated effort (e.g. Karanth *et al.* 2012).

In this study I developed maximum entropy models in MaxEnt (Phillips *et al.* 2006) and current flow models in Circuitscape (McRae & Shah 2009) to 1) investigate current suitability of habitat for cheetahs and wild dogs within South Africa to identify important areas for their conservation and assisted range expansion through the managed metapopulation approach; 2) identify important areas of connectivity between suitable patches of habitat and 3) evaluate how effective the current protected area network is in conserving suitable habitat for cheetahs and wild dogs.

2.3 METHODS

2.3.1 Habitat suitability modelling

The maximum entropy approach to species distribution modelling was used to determine habitat suitability and current potential distribution of cheetahs and wild dogs in South Africa using MaxEnt 3.3.0 (http://www.cs.princeton.edu/~schapire/maxent/; Phillips *et al.* 2006). MaxEnt and its performance are described in detail by several authors (e.g. Soberón & Peterson 2005, Phillips & Dudík 2008, Elith *et al.* 2010), and was chosen because it performs well (Elith *et al.* 2006) and it is not affected by correlated environmental variables (Phillips *et al.* 2006; Elith *et al.* 2010), the number of occurrence points (Elith *et al.* 2006, Wisz *et al.* 2008), or by spatial error (Graham *et al.* 2008). These factors are important when modelling for species that only occupy part of their potential habitat (Engler *et al.* 2004) such as cheetahs and wild dogs in South Africa.

2.3.2 Occurrence records

I collected 845 cheetah and 792 wild dog occurrence records from the following sources (Figure 2.1):

1. questionnaire surveys on the western boundary of the Kruger National Park (Watermeyer 2012)
2. questionnaire surveys outside protected areas on Limpopo and North West Provinces between 2000 and 2012 (KM unpublished data);
3. a register of sightings of wild dogs outside protected areas between 2009-2011 maintained by the Endangered Wildlife Trust on behalf of the Wild Dog Advisory Group of South Africa (WAG-SA www.wagsa.org.za);
4. sightings records from the 2009 photographic survey in the Kruger National park (Marnewick *et al.* 2014);
5. Cybertracker records from the Kruger National Park (Data supplied by SANParks)
6. tourist sightings in the Kgalagadi National Park (M.G.L Mills unpublished data)

No occurrence data from reintroduced populations were included. Each data point included a GPS coordinate, date and spatial error and was projected into an Albers Equal Area projection. GPS locations with a spatial error of 18 km^2 and smaller were used. All occurrence records were combined and projected into UTM Zone 35.

2.3.3 Predictor variables
I used 11 environmental predictor variables that were shown to be important for large carnivores (Swanepoel *et al.* 2013) as the variables specific to cheetahs and wild dogs are unknown. These included: cattle density, distance from roads, distance from villages, human density, small ruminant density, distance from rivers, a digital elevation model, topographic roughness, grazing capacity, normalised difference vegetation index and land cover. Data for all environmental layers are given in Table 2.1. All environmental layers were scaled to cell size of 3.366 km X 3.366 km using ArcMap10 (ESRI 2010) and projected into Albers Equal Area with two standard parallels at 19.00 and 31.00 with a geographic coordinate system of WGS1984. This scale was felt to be reasonable given that both species have home ranges much larger than the predictor variable resolution. Additionally, the resolution of the presence data was unlikely to be at a finer scale than the predictor variables because much of the data were collected from questionnaires and tourist reports.

2.3.4 MaxEnt model
MaxEnt was run using a random sample of 30% of the location points for model training. The models were run for 500 iterations, using 10 000 random background points, and default regularization parameters as these are reported to perform well (Phillips & Dudík 2008). While the extent of the background subsample can affect the MaxEnt output (Vanderwal *et al.* 2009), the background sample was not restricted as both species are habitat generalists. The accuracy of the MaxEnt models was

measured using the area under curve (AUC) of the receiver operating characteristic curves (ROC) and the regularized model gain (Fielding & Bell 1997; Phillips *et al.* 2006; Phillips & Dudík 2008).

Figure 2.1: Latest published distribution of cheetahs and wild dogs (shown in grey) in South Africa with presence points used for MaxEnt modelling (black dots). Cheetah distribution from Marnewick *et al.* (2007), wild dog distribution from Friedmann & Daly (2004).

Cheetah

Wild dog

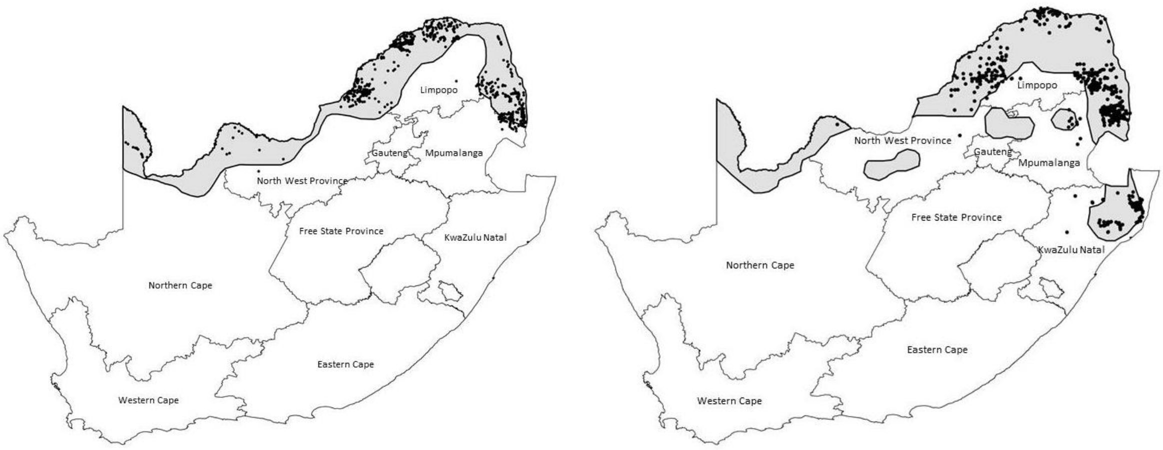

Table 2.1: Environmental layers used for MaxEnt modelling to produce habitat suitability maps for cheetahs and African wild dogs in South Africa.

Environmental variable	Description	Unit or classes	Data source	Predicted effect on habitat suitability
Cattle density	Number of cattle / km^2	0-701 / km^2	Food and Agriculture Organisation on the United Nations (2005) www.fao.org	More cattle, decreased suitability due to conflict potential
Distance from rivers	Euclidian distance from rivers and streams	0-50 km	Created with Euclidian distance tool in Spatial Analyst using drainage data from Department of Land Affairs and Department of Water Affairs and Forestry, RSA	Nearer rivers, more suitable for wild dogs due to preferred prey in riparian zone. Further from rivers, more suitable for cheetahs due to preferred prey habitat.
Distance from roads	Euclidian distance from primary and secondary roads	0-500 km	Created with Spatial Analyst using road data from Department of Land Affairs, RSA	Further from roads, more suitable due to less disturbance, but roads often used for travelling by both species.
Distance from villages	Euclidian distance from villages	0-500 km	Created with distance tool in Spatial Analyst using village data from Department of Water Affairs and Forestry (DWAF) (2006), RSA	Further from villages, more suitable due to decreased disturbance and conflict potential.
Grazing capacity	Potential biomass available for grazing animals in hectares (ha) per animal unit (AU)	1-100 ha / AU	Institute for Soil, Water and Climate, National Agricultural Research Council (ARC), RSA	Higher more suitable as higher biomass likely supports higher prey density.
Human density	Number of people per km^2	0-9950 / km^2	Statistics South Africa (2001) www.statssa.gov.za, Accessed on FUNDISA Disk	Lower, more suitable due to decreased disturbance and conflict potential.
Normalised Difference Vegetation Index (NDVI)	Measure of vegetation greenness including plant growth, cover and vigour	Micrometers	Moderate Resolution Imaging Spectroradiometer (MODIS)	Higher more suitable as higher biomass likely supports higher prey density.
SA Digital Elevation Model (SA-DEM)	Altitude in meters above sea level	0-3322 m	Shuttle Radar Topography Mission (SRTM) www2.jpl.nasa.gov/srtm/Africa_radar_images.htm	Unknown effect, high altitudes unlikely to be suitable due lower biomass potential, expect a range in the lower altitudes to be suitable.
SA Land Cover	Land Cover Classes	6 classes	SA Land Cover Database (2001) www.arc.gov.za	Data are categorical; expect land covers associated with prey presence to be more suitable. Highly modified areas, large water sources, etc to be less suitable
Small ruminant density	Number of sheep and goats per km^2	0-3613 / km^2	Food and Agriculture Organisation on the united Nations (2005) www.fao.org	More cattle, decreased suitability due to conflict potential. Possibility of increased suitability due to prey availability.
Topographic roughness	Measure of topographic ruggedness or roughness	1 (level) – 2 (extremely rugged)	Created with Surface Tools (Jennes 2010). DEM surface Tool for Arc GIS v 2.1.254, Jennes Enterprises using the SA-DEM data	Expect a range in the lower index to be suitable.

2.3.5 Determining habitat suitability

The total amount of suitable habitat for each species was determined using the logistic output and a 10% percentile threshold was used to determine suitable and unsuitable habitat. The 10 percentile training presence was used and this assumes that spatial error affects at least 10% of the presence points for cheetahs and wild dogs (Raes *et al.* 2009). The area of habitat suitable for both species combined was determined by calculating the intersect of the habitat suitability maps of each species i.e. the intersect of the 10% training presence maps for cheetahs and wild dogs.

2.3.6 Modelling habitat connectivity

Modelling habitat connectivity is important for conservation planning (Rouget *et al.* 2006, Beier *et al.* 2008) because habitat corridors allow for movement of animals and genes. Circuit theory attempts to quantify the overall resistance of the landscape to movement by the animal (McRae 2006, McRae *et al.* 2008). Connectivity between focal clusters was modelled using circuit theory in Circuitscape V 3.5.8 (McRae & Shah 2009). Circuitscape uses a resistance layer and focal nodes to assess connectivity across the landscape. The output from the MaxEnt model was used as a resistance layer for Circuitscape as it is assumed that more suitable habitat provides less resistance to movement than less suitable habitat.

The MaxEnt output raster maps were then used to define focal nodes for Circuitscape input by reclassifying them into five habitat classes using Jenks natural breaks. Class 1 represented the most suitable habitat and class 5 the least suitable habitat. Habitat class 1 (the most suitable) was extracted for both cheetahs and wild dogs and used to represent focal nodes for each species. This ensured that only the most suitable habitat was identified as possible sources for the connectivity model.

The focal nodes, together with the habitat suitability maps from MaxEnt (i.e. the original model output not only using the 10 percentile training presence), were used as inputs into Circuitscape to investigate landscape resistance to movement of cheetahs and wild dogs. The model was run using all to one source/ground modelling mode with all other settings on default (focal regions, habitat data specified per cell conductances, eight neighbour cell connection scheme and average resistance cell connection calculation). To attempt to identify the minimum areas required to maintain connectivity, an elimination system was used. The Circuitscape outputs were reclassified into 10 classes using Jenks natural breaks. The class with the most resistance to movement, i.e. the lowest class, was systematically removed until connectivity was visually disrupted.

2.4 RESULTS

2.4.1 Model performance and response variables

MaxEnt models for cheetahs and wild dogs performed well (Table 2.2) and the resulting outputs reflect what is expected from prior knowledge of the country. The most important response variables and their contribution to the cheetah model were land cover (36.2%; main contributing class - woodland), DEM (21.1%; areas <1000m) and small ruminant density (9.4%, density <1/km^2), while for the wild dog model it was land cover (24.1%, main contributing class - woodland), cattle density (19.7%, density <0.05/km^2) and DEM (17.8%, areas <750m) (logistic threshold cheetahs = 0.781, wild dogs = 0.856).

2.4.2 Habitat suitability for cheetahs and wild dogs

As expected, there is more unsuitable than suitable habitat for cheetahs and wild dogs in South Africa (Figure 2.2). A total of 21 410km^2 of habitat is suitable for both species in South Africa when using the 10 percentile training presence (logistic threshold cheetahs = 0.793, wild dogs = 0.864) as suitable habitat. The union of both cheetah and wild dog habitat suitability maps indicated that the northern, eastern and western sections of Limpopo province are important areas in conserving both species simultaneously (Figure 2.3 Areas 1, 2, 3). The Kruger National Park is an important conservation area for cheetahs and wild dogs. The many private reserves on the western boundary of Kruger (Figure 2.3 Area 1) are well placed for conserving habitat suitable for both cheetahs and wild dogs that is contiguous with Kruger. The northern parts of Kruger are less suitable than the southern parts and this is to be expected as there is a decrease in gradient from south to north in prey biomass and rainfall (Ferreira and Funston 2010) there is also a resultant decrease in density of cheetahs and wild dogs from south to north (Marnewick *et al.* 2014). For the rest of Limpopo, the protected area network is insufficient in size and location to protect cheetah and wild dog populations that occur here naturally (Figure 2.3).

2.4.3 Habitat connectivity for cheetahs and wild dogs

Circuitscape outputs show areas of connectivity for cheetahs and wild dogs in South Africa (Figure 2.4). Important areas of connectivity are in Limpopo province, along the western boundary of the Kruger National Park and the Eastern Cape. Areas in Kgalagadi are unique to cheetahs with northern KZN being unique for wild dogs. The top nine classes of connectivity need to be retained in order to maintain connectivity. With only eight classes maintained, connectivity between the populations in the Kruger National Park and Limpopo is lost along with areas in northern KZN (Figure 2.4, circles on maps in class 7). It is important that the connectivity between Kruger, other parts of Limpopo and neighbouring countries is maintained (Figure 2.4, rectangles on maps in 8 classes) to prevent this population from becoming isolated.

Table 2.2: The performance of the MaxEnt models for cheetahs and African wild dogs in South Africa.

	Species	
Model output	Cheetah	Wild dog
Number of training samples	332	310
Regularized training gain	2.4978	2.4038
Unregularized training gain	2.9742	3.0434
Iterations	500	500
Training AUC	0.9981	0.9983
Number of test samples	142	132
Test gain	2.2463	1.7035
Test AUC	0.9527	0.9259
AUC standard deviation	0.0078	0.0108
Number of background points	10301	10280

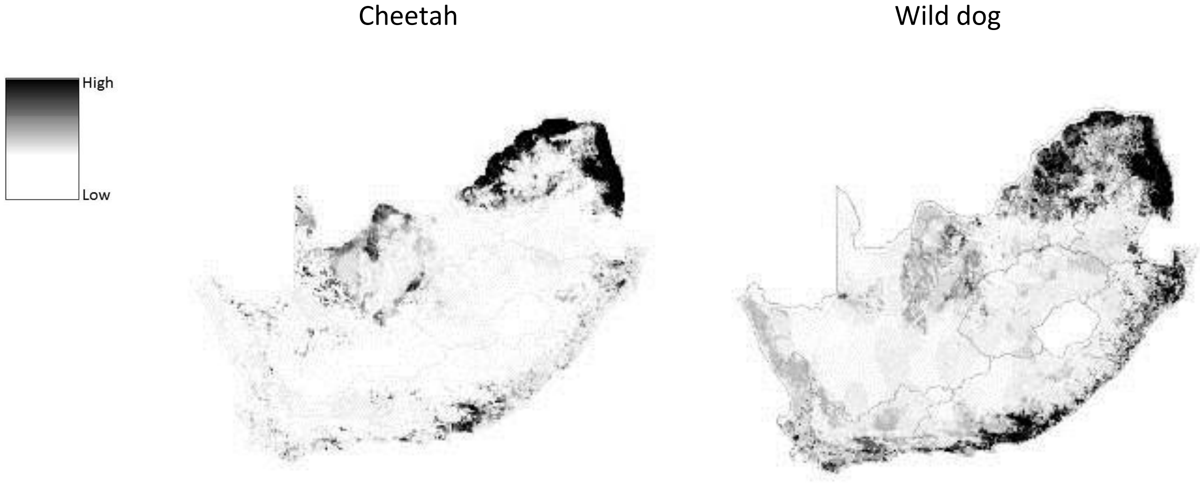

Figure 2.2: Complete habitat suitability maps from MaxEnt modelling for cheetahs and wild dogs in South Africa with no thresholds applied. Darker colours are more suitable habitat and lighter colours are less suitable habitat.

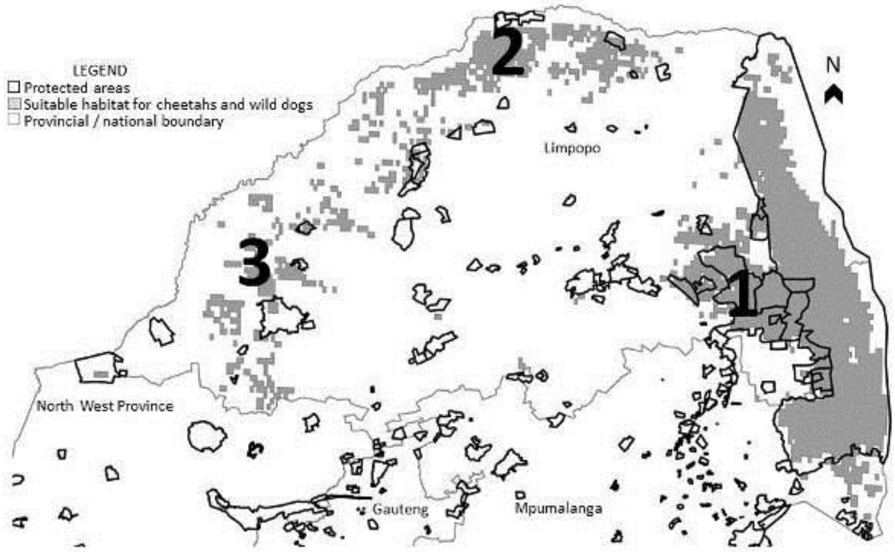

Figure 2.3: Formally protected areas in relation to suitable habitat for both cheetahs and African wild dogs (grey) from the MaxEnt habitat models defined using the 10 percentile training presence. With the exception of the Greater Kruger National Park, the protected area network is not effective in conserving habitat for these two species. Numbers denote important areas for conservation action which is discussed further in the text.

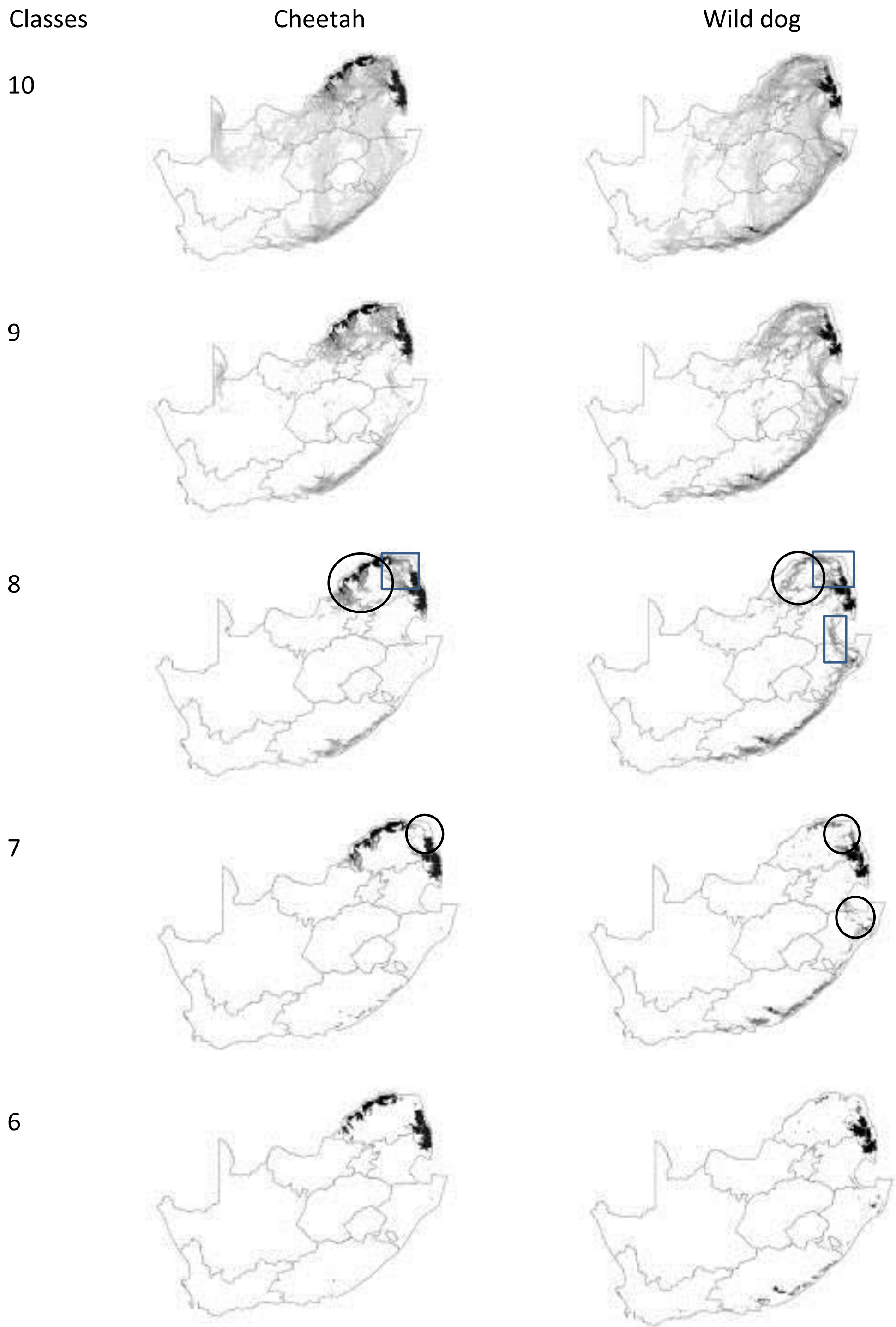

Figure 2.4: Connectivity of habitat for cheetahs and wild dogs in South Africa as derived from Circuitscape. The output is reclassified into 10 classes for each species then the lowest classes are removed consecutively to identify at which stage connectivity is lost. The minimum required to still maintain important connectivity is eight classes. Rectangles in class 8 show important areas of connectivity between the Kruger national Park and other populations. Circles in class 8 show important areas of connectivity for the unprotected populations. The circles denote important areas of connectivity that are lost if only the top 7 classes of connectivity are maintained.

2.4.4 *Implications for conservation planning*

Cheetahs and wild dogs have been reintroduced into several smaller fenced reserves (Figure 2.5). Wild dog reintroductions have been done into nine reserves all of which are placed in suitable habitat (Figure 2.5a). A key area that contains highly suitable habitat but does not yet have any reserves that support wild dogs is the Eastern Cape (Figure 2.5a, circled area). For cheetahs, reintroductions have been done in most areas that contain suitable habitat (Figure 2.5b).

Improved connectivity between these fragmented populations can improve the persistence of the managed metapopulations (Di Minin *et al.* 2013). This can be achieved through assisted dispersal between these reserves to allow for decreased management intensity and long-term increased sustainability of these populations. There are areas in Limpopo suitable for this for cheetahs (Figure 2.5d circles), but importantly an opportunity exists in KwaZulu-Natal where this can realistically be developed for both cheetahs and wild dogs (Whittington-Jones 2011) (Figure 2.5c and d broken circles).

2.5 DISCUSSION

2.5.1 *Distribution of suitable habitat*

The MaxEnt models identified areas of suitable habitat in northern and north-eastern South Africa where cheetahs and wild dogs are known to occur. Additionally, areas in the Eastern Cape and KwaZulu-Natal are also suitable even though neither species presently occurs there naturally. It is known from existing reintroduction projects that cheetahs and wild dogs do survive and breed in these areas. However, our models were not able to find any suitable habitat in the central parts of South Africa. This could be due to two reasons: 1) the occurrence records for both species are almost exclusively from the northern parts of South Africa, these areas are of lower altitude than the central areas of the country and this could be driving the model outputs and would explain why the DEM was an important response variable in the models for both species; 2) the environmental variables used were not able to detect the factor that affects distribution in this part of the country – namely conflict and the resultant killing of carnivores. Areas that are suitable for cheetahs and wild dogs have a low altitude, low livestock densities and woodland land cover type.

2.5.2 *Effect of environmental variables*

The key environmental predictors that influenced the cheetah model were land cover, the DEM and small ruminant density and for wild dogs were the land cover, cattle density and DEM. This supports

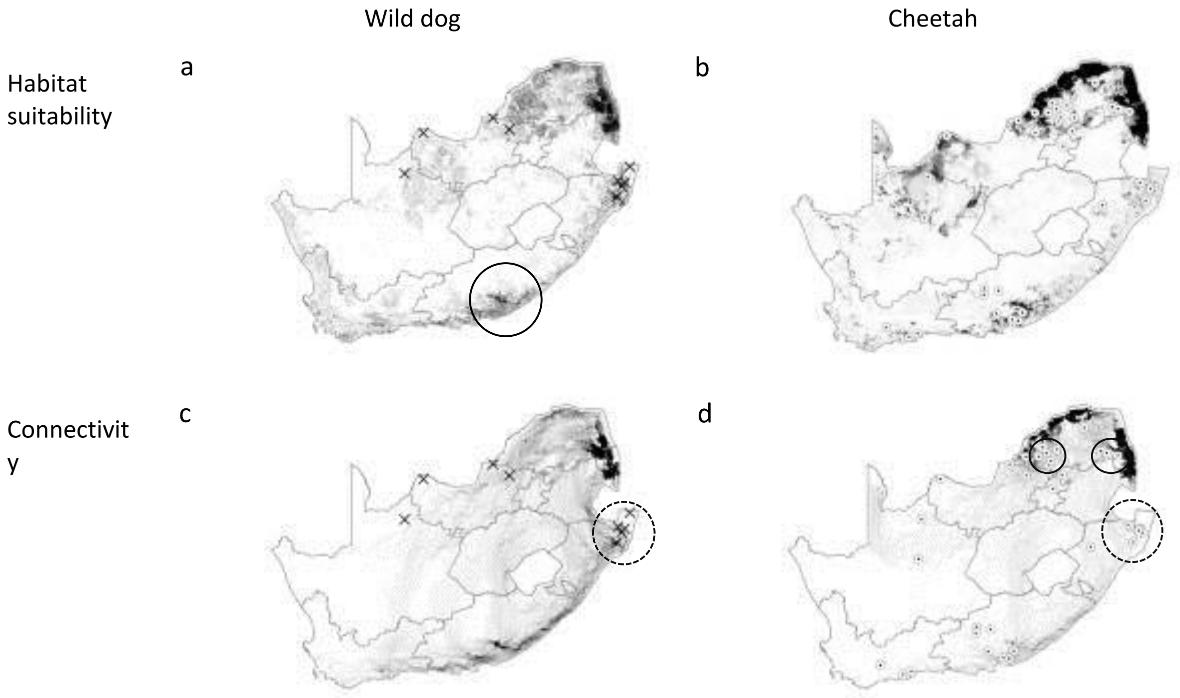

Figure 2.5: Location of small fenced reserves in South Africa where cheetahs and wild dogs have been reintroduced. Each is shown with a back ground of habitat suitability (MaxEnt output) and connectivity (Circuitscape output). The circle in map a indicates an area with suitable habitat that does not currently contain any reintroduced wild dogs. The broken circles in maps c and d indicate areas that are suitable for developing connectivity between reintroduced populations for both cheetahs and wild dogs. The circles in map d indicate areas where connectivity between reintroduced populations could be developed for cheetahs.

the assumptions above that the limited spatial distribution of the occurrence records and conflict could be affecting the ability of the models to detect suitable habitat in the central parts of South Africa. Areas with higher densities of both small and large livestock are likely to have less natural prey and experience higher conflict than areas under wildlife utilisation.

MaxEnt models do not explain how the predictor variables individually affect the habitat suitability of the modelled species. Quantifying the range and sensitivity of each predictor variable on habitat selection for cheetahs and wild dogs would be useful, this is not within the scope of this study but should be considered for future research.

Anecdotal information suggests that in South Africa the distribution of cheetahs in particular has spread further south in the last 50 years. This has been attributed to a change in land-use from cattle to wildlife ranching that provides more suitable prey for cheetahs. However, this comes paired with conflict (Thorn *et al.* 2013) that could limit the distribution of both species. In these unprotected areas, the threats to cheetahs and wild dogs that need to be mitigated include persecution, habitat fragmentation, road accidents and trade.

2.5.3 Significance for reintroductions

Because cheetahs and wild dogs have been extirpated from most of South Africa (Lindsey & Davies-Mostert 2009), there have been several reintroductions done into smaller fenced reserves. These reintroductions have been guided by reported historical distribution and the willingness of reserve management to partake in the reintroduction. However, habitat suitability should be a factor when planning reintroductions at a national level.

The Eastern Cape has areas that are suitable for both cheetah and wild dogs and several cheetah reintroductions have been done successfully into reserves in this area. However, opportunities for future wild dog reintroductions exist as the habitat is suitable and several large fenced reserves are present. Additionally, suitable habitat exists in KwaZulu-Natal, where it is known that both cheetah and wild dog introductions have been very successful (wild dogs: Somers *et al.* 2008; cheetahs: EWT unpublished data). While some reintroductions have been done into areas that our models do not show as highly suitable, they have none the less been successful at a reserve scale. This is probably due to the presence of prey and because cheetahs and wild dogs are generalist species.

These reintroduced populations of cheetahs and wild dogs are managed by artificially simulating dispersal between reserves by translocations (Marnewick *et al.* 2009, Davies-Mostert, *et al.* 2009) which is expensive, logistically challenging and requires immobilisation, transportation and artificial formation of social groups – all of which carry risks to the animals. Ideally, areas need to be developed where cheetahs and wild dogs can disperse naturally between these reintroduced populations. This is viable in areas with suitable and connecting habitat where reserves are in close enough proximity to each other for the animals to move between them. This would increase the resilience of the population (Di Minin *et al.* 2013) but would require buy in from landowners and managers who may be concerned about libel issues and animal safety outside of protected areas.

2.5.4 Connectivity and species conservation

The results of the Circuitscape modelling show several areas of connectivity in South Africa that should be maintained to ensure population connectivity between geographical areas. There are few data available on dispersal events in South Africa and it is likely that many of these areas are not useful due to potential conflict – a factor that cannot be modelled at this stage. Several long distance wild dog dispersals have been recorded between protected areas in southern Africa (Davies-Mostert *et al.* 2012) and while the actual route these wild dogs took is unknown it is likely that they used areas in Limpopo where our models show both suitable habitat and connectivity. However, no dispersals have been recorded to or from the Greater Kruger population (Davies-Mostert *et al.* 2012) despite the fact that our models show connectivity exits. This raises concern that the Kruger population may become isolated from other populations in the region and emphasises the importance of areas of suitable habitat and connectivity. While our models do show areas of suitable habitat and connectivity, one of the key limiting factors for carnivore movement is killing due to conflict. The models are not able to simulate the effect of this and future conservation planning should investigate methods of doing this.

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CHAPTER 3: Evaluating the Status of African Wild Dogs *Lycaon pictus* and Cheetahs *Acinonyx jubatus* Through Tourist-based Photographic Surveys in the Kruger National Park.

Kelly Marnewick, Sam M. Ferreira, Sophie Grange, Jessica Watermeyer, Nakedi Maputla &

Harriet T. Davies-Mostert

2014; PLoS ONE 9(1): e86265. doi:10.1371/journal.pone.0086265

3.1 ABSTRACT

The Kruger National Park is a stronghold for African wild dog *Lycaon pictus* and cheetah *Acinonyx jubatus* conservation in South Africa. Tourist photographic surveys have been used to evaluate the minimum number of wild dogs and cheetahs alive over the last two decades. Photographic-based capture-recapture techniques for open populations were used on data collected during a survey done in 2008/9. Models were run for the park as a whole and per region (northern, central, southern). A total of 412 (329-495; SE 41.95) cheetahs and 151 (144-157; SE 3.21) wild dogs occur in the Kruger National Park. Cheetah capture probabilities were affected by time (number of entries) and sex, whereas wild dog capture probabilities were affected by the region of the park. When plotting the number of new individuals identified against the number of entries received, the addition of new wild dogs to the survey reached an asymptote at 210 entries, but cheetahs did not reach an asymptote. The cheetah population of Kruger appears to be healthy, while the wild dog population size and density are of concern. The importance of long-term monitoring to guide conservation action is highlighted as well as the effectiveness of tourist-based surveys for estimating population sizes through capture-recapture analyses.

3.2 INTRODUCTION

African wild dogs *Lycaon pictus* and cheetahs *Acinonyx jubatus* are threatened throughout their range and the Kruger National Park (hereafter Kruger) and its neighbouring conservation areas represent an essential core area for their conservation *(*Woodroffe *et al.* 2004; Lindsey *et al.* 2005*)*. Both species are sub-dominant members of the African large carnivore guild with lions *Panthera leo* and spotted hyaenas *Crocuta crocuta* being dominant over them through exploitive competition (Creel & Creel 1996; Durant 1998). Additionally, cheetahs and wild dogs have large space requirements and thus occur at low densities (Durant 1998; Creel 2001) even in large protected areas (Palomares & Caro 1999).

Small populations pose conservation challenges for two key reasons. Firstly, extinction risk in small populations is potentially higher since it is mainly driven by demographic and environmental stochastic effects and random catastrophes (Lande 1993). Secondly detecting trends and thus local extinction risks in small populations is statistically challenging (Ginsberg *et al.* 1995).

The wild dog population in Kruger has been monitored using photographic surveys in 1988/9 (survey period June 1988-June 1989) (Maddock & Mills 1994), 1994/5 (survey period June 1994-June 1995) (Wilkinson 1995), 1999/2000 (survey period May 1999-June 2000) (Davies 2000) and 2004/5 (survey period October 2004-April 2005) (Kemp & Mills 2005) with cheetah being included in the surveys during 1990/1 (Bowland 1994) and 2004/5 (Kemp & Mills 2005). All photographic surveys gave a population estimate of the minimum number of animals alive on 1 January of the survey period (Maddock & Mills 1994). While the minimum number of animals alive on the census date was a useful measure of the status of the population, more robust methodologies now can be applied to photographic data to obtain more accurate population estimates with confidence intervals.

This study assesses the status of cheetahs and wild dogs in Kruger using capture-recapture models applied to data obtained from tourist photographic surveys. The survey intensities necessary for obtaining reliable population estimates were determined to help inform effective future monitoring systems.

3.3 MATERIALS AND METHODS

3.3.1 Study area

The study was conducted in the 21 353 km^2 Kruger National Park and neighbouring private reserves in South Africa with permits issued by SANParks under registered research project number DMOHT582. Field work and advertising were restricted to the Kruger National Park, thus no permits or permissions were required to obtain entries from neighbouring areas. The analysis was based on three separate regions: southern region (south of the Sabie River); central region (between the Sabie and Olifants rivers) and northern region (north of the Olifants River) (Figure 3.1). These were defined by differences in prey biomass (Ferreira & Funston 2010) and tourist numbers (Maddock & Mills 1994) which can collectively lead to variations in carnivore density, frequency of observation and detection. There is a decrease in gradient from south to north in prey biomass, density of roads and infrastructure, and tourist volumes. These differences can lead to variations in sample effort in both time and space.

3.3.2 Data collection

The latest tourist photographic survey for cheetahs and wild dogs was done from 1 July 2008 to 30 April 2009 using methodology following Maddock & Mills (1994). Wild dogs breed annually at mid-year making this a good time to estimate wild dog numbers and cheetahs breed aseasonally making survey timing irrelevant. During this time, tourists and park staff were asked to submit sighting details to the project with photographs, dates and locations. The survey was promoted through a photographic competition, and flyers and posters were distributed throughout the park at gates and camps. A web site was developed and several local radio adverts were broadcast. A Census Hotline Number was established that tourists could text to report sightings of cheetahs or wild dogs that could be followed up by a field worker. Promotional material was actively distributed to tourists and staff to encourage submission. Entries were received by e-mail, post and by hand. All animals photographed were identified using their unique pelage patterns. Locations were georeferenced using the description given by the entrant.

3.3.3 Sampling effort

To investigate possible differing detection rates between regions, the number of day visitors and tourist bed nights occupied in each camp were collated (data provided by South African National Parks). Where access gates or rest camps were located on the boundaries defining the three regions, half of the bed nights and day visitors were assigned to each region. The average daily number of visitors was calculated at weekly intervals.

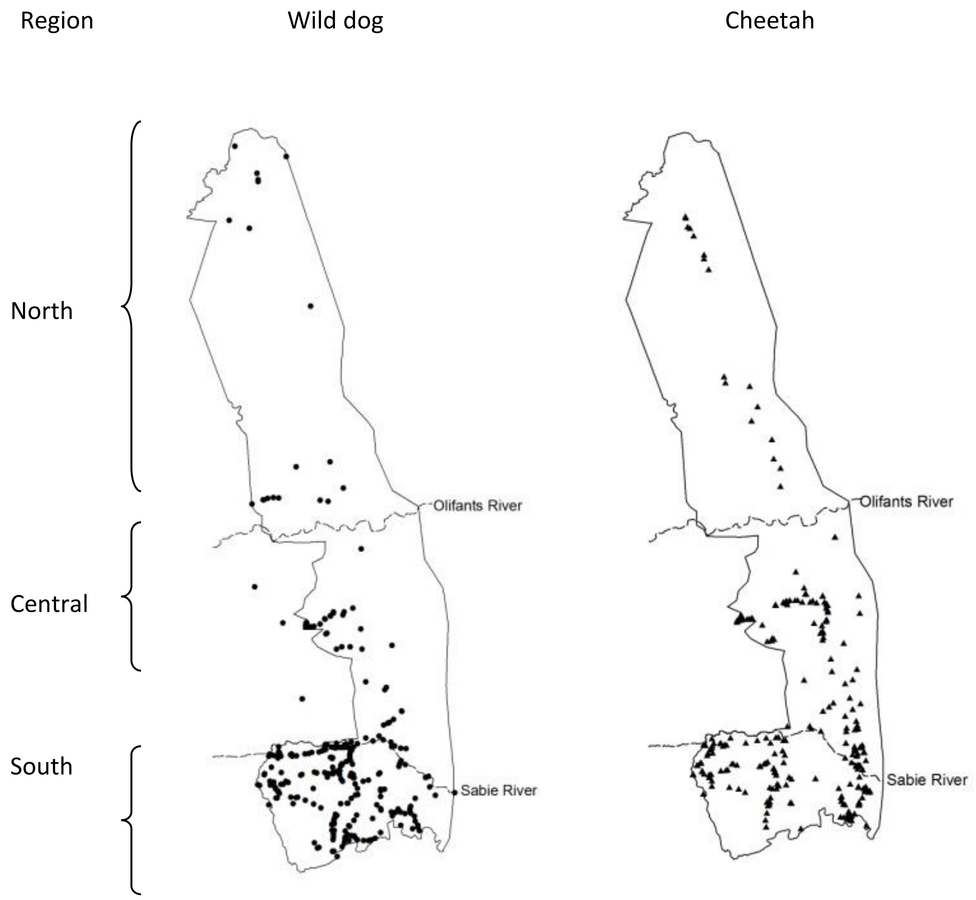

Figure 3.1: Wild dog and cheetah sightings in the Kruger National Park during the 2008/9 tourist photographic survey. The regions for analysis are delineated as follows: southern = south of the Sabie River, central = between Sabie and Olifants Rivers, north = north of Olifants River.

To determine the relationship between population estimates and tourist-related effort, an effort index was developed which scaled tourist volumes to the area and road density in each region (n/km/km^2). This index was plotted against the accumulation of newly identified individual animals to define an accumulation curve described by the negative exponential model ($y=a[1-e^{-bx}]$). The derivative of this model allowed for estimating the effort at which new individuals were recorded, less than 0.1 individuals added per unit of increasing tourist effort was considered evidence that an asymptote had been reached.

The number of entries was predicted to increase with time as awareness of the photographic competition increased. Entries were thus related to weeks into the competition using non-linear curve fitting. To evaluate the assumption that more observers lead to more observations, the residual values for entries were calculated to remove the effect of time on entries and these were related to the average daily number of tourists present in that week. A tourist-related effect on sampling was concluded if this linear relationship was significant ($p<0.05$).

3.3.4 Population estimates

The data for cheetahs and wild dogs were prepared for capture-recapture analyses by using all captures for the period 1 July 2008 to 30 April 2009. The data were collapsed to form 10 capture occasions where, one month was equated to one capture period. Thus any animal photographed at any time during that month was considered captured during that month.

Life histories were compiled for each identified individual photographed and consisted of 10 occasions of capture coded as "1" for a captured individual and "0" for a non-captured individual. Each individual was assigned to a region of the park based on the majority of recorded sightings, allowing for regional population estimates.

Goodness-of-fit (GOF) tests were run in U-CARE (Choquet *et al.* 2009) to detect potential problems in the structure of the data files. The appropriate data files were selected and used to run open capture-recapture models (POPAN) in MARK (White & Burnham 1999) to estimate population sizes of cheetahs and wild dogs.

For cheetahs, adult males are associated with each other in small coalitions (2-3 individuals), whereas each adult female is associated with her cubs. For wild dogs, animals of all ages are associated with specific packs. These social structures are likely to result in heterogeneity in individual life histories; because individuals in the same social group are more likely to be captured during the same occasion than individuals in other groups. This violates the assumption of the capture-recapture models that all individuals in a population have equal capture probabilities. To account for this, sub-sets of the data were built which took the social structure of the species into account.

Firstly, datasets were built at a park-wide scale (i.e. data from all three regions were used). For cheetahs, the datasets including one adult male per coalition, adult females and adult unknowns could not be used because the data structure was not suitable (GOF test: $p=0.02$). A dataset including 145 adults and sub-adults classified by sex (male, female, unknown) was selected for cheetahs (GOF test: $p=0.82$). No cheetah cubs were included in the analyses because cubs are always associated with their mothers. These animals were accounted for by estimating the mean size of family groups (one female and her offspring) (4.87 ±0.44 SE; $n=15$) to calculate the total number of adult females and cubs in the population. The final number of females from the capture-recapture estimate was multiplied by the mean female group size and added to the population estimate to produce a result that accounted for these groups.

For wild dogs each pack was used for the capture-recapture modelling i.e. if an individual in a specific pack was captured, the whole pack was considered captured. This resulted in the selection of a dataset that included 21 packs (155 wild dogs with all age- and sex-classes combined) (GOF test: $p=0.14$). Capture-recapture models were used to estimate the total number of packs in Kruger. The mean pack size was then estimated (7.381 ±1.343 SE; $n=21$) and multiplied by the number of packs from the capture-recapture modelling to estimate the total number of wild dogs in the population.

Secondly, datasets were built for each region (three per species: northern, central and southern regions). For cheetahs, datasets that included adults and sub-adults classified by sex (male, female, unknown) were selected (central region: n=53, GOF test: p=0.93; southern region: n=79, GOF test: p=0.98). The sample size for the northern region (n = 13) was not sufficient to run GOF tests. For wild dogs, a dataset including 21 packs classified into three regions was selected (GOF test: p=0.70).

Finally, POPAN models using selected datasets for the park and for each region were run. In each instance, the model selected had the lowest Akaike Information Criterion (AICc for small sample size) and lowest number of parameters (Burnham & Anderson 2002).

3.3.5 Population characteristics

Population structures for cheetahs and wild dogs were determined. Wild dogs were assigned to adult/yearling (>1 year old) and pup (< 1 year old) age classes for males, females and animals of unknown sex. Cheetahs were assigned to cubs and adult male, female and unknown. Capture-recapture models were able to be used to determine the abundance of the three adult sex classes for cheetahs. Due to the dependency of capture probabilities between pack members, wild dog age and sex structure could not be determined using capture-recapture models; instead counts using the photographic records were used.

3.3.6 Optimal survey intensity

Optimal survey intensities were determined by calculating a series of population estimates using mark-recapture, with the associated confidence intervals, from sub-samples of entries, ranging from 15 entries to the complete datasets for both species. Each confidence interval was expressed as a percentage of the estimate, i.e. a percentage confidence limit (PCL) (PCL= $\frac{2CL}{\bar{\chi}}$) (Ferreira & van Aarde 2009). PCLs of 20% typically translate to a coefficient of variance of ≈5% while those of 40% translate to ≈10%. The number of entries required to produce population estimates with CVs of ≈5% and ≈10% were determined using the fitted equation $y=1.558x^{-0.373}$ for wild dogs and $y=1.464x^{-0.212}$ for cheetahs where y=PCL and x=number of entries.

3.4 RESULTS

3.4.1 Data collection and sampling effort

The number of photographic entries varied over time and between regions with a general trend of more entries being received from the southern regions (Table 3.1 & Figure 3.1). The number of entries per week for both species increased exponentially over time (Figure 3.2). The number of wild dog entries was not associated with the number of tourists once the effect of time was accounted for ($F_{1,42}$=4.03, p=0.06; Figure 3.2B) while the number of cheetah entries increased as tourist numbers increased ($F_{1,42}$=6.02, p=0.02; Figure 3.2B).

In all three study regions, the accumulation of new wild dogs per unit effort reached asymptotes i.e. less than 0.1 individuals added per unit of increasing tourist effort (Figure 3.2C, Northern: $y=26.99[1-e^{-11.44x}]$, $R^2 = 0.82$; Central $y=243.88[1-e^{-2.04x}]$, $R^2 = 0.91$; Southern: $y=135.06[1-e^{-6.57x}]$, $R^2 = 0.92$). For cheetahs, no asymptotes were reached (Figure 3.2C, Northern: $y=8523.92[1-e^{-0.04x}]$ $R^2 = 0.80$; Central: $y=2844.42[1-e^{-0.21x}]$, $R^2 = 0.99$; Southern: $y=533.54[1-e^{-0.97x}]$, $R^2 = 0.98$).

The rate of accumulation of new wild dogs decreased with increasing entries (Figure 3.2D, Southern: $y=99081[1-e^{-0.03x}]$, $R^2 = 0.99$; Central: $y=48.08[1-e^{-0.06x}]$, $R^2 = 0.97$; Northern: $y=12.20[1-e^{-0.09x}]$, $R^2 = 0.83$). Less than 10% new wild dog additions per week were obtained at 126, 56 and 28 entries in the southern, central and northern regions, respectively.

The rate of accumulation of new cheetahs decreased with increasing entries (Figure 3.2D, Southern: $y=134.76[1-e^{-0.01x}]$, $R^2 = 0.96$; Central: $y=71.14[1-e^{-0.03x}]$, $R^2 = 0.97$; Northern: $y=63.43[1-e^{-0.01x}]$, $R^2 = 0.98$). Less than 10% new individuals per week were obtained at 157, 105 and 338 entries from the south, central and northern, respectively.

Table 3.1: Population estimates of cheetahs and African wild dogs derived from POPAN models in MARK. Data collected through a tourist photographic survey during 2008-2009 with the number of entries received per region displayed.

	Cheetahs					Wild dogs				
Park region	Number of entries	POPAN Model	Estimate	SE	95% CI	Number of entries	POPAN Model	Estimate	SE	95% CI
North	24	NA[1]	NA[1]	NA[1]	NA[1]	24	ϕ(g*t) p(g) β(t) N(g)	24	1.60	19-29
Central	107	ϕ(.) p(g) β(g*t) N(g)	137	26.72	83-191	89		23	1.15	20-27
South	312	ϕ(g) p(g) β(t) N(g)	236	31.24	174-298	450		89	0.91	87-91
Total	454[2]	ϕ(i) p(g*t) β(t) N(g)	412	41.95	329-495	564[3]	ϕ(i) p(i) β(t) N(i)	151	3.21	144-157

[1]: Sample size insufficient
[2]: 1 unknown region
[3]: 11 unknown region

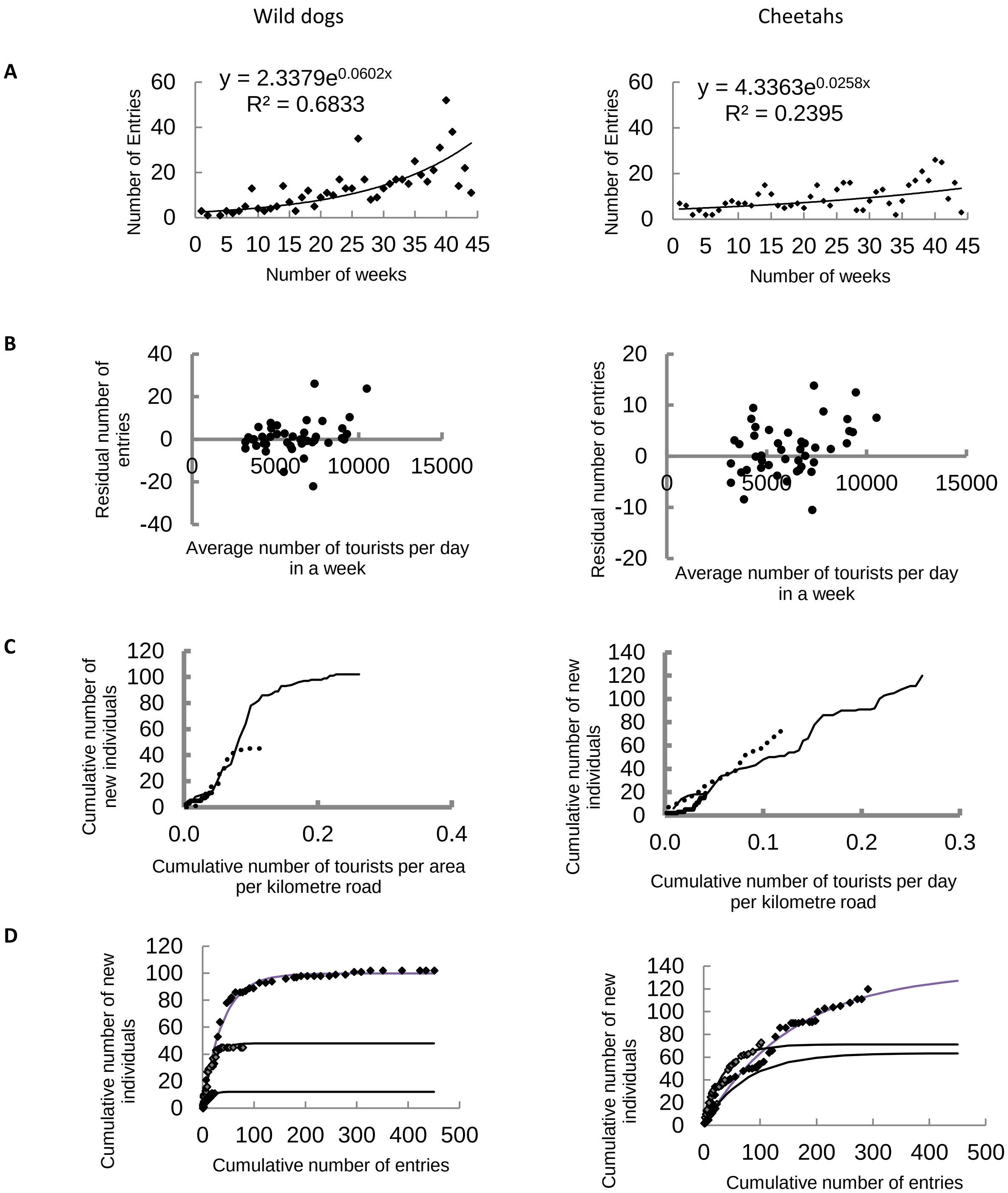

Figure 3.2: Sampling effort in the 2008/9 Kruger National Park tourist photographic survey of cheetahs and wild dogs. A: The weekly number of entries received over time. B: The relationship between the weekly number of entries and available tourists during that time - effect of time removed. C: Accumulation of new individuals as the number of tourists per area and available roads in a region increases. (northern – solid line, central – broken line, southern – solid thin line. D: Accumulation of new individuals as the number of entries increases (northern – open symbols, central – shaded symbols, southern – solid symbols).

3.4.2 Population estimates

Cheetahs

For the whole park, the selected model included a group (sex) effect on the estimated population size, with 94 (±6.66 SE) adult males, 38 (±4.49 SE) adult females and 134 (±35.18 SE) unknown adults estimated. In total, the number of adult cheetahs was estimated at 266 individuals in Kruger as a whole. Using the average size of cheetah families (4.867 ±0.435 SE; N=15), the total population size of cheetahs in Kruger was therefore estimated at 412 individuals (Table 3.1). There was no estimate of population size for the northern region since the sample size was too small to run models.

For the central region, the selected model included a group (sex) effect on the estimated population size, with 28 (±3.84 SE) adult males, 7 (±1.62 SE) adult females and 74 (±25.25 SE) unknown adults. The total number of adult cheetahs was estimated at 110 individuals in the central region. Using the average size of cheetah groups (4.867 ±0.435 SE; N=15), the total population size of cheetahs in the Central region was estimated at 137 individuals (Table 3.1).

For the southern region, the selected model included a group (sex) effect on the estimated population size, with 57 (±5.45 SE) adult males, 26 (±3.20 SE) adult females and 52 (±26.51 SE) unknown adults. The total number of adult cheetahs was estimated at 135 individuals in the southern region. Using the average size of cheetah groups (4.867 ±0.435 SE; N=15), the total population size of cheetahs in the southern region was estimated at 236 individuals (Table 3.1).

Wild dogs

For the whole park, the selected model did not include any effect on the estimated population size, with 20 (±0.44 SE) packs. The total number of wild dog packs was estimated at 20 packs in the whole of Kruger. Using the average pack size (7.381 ±1.343 SE; n=21), the total population size of wild dogs in Kruger was estimated at 151 individuals (Table 3.1).

When regions were considered, the selected model included a regional effect on the estimated population size, with three (±0.16 SE) packs in the central region, three (±0.22 SE) packs in the northern region and 12 (±0.12 SE) packs in the southern region. Using the average size of a pack (7.381 ±1.343 SE; N=21), the total population size of wild dogs was estimated at 23 individuals in the central region, 24 in the northern region and 89 in the southern region (Table 3.1).

3.4.3 Population characteristics

Capture–recapture models were able to be used to determine the adult cheetah sex structure per region with the exception of the northern region where the sample size was too small to run the models (Table 3.2). Cheetah estimates are biased towards males for the sexed adults. Wild dog sex ratios from photographic counts were near parity for the whole park (Table 3.3).

3.4.4 Optimal survey intensity

PCLs of estimates declined with increasing numbers of entries for wild dogs (R^2=0.848) and cheetahs (R^2=0.711) (Figure 3.3). Wild dogs required 250 and 38 entries to return 20% and 40% PCLs, respectively (i.e. CVs of ≈5% and ≈10%). For cheetahs an unrealistic 11670 entries were required to return 20% PCL; a more achievable 451 entries were required for 40% PCL.

3.5 DISCUSSION

3.5.1 Effectiveness of tourist photographic surveys for monitoring wild dogs and cheetahs

Estimating population sizes for sub-dominant carnivore guild members is challenging both statistically and logistically. Photographic-based surveys have been used for several species (Marnewick *et al.* 2008) with capture-recapture estimates being applied when species have distinct pelage patterns, like cheetahs (Caro & Colins 1987) and wild dogs. Public participation in photographic-based surveys is less used, but can generate data suitable for capture-recapture analyses.

Generating sufficient data through tourist-based surveys is integral to ensuring sampling success. In this survey, the number of photographic entries was sufficient to generate a reliable estimate for wild dogs and cheetahs at a park-wide scale and per park region except for the northern region for cheetahs. However, the wild dog population estimates from capture-recapture models had lower standard errors suggesting more effective sampling for wild dogs than for cheetahs.

Table 3.2: Population estimates of cheetahs in the different regions of the Kruger National park derived from POPAN models in MARK. Data collected through a tourist photographic survey during 2008-2009.

	Adult male			Adult female			Adult unknown			POPAN model	Total	
Park Region	Population estimate	SE	95% CI	Population estimate	SE	95% CI	Population estimate	SE	95% CI		Adults	All ages
North	NA[1]	NA[1]	NA[1]	NA[1]	NA[1]	NA[1]	NA[1]	NA[1]	NA[1]	NA[1]	NA[1]	NA[1]
Centre	28	3.84	21-36	7	1.62	4-40	74	25.25	25-124	ϕ(i) p(g) b(g*t) N(g)	110	137
South	57	5.45	46-67	26	3.2	20-32	52	26.51	0-104	ϕ(g) p(g) b(t) N(g)	135	236
Total	94	6.66	81-107	38	4.49	29-47	134	35.18	65-203	ϕ(i) p(g*t) b(t) N(g)	266	412

[1] Sample size insufficient

Table 3.3: Population estimates of African wild dogs in the different regions of the Kruger National park derived from count data collected through a tourist photographic survey during 2008-2009.

	Adult				Pup				Total
Park region	Male	Female	Unknown	Total	Male	Female	Unknown	Total	All ages
North	3	6	0	9	1	2	0	3	12
Central	10	11	4	25	5	12	2	19	44
South	29	35	6	70	9	12	9	30	100
Total	42	52	10	104	15	26	11	52	156

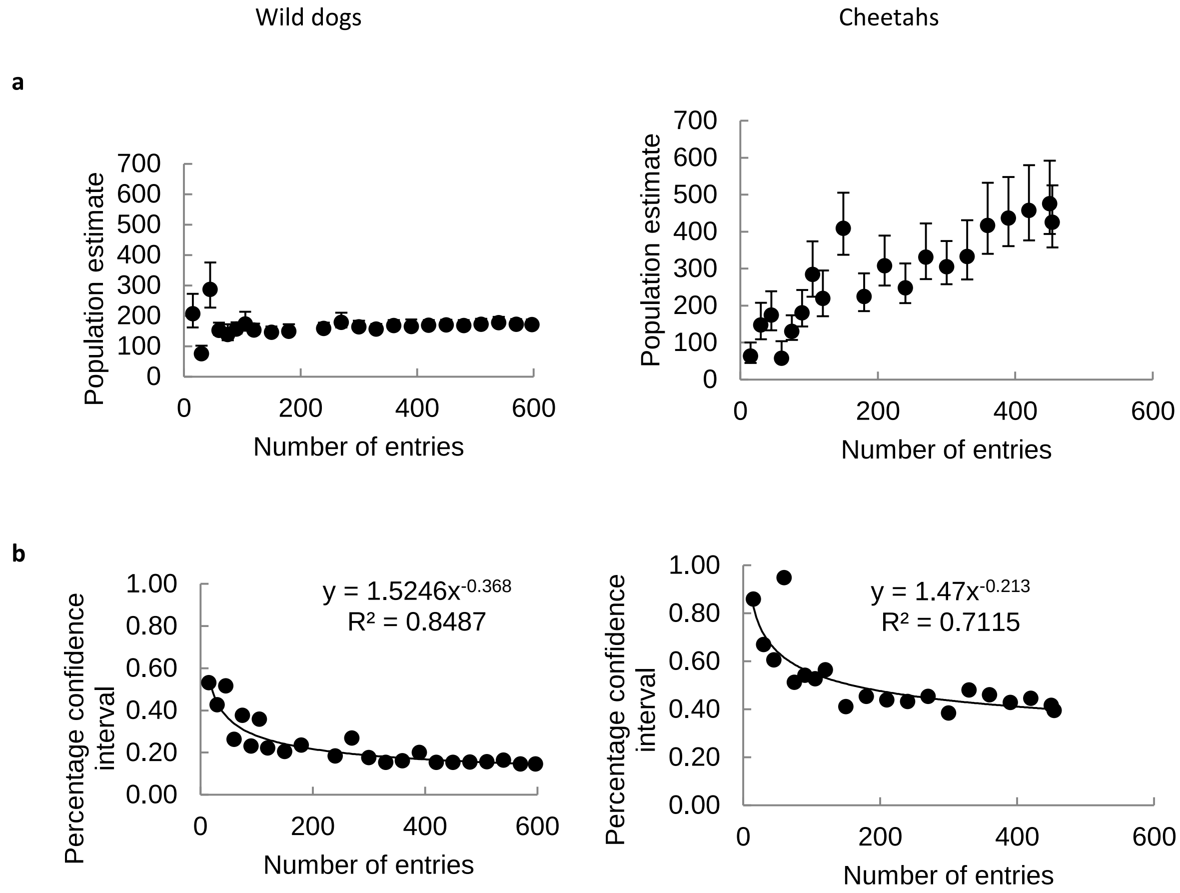

Figure 3.3: Effect of the number of entries on estimates. Population estimate (a) and percentage confidence intervals (b) for wild dogs and cheetahs in the Kruger National Park using tourist photographic surveys.

Analysis of results from public-generated data present challenges through biases introduced through a lack of control over survey effort and area. This makes survey effort difficult to measure and data may be biased towards areas with higher visitation rates. In this study, survey effort was not uniformly distributed with a higher density of tourists and roads in the south which decreased in a gradient towards the north. This can lead to variations in capture probability which can affect the outcomes of the capture-recapture models. However, this was accounted for by dividing the study area into the three separate regions (northern, central, southern) based on differences in tourist volumes, infrastructure and prey density.

Individual capture-recapture models were run for each region separately to account for these spatial differences across the study area. For wild dogs the regional models showed that the capture probability varied by region meaning that some of these spatial differences could be affecting the survey for wild dogs, but not for cheetahs.

The selected cheetah capture-recapture model for the whole park showed that the capture probability of cheetahs was dependent on time i.e. the number of entries, but this was not relevant at the regional level or for any of the selected wild dog models. This means that capture probability was not affected by time or number of entries for any of the selected models, except for cheetahs at a park-wide scale.

The number of entries received was not influenced by the number of tourists, but was most likely associated with the chance of encountering animals. The higher number of entries in the southern region is probably a consequence of larger population sizes for both species in this region.

While there are more cheetahs (n=412) than wild dogs (n=151) in the park, more entries were received for wild dogs than cheetahs. This difference may be related to social behaviour. Cheetah females occur as singletons, unless with cubs, and males either singly or in coalitions comprising two to three individuals (Broomhall *et al.* 2003). This could lead to cheetahs being less detectable than wild dogs which occur in large packs. Group size also affects detection probabilities for other species like feral horses (Ransom 2012). Additionally, wild dogs are wider ranging than cheetahs and frequently use roads to traverse large distances.

3.5.2 Survey intensity

In this study, it was more difficult to obtain precise population estimates for cheetahs than for wild dogs through tourist surveys. More than 11 000 cheetah entries are required to achieve estimates with PCLs of 20% while wild dogs require only 250 entries. Thus, it is more feasible to aim at obtaining cheetah estimates with PCLs of 40% for which approximately 450 entries are required.

3.5.3 Population status

The male-biased sex ratio of cheetahs in Kruger is potentially an artefact of the survey method. Males are probably easier to sex from photographs than females due to the former's external genitalia. Additionally, male cheetahs are probably more detectible than females because they occur in coalitions (Caro & Colins 1987), use roads and prefer more open habitat (Broomhall *et al.* 2003). This trend was confirmed by the selected capture-recapture models for cheetahs at the park-wide scale that showed the probability of cheetah capture varied with sex for male, female, unknown sex models. The observed patterns in the sex structure of cheetahs in Kruger are therefore likely to be a result of limitations of the survey method and animal behaviour rather than biological effects that would suggest consequences for their conservation status.

Wild dog sex ratios are near parity as would be expected. The effect of sex could not be tested using capture-recapture models due to packs being used in the models and not individuals. However, it makes biological sense that wild dogs of both sexes would have similar capture probabilities. Wild dogs live in packs and the behaviour of males and females is not different enough to affect capture probabilities as it does for cheetahs.

The estimated cheetah population of 412 individuals translates to a density of approximately 0.193 cheetahs/km^2 in the whole of Kruger. While there are no appropriate historical data to compare this estimate to, in other areas cheetahs have been recorded at lower densities of 0.016-0.0438/km^2 in the Serengeti (Gros 2002) and 0.009-0.102 cheetahs/km^2 in Kenya (Gros 1998). From these estimates, there is currently no reason for conservation concern around the Kruger cheetah population.

The estimated wild dog population of 151 individuals in 18 packs translates to a density of approximately 0.007 wild dogs/km^2 in the whole of Kruger. This is low in comparison to historical data when in 1994 an estimated minimum count of 357 wild dogs (0.017 wild dogs/km^2) in 26 packs was recorded (Maddock & Mills 1994). In other protected areas wild dogs occur at densities of varying between 0.040 in the Selous to 0.015 in Hwange (Creel & Creel 1996). This small size and apparent declining nature of the Kruger wild dog population is of concern as this is South Africa's largest protected population and for one of the key populations in Africa. This needs to be further investigated.

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CHAPTER 4: Home ranges of cheetahs outside protected areas in South Africa

Kelly Marnewick & Michael J. Somers

2015 African Journal of Wildlife Research, Special Carnivore Issue 45(2): 223–232

4.1. ABSTRACT

As many carnivores occur outside protected areas they are vulnerable to anthropogenic threats. In South Africa, the largest proportion of the distribution range of cheetahs *Acinonyx jubatus* is outside protected areas along the northern border of the country. Lions *Panthera leo* and spotted hyaenas *Crocuta crocuta* have been extirpated from these areas, leaving the depauperate carnivore guild dominated by cheetahs, leopards *Panthera pardus* and brown hyaenas *Hyaena brunnea*. To determine how cheetahs use these areas, tracking collars were fitted to nine individuals from September 2003 to July 2009 in the Thabazimbi area, Limpopo, South Africa. Local Convex Hulls (αLoCoH) were used to determine home range sizes and 50 and 95 utilisation distributions (UDs) were calculated. Male 95UDs ranged from 121.5 km^2 to 607 km^2 while females ranged from 14.7 km^2 to 703.3 km^2. Cheetahs utilised several ranches and mean home ranges sizes were larger than mean ranch size and larger than cheetah home ranges recorded in other southern African countries, with the exception of the more arid Namibia. This study provides valuable and relevant data on cheetahs and aids conservation practitioners in mitigating human-cheetah conflict on South African farmland.

4.2. INTRODUCTION

4.2.1 Large carnivore conservation and protected areas

A key function of protected areas is to separate biodiversity elements from processes that threaten them (Margules & Pressey 2000). The designation of protected areas has seldom been done in a systematic way and as a result protected areas are not always effective in contributing to biodiversity conservation (Margules & Pressey 2000). This means that many species which occur outside protected areas in regions of anthropogenic use are vulnerable to the effects of habitat fragmentation (Ranta *et al.* 2009), conflict related killings (Swanepoel *et al.* 2014) and other threats.

Large carnivores are particularly vulnerable to threats in fragmented landscapes as they have high space requirements, live at low densities and inevitably come into conflict with humans (Purvis *et al.* 2000; Cardillo *et al.* 2005). While protected areas are important for carnivore conservation, they are seldom effective in their conservation (Woodroffe & Ginsburg 1998). Conservation of carnivores therefore cannot rely solely on protected areas, and needs to be addressed both within and beyond the boundaries of these areas.

4.2.2 The South African context

In South Africa, the protected area network alone is not sufficient for conserving populations of large carnivores. For example: leopards *Panthera pardus* are vulnerable to edge effects (Balme *et al.* 2010), habitat fragmentation and ineffective positioning of protected areas (Swanepoel *et al.* 2013); and only two protected populations of lions *Panthera leo* (Kruger National Park and Kgalagadi Transfrontier Park) are classified as viable (IUCN/SSC 2006), with lions in smaller protected areas being vulnerable to genetic, ecological and stochastic effects (Miller *et al.* 2013). Ecological niche modelling shows that the protected area network is also not effective in conserving the most suitable habitat for cheetahs *Acinonyx jubatus* and African wild dogs *Lycaon pictus* in South Africa (K.M., unpublished data).

The Kruger National Park and the Kgalagadi Transfrontier Park hold the only substantial populations of cheetahs inside protected areas in South Africa (Lindsey & Davies-Mostert 2009), with the largest portion of the national cheetah distribution range occurring outside protected areas along the northern border of the country (Marnewick *et al.* 2007). Lions and spotted hyaenas *Crocuta crocuta* have been extirpated from these areas leaving the depauperate carnivore guild dominated by cheetahs, leopards and brown hyaenas *Hyaena brunnea*. In these areas, land is privately owned and utilised for wildlife ranching, livestock ranching or a combination thereof. Both livestock and wildlife have an economic value to the landowner; livestock through live sale or the meat industry and wildlife through sport hunting and live sale. Thus when carnivores prey on these animals, conflict results and the suspected carnivore is often killed in retaliation or in an effort to prevent further losses (Thorn *et al.* 2013). Cheetahs are classified as Vulnerable in the South African Red Data Book of Mammals (Friedmann & Daly 2004) and the South African population is contiguous with the populations in Botswana, Namibia, Zimbabwe and Mozambique (IUCN/SSC 2007). These factors make the cheetah population outside of protected areas important for conservation of the species.

Few data exist on cheetahs outside protected areas in South Africa. Some landowners perceive cheetahs to be problematic as they claim cheetahs do not behave naturally in these areas. Ranches are heavily stocked with game and supported by supplying food and water. Because the ranches are fenced and the prey is sedentary many landowners believe that cheetahs do not use large home ranges as is typical in other areas. This means that the impact of cheetahs on any individual ranch is perceived to be high (K.M., unpublished data).

These perceptions are important in driving killing of cheetahs and thus their long-term survival outside protected areas. Data relevant to the landowners are required to address these perceptions and to implement cheetah conservation actions. This study therefore attempts to quantify the home ranges of cheetahs outside of protected areas on private ranches.

4.3. STUDY AREA

The Thabazimbi District in the Limpopo province was the core study area. The area was selected because previous surveys had been done in the district and a relationship had been developed with the landowners (Marnewick & Cilliers 2006; Marnewick *et al.* 2006; Wilson 2006). Thus, landowner buy-in had been obtained for the study with the resulting permissions to trap, collar and release cheetahs on several properties. The mean ranch size in the district is approximately 18 km^2 with the main form of land-use being wildlife ranching, or a combination of wildlife and stock ranching (Wilson 2006). The area is topographically flat with little change in elevation and few distinguishing geographic features.

The Thabazimbi District lies in the Savanna Biome of South Africa and the main vegetation type is Mixed Bushveld dominated by the red bushwillow *Combretum apiculatum*, common hook-thorn *Acacia caffra*, sickle bush *Dichrostachys cinerea*, live-long *Lannea discolour* and marula *Sclerocarya birrea* (Low & Rebelo 1996). Where the soil is more clayey, Clay Thorn Bushveld occurs which is dominated by Acacia species (Low & Rebelo 1996). The area has been historically used for cattle ranching and the bush is encroached over a large portion of the district (personal observations). There are some previously ploughed areas that have since been left fallow. The edges between these areas and the surrounding more dense, bushy areas are generally hard and linear.

The annual, mainly summer rainfall for the study area varies from 350 mm to 650 mm per year with temperatures ranging from -8°C to 40°C with an annual mean of 21°C (Low & Rebelo 1996). Human population density is low at 2/km^2 (Statistics South Africa (2001) www.statssa.gov.za accessed on FUNDISA Disk).

4.4. METHODS

4.4.1 Cheetah capture

Cheetahs were trapped from September 2003 to July 2009 using double door box traps along frequently walked fence lines, at scent marking posts and using live bait. For more detailed information on trapping procedure see Marnewick and Cilliers (2006). Trapped cheetahs were immobilised by a wildlife veterinarian and fitted with tracking collars. All activities involving cheetah handling and research were done under a University of Pretoria Animal Ethics Committee permit (Nr EC030-09) and permits issued from Limpopo Department of Economic Development, Environment and Tourism (the local government conservation authority).

If coalitions were caught then only one member of the group was collared as this group structure is normally stable and these males can be expected to remain together (Caro 1994). Initially VHF collars (African Wildlife Tracking, Pretoria, South Africa) were fitted and the cheetahs monitored by microlight aircraft. Once the technology was available and affordable, GPS/GSM collars (African Wildlife Tracking, Pretoria South Africa and Hot Group, Pretoria, South Africa) were used to obtain more robust data and set to take two to four GPS locations per day; at 12h00 and 00h00 for the collars set for two daily locations, and with 06h00 and 18h00 included for the collars with four daily locations. The cheetahs were allowed to recover from immobilisation in the trap cage and once fully recovered, were released at the site of capture. Cheetahs were monitored for the extent of their life or the life of the collar. On two occasions, the collars were replaced due to deteriorating batteries by darting the cheetahs from a helicopter. Three female and six male cheetahs were collared. Four of the males were singletons, one from a collation of three and one from a coalition of two, resulting in nine monitoring units (Figure 4.1). None of the females had cubs or showed any signs of lactation.

Trapping success was low with approximately 278 trap days required to trap a cheetah, or monitoring unit. Cheetahs were monitored from 28 days to 2 119 days depending on the life of the cheetah or the collar (see Table 1). The two male (AM196) and three male (AS68) coalitions were initially monitored using VHF collars resulting in 56 (2.8% of total) and 12 (8.6% of total) data points being obtained respectively.

4.4.2 Data analyses

Local Convex Hulls (αLoCoH) (Getz & Wilmers 2004; Getz *et al.* 2007) were used to determine home range sizes, using the computer programme R v 2.10.1 (The R Foundation http://www.R-project.org/). Utilisation distributions (the two dimensional distribution of the position of an animal (Worton 1989)) were considered at two spatial scales where 50 utlisation distributions represented core areas and 95 utilisation distributions represented total ranges. K, the number of nearest neighbour points used to construct local hulls to obtain a utilization distribution, was calculated using the square root of the total number of data points per animal (Getz *et al.* 2007).

LoCoHs have been shown to outperform kernels and provide a more accurate representation of the animals' home range, especially in areas with hard boundaries (Getz *et al.* 2007). Minimum Convex Polygons (MCP) (Jenrich & Turner 1969) (Hawth's Analysis Tools ARC GIS V 3.27 2006. www.spatialecology.com/htools) were determined and used to allow for comparison to other studies, because the method is widely used (Harris *et al.* 1990). For area calculations, the data were projected into UTM. Home range size using MCPs was plotted against sequential GPS locations in the software package Abode Beta V2 (Laver 2005; http://fishwild.vt.edu/abode/abodeweb.html) to visually determine if home ranges reached asymptotes. Relationships between male and female home range sizes, maximum distances moved and proportion between total and core ranges were tested using appropriate statistical tests.

4.5. RESULTS

4.5.1 Fate of the collared cheetahs

Two of the females were shot by landowners and one was killed in a road accident. The coalition of three males was shot as was one of the single males, the coalition of two died from what appeared to be natural causes, three single males have unknown fates as the collar downloads stopped. They either died and the collars were destroyed, were out of cell phone reception, or the collars malfunctioned. Five of the nine collared cheetahs died due to anthropogenic causes.

4.5.2 Home range sizes

The home range sizes of all females reached an asymptote. Male home ranges appeared to be larger than female ranges but they did not all reach asymptotes (Figure 4.2) and these differences were not significant for the MCP ($t(7) = -0.8$, $P = 0.22$), 95UD ($t(7) = -0.7$, $P = 0.46$) or 50UD ($t(7) = 0.77$, $P = 0.23$). Male 95UDs ranged from 121.5 km^2 to 607 km^2 while females ranged from 14.7 km^2 to 703.3 km^2 (Figure 4.3a). The 50UD (Figure 4.3b) as a percentage of the 95UD was 18% for females, 10% for males and 12% across all sexes. There was no significant difference between the maximum distances between points for males and females ($t(7) = -1.14$, $P = 0.15$).

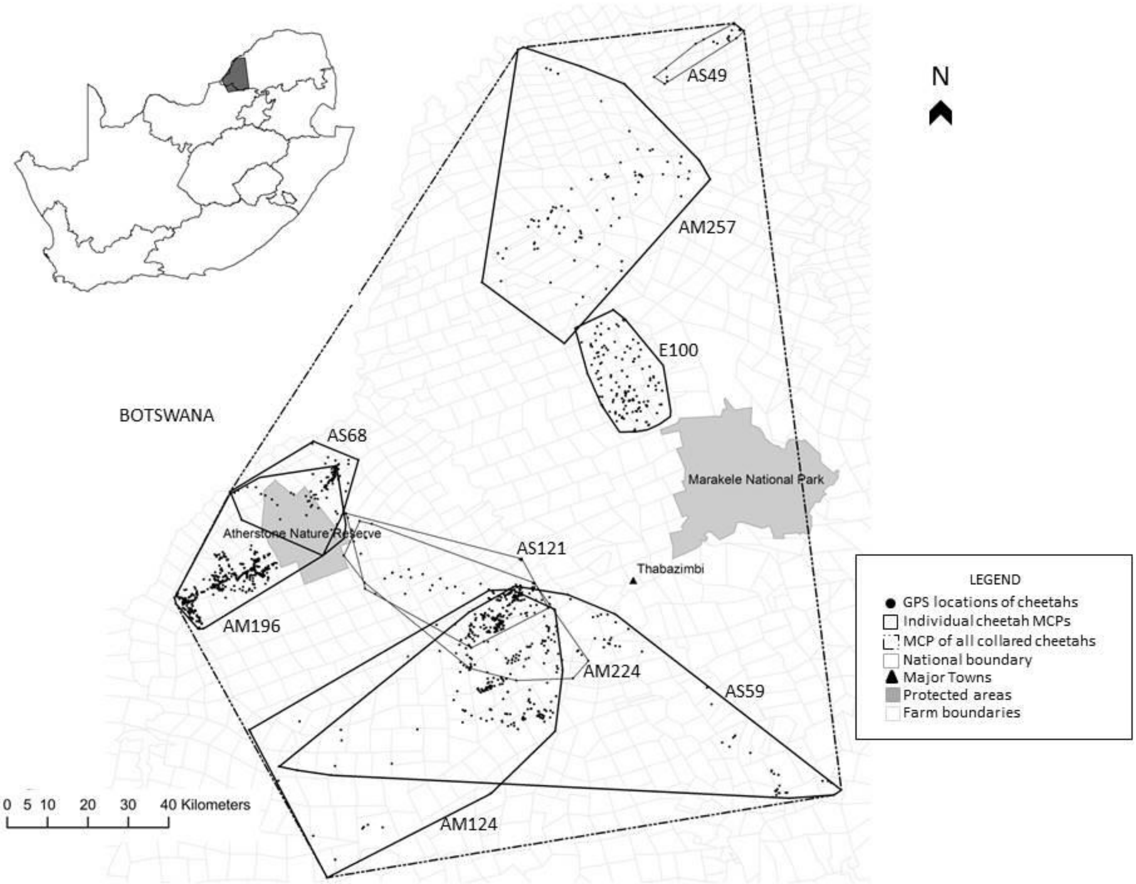

Figure 4.1: The study area in Limpopo province, South Africa where free roaming cheetahs were collared. MCPs for each cheetah are shown along with protected areas, farm boundaries and major towns.

Table 4.1: Details of cheetahs collared on cattle and game ranches in the Thabazimbi District, Limpopo province, South Africa.

Animal ID	Social	Sex	Date start	Date end	Fate	Nr days	Nr Locations	95 UD	50 UD	MCP	Nr Hulls	k value	Max distance between points (km)
AS59	Single	Male	2006/08/03	2006/10/13	Shot	71	150	607.0	86.6	2761.8	12	18	122
AM124	Single	Male	2006/07/14	2007/03/21	Unknown	250	394	506.2	42.0	2172.0	20	70	76
AM224	Single	Male	2007/06/15	2007/10/16	Unknown	123	43	314.2	44.8	824.2	7	18	57
AM257	Single	Female	2007/05/18	2007/11/15	Road kill	181	90	703.3	102.0	1717.3	9	12	65
AS49	Single	Female	2007/12/12	2008/01/09	Shot	28	31	14.7	0.2	61.1	6	10	21
AS68	Coalition of three	Male	2004/05/03	2008/02/09	Shot	1377	140	171.2	4.2	367.1	12	30	28
E001	Single	Female	2007/09/20	2008/04/17	Shot	211	167	183.23	56.485	315.6	13	16	28
AS121	Single	Male	2008/07/04	2008/11/21	Unknown	140	196	192.0	11.7	631.0	14	30	48
AM196	Coalition of two	Male	2003/09/18	2009/07/07	Dead - natural	2119	1954	121.5	0.0	662.0	44	60	45
Averages													
Males	Males	Males	2003/09/18	2009/07/07		2119	2877	319	32	1597.2			
Females	Females	Females	2007/05/18	2008/04/17		336	288	300	53	698			
All	All	All	2003/09/18	2009/07/07		2119	3165	313	39	1057			

K value: The number of nearest neighbours minus one out of which convex hulls were created
UD: Utilisation distribution
MCP: Minimum convex polygon

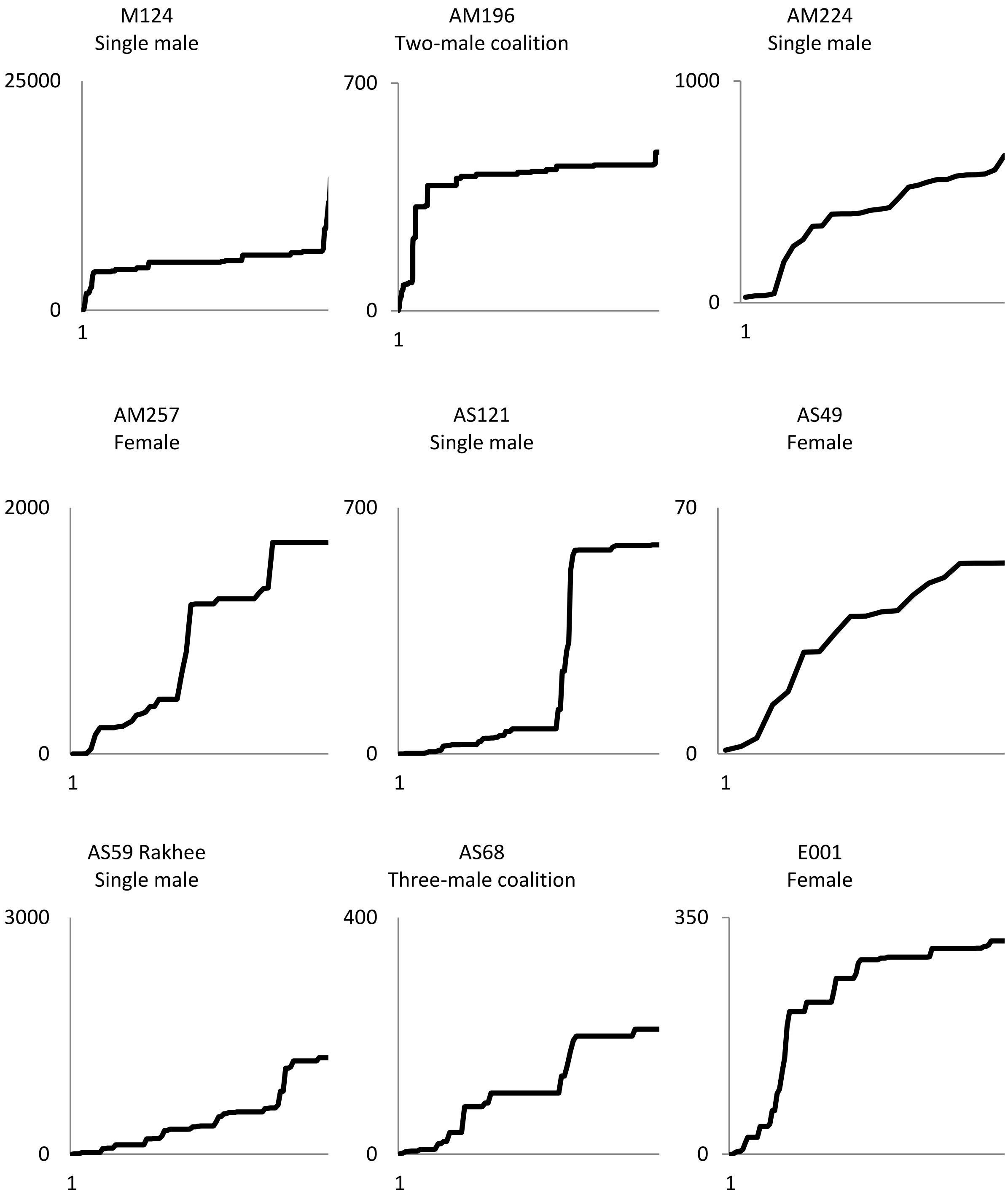

Figure 4.2: Determining if home ranges have reached asymptotes for cheetahs in Limpopo by plotting incremental increases in home range size with addition of consecutive GPS locations. Y-axis denotes the size of the home range in km^2 and the x-axis denotes the number of GPS locations used in the analysis.

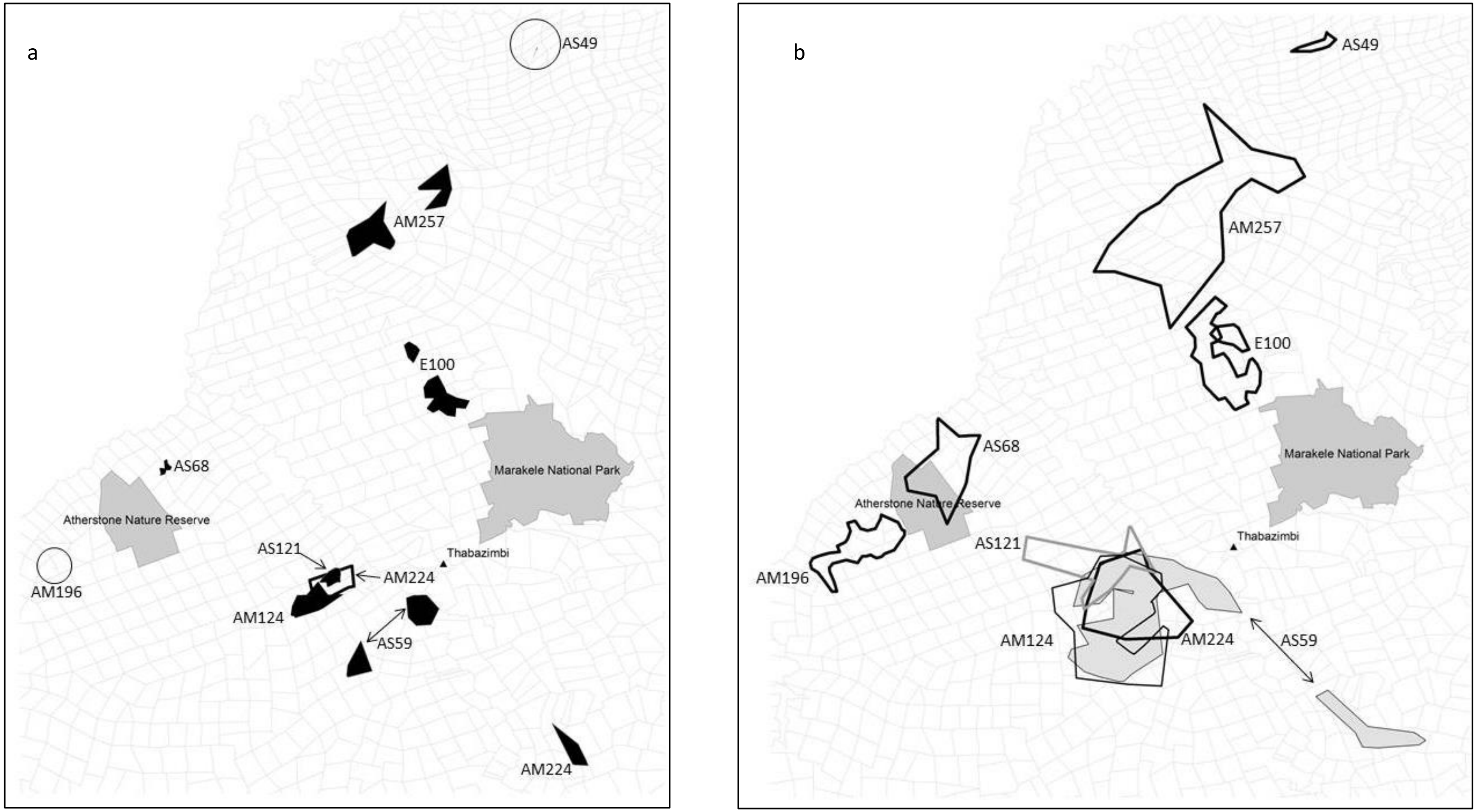

Figure 4.3 a & b: 50 utilisation distributions and 95 utilisation distributions for cheetahs on cattle and game ranches in the Thabazimbi district, Limpopo province.

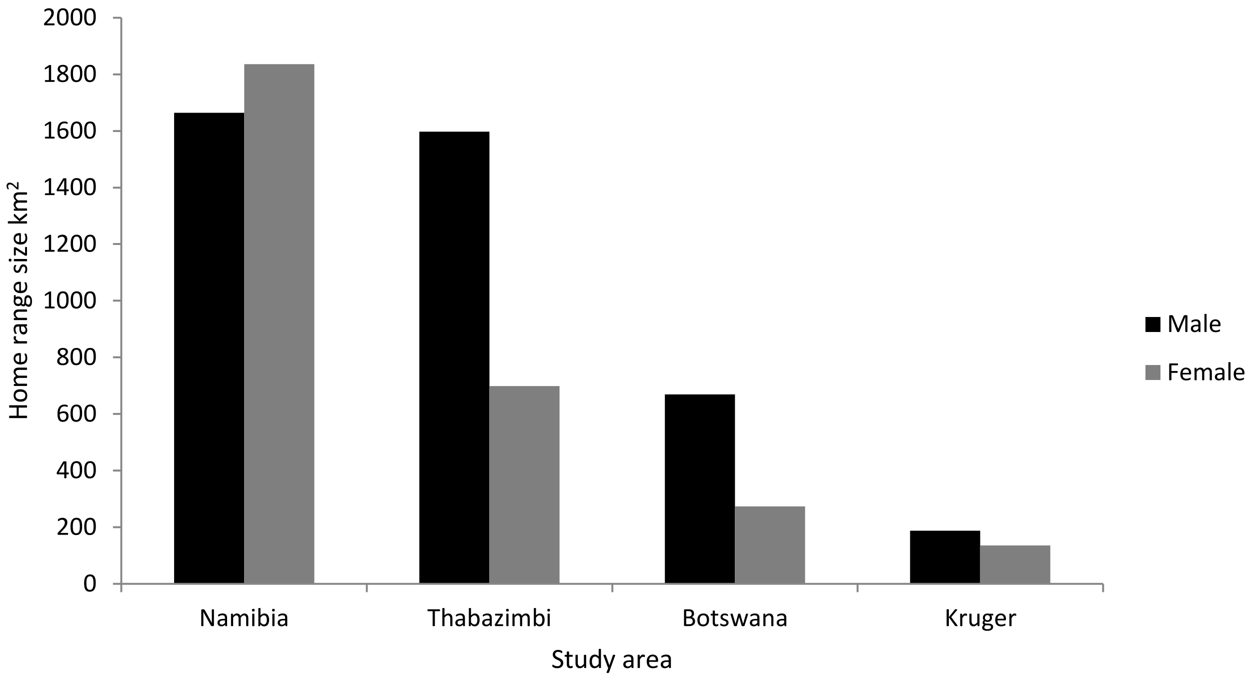

Figure 4.4: Comparison of mean male and female cheetah home ranges sizes across study areas in southern Africa. Namibia (Marker *et al.* 2007), Botswana (Houser *et al.* 2009) and Kruger (Broomhall *et al.* 2003) using 95MCPs and Thabazimbi using MCPs.

4.6. DISCUSSION

4.6.1 Sample sizes

Owing to the low trapping success of 278 trap nights per cheetah our sample size was low. The data collected did not allow for analysis of seasonal range use as only the coalition of two males were monitored for longer than one year. However, this study is still valuable in assessing cheetah movement in a ranching area and provides new information to assist conservation practitioners in conflict mitigation and conservation researchers on the effort required to derive robust home range estimates for cheetahs (*ca* 343 locations).

4.6.2 Home range sizes and implications for conservation

Cheetahs in Thabazimbi have large home ranges similar to cheetahs outside protected areas in other southern Africa countries. All studies on cheetahs outside protected areas show larger home ranges than cheetahs in the Kruger National Park (Figure 4.4). Home ranges were generally larger than the average ranch size of 18 km^2 with the average 95UD for all cheetahs covering approximately 18 properties. The average area of 12% of core utilisation in relation to the 95UD in this study comprised similar percentages to those found in other studies in southern Africa: Namibia (average 13.9%; Marker *et al.* 2007), Botswana (males 11%, females 10%; Houser *et al.* 2009) and Kruger (average 13%; Broomhall *et al.* 2003) (Figure 4.4), despite the large variation in home range sizes recorded between the studies. The reason for this is unknown and warrants further investigation.

The average size of the 50UDs for all cheetahs in this study is 42 km^2 (Table 1) and is more than twice the size of the mean property size in the study area. The largest MCP was 2 761.8 km^2 for a male cheetah, this cheetah also had the second largest 95UD of all cheetahs. This is probably because he was a young male and dispersing from his maternal range. He moved over a large area and was eventually shot *ca* 78km from the capture site. The coalition of two males had a very small 50UD, this was centred on a property that had a large area of relatively open vegetation where plains game congregated at an artificial feeding site. The landowner of the property in which the 50UD was focussed was fortunately cheetah friendly (pers. obs.) and some anti-predation measures were taken to prevent excessive damage to the prey population. Predator-proof camps were constructed for a breeding project for expensive antelope types, these camps would have been constructed regardless of the cheetahs' presence to eliminate predation by other carnivores. The camps did present a problem in the form of small artificial watering point outside one of the camps. Antelope would congregate around the water point and the cheetahs chased the herds into the fence on a few occasions. This resulted in several antelope being injured and the fence getting damaged. This was finally resolved by closing the small water point.

The two male coalition was the longest monitored in the study and while their home range appeared to reach an asymptote the last few GPS fixes showed an increase in the range size. This could be explained by the death of the coalition partner which has been shown to result in an increase in range by the remaining cheetah (Caro 1994; Marker *et al.* 2007).

Cheetahs did not limit their movement to one individual property and moved over large areas as is generally typical for cheetahs in savannah habitats. This is despite the estimated high abundance of food and water, sedentary prey and the lack of intra-guild competition. The large home ranges of cheetahs in the Serengeti (>800 km^2 females and >777 km^2 males; Caro 1994) and the Kalahari (>320 km^2; Mills 1998) could be due to prey mobility; while the smaller ranges in

Matusadona (<100 km^2) could be due to prey congregating on the foreshore grassland (Purchase & du Toit 2000). However, patchy distribution of suitable hunting habitat could drive large range use, and especially in felids, suitable hunting habitat may influence range size more than prey availability (Kruuk 1986). Cheetah movements in woodland areas are influenced by the search for more open habitat suitable for hunting (Hunter 1998). This could be the case in Thabazimbi as the bush is dense and open areas are scarce. The areas where the male coalitions centred their movement were previously ploughed, open grassland habitats in contrast to the hard boundaries of the surrounding densely wooded areas (pers obs.).

With the data available and no data on prey numbers and distribution, it is not known what drives the large range use of cheetahs in Thabazimbi. However, this study does provide useful information on the movement of cheetahs and shows that generally, cheetahs do not limit their movement to one property, thus causing excessive damage to the prey base on individual properties. However, there may be cases, like the two male coalition, where cheetahs do have small areas of core utilisation that could result in escalated conflict.

The patchy distribution of hunting habitat could also explain why cheetahs outside protected areas have larger ranges than cheetahs in Kruger. Ranching areas are prone to being over utilised for long periods of time and as a result the vegetation becomes encroached. This makes more open areas sought after as hunting habitat for cheetahs. Additionally cheetahs outside protected areas are affected by human disturbance that could require them to move larger distances to avoid conflict (Houser *et al.* 2009). It is likely that the large ranges of cheetahs outside protected areas are driven by the search for suitable habitat in an encroached environment and by human avoidance where cheetahs in Kruger have other range use drivers.

4.6.3 Survival of collared cheetahs

In this study, 44% of the collared cheetahs were shot by landowners while in Botswana 55% of collared cheetahs were shot (Houser *et al.* 2009). These high levels of persecution highlight the need for effective conflict mitigation projects outside protected areas as high levels of human-induced mortality could outweigh the advantages of a lack of intra-guild completion and a plentiful food and water resource. Most of the Southern Africa's cheetah population and distribution range occurs outside protected areas with approximately 22% (258 264 km^2 of 1 170 479 km^2) of cheetah range being protected and 23% (1 460 of 6 260) of cheetahs occurring inside protected areas (IUCN/SSC 2007), conflict can pose a significant challenge to the survival of the species.

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CHAPTER 5: Survival of cheetahs relocated from ranchland to fenced protected areas in South Africa

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5.1 ABSTRACT

In South Africa, wildlife can be privately owned and utilized for economic gain, with the consequent formation of thousands of wildlife ranches that are stocked with wildlife for the main purpose of hunting and live sale. When predators prey on antelope, the economic value attached to wildlife results in conflict. The cheetah *Acinonyx jubatus* is protected by legislation in South Africa, and cheetahs have thus been illegally shot and trapped in an attempt to reduce losses. A compensation–relocation programme for "problem" cheetahs was therefore initiated in South Africa by landowners, conservation officials and biologists; this programme allowed landowners to legally capture "damage-causing" cheetahs on their property for relocation into fenced protected areas. Trapped cheetahs were temporarily placed in a specially designed holding facility to habituate them to humans to facilitate monitoring and future viewing for ecotourism. Cheetahs were released into approved reserves using a soft-release method and were subsequently monitored. A total of 29 reserves and 189 cheetahs (92 adults: 59 males and 33 females, plus 94 cubs born on the reserves) were included in the survival analyses using the Kaplan-Meier (product limit) estimator with staggered entry. The mean annual survivorship for all cheetahs, including cubs born in this study, was 82.8%. The final survivorship value for all adult cheetahs was 0.23 and for cubs was 0.04. Cubs had significantly higher survival on reserves where other competing predators were absent. The median survival time was 38 months for adult males and more than 53 months for adult females, which is higher than the corresponding 17 months for adult males and 8 months for adult females on Namibian ranchland.

5.2 INTRODUCTION

5.2.1 Cheetahs and landuse in South Africa

The land use system in South Africa is unique in Africa in that land and wildlife can be privately owned and utilized for commercial purposes (Benson 1991; Lindsey *et al.* 2009). This has resulted in more than 10 000 000 ha of land being fenced to form more than 5 000 wildlife ranches that are stocked with various wildlife species for the main purpose of sport hunting (Eloff 2002). Wildlife is therefore consumptively utilized for economic gain by landowners, which provides concomitant habitat conservation (Hayward 2005). Lions *Panthera leo* and spotted hyaenas *Crocuta crocuta* have been extirpated from most ranchlands in South Africa, but leopards *Panthera pardus*, cheetahs *Acinonyx jubatus* and brown hyaenas *Hyaena brunnea* still persist

(Wilson 2006). In the Thabazimbi district, the mean ranch size is 1800 ha and the ranches are enclosed in game fencing, which is not predator proof (Wilson 2006), allowing predators to move either under or over the fences. Large predators can only be legally reintroduced onto a property when, among other considerations, predator-proof fencing has been erected. This means that only larger properties are able to sustain confined large predators like lions and spotted hyaenas, and thus the average wildlife ranch will not be able to benefit from their value as trophy animals. Additionally, lions pose a threat to ranch staff, who work mostly on foot and unarmed, so their presence is not desired. For these reasons, only leopards, cheetahs and brown hyaenas persist on ranchland in South Africa.

In some areas, cheetahs may fare better outside than inside conservation areas, owing to the lack of intra-guild competition (Laurenson 1995). Additionally, prey species on wildlife ranches are often maintained at artificially high densities (van der Waal & Dekker 2000), by means of supplementary feeding and water provisioning, which further improves conditions for cheetahs in these areas. While ecological conditions may theoretically favour cheetahs outside reserves, conflict with landowners frequently occurs owing to the perceived threat of cheetahs to ungulate populations and domestic stock (Marker 2002; Wilson 2006). This is exacerbated when ranchers stock expensive rare or endangered antelope or rare colour variations, e.g. black impala *Aepyceros melampus* or white blesbok *Damaliscus pygargus phillipsi* (K.M., unpublished data). This often results in landowners illegally shooting, trapping and removing cheetahs from their land (K.M., unpublished data).

There is a booming non-consumptive, photographic ecotourism market in South Africa, which has resulted in many privately owned reserves being established. In order to attract tourists, these reserves are reintroducing a diverse range of species from antelope to the Big Five (lion, leopard, elephant *Loxodonta africana*, African buffalo *Syncerus caffer* and white rhinoceros *Ceratotherium simum*). Such reserves find great economic benefit from the presence of cheetahs on their property (Lindsey *et al.* 2009).

5.2.2 Cheetah relocation project

In 2000, a group of landowners from the Thabazimbi district in the western part of South Africa's Limpopo province (Figure 5.1) approached the then De Wildt Cheetah and Wildlife Trust looking for solutions to the conflict between landowners and cheetahs. As a result, the National Cheetah

Management Program (now known as the National Cheetah Conservation Forum of South Africa) was formed and included most role-players in South Africa who had an interest in cheetahs, from landowners to conservation officials and researchers. Several issues were discussed around the conflict, and a compensation–relocation programme was initiated as one of the short-term methods of reducing conflict while ensuring cheetah survival.

The compensation–relocation programme made legal provision for landowners, who were experiencing problems with cheetah predation, to trap them live rather than using lethal control methods. The landowner would then be compensated by a pre-determined amount (currently ZAR 10 000—approximately US$ 1 500) per cheetah. The cheetah would then be relocated to a conservation reserve in South Africa where cheetahs were required for ecotourism purposes. The relocation venue would then pay a minimum donation (currently ZAR 15 000—approximately US$ 2 200) for the cheetah. The ZAR 5 000 (approximately US$ 700) excess would be used to cover any incidental and holding costs for the cheetahs.

5.2.3 Relocation procedure

In order to prevent some of the problems that are common to relocations, the cheetahs are relocated only into fenced protected areas. This ensures that they are not able to return to the site of capture (Hunter 1998) or to become problem animals in the relocation area as occurs in many relocation programmes (Linnell *et al.* 1997). Additionally, all releases were soft releases, which further increase the chances of success (Hunter 1998; Moehrenschlager & Somers 2004).

5.2.4 Relocation in response to conflict

Finally, this compensation–relocation programme is not seen as a long-term solution to conflict, but rather as a short-term method of buying some time while other mitigation measures, such as education, improved livestock husbandry practices, research and non-lethal damage prevention are implemented. While in some cases landowners trapped cheetahs specifically for the financial benefit of compensation, in other cases cheetahs that would otherwise have been killed were made available for relocation owing to the financial gain. It is not possible to quantify how many cheetahs would have been killed or would not have been trapped if compensation was not offered.

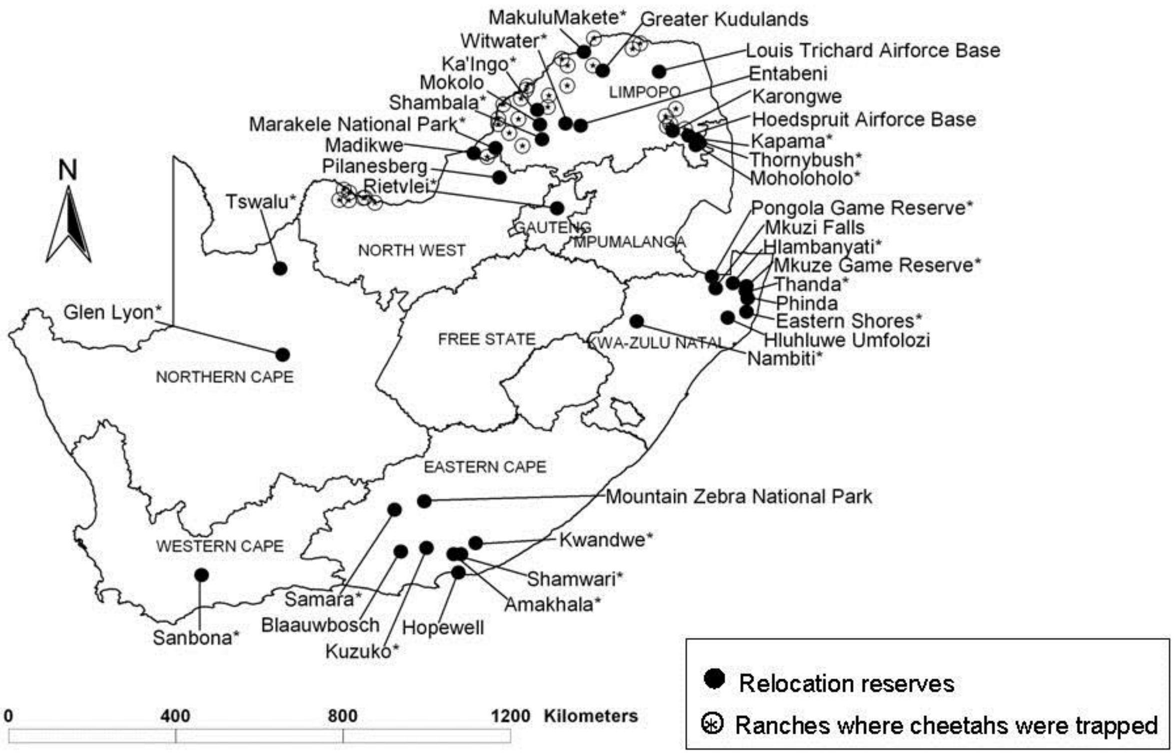


Figure 5.1: Locations where cheetahs were trapped, as well as relocation reserves in South Africa. Reserves marked with an asterisk were included in the analyses. Other reserves were omitted either because no data were supplied or because relocations began after the start of data analysis.

Trapping cheetahs on ranchland is not easy—it is time consuming and labour intensive. It requires investigation into a good trapping site, chopping down trees to build a boma, obtaining and daily feeding a goat if live bait is used, maintenance of the trap and trap time lost in capturing non-target animals. Even then, there is still no guarantee that the cheetah will be caught. In a study on ranchland in the Thabazimbi district, it took approximately 1 500 trap nights to trap five cheetahs (Marnewick & Cilliers 2006). Thus, many ranchers feel that it is not worth the effort setting traps and maintaining them if they are not going to receive any benefit from trapping the cheetah; they feel that shooting is cheaper and quicker, with immediate results and some sense of satisfaction. In contrast to this, other ranchers are happy to leave cheetahs on their ranches because they know that they can obtain help if they feel that the cheetahs can no longer be tolerated. The above demonstrates that there are several issues of concern in this compensation–relocation programme pertaining to conservation principles and long-term sustainability. Nonetheless, from the human perspective, this has encouraged cooperation from landowners, who often feel conflicted with and marginalized by predator conservationists and governmental authorities.

5.2.5 Historical cheetah relocations

Previously, several attempts have been made to relocate cheetahs from ranchlands to reserves. In Zimbabwe, cheetahs were successfully relocated from ranches to Matusadona National Park (Purchase & Vhurumuku 2006). A similar relocation project in Suikerbosrand Nature Reserve in South Africa (Pettifer 1981) was less successful. Here, eight adult cheetahs were released onto the 13 400 ha reserve over a period of 15 months. The population had grown to approximately 24 individuals after two years, and the prey population became depleted owing to overpopulation of cheetahs (Hayward *et al.* 2007c), and the prey then had to be supplemented. The rapid increase of the cheetah population was attributed to the absence of other large, competing predators.

Cheetahs were also relocated from Namibian ranchlands to Pilanesberg and Madikwe Game Reserves in South Africa (Hofmeyr & van Dyk 1998). At Pilanesberg, seven cheetahs were reintroduced in 1981/1982 from the De Wildt Cheetah Breeding Centre, but most of these were later removed to protect antelope populations. A further 16 cheetahs were introduced from Namibia in 1995/1996, after which the population remained stable at 17 individuals (Hofmeyr & van Dyk 1998) before rising to 20 by 2001 (van Dyk & Slotow 2003). Nineteen cheetahs were reintroduced to Madikwe from 1994. However, only four reintroduced individuals still survived in 1998 (Hofmeyr & van Dyk 1998).

Cheetahs that were relocated from Namibia to the Zambezi National Park in Zambia (Anonymous, 1995) all died after release, owing to snaring and conflict with other cheetahs. Cheetahs were reintroduced into Phinda in 1992 (Hunter 1998) and into several other reserves in the Eastern Cape of South Africa since 2000 (Hayward *et al.* 2007b), many of which are included in this study.

5.3 METHODS

5.3.1 Trapping

Perceptions of the landowner are often stronger than reality and can strongly influence attitudes towards predation (Mech 1981). Negative attitudes towards large predators are normally motivated by fear of economic loss (Kellert 1985; Marker 2002) as opposed to actual losses. Therefore, as it was not possible to quantify actual losses on every ranch, in situations where the landowner could not be convinced otherwise, cheetahs that were perceived to be causing damage were trapped on cattle and wildlife ranches in Limpopo and the North West Province (Figure 5.1.). Cheetahs were trapped by landowners, conservation officials and field staff of the members of the National Cheetah Conservation Forum of South Africa. Where landowners were trapping independently, it was impossible to attempt to convince them to leave the cheetahs on the property.

Double-door, box trap cages were mostly used (Marnewick & Cilliers 2006). De Wildt occasionally received cheetahs that had been trapped by landowners using undesirable methods that led to the cheetahs being injured. If these injuries were considered severe enough to prevent relocation of the cheetah, then the cheetah was placed in a reputable captive-breeding centre (e.g. De Wildt Cheetah Breeding Centre, Cango Wildlife Ranch or Hoedspruit Centre for Endangered Species). Such injuries included broken jaws, loss of limbs or part of limbs and, in some cases, broken bones that did not recover well after veterinary care. Some cheetahs were released and survived after pinning and plating of bones, blindness in one eye, or after surgery on lacerations caused by snares and dogs during capture. However, the eventual hunting success seems to be dependent on the specific injury and the degree of recovery of the cheetah.

Trapped cheetahs were then transported in a crate to one of three holding facilities located in the Limpopo province. De Wildt Shingwedzi near Bela-Bela is now the main holding facility as it is specifically designed to hold wild cheetahs, is separate from any captive cheetahs and has staff experienced in managing wild cheetahs. The cheetahs were usually not immobilized or sedated for transportation, but were simply moved from the capture cage into the crate. Immobilization was used only if it was not possible to remove the cheetah from the capture cage.

5.3.2 Holding

The holding facility was specifically designed to hold wild cheetahs (Figure 5.2). As the cheetahs were not habituated to humans, the facility was intentionally small in size, with the limited amount of space preventing injuries when the cheetahs tried to flee from human presence during holding. Unable to build up enough speed in the small camps, the cheetahs could not hurt themselves by running into fences. To habituate the cheetahs to human activities and vehicles for both viewing and monitoring purposes, the holding facility was situated near a major road on the ranch. While in captivity, the cheetahs were fed daily and became accustomed to humans. This practice contrasts with plans for the Amur leopard (Christie 2009), because the economic value of the cheetahs drives their conservation at the reintroduction sites, whereas the leopards will be at risk from human poaching at their reintroduction sites.

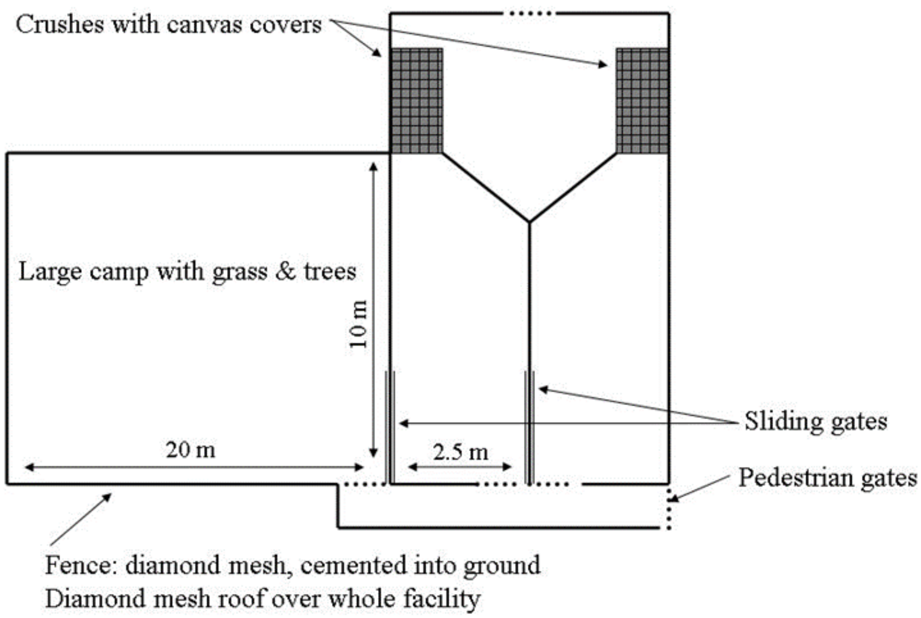


Figure 5.2: Schematic aerial view of the temporary holding facility for wild cheetahs.

Cheetahs were held here for approximately 3–4 months, with the time dependent on the availability of relocation venues, how habituated the cheetahs became and any injuries that needed attention.

Prior to relocation to a suitable reserve, the cheetahs were immobilized and fitted with a radio telemetry collar and a microchip implant. Measurements and bio-samples were taken and a general health check was carried out by qualified veterinarians. If females were released onto reserves with males, they were sometimes contracepted for the first year using Suprelorin (Peptech Animal Health, Sydney, Australia; Bertschinger *et al.* 2002; Bertschinger *et al.* 2006) to prevent unwanted growth of the cheetah population in confined reserves. Such unwanted growth is the biggest problem faced in managing many reintroduced predators once the agents of their decline have been removed (Hayward *et al.* 2007c).

Males received as individuals were bonded artificially to form coalitions as this is believed to be more suitable for relocation purposes (Hunter 1998). Males were first put in adjoining camps (Figure 5.2) to allow them to become accustomed to each other. Once they were observed lying next to each other, either side of the fence, and showing no obvious signs of aggression, the sliding gate between the two camps was opened. They were further monitored and, if there was no fighting over food, the bonding was considered successful. Once the cheetahs were habituated to the presence of humans and vehicles, and the male groups formed, the sliding gate was opened into the larger camp (200 m^2), where they remained until relocated to a reserve.

The cheetahs were again transported in crates without drugs to the relocation reserve, where they were released into a suitably fenced holding boma of approximately 1 ha in size. If males and females were to be released on the same reserve, they were held in separate but adjoining bomas in order to become accustomed to each other through the fence. If possible, the female was released first to allow her time to settle into a range before the males were released.

The cheetahs were monitored several times per day (ideally for several minutes at a time) to further habituate the cheetahs to humans and vehicles. Tourist game drives were taken past the boma to allow the cheetahs to habituate to the game-viewing vehicles. If the relocation reserve wanted to view their cheetahs on foot after release, it was recommended that reserve staff spend time with the cheetahs in the boma on foot to ensure that they were fully habituated before release. Many reserves obtained very relaxed cheetahs by allowing a staff member to spend several hours at a time in the boma working on a lap top or reading a book out loud to accustom the cheetahs to human voices.

Although wild cheetahs pose little threat to adult humans, staff were urged to always carry a stick whilst on foot in the boma and were told to never sit down on the ground and to always respect the comfort zone of the cheetah. While it may be irregular to habituate other large carnivores to humans on foot, cheetahs are unique in that they can be safely approached and observed. Additionally, it is necessary to have the cheetahs habituated for effective monitoring as, on many reserves, it is not possible to obtain visuals from a vehicle if the cat has moved off the road. Habituated cheetahs are also easier to manage in case of injury or escape. The first release of wild cheetahs onto a reserve in this project was done without habituating the cheetahs and, after release, it was not possible to obtain visuals of the cheetahs. Additionally, one of the reasons that reserves introduce cheetahs is for tourism. Cheetahs can make excellent viewing animals, but need to be habituated to humans if walking safaris are to be offered.

The frequency of feeding was gradually decreased from daily to weekly (as is usual in wild cheetahs). It was recommended to the managers that, when feeding, a whistle should be blown prior to the cheetahs being fed. This resulted in the cheetah being conditioned to the sight of a human *and* the sound of a whistle equating to food being given. Human presence, without the whistle being blown, did not result in food for the cheetah. This practice desensitized the cheetah to human presence by beneficial association. It also conditioned them to only expect food when both stimuli (human and whistle) were present (S. McKay, per comm.[1]). The whistle can also be useful after release for management reasons, such as recapture after escape or darting to administer veterinary care (Hayward *et al.* 2007a). If a cheetah heard a whistle, it would be inclined to look for a human being in order to complete the conditioned behaviour sequence and thus receive food.

Relocation venues needed to comply with certain criteria before being considered for releases. Such criteria included an ecological management plan, and this required proof that the reserve could support the cheetahs for a minimum of two years without supplementing the prey population. A model was used to quantify this ecological management plan; stocking rates of the

[1] Shannon McKay, Animal Behaviour Consultant, e-mail: chairperson@animal-behaviour.org.za

reserve, as well as consumption rates of cheetahs, preferred prey availability and prey growth rates were included (J.W. Kruger, unpublished data). The precision of this model may not be satisfactory (as reserves as small as 1 500 ha have been included), so predicting the carrying capacity of a reserve based on the biomass of preferred prey should provide more robust estimates of the sustainability of a reintroduced cheetah population (Hayward *et al.* 2007c). The reserve must be fenced according to specifications and a monitoring programme must be in place. Additionally, the relevant permits and permissions must be obtained from government, and a memorandum of understanding must be signed which includes agreements to monitoring, confirmation that the cheetahs remain wild and are not held in small camps, and confirmation that they will not be sold or hunted. Only two reserves had cheetahs from previous introductions and reserve was omitted from the analyses owing to lack of feedback from managers. Dominant competitors (lions and/or spotted hyaenas) were present on 13 of the 23 reserves included in the data analyses.

5.3.3 Release

The cheetahs were held in bomas for at least three months before they were released onto the reserve. If males and females were to be released, females were released first to give them the opportunity to settle into the range before the males were released. During the release, cheetahs were lured out of the boma by dragging an antelope carcass or hind-quarter on a piece of rope until the cheetah was far enough away to allow the gate to be closed without frightening the cheetah. Although it is feasible to open the gate and let the cheetahs leave at their own accord, the cats were lured out to reduce the risk of other animals entering the open boma and possibly injuring or killing the confined cheetahs.

After release, the cheetahs were closely monitored using telemetry for the first few weeks until reserve staff were satisfied that the cheetahs had settled in and were hunting effectively. If they were not hunting, supplementary feeding was considered. This was seldom necessary and only occurred if the cheetah had not eaten for a period of approximately seven days; the timing varied according to the individual cheetah and how well it retained condition. If supplementary feeding took place, only a small amount of food (e.g. a hind-quarter) was fed in order to maintain condition and energy levels, but to leave the cat hungry. It was recommended that monitoring should continue on a daily basis after release.

5.3.4 Data collection

Basic data on release and death dates (accurate to the nearest month) for the Kaplan-Meier analyses were collected from relocation reserve managers; this provided information for 29 reserves and 186 cheetahs for a complete five year period (Figure 5.1). Many reserves offered this information for all their cheetahs, including those that had been relocated privately between reserves and not through the compensation–relocation programme—and these were also included in the analyses. Information collected included month of release and month of death or censoring if applicable. For cubs born on reserves, managers were asked to report the month in which the cubs were born and how many cubs there were, and also to note the months in which cubs were seen to have died or gone missing. Females were generally carefully monitored, and managers were able to give data on cubs from a young age (normally still in the lair).

5.3.5 Data analyses

Because the cheetahs were not all reintroduced at the same time, but rather over a period of several years, survivorship was measured using the Kaplan-Meier estimator (product limit estimator) with staggered entry (Pollock *et al.* 1989). This allows for the staggered entry of animals and compares survival functions using the log rank test (χ^2). The Kaplan-Meier estimator also allows for inclusion of data from censored animals (e.g. those who escaped and could not be found or whose fates were unknown). Log rank tests were used to compare the overall survival curves obtained from the Kaplan-Meier analyses (Pollock *et al.* 1989). The Z-test was used to compare survivorship values at the end of the six year study period. Median survival times were estimated as the smallest survival time for which the survivorship function was less than or equal to 0.5 (i.e. the value on the *x*-axis where the *y*-axis value is equal to 0.5).

5.4 RESULTS

5.4.1 Capture of cheetahs

From 2000 until the end of 2006, 136 cheetahs were received through the compensation–relocation programme; of these, 20 individuals were retained in captivity as they were either too young (unweaned cubs) to be released or were injured (e.g. badly broken limbs, broken jaws, etc.) and deemed unfit for release. Methods are currently being developed to rehabilitate young cheetahs to ensure that they seldom end up in captivity (K.M. unpublished data).

5.4.2 Cheetah and reserve data

Sufficient data for the Kaplan-Meier analyses were obtained for 186 cheetahs, of which 92 were adults (59 males and 33 females) and 94 were cubs born on reserves. Owing to inaccurate information or to a lack of response from the reserves, 35 cheetahs were omitted from the analyses. These cheetahs were relocated in the same manner as all the other cheetahs in the study, and it is not likely that the managers' non-response to requests for data could bias survival of cheetahs. The fate of most of these cheetahs is known, and some of the omitted cheetahs are on reserves where monitoring is excellent—however, accurate information for analyses was not able to be obtained.

The cubs were born from 23 females, of which two had two litters each. Litter size ranged from two to seven cubs per litter (mean=4.5 ± 1.87). The litter sizes could have been underestimated in some cases as some cubs could have died before emerging from the lair. However, because most of these relocated cheetahs were thoroughly habituated to humans on foot, monitoring staff were often able to observe cubs from a very young age. In the Serengeti, the litter size ranged between one and six cubs (mean=3.5 ± 1.87) (Laurenson 1995).

The relocations from which data were collected took place from September 2000 to September 2007. The relocation reserves ranged in size from 1 500 ha to 70 000 ha, with a mean reserve size of approximately 36 000 ha.

5.4.3 Cost of relocations

While the principal aim of the relocation programme is for it to be financially self-sustaining (with funds paid out and paid into the compensation fund), this is not the case. For a normal relocation, where the cheetah is not injured or ill and does not require any additional veterinary attention, the cost is roughly ZAR 18 250 (approximately US$ 2 700). These costs include the cost of food, collars, general veterinary care, permits, staff salaries and transportation. Excluded are the fixed costs of building and maintaining the holding facilities, fencing the protected areas and any costs incurred at the relocation venue. The ZAR 5 000 deficit from the relocation venue donation contributes to these expenses, making the actual cost approximately ZAR 13 250 (approximately US$ 1 900). These costs soar when the cheetah requires surgery, or when the cheetah is received at a young age, is held for extended periods and needs to go through a re-wilding programme. The costs of the actual capture are also not included: capture cages, labour, bait animals and their food, health care, etc.

5.4.4 Survival of relocated cheetahs

Survivorship was determined for each sex, age group and year and for cheetahs with and without the presence of other large predators (Table 5.1; Figure 5.3a and 5.3b). Cheetahs survived significantly longer at sites where other competing predators (lions and/or spotted hyaenas) were not present than at sites where they were sympatric (Table 5.2). There was a significantly higher final survivorship value for adults when compared to cubs, and adult female cheetahs survived significantly longer than males (Table 5.2).

The mean annual survivorship for all cheetahs, including cubs born in this study, was 0.14 for the complete five year period of the study, and a cheetah in the reintroduced population had an 82.8% chance of surviving for one year. Only adult cheetahs were reintroduced, and the final survivorship value for all adult cheetahs was 0.23 (95% CI = 0.1707−0.2869). This means that any adult cheetah released as part of the relocation programme has a 23% chance of surviving for five years or an 84.6% chance of surviving for one year.

A highly significant difference in cheetah survivorship existed between the different complete years ($Z = -21.47$; df = 5; $p < 0.001$). Survivorship was lowest during 2003, owing to eight cheetahs being placed on a reserve where six of them were killed by lions. During the same year, three cheetahs escaped from another reserve and died, and four other cheetahs were not monitored and were classified as censored according to the Kaplan-Meier method (censored animals are those who escaped and could not be found, or whose fates were unknown).

The first cubs from reintroduced parents were born in February 2002. The final survivorship value for cubs was 0.04 (95% CI = 0.0327−0.0570), which meant that cubs born from relocated cheetahs have a 4% chance of surviving for five years or an 80.8% chance of surviving for one year. However, the final survivorship value for cubs on reserves where competing predators were absent was 0.76 (95% CI = 0.6034−0.9148), compared to a final survivorship value of 0.04 (95% CI = 0.0228−0.0474) when competitors were present. This highly significant difference ($Z = 9.09$; df = 1; $p < 0.01$) highlights the impact of dominant competitors on cub survivorship, with an annual survivorship for cubs without competitors of 95.2% and with competitors of 80.8%. Importantly, cub survivorship is not as important as adult survivorship in long-term population persistence (Crooks *et al.* 1998), and all of the reintroduced populations still persisted seven years after the reintroduction programme began. In one population, all but one of the cheetahs were killed by lions, and management decided not to introduce additional cheetahs from ranchlands as they expected that the cheetahs would meet the same fate. The lions here were captive bred—which may have contributed to the problem. However, cheetahs have subsequently been introduced into the study area from other reserves where lions did occur, and these cheetahs are reportedly doing well.

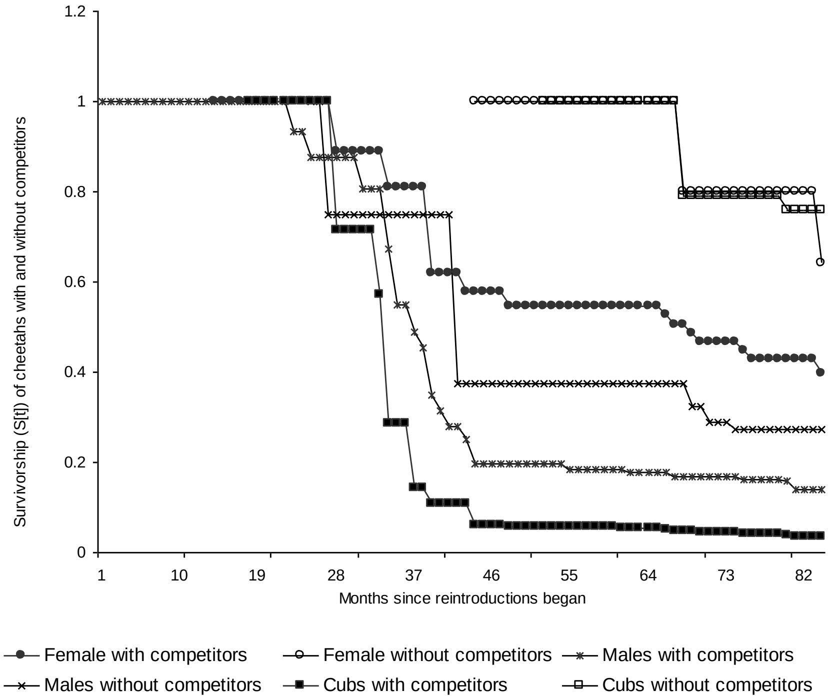
Cheetah cub survival increases dramatically with increase in the age of the cubs. Here, cheetah cubs were not able to be accurately divided into age groups, which could result in the survival values being overestimated. In studies elsewhere, it was found that estimating cub survival after emergence can inflate survival by up to 300% and estimating survival two weeks after emergence can overestimate survival by another 150%. (S. Durant, pers comm.). Ideally, cub survival should be analysed in age-specific analyses such as mixed linear models (Durant *et al.* 2004). However, such models do not take into consideration the staggered entry of the reintroductions.

5.4.5 Comparison of survivorship between cheetah populations

The mean annual juvenile survival in the Serengeti was estimated at 0.10 (Kelly & Durant 2000). This was far lower than that for cubs from reintroduced parents where other competitors were present on the reserve (80.8% annual survivorship; Table 5.1), which is surprising given that cub survival is so low in the Serengeti (Laurenson 1994). However, Laurenson (1994) did count cubs in the den and monitored them intensively thereafter, which could account for the differences noted between the two studies.

The median survival time for adult males in our study was 38 months and for adult females was more than 53 months (50% survivorship had not yet been achieved for adult females; Table 5.1). On Namibian ranchlands, the median survival for marked adult males was approximately 17 months and for females was eight months (Marker *et al.* 2003). (The median survival time of Namibian cheetahs was obtained from Figure 8 in the source by estimating the shortest survival time for which the survivorship function was less than or equal to 0.5—i.e. the value on the *x*-axis where the *y*-axis value is equal to 0.5—as used here). On Namibian ranchland, competition with other large carnivores is minimal, whereas persecution from landowners is the main threat (Marker-Krause *et al.* 1996).

a



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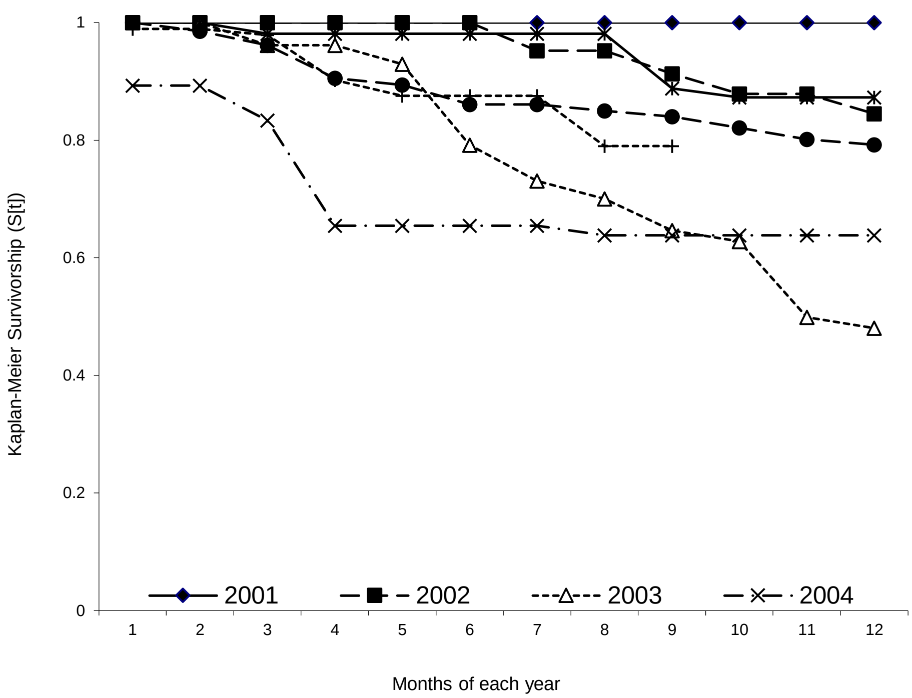

Figure 5.3 a & b: Kaplain-Meier survivorship of cheetahs on relocation reserves (a) with and without other competing predators and (b) for different years.

Table 5.1: Kaplan-Meier survivorship estimates with variance and median survival time in months for various age and sex classes of relocated cheetahs and years of relocation. Annual survivorship is the percentage chance that a reintroduced animal will survive for 1 year. Cubs are those that were born on reserves as a result of relocated cheetahs.

Group	Sample size n	Survivorship for 5-year study period	Variance	Median survival time (months)	Annual survivorship, %
All adults	92	0.23	0.001	28	84.6
Females	33	0.45	0.005	>53 (50% survivorship not reached)	89.0
Males	59	0.19	0.001	38	83.8
All individuals (males, females and cubs)	168	0.14	0.000	38	82.8
With competitors	106	0.25	0.001	39	85.0
Without competitors	62	0.26	0.001	41	85.2
All cubs	94	0.04	0.000	16	80.8
With competitors	57	0.04	0.000	16	80.8
Without competitors	37	0.76	0.006	>36 (50% survivorship not reached)	95.2
All females	65	0.12	0.000	8	82.4
With competitors	44	0.40	0.004	54	88.0
Without competitors	21	0.64	0.011	>41 (50% survivorship not reached)	92.8
All males	103	0.12	0.000	37	82.4
With competitors	62	0.19	0.001	36	83.8
Without competitors	41	0.27	0.002	40	85.4
Year 2001		1	0.000	50% survivorship not reached	n/a
Year 2002		0.85	0.004	50% survivorship not reached	n/a
Year 2003		0.48	0.004	11	n/a
Year 2004		0.64	0.003	50% survivorship not reached	n/a
Year 2005		0.87	0.002	50% survivorship not reached	n/a
Year 2006		0.79	0.002	50% survivorship not reached	n/a

n/a, invalid assessment.

Table 5.2: Comparison of the survival of reintroduced cheetahs analysed by age, sex, presence of dominant competitors and year of reintroduction.

Category	Z-test results				Log rank test results		
	Z statistic	Z squared	Degrees of freedom, df	Probability	Chi-square	Degrees of freedom, df	Probability
Years	−21.47	460.78	5	<0.001			
Adults versus cubs	6.02	36.20	1	<0.001	164.8362	83	<0.001
Males versus females	−0.19	0.04	1	0.849	113.1246	83	>0.10
Females with versus without competitors	−1.99	3.95	1	0.047	110.7239	70	<0.001
Males with versus without competitors	−1.45	2.10	1	0.147	218.1531	83	<0.001
Cubs with versus without competitors	9.09	82.56	1	<0.001	134.1494	67	<0.001
All cheetahs with versus without competitors	−0.11	0.01	1	0.912	268.6893	83	<0.001

The lowest median survival time (eight months) was for the total female group (including adults and cubs and in reserves both with and without competitors), which is the same as that recorded on Namibian ranchland for adult females. The highest median survival time (54 months) was for the same group of females but on reserves with competitors present; however, females on reserves without competitors had not yet reached a 50% survivorship after 41 months. Adult females generally had the highest survivorship value (S[t] = 0.45; 95% CI = 0.3105−0.5894). All females had higher survivorship values than all males, but this was not significantly different ($Z = -0.19$; df = 1; $p = 0.849$). There was also no significant difference between survival values of females and males in Namibia, although females also had higher survivorship (Marker *et al.* 2003). In the Serengeti, adult females had mean annual survival of 0.8516 (Durant *et al.* 2004), which is comparable to the female survival of 0.8960 obtained in this study. Serengeti males had a mean annual survival of 0.6837 (Durant *et al.* 2004), which is lower than the adult male survival of 0.83 obtained in this study.

Comparison of survival of cheetahs in different study areas is difficult and has some inherent problems including monitoring methods and intensity, age group classifications of cheetahs and different methods of data analyses.

5.5 DISCUSSION

5.5.1 Cheetah survival and lions

Our data show that cub survival on reserves where other large predators were present was lower than adult survivorship. This supports Laurenson's (1995) assertion that cub mortality in the Serengeti limits recruitment and that it may also limit recruitment in reintroduced populations where other large carnivores are present. Some authors have suggested that cub survivorship is not as important as adult survivorship for population persistence, however (Crooks *et al.* 1998). This reinforces Mills' (2005) view that high levels of cub mortality and intraguild predation are natural elements of cheetah population dynamics.

Reintroduced cheetahs originated from ranchland areas where other competing predators (lions and spotted hyaenas) were not present. It is possible that these females were naive to the dangers of competing predators and were thus not able to effectively protect their cubs. Additionally, cheetahs are thought to avoid competition by seeking out areas of "competition refuge" that have low lion and spotted hyaena densities (Durant 1998), which is more difficult in small, fenced protected areas like those studied here. Kelly & Durant (2000) predicted that cheetah populations would go extinct within 50 years when lion abundance was average or high but that cheetah populations could persist at low lion densities. At first glance, such a prediction appears to cause confusion as to how such an interaction evolved. However, the heterogeneity of African ecosystems would originally have supported diverse herbivore communities that would have favoured lions when their preferred prey were present, and cheetahs when their smaller preferred prey weight range was dominant (Hayward *et al.* 2007c). This becomes problematic for cheetah conservation today because many reserves are small or homogeneous, such that they lack refuges, or are stocked at artificially high densities to support tourist-attracting species, like lions.

5.5.2 Survival after release

A sudden decrease in cheetah survival was apparent between 20 and 40 months after reintroduction for all groups of cheetahs (Figure 5.3a), suggesting that this is a critical time in which cheetahs need to adapt to their environment in order to survive. This also supports the findings of Marker *et al.* (2003) that time spent in captivity does not affect survival. If it did, the cheetahs would be expected to die soon after release as most had been in captivity for several months by this stage.

In South Africa (this study), Namibia and the Serengeti, female cheetahs have higher survival rates than males, although this was not always significant. Caro (1994) attributed this lower male survival to intra-male aggression. Cheetahs have been killed by other cheetahs in this reintroduction programme when a coalition of males killed three cheetahs on one reserve (Hayward *et al.* 2007b). A coalition of three males is reported to have killed several cheetahs on Madikwe Game Reserve in the North West Province (M. Hofmeyr, pers comm.). However, most (n = 10) of the cheetahs killed by predators in this study were killed by lions (Table 5.3).

Several alternative methods can be used to define a successful reintroduction, but most of these definitions do not apply in small isolated populations of large predators, as in this study (Hayward *et al.* 2007b). This reintroduction programme is still young and no long-term success can be claimed as yet. However, in the short term, the same definition can be used as for the evaluation of success of predator reintroduction into confined reserves in the Eastern Cape of South Africa: a reintroduction is considered successful when a three year breeding population exists in which recruitment exceeds the adult death rate (Hayward *et al.* 2007b). Consequently, with the exception of the cheetah population that was reduced to one individual, all reintroductions described here are considered successful, at least in the short term, with females breeding and a general increase in the number of cheetahs in confined reserves. The real measure of success will be the long-term survival of these reintroduced populations.

Table 5.3: Causes of post-release death in relocated cheetahs broken down into age and sex categories.

	Male		Female		
Cause of death	Sub-adult	Adult	Sub-adult	Adult	Total
Natural	0	2	3	1	6
Predators	0	5	2	4	11
Unknown	0	1	0	1	2
Escape/missing	0	5	0	2	7
Disease	2	2	0	0	4
Other	1	1	1	0	3
Total	3	16	6	8	33
	19		14		

5.5.3 Implications for conservation

The challenge now is to manage these small isolated populations under one metapopulation management plan (Davies-Mostert *et al.* 2009). This will require the cooperation of all reserve owners and managers and nature conservation authorities. Alternatively, where several smaller reserves are clustered together, the possibility of dropping fences and managing the area as a single unit will further increase the long-term viability of reintroduced cheetah populations without excessive management. Larger areas may also remove some of the pressure on cheetahs as a result of the presence of lions and spotted hyaenas. Long-term permanent management, however, will be required for the conservation of cheetahs in fenced protected areas (Hayward *et al.* 2007a). A national cheetah DNA database for cheetahs in fenced conservation areas needs to be developed and maintained; this database will form the basis of a studbook which will allow reserve managers to intelligently swap cheetahs between reserves to ensure maintenance of genetic diversity (Hayward *et al.* 2007c). Incorporation of pelage patterns (Kelly 2001) in the studbook would minimize the need for intrusive management interventions aimed at simply identifying individuals requiring translocation (Hayward *et al.* 2007c). A studbook and organized metapopulation management plan are of vital importance to ensure long-term viability of this fragmented cheetah population in South Africa. This would require cooperation from all the reserves and would mean that this studbook should be consulted before any cheetahs are moved between reserves.

While the relocation of cheetahs is successful, relocation should not be seen as a solution to conflict on ranchlands. There is a large difference between adult cheetah survival on reserves without lions and adult cheetah survival on Namibian ranchland—with lower survival on ranchlands. Namibian ranchlands generally have no large predators present, so survival rates would be expected to be comparable to those on reserves without large predators, but this is not the case. This shows how detrimental persecution can be to the survival of cheetahs outside protected areas. Additionally, the removal of adult cheetahs has been shown to be more detrimental to the survival of the population than the removal of cubs (Crooks *et al.* 1998). Cheetahs removed from ranchland are mostly adults (this study; Marker *et al.* 2003) and often males which are trapped at scent-marking posts (McVittie 1979; Marker 2002; Wilson 2006). The effect of these removals on the source population on ranchlands must also be considered and weighed up against the benefits of the reintroductions and the likelihood of the captured individual surviving human persecution on the ranchland.

In this study, relocated cheetahs had a higher median survival time than cheetahs on Namibian ranchlands. No survival data are available for South African ranchlands, so a direct comparison is not possible. This difference in survival could suggest that ranchlands are not ideal conservation areas for cheetahs, as has been suggested by Laurenson (1995) and Kelly & Durant (2000). This also highlights the impact that human conflict can have on cheetah survival outside conservation areas. However, it must be considered that relocated cheetahs are given every possible opportunity to survive, including inoculations and veterinary care for injuries. Cheetahs on ranchlands have to contend with persecution, illegal hunting, illegal capture and trade (Marnewick *et al.* 2007), road accidents and disease.

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CHAPTER 6: SUMMARY AND CONCLUSIONS

6.1 INTRODUCTION

The aim of this concluding chapter is to summarise the finding of the thesis, to highlight further areas of study required and identify key conservation actions required for cheetahs *Acinonyx jubatus* and wild dogs *Lycaon pictus* in South Africa. Cheetahs and wild dogs are grouped together in this thesis as they are both wide ranging carnivores that occur at low densities, have overlapping distribution ranges and face similar threats. While the focus is on cheetahs and wild dogs it is likely that conservation action aimed at these two species will benefit other members of the carnivore guild that face threats due to persecution and habitat fragmentation.

6.2 HABITAT SUITABILITY AND CONNECTIVITY FOR CHEETAHS AND AFRICAN WILD DOGS IN SOUTH AFRICA

In South Africa, conservation planning for these two threatened large carnivores is hampered by a lack of national-level data on suitable habitat and connectivity. I used ecological niche models in MaxEnt (Phillips *et al.* 2006) and current flow models in Circuitscape (McRae and Shah 2009) to; 1) quantify current suitability habitat for cheetahs and wild dogs within South Africa and to identify important areas for their conservation and assisted range expansion; 2) identify important areas of connectivity between suitable habitat patches and 3) evaluate how effective the current protected network is in conserving suitable habitat for cheetahs and wild dogs. We found that a greater proportion of South Africa had suitable habitat for wild dogs than cheetahs. Overall about 21 410km^2 of South Africa had suitable habitat for both species. While the Kruger National Park and its bordering reserves were important for conserving suitable habitat for both species, the rest of the protected area system in South Africa was ineffective in capturing suitable habitat for both species. Through connectivity analysis we identified important areas of connectivity in the Limpopo province, along the western boundary of the Kruger National Park and in the Eastern Cape. Key areas for conservation action, range expansion and reintroduction included areas of Limpopo, KwaZulu-Natal (KZN) and the Eastern Cape Provinces. Dispersal areas between fenced populations in KZN and the Eastern Cape were identified that could allow for decreased management intensity and increased long-term sustainability of small isolated populations of both species.

While our models do show areas of suitable habitat and connectivity, one of the key limiting factors for carnivore movement is killing due to conflict (Woodroffe *et al.* 2007). The models are not able to simulate the effect of this and future conservation planning should investigate methods of doing this.

6.3 EVALUATING THE STATUS OF CHEETAHS AND AFRICAN WILD DOGS THROUGH TOURIST-BASED PHOTOGRAPHIC SURVEYS IN THE KRUGER NATIONAL PARK

The Kruger National Park is a stronghold for African wild dog and cheetah conservation in South Africa thus monitoring the status of these populations is important. Tourist photographic surveys have been used to evaluate the minimum number of wild dogs and cheetahs alive over the last two decades (Chapter 3). Photographic-based capture-recapture techniques for open populations were used on data collected during a survey done in 2008/9. Models were run for the park as a whole and per region (northern, central, southern). A total of 412 (329-495; SE 41.95) cheetahs and 151 (144-157; SE 3.21) wild dogs occur in the Kruger National Park. Cheetah capture probabilities were affected by time (number of entries) and sex, whereas wild dog capture probabilities were affected by the region of the park. When plotting the number of new individuals identified against the number of entries received, the addition of new wild dogs to the survey reached an asymptote at 210 entries, but cheetahs did not reach an asymptote. The cheetah population of Kruger appears to be healthy, while the wild dog population size and density are of concern. The importance of long-term monitoring to guide conservation action is highlighted as well as the effectiveness of tourist-based surveys for estimating population sizes through capture-recapture analyses.

This small size and apparent declining nature of the Kruger wild dog population is of concern as this is South Africa's largest protected population and for one of the key populations in Africa. This needs to be further investigated as well as the possibility that the Greater Kruger National Park is acting as a wild dog sink or ecological trap as has been shown in Hwange National Park in Zimbabwe (Van der Meer 2013).

6.4 RANGE USE OF CHEETAHS OUTSIDE PROTECTED AREAS IN SOUTH AFRICA

Protected areas are not always effective in conserving carnivores (Woodroffe & Ginsburg 1998). Many carnivore populations occur outside of protected areas where they are vulnerable to anthropogenic threats (Purvis *et al.* 2000; Cardillo *et al.* 2005). In South Africa most of the cheetah population lives outside protected areas along the northern border of the country. Lions and spotted hyaenas have been extirpated from these areas leaving the carnivore guild dominated by cheetahs, leopards and brown hyaenas. Land is privately owned and utilised for wildlife ranching, stock ranching or a combination thereof. The economic value attributed to prey species often leads to conflict between land owners and cheetahs. Many misperceptions exist on the spatial ecology of these cheetahs and these further exacerbate the conflict. To collect accurate and relevant data on the spatial use of cheetahs living in these areas, collars were fitted to nine cheetahs from September 2003 to July 2009 in the Thabazimbi area, Limpopo. Local Convex Hulls (αLoCoH) (Getz & Wilmers 2004; Getz *et al.* 2007) were used to determine home range sizes and 50 and 95 utilisation distributions (UDs) were calculated. Male 95UDs ranged from 121.5 km^2 to 607 km^2 while females ranged from 14.7 km^2 to 703.3 km^2. Cheetahs utilised several ranches and mean home ranges sizes were larger than mean ranch size. This study provides valuable and relevant information on cheetahs and aids conservation practitioners in mitigating human-cheetah conflict on South African farmland.

In this study, 44% of the collared cheetahs were shot by landowners and in Botswana 55% of collared cheetahs were shot (Houser *et al.* 2009). This highlights the need for effective conflict mitigation projects outside protected areas as high levels of human-induced mortality could outweigh the advantages of a lack of intra-guild completion and a plentiful food and water resource. With most of the continents cheetah population occurring outside protected areas, this threat can pose a significant conservation challenge to the species.

6.5 SURVIVAL OF CHEETAHS RELOCATED FROM RANCHES TO FENCED PROTECTED AREAS IN SOUTH AFRICA

In South Africa, wildlife can be privately owned and utilized for economic gain, with the consequent formation of thousands of wildlife ranches that are stocked with wildlife for the main purpose of hunting and live sale (Benson 1991; Lindsey *et al.* 2009). When predators prey on antelope, the economic value attached to wildlife results in conflict. The cheetah is protected by legislation in South Africa, and cheetahs have thus been illegally shot and trapped in an attempt to reduce losses. A compensation–relocation programme for 'problem' cheetahs was therefore initiated in South Africa by landowners, conservation officials and biologists; this programme allowed landowners to legally capture "damage-causing" cheetahs on their property for relocation into fenced protected areas. Trapped cheetahs were temporarily placed in a specially designed holding facility to habituate them to humans to facilitate monitoring and future viewing for ecotourism. Cheetahs were released into approved reserves using a soft-release method and were subsequently monitored. A total of 29 reserves and 189 cheetahs (92 adults: 59 males and 33 females, plus 94 cubs born on the reserves) were included in the survival analyses using the Kaplan-Meier (product limit) estimator with staggered entry (Pollock *et al.*1989). The mean annual survivorship for all cheetahs, including cubs born in this study, was 82.8%. The final survivorship value for all adult cheetahs was 0.23 and for cubs was 0.04. Cubs had significantly higher survival on reserves where other competing predators were absent. The median survival time was 38 months for adult males and more than 53 months for adult females, which is higher than the corresponding 17 months for adult males and 8 months for adult females on Namibian ranches (Marker *et al.* 2003).

6.6 CONCLUSION

In South Africa cheetahs are classified as Vulnerable and wild dogs as Endangered (Friedmann & Daly 2004), making them the countries most threatened carnivores. As such, conservation of these two species and their habitats are a priority. However, conservation planning and the focus of key interventions are inhibited spatially by a lack of information on habitat suitability and connectivity at a national level. Here I have shown that suitable habitat exists for both species inside and outside their current distribution ranges. Large, contiguous areas of suitable habitat in their current distribution ranges are situated in the Limpopo province.

The necessity for this information is highlighted by the fact that the results from the habitat suitability and connectivity modelling of this study have been requested for integration into the Conservation Plan for Limpopo province. This plan is being developed by the provincial conservation authority and will guide conservation prioritisation in the province. This is the first time that large carnivores are being incorporated into the conservation plan, which has historically only focussed on protected flora and ecologically sensitive areas.

One of the key anthropogenic threats to cheetahs and wild dogs is conflict-driven killing e.g. in Limpopo, 44% of the collared cheetahs were shot by landowners. As a result, much of the conservation work for the species has been aimed at conflict mitigation. However, this has been done spatially in an ad-hoc manner with key focus areas being selected by expert intuition or where landowner complaints are most vociferous. With important areas of suitable habitat and connectivity identified through this study, sparse conservation resources can now be allocated strategically to core areas to maximise conservation benefit to both species.

One of the gaps in mitigating conflict between landowners and cheetahs has been a lack of information on cheetah spatial utilisation outside of protected areas. As a result, many misperceptions exist around the behaviour of cheetahs in ranching areas. With the high density of sedentary prey, continual water supply and lack of intraguild predation, many landowners believe that cheetahs and wild dogs do not move over large areas and are locally overabundant. These perceptions can only be addressed by providing accurate and relevant information that the landowners can trust and relate to. This study found that cheetahs outside protected areas are using large home ranges as is typical for the species with the average 95UD for all cheetahs covering approximately 18 properties.

This means that the impact is spread across several properties and that cheetah home range use is driven by factors other than prey availability. When these data have been presented to landowners during extension work visits, it was found that they were more receptive to discussion, and ultimately likely to be more tolerant, as the information is pertinent to the region. Home range data are currently being gathered for wild dogs outside of protected areas and these data have also proved very useful in conflict mitigation extension work.

Cheetahs and wild dogs have been extirpated from large areas of South Africa with free roaming populations only occurring along the northern border of the country. Areas of suitable habitat outside the current distribution range should be targeted for reintroduction and range expansion efforts. Relocation of 'problem' cheetahs was used as a conflict mitigation measure in the past, however, it was ceased as it does not solve conflict and the impacts on the source population were of concern. The survival of cheetahs relocated into fenced protected areas is good but the population requires intensive management to ensure demographic and genetic viability. There should be an attempt to cluster reintroductions into areas that can be connected through corridors – these are situated in northern KwaZulu-Natal and the Eastern Cape provinces. Natural dispersal between these areas can then be facilitated to minimise the management intensity required for fenced populations. During the last year, this has proved viable in KwaZulu-Natal as a group of wild dogs dispersed naturally between two reserves (B. Whittington-Jones pers comm.). Additionally, in the same region, two unknown single cheetahs have been sighted outside of reserves that have resident populations (V. van der Merwe pers comm.). This shows that both cheetahs and wild dogs are able to disperse from reserves and survive.

With the exception of the Kruger National Park (Kruger), the protected area network in South Africa is ineffective in conserving suitable habitat for cheetahs and wild dogs. Kruger is a key conservation priority and is the largest protected, viable, unmanaged population for both species in the country. The park is also the only large area of suitable habitat for both species. This means that monitoring of these populations is important to ensure that their conservation status in the park is maintained. The value of citizen science in monitoring wildlife has been recognised, but there have not been any attempts to use it for obtaining accurate population estimates, with confidence limits, through capture-recapture surveys for large carnivores. In this thesis I have shown that tourist surveys can be used for effectively and accurately monitoring cheetahs and wild dogs. Additionally, I have for the first time provided recommendations for more effective monitoring regimes that are specific for each species and its unique monitoring challenges. These findings make accurate, measurable and cost-effective monitoring of the population viable. Consequently, the next tourist photographic survey that started in September 2014 will use and test the monitoring frameworks suggested.

This thesis addresses issues of conservation importance to cheetahs and wild dogs at various scales from range use in one district to habitat suitability at a national level. Many of the results presented have already been used in conservation action showing the necessity for studies that have been done here.

Conservation resources are scarce and work must be done in a focussed, cost effective way to ensure that the resources available for conservation are used prudently (Botril *et al.* 2008). This thesis contributes to this, for cheetahs and wild dogs, through clumping two species under one conservation plan, by providing spatial prioritisation for conservation action, and by suggesting optimal monitoring regimes in the largest protected area.

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